STUDIES ON BRACHIOPODA FROM THE OOLITE MARL (JURASSIC) OF THE COTSWOLDS

Submitted for the Degree of Doctor of Philosophy

in the University of Leicester

by

P.G. BAKER

January 1972

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Studies on Brachiopoda from the Oolite Marl (Jurassic) of the Cotswolds

by P.G. Baker

The most comprehensive accounts of the geology of the Cotswolds are to be found in Buckman (1895, 1897, 1901) and Richardson (1904a, 1910, 1929, 1933) although these two very active workers have made numerous other important contributions (Buckman, 1910), (Richardson 1903, 1904b, 1906, 1908, 1925). The stratigraphy, summarised by Arkell (1933) places the Oolite Marl in the Upper Aalenian, a view supported by Murray (1969). An anonymous editor (Baker, 1971) supports the Geological Society's view (George, T.N. et al. 1969) that Aalenian is unacceptable and favours the adoption of Lower Bajocian as the appropriate Age-Standard Stage. However, agreement is by no means universal (ibid. p.153 recommendation 15.2.3) and Torrens (1971, personal communication) claims that a dogmatic view is unjustified.

The suggestion that a re-study of the Brachiopoda of the Oolite Marl was long overdue was made by the late Dr. Helen Muir-Wood because, although the extensive collections of Buckman, Richardson, Upton and Walker during the period 1895-1933 proved a diverse brachiopod fauna in the Oolite Marl, the deposit had subsequently received scant attention. Moore (1855, 1861) had described micromorphic species from the Inferior Oolite of Dundry but no parallel investigations were undertaken in the mid-Cotswolds. The apparent recent lack of interest seems strange as immature zeilleriids were certainly recognised by Richardson (1929) in Westington Hill Quarry (Appendix fig. 1 - 3. Appendix Pl. 1, 2) and ontogenetic stages of zeilleriid genera have been sought for a number of years. In fact, bulk samples of the marl from this locality have yielded such a rich fauna of micromorphic and juvenile brachiopods that the current research has necessarily been restricted to micromorphs and to ontogenetic studies involving the juvenile zeilleriids.

An obvious preliminary course of action was to attempt to correlate juveniles of a species with their respective adults. During these investigations it was noticed that the secondary shell mosaic of some specimens was often very well preserved. In the light of Williams' very important contribution to microstructure studies, first with the aid of the transmission electron microscope and subsequently with the aid of the scanning electron microscope, it was decided to obtain as much new microstructural data from the material as possible, in addition to ontogenetic, morphological and systematic studies.

The species recognised have been studied separately and the sections are listed below together with the various aspects investigated.

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2. Zellania davidsoni (Moore) p. 76

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3. Nannirhynchia longirostra sp. nov. p. 101

Systematics. Microstructure. Ontogeny.

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I am indebted to Dr. J.D. Hudson for supervision of the entire project and to Mr. G. McTurk for preparing the stereoscan negatives. I am grateful to Professor A. Williams, Department of Geology, The Queen's University, Belfast, for stimulating my ideas and to Dr. H. Torrens, Department of Geology, The University of Keele, for help with the, often

difficult, location of type material. Finally I wish to thank Professor P.C. Sylvester-Bradley for use of the research facilities of the Department of Geology and the Board of Governors, Derby and District College of Technology, for research relaxation.

Section 1

Moorellina granulosa (Moore)

Introduction

Organo-detrital residues obtained from treated marl samples have yielded a collection of shells ranging from 0.2 - 1.8 mm. brachial valve width. Among the separated valves an ontogenetic series is recognised. Some of the complete specimens were very well preserved and upon sectioning enabled microstructural investigations to be conducted.

Part A

Extraction. Brachial valve morphology. Ontogeny.

THE ONTOGENY OF THE THECIDEACEAN BRACHIOPOD *MOORELLINA GRANULOSA* (MOORE) FROM THE MIDDLE JURASSIC OF ENGLAND

by P. G. Baker

ABSTRACT. Investigation of fifty-five brachial valves and several sectioned shells from a new locality has led to the conclusion that in *Moorellina granulosa* the brachial apparatus shows progressive elaboration from simple tubercles to very delicate convoluted lobes which are in the form of a ptycholophe. Also that *Thecidium forbesi* Moore (1855) should be regarded as an early pre-brachial lobe stage of *M. granulosa*.

Five ontogenetic stages are described. The argument for an ontogenetic series is strengthened by the changes occurring in the cardinal process, coincident with the development of the brachial apparatus. Reference is made to the improbability of finding detached brachial valves showing adult characteristics. It is considered that the generic distinction between *Moorellina* Elliott (1953) and *Rioultina* Pajaud (1966) should be based on the form of the brachial lobes and not merely on their presence or absence. Specific determination based on the morphology of the brachial valve is considered unsatisfactory and a technique has been developed for the study of the internal characters of complete specimens.

The paper records the occurrence of thecidellinids in the Oolite Marl of the Mid-Cotswolds. The deposit is rather variable and outcrops at a number of localities. It is well developed on Cleeve Cloud near Cheltenham where it attains a thickness of over 4 m. The Marl is typically a pale, cream-coloured marl, relatively harder and more oolitic in the upper layers, softer and with the ooliths more scattered towards the base. It thins in a north-easterly direction towards Chipping Campden and changes lithologically in a south-westerly direction, becoming indurated south from Painswick until it is indistinguishable from the overlying limestone.

Stratigraphically the Oolite Marl was placed by Arkell in the Lower Inferior Oolite (Upper Aalenian, *murchisonae* zone). It rests on a clearly

recognizable bored surface of Lower Freestone but cannot be structurally separated from the overlying Upper Freestone, into which it passes laterally in the vicinity of Stroud.

The material described in this paper was obtained from the northernmost outcrop of the Oolite Marl two miles to the south of Chipping Campden at Westington Hill quarry, grid. ref. SP 142368. The Marl occurs at the top of the quarry which exposes almost 8 m. of Lower Freestone. The collection was made from a bed of soft, pale marl 30 cm. thick, which occurs in the north face of the quarry between two harder bands and about 60 cm. above the top of the Lower Freestone.

The thecidellinids from this locality occur together with a variety of organo-detrital remains which are recorded in tabular form in the text. This fauna is essentially similar to the surf-zone fauna recorded by Nekvasilová (1967) (Nekvasilová in Ager 1965, p. 146). The occasional large brachiopods which occur are forms which are anatomically characteristic (Ager 1965) of peri-reefal deposits.

PREPARATION OF MATERIAL

Weathered marl samples were dried and crumbled through a 6 mm. sieve to remove large fragments. The sieved material was immersed in water and cleaned for ten minutes in a Dison electrosonic cleaner, marketed by Headland Engineering Developments Ltd. The samples were then washed until a clean residue was obtained. This was dried and passed through 2 mm., 422 μ and 152 μ sieves, each residue size being analysed for faunal content (Table 1). Experience has shown that only the material retained on the 422 μ mesh is likely to yield thecidellinids. The cleaned residue was hand-picked under a binocular microscope and the brachiopods transferred to glass tubes for further cleaning. The individual tubes were replaced in the cleaner for periods of 10-20 seconds until the matrix had been removed. The shells were examined at each phase of cleaning to determine whether the treatment

TABLE 1

Residue retained on sieve mesh						
Residue type	2mm. mesh		422μ. mesh		152μ. mesh	
	Av. ten 5gm.samps.	Av. % sample	Av. ten 5gm.samps	Av. % sample	Av. ten 1gm.samps.	Av. % sample
Oolite fragments	3·8	4·7	40·8	0·78	–	–
Ooliths	–	–	1198·8	22·9	148·8	0·8
Brachiopod shell fragments	69·9	84·3	3555·0	68·0	17064·0	98·4
Bivalve shell fragments	3·8	4·7	45·0	0·84		
Echinoderm debris	1·8	2·2	214·8	4·1	64·5	0·3
Gastropods	–	–	0·3	0·006	–	–
Thecidellinids	0·2	0·24	14·4	0·27	2·6	0·01
Other brachiopods	1·4	1·6	13·8	0·26	5·7	0·03
Ostracods	–	–	8·4	0·16	38·9	0·2
Polyzoa fragments	1·7	2·0	112·2	2·1	2·0	0·01
Annelid worms	0·4	0·48	19·1	0·36	3·5	0·01
Total	83·0		5222·6		17330·0	

should be continued. It should be emphasised that this is a very slow method of collecting as the thecidellinid content of the residue is approximately 0.3%. The collection of 172 specimens is comprised as follows:

Brachial valves	55
Pedicle valves	16
Complete specimens	43
Broken valves with significant detail	58
	172

Complete specimens selected for sectioning were cemented to glass slides, using a mixture of Lakeside cement (obtainable from Cutrock Engineering Co.) and chloroform. This remains plastic for sufficient length of time to allow correct orientation of the specimen under a binocular microscope. When the cement has hardened, the orientation of the specimen is checked and a plasticine mould is built round it. The mould is then filled with Ceemar cold setting resin, which, when hardened, allows the block (attached to the slide) to be serial sectioned on a Croft parallel grinder (see Hendry et al. (1963) for other methods). Although the theory of sectioning such small specimens at 0.02 mm. intervals is sound it is found to be inaccurate in practice. Better results are obtained if acetate peels are taken after a standard number of 30-50 revolutions (depending on the area of the block face). The length of the specimen is divided by the number of peels obtained, thus averaging out any error.

ANALYSIS OF RESIDUE

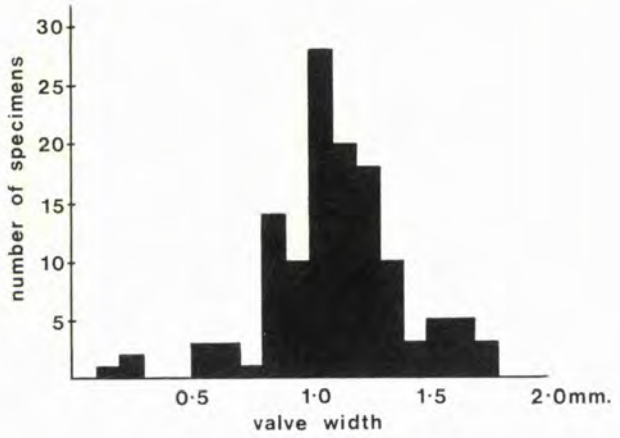
Residue obtained by the method described was found to constitute approximately 40% of the Oolite Marl from the Westington Locality. An analysis of the composition and faunal content of the cleaned residue is shown in Table 1.

In all size ranges, the bulk of the residue is composed of brachiopod shell fragments which may be identified as rhynchonellid and terebratuloid.

Occasional specimens of Globirhynchia subobsoleta (Dav.), Epithyris submaxillata (Morris), and Plectothyris fimbria (Sow.) occur in the coarse residue and it is probable that the shell debris was formed from the remains of these species. The bivalve shell fragments may be identified as Ostrea and Lopha species. The echinoderm debris consists of unidentified echinoid spines and plates, crinoid ossicles of Pentacrinus type, unidentified ophiuroid plates and vertebrae. Three very small gastropods of Nerinea type were recovered from the 422μ sample. The polyzoa fragments have been identified by Dr. A. W. Medd as Actinopora sp., Berenecea sp., Meliceritites sp., and Spiropora sp. The ostracods are Bairdia sp., Cytherella sp., and several unidentified cytheracean genera.

The analysis probably shows a bias towards brachiopod shell fragments as the true nature of the shell type was frequently obscured by adherent matrix. It is possible therefore, that some fragments included in the brachiopod count may in fact have been bivalve material. In addition, quite large echinoid spines appear in the 422μ sample as their diameter is the critical factor. In the 152μ size range it was not possible to distinguish between brachiopod and bivalve shell material with any degree of accuracy and they are therefore grouped. However, as the proportion of brachiopod shell material is so large it is considered that the probable error is of no significance. Analysis of the brachiopod content was very critical and it is unlikely that any specimens escaped attention, even in the 152μ samples. Although the number of ostracods shows a marked rise in this size range, they still represent approximately the same percentage of the sample.

The thecidellinid material shows the same ranges of variation of shell shape noted by Elliott (1948) during his study of Bifolium and by Nekvasilová (1967) during her study of Thecidiopsis. It appears to be correlated with the size of the area of attachment and is almost certainly the result of environmental influence (Rudwick 1962). The dangers of using



TEXT-FIG. 1. Histogram to show the size distribution of 126 brachial valves of *Moorellina granulosa* (Moore) from Westington Hill Quarry. Number of individuals plotted against width of the brachial valve.

a single character are evident but for the purpose of expressing size distribution (text-fig. 1) width of the brachial valve is used, as this appears to be one of the least variable growth characteristics. This feature is particularly useful as over half the material consists of complete or broken brachial valves.

Scars of the area of attachment on the pedicle valve occasionally show portions missing and occasionally, the pedicle valves are still cemented to shell fragments. Nekvasilová (1967) has shown that the form of the area of attachment is consistent with Thecidiopsis being attached, either to the valves of living oysters (liberated on the decay of conchiolin), or settled directly to some firm rocky substratum. The author is in agreement with her views on the ecology of Thecidiopsis and the evidence suggests that Moorellina occupied a similar environment, that is, belonged to the epifauna of the inner sub-littoral zone. This opinion is further supported by their association with peri-reefal brachiopods and the nature of the organo-detrital remains with which they are deposited (ref. Table 1).

A consideration of the evidence indicates that the collection represents a transported death assemblage, the size-frequency distribution (text-fig. 1) showing moderate positive skewness. This may be regarded as the product of a normal growth-mortality rate if compared with the histograms plotted by Hallam (1967) in his work on molluscan death assemblages.

The fragmentation of thecidellinids, other brachiopods, bivalves, and Polyzoa indicates that the debris was formed in a turbulent environment. However, the lack of abrasion of the fragments together with the persistence of occasional bridges and brachial lobes in detached brachial valves of thecidellinids would suggest that the organo-detrital remains were

transported only a short distance. Reference to Table 1 will show that thecidellinids are most common in the 422μ size range whereas ostracods are most common in the 152μ size range. Brachiopod shell fragments represent a high percentage of the material in all size ranges. These data and arguments advanced by Hallam (1967) suggest that no significant sorting of the population has occurred. The absence of appreciable numbers of small thecidellinids which would reflect the normally expected high juvenile mortality rate may simply be the result of selective shell breakage (Hallam 1967, p. 35). The presence of brachiopod shell fragments in excess of 2 mm. diameter, the absence of large thecidellinids and particularly the absence of large thecidellinid shell fragments, is considered to indicate that thecidellinids with a brachial valve width of more than 2 mm. are not represented in the population. Sedimentation factors are not thought to have affected the upper size limit as ooliths larger than the largest complete thecidellinid shells are common in the 422μ sample. Clearly, therefore, the larger size-distributions of the sample may be regarded as adult shells. This is a much smaller population than that studied by Nekvasilová (1967) but the ratio of brachial valves to pedicle valves and complete shells within the sample is similar.

The material shows a number of progressive changes, such as, the development of the cardinal process, the development of the border and the appearance and progressive elaboration of the sub-peripheral rim. The brachial apparatus develops in the same manner and, in the tuberculate stages, forms with from one to five pairs of brachial tubercles are present. For reasons to be described later it is thought that some of these latter are damaged adults. All the structures, with the exception of the adult brachial lobes, show varying degrees of development in the material studied. This shows the presence of an intimate relationship between the progressive development of the various growth features with general size increase.

The collection of the material from one sample from a single bed, the size distribution and the close parallel between the growth stages of Moorellina and the ontogenetic development of Bifolium (Elliott 1948), Lacazella (B.) lacazelliforme (Elliott) (Nekvasilová 1964), and Thecidiopsis (Nekvasilová 1967) leaves little room for doubt that the material from Westington Hill quarry represents the ontogenetic stages of a single species.

Comparison of the forms having a single pair of brachial tubercles with Thecidium forbesi Moore 1855 indicates that there is no valid basis for the separation of T. forbesi from Moorellina granulosa. It is proposed, therefore, that the adolescent growth stages showing this degree of development of the brachial apparatus should be designated forbesiform. It is considered that five ontogenetic stages may be recognised, each marked by the appearance of a characteristic feature (text-fig. 3A-F). The dimensions recorded are those of the specimens figured in Plate 73 and are intended to indicate only the general size relationship, the stages represented being obviously subject to natural size variation.

	Length mm.	Width mm.	Thickness mm.
A. Brephic valve	0.47	0.5	0.2
B. Pre-forbesiform stage	0.9	1.0	0.3
C. Early forbesiform stage	1.0	1.2	0.35
D. Late forbesiform stage	1.2	1.6	0.35
E. Post-forbesiform stage	1.4	1.7	0.4
F. Adult valve	1.1	1.3	0.4

MORPHOLOGY

The present paper is concerned only with the morphology of the interior of the brachial valve (text-fig. 2A) but it is felt that some attempt should be made to reconcile the interpretations of Elliott (1948) and Pajaud (1963) with the glossary laid out in the Treatise on Brachiopoda but without adding to the existing confusion. Briefly the new morphological terms and the justification for their introduction are as follows:

Border. The term is introduced to define the flat region of the valve between the sub-peripheral rim and the periphery of the valve. This unites the limbe-marginal and bord frontal of Pajaud and enables the distinction between anterior, lateral and posterolateral regions to be made. It is felt that this is necessary as it is noted that the posterolateral border is the first to appear during the pre-forbesiform stage of development (text-fig. 3B).

Brachial shelf. The term is introduced to define the raised flat areas, within the lophophorian area, from which the brachial tubercles develop. The inner boundary of the shelf is occasionally raised to form low ridges which may correspond, in part, to the ridge extensions described by Elliott (1948) during the early ontogeny of Bifolium faringdonense (Davidson).

Brachial tubercle. The dotted brachial ridge (Elliott) is not thought to be sufficiently explicit. The rounded dots (Elliott 1948, p. 9) are by definition tubercles (Williams 1965, H154) and the term brachial tubercle is introduced as these structures are of considerable importance in the development of the brachial apparatus.

Socket ridges. As defined in the glossary, inner and outer socket ridges are present (Pl. 74, fig. 3).

The recommendation of the glossary (op. cit. H148) that the term marginal flange should be replaced by sub-peripheral rim is adopted but it is noted that this has a postero-lateral extension demarcating the outer boundary of the cardinal area. The term brachial lobe introduced by Pajaud (1966b) for the establishment of the genus Rioultina is adopted, particularly as lobes are referred to in Moore's original description of Moorellina granulosa (Moore 1855). One must recognise however, that the brachial lobes of M. granulosa are convoluted and not as in Rioultina, auriform.

Ontogenetic stages recognized. The brephic valve (text-fig. 3A; Pl. 73, fig. 1) is the first stage represented and is 0.5 mm. wide. The valve is almost circular, thick, and cap-like. The cardinal margin is almost straight and approximately two-thirds of the width of the valve. The cardinal process is the only recognizable thecidellinid feature, being low and broad, occupying a little more than half the hinge-line and projecting slightly beyond the cardinal margin (text-fig. 2B). There is no median septum but the posterolateral border is just discernible. The dental sockets are poorly developed but clearly bounded anteriorly by the lateral divergence of the sides of the cardinal process, forming inner socket ridges where they turn down to unite with the posterior margin of the valve. No sub-peripheral rim is present at this stage. Three valves show this stage of development.

Stage two is marked by the appearance of the median septum which is considered to be a neanic feature (text-fig. 3B; Pl. 73, fig. 2). The valve is still nearly circular, relatively thick, markedly convex, and in the specimen figured, 1 mm. wide. The cardinal margin is slightly curved and somewhat less than half the width of the valve. The cardinal process is more strongly developed (text-fig. 2C) and turns down sharply into the floor of the valve anteriorly. The postero-lateral border is now clearly defined, also the dental sockets. The sub-peripheral rim is represented by a row of denticles which, posteriorly, mark the inner boundary of the postero-lateral border, not, as in Elliott (1948), trending inwards to form the sides of the cardinal process. Laterally the denticulate rim is almost peripheral so that there is no noticeable border. It will be noticed that the bridge extensions do not unite with the inner socket ridges and that they merge laterally with the sub-peripheral rim. The median septum is fairly thick, developing from the anterior margin and extending posteriorly, the posterior portion being free from the floor of the valve. This stage is designated pre-forbesiform by virtue of the fact that the brachial tubercles of T. forbesi Moore (1855) are not yet developed. Six valves show this

EXPLANATION OF PLATE 73

Figs. 1–6. Stereoscan photomicrographs of brachial valves of *Moorellina granulosa* (Moore) collected from the Oolite Marl, Westington Hill Quarry near Chipping Campden. All the figures are interior views of specimens coated with evaporated aluminium before photography. The bridge is broken on specimens fig. 3–5. 1. Brephic valve (37500), shell recrystallized. × 75. 2. Pre-forbesiform stage of development (37503) showing the development of the median septum. Cardinal process slightly damaged. × 50. 3. Early forbesiform stage (37505) showing the brachial shelf and appearance of the first pair of brachial tubercles. × 50. 4. Late forbesiform stage (37507) showing four pairs of brachial tubercles, well defined sub-peripheral rim and border. × 50. 5. Post-forbesiform stage (37508) showing the expanded brachial tubercles, uniting posteriorly to form arches. Cardinal process slightly damaged. × 50. 6. Adult valve (37509) showing the form of the right brachial lobe. Cardinal process slightly damaged. × 50.

Studies on Brachiopoda from the Oolite Marl (Jurassic) of the Cotswolds.

Ph.D.thesis 1972 - University of Leicester

by P.G.Baker.

Abstract. The Oolite Marl (Upper Aalenian, murchisonae zone) has proved to be a very favourable medium for the preservation of brachiopods. Organo-detrital residues obtained from treated bulk samples yielded moderately large collections of micromorphic and macromorphic genera. Analysis of characters exhibited by shells in different size ranges enables the recognition of ontogenetic series for several genera. Shells from certain horizons are exceptionally well preserved and may be used for microstructural studies. Evidence obtained from ontogenetic stages of the thecidellinid Moorellina granulosa (Moore) indicates that the species includes forms such as Thecidium forbesi Moore, also that some members of the genus were ptycholophous. New data has been obtained regarding rare micromorphic brachiopods such as Zellania davidsoni Moore and the presence of a new species, Nannirhynchia longirostra indicates that micromorphic forms are probably more common than is generally supposed. Work on ontogenetic series of Zeilleria leckenbyi (Davidson ex Walker Ms) has enabled determination of the microstructure and development régime of the loop. Serial sectioning reveals that in Zeilleria a loop of adult character is formed by the time that the brachial valve is about 4.0 mm in length and that during early loop development a connected phase is present. The growth pattern of the median septum indicates that it makes only a limited contribution to loop development in the Zeilleriidae.

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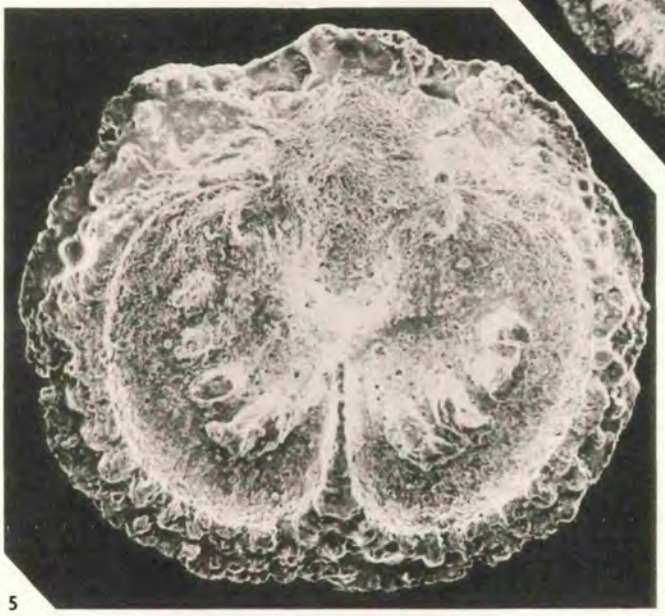

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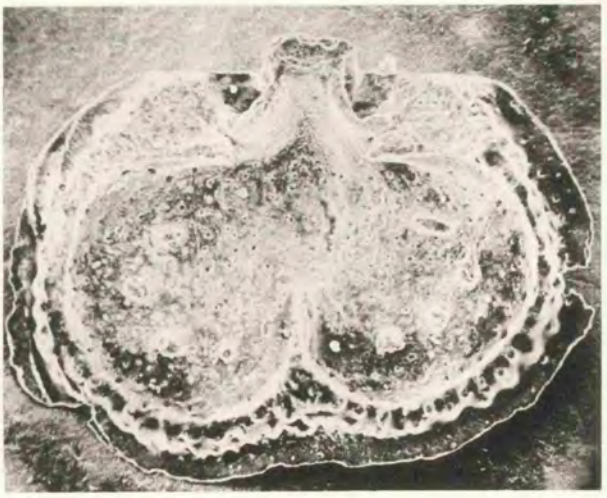


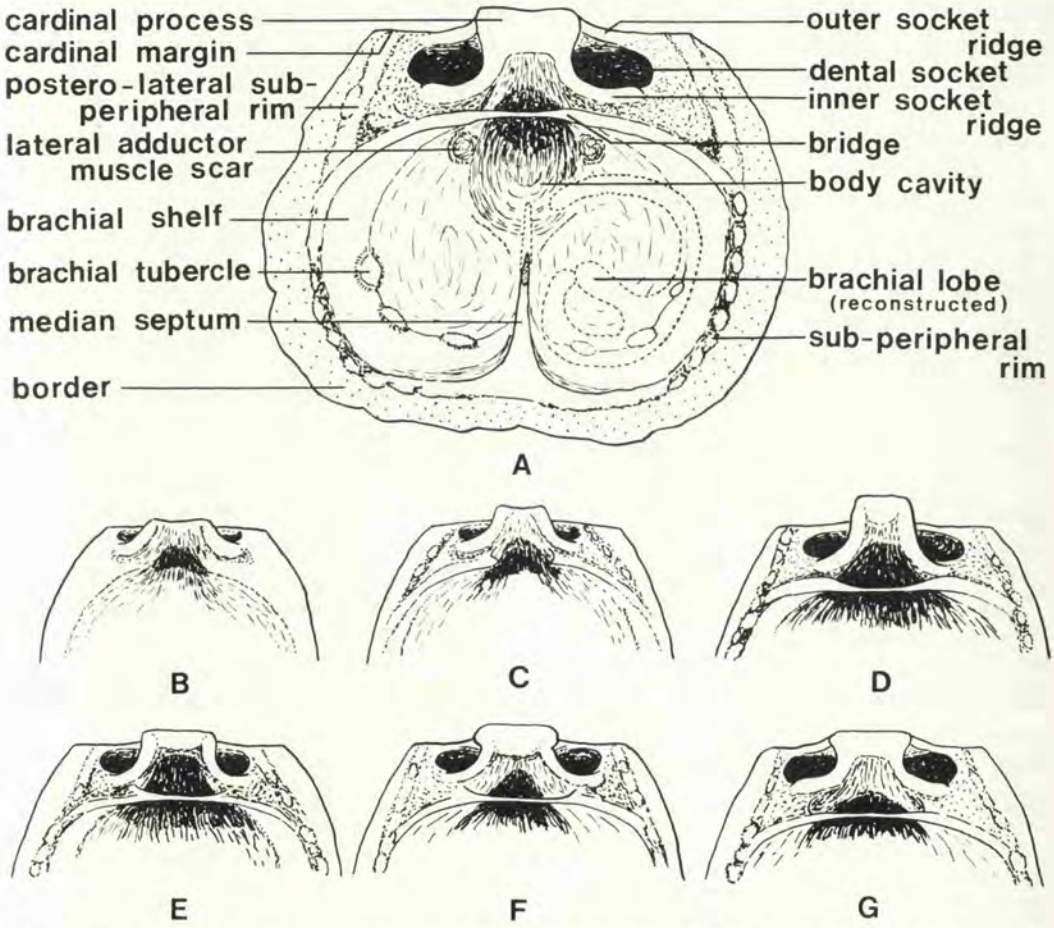
4

BAKER, *Moorellina granulosa*

stage of development.

The two stages described correspond closely with the first two ontogenetic stages of Bifolium faringdonense (Davidson) described by Elliott (1948) but the subsequent stages showing the development of the brachial apparatus are quite different.

Stage three is marked by the appearance of the brachial tubercles characteristic of T. forbesi and is accordingly designated the forbesiform stage, early and late features being distinguishable (text-fig. 3C. D; Pl. 73, figs. 3, 4). The valve is now slightly wider than long. The cardinal margin is well-defined, slightly curved, and just less than half the width of the valve. The cardinal process is by now a prominent feature, projecting markedly beyond the cardinal margin. The dental sockets are deep and the posterolateral border inclined to the plane of the valve. The sub-peripheral rim is well developed so that the lateral and anterior portions of the border are now visible. At this stage the bridge is usually complete (broken in the specimen figured during cleaning) but without the marsupial notch (Elliott 1948). The posterior portion of the median septum is quite clearly free from the floor of the valve and is usually slightly larger than that shown. The floor of the valve is now characterized by two raised areas (brachial shelf), along the inner boundary of which the brachial tubercles develop, usually appearing in pairs. Valves with one or two pairs of tubercles are said to constitute an early forbesiform stage, whilst those with four to five pairs are said to constitute a late forbesiform stage. Attention is drawn to the fact that the tubercles are regularly arranged and without the random distribution figured by Pajaud (1966b) in his work on material from the Inferior Oolite of Dundry. During the early forbesiform stage the cardinal process begins to lose its concavity posteriorly (text-fig. 2D, E) eventually forming a flattened region which gives rise to the outer socket ridges during the late forbesiform stage (text-fig. 2F; Pl. 74, fig. 3). The bulk of the valves show this stage of development.



TEXT-FIG. 2. A. Composite drawing from brachial valves 37509 and 37510 to show the morphological features of the interior of the adult valve. Brachial lobe and median septum reconstructed from specimen 37510. B–G. Drawings to show the form and modification of the cardinal process during ontogeny, together with the development of the inner and outer socket ridges. B, brephic 37500. C, preforbesiform 37503. D, E. early forbesiform 37505, 37506. F, late forbesiform 37507. G, post forbesiform 37508.

The beginning of stage four may be recognized by the fact that the distal ends of the brachial tubercles expand and develop projections which ultimately unite with those of adjacent tubercles to form delicate arches. This degree of organisation is taken to represent a post-forbesiform stage (text-fig. 3E; Pl. 74, fig. 1). The cardinal margin is, by definition, a hinge line. The outer socket ridges, developed from the posterior of the cardinal process are now clearly visible (text-fig. 2G; Pl. 73, fig. 5). The median septum extends back almost as far as the edge of the body cavity. The floor of the valve is characterized by expanded brachial tubercles showing the development of arches and inward pointing projections. The brachial shelf is now hardly visible, its decline is probably to be correlated with the higher development of the brachial apparatus. Five valves show this stage of development.

In the adult state, stage five, the arches of the post-forbesiform stage are united, thickened, and extended to form convoluted lobes (text-fig. 3F). Two specimens were found at this stage of development, 37509 with the right brachial lobe intact (Pl. 73, fig. 6; Pl. 74, fig. 2) and 37510 with the left brachial lobe intact. The brachial lobes of both specimens could be seen to be joined to brachial tubercles anteriorly. An attempt to clean specimen 37510 in order to provide conclusive evidence for the view that the brachial lobes are attached to the valve solely by brachial tubercles, resulted in the loss of the remaining brachial lobe. Specimen 37509 has therefore been subjected only to partial cleaning, this in itself being sufficiently destructive to remove part of the bridge. This specimen is remarkable in possessing a very young form cemented to its anterior border in front of the median septum (Pl. 74, fig. 4).

For reasons to be mentioned later, very little appears to be known about the adult brachial valve of M. granulosa. The above specimens are almost certainly examples of the type referred to by Davidson (1874, p. 110) in Moore's collection from Dundry and almost identical with Moore's type

EXPLANATION OF PLATE 74

Figs. 1–8. *Moorellina granulosa* (Moore) 1. Stereoscan photomicrograph (37508) showing the brachial arches. Postero-lateral view, angle of incidence 48° to the plane of the valve. ×250. 2. Stereoscan photomicrograph (37509) showing the brachial lobe free from the floor of the valve. X indicates the point of attachment to one brachial tubercle. Antero-lateral view, angle of incidence 36° to the plane of the valve. ×100. 3. Stereoscan photomicrograph (37507) normal to the plane of the valve showing the cardinal process with inner and outer socket ridges. ×100. 4. Very young form cemented to the anterior border of specimen 37509. ×250. 5. Photomicrograph, reflected light. Vertical transverse section through specimen (37511) showing the posterior extensions of the brachial lobes and median septum. ×46. 6. Retouched copy of fig. 5. 7, 8. Photomicrographs prepared from acetate peels of vertical transverse sections of specimen (37511) at 0·68 and 0·7 mm. from the umbo, showing the form of the brachial lobes and their attachment to the floor of the valve by brachial tubercles. ×50.

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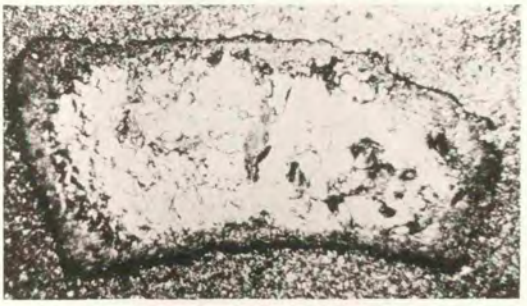

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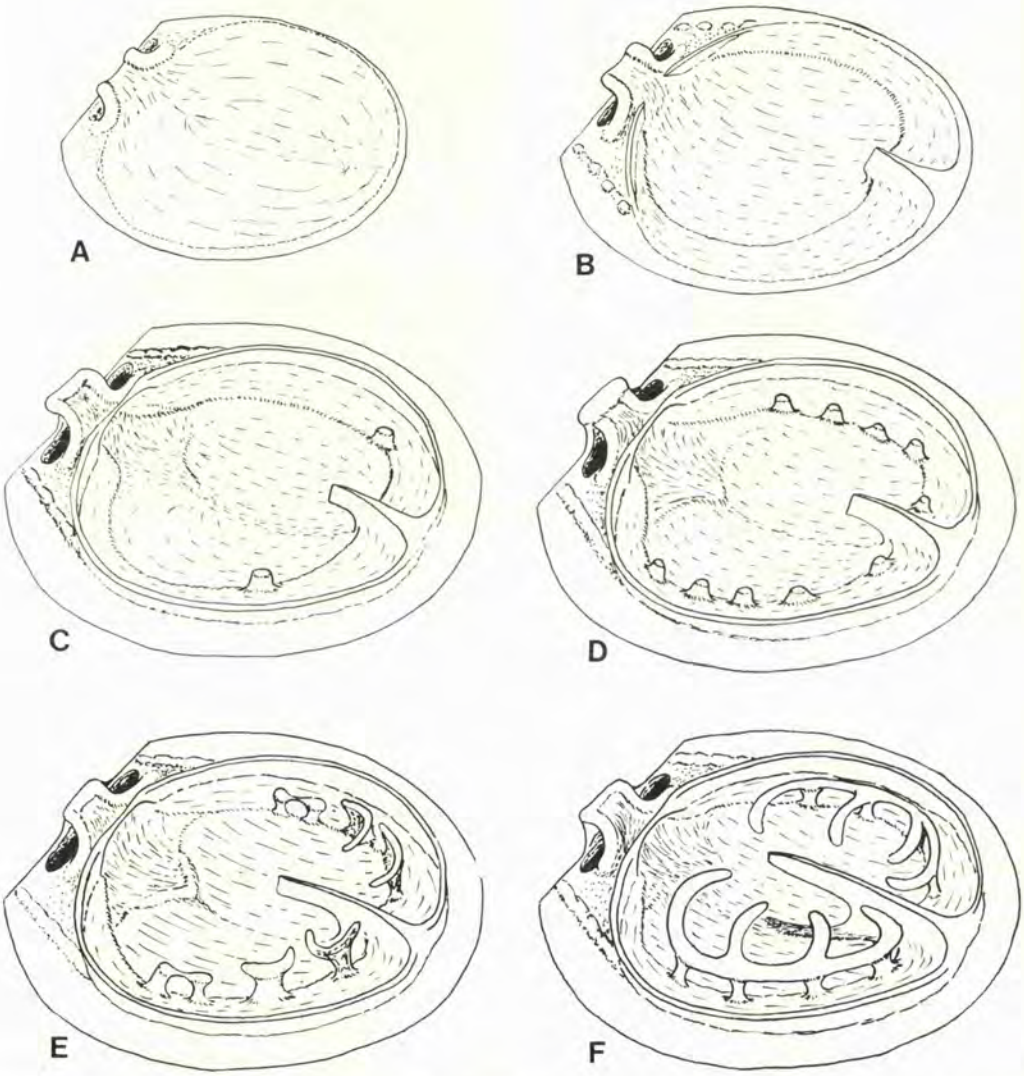
BAKER, *Moorellina granulosa*

specimens, M2850, Nos. 2, 5, and 6 held in the basement of the City of Bath Reference Library. The Westington Hill specimens are smaller than the examples of M. granulosa held at the British Museum. These have a brachial valve width of 2.5 - 3.5 mm. whereas the largest specimens from Westington Hill have a brachial valve width of only 1.7 mm. (Moore's types 1.2 - 1.8 mm.). In addition, the posterior region of the sub-peripheral rim is different, the rim being inclined posteriorly in the majority of the large Dundry specimens and forming quite pronounced angles where it turns to unite with the bridge. In the Westington Hill and Moore's type material the rim remains vertical in this posterior region (Pl. 73, figs. 3 - 6). It is felt, therefore, that re-study of the larger forms must be undertaken in order to ascertain whether they are properly assigned to M. granulosa. Although the stages show a general size increase, size is found to be no criterion of stage of development. This morphological variation is judged by Elliott (1948, p. 24) to be the natural result of intra-specific variation.

GENERAL OBSERVATIONS

As it appears almost impossible to clean brachial valves without destroying the brachial lobes, if present, a technique for serial sectioning oriented complete shells at 0.02 mm. intervals has been developed in order to discover the true nature of the brachial lobes and the nature of their attachment to the brachial valve. Sections show that the brachial lobes are extremely delicate (approximately 0.03 mm. thick) when first formed. They are, in fact, developed from the brachial tubercles in the manner described and extend posteriorly as crescentic horns, turned inwards, towards, but not uniting with, the posterior termination of the median septum (Pl. 74, fig. 5 - 8).

As, in the forms studied, the brachial lobes are only attached to the valve floor by the slender brachial tubercles, one feels that this must surely be the explanation for the general absence of brachial lobes in detached brachial valves of M. granulosa, although the remains of the brachial tubercles



TEXT-FIG. 3. Series of three-quarter profile drawings to show the development of the morphological features of the interior of the brachial valve of *Moorellina granulosa* (Moore) during ontogeny. A. brephic valve, B. pre-forbesiform stage, C. early forbesiform, D. late forbesiform, E. post-forbesiform F. adult valve.

are quite common. On separation of the valves, such delicate structures could hardly be expected to survive in the accepted environment of the thecidellinids (Ager 1965, Nekvasilová 1967). It is probable that the bridge also is usually broken in detached valves, a view supported by the fact that the bridge is present in all sectioned shells with a brachial valve width of more than 0.8 mm.

Distinction between the post-forbesiform stage and the adult is not possible in brachial valves, in which only the broken tubercles remain. As size is found to be no criterion of stage of development, it might be better at present to include all forms with expanded tubercles in the adult stage.

Study of the Oolite Marl material may resolve the difficulty observed by Pajaud (1966b) concerning the division of the sub-family Moorellininae Pajaud 1966 into the genera Moorellina Elliott 1953 and Rioultina.

The criterion of distinction between these genera is said to be the absence of brachial lobes (Moorellina) or the presence of well established auriform brachial lobes (Rioultina). The genus Elliottina Pajaud 1963 created on the form of the area is wisely reduced to sub-generic rank. Pajaud maintains that Rioultina is evolved from Moorellina stock. The Westington Hill specimens might logically be considered to occupy an intermediate position in time (Moorellina, Rhaetic to Bajocian, Rioultina, Pliensbachian to Oxfordian). Careful comparison of the thecidellinid material of the British Museum and the Institute of Geological Sciences with that collected from Westington Hill shows a range of features in the Westington material which grade from moorellinid to rioultinid so that the only real difference is that of size. Rudwick (1962, p. 334) notes the occurrence of typically adult shells of Terebratella inconspicua (Sowerby) which are much below the normal size and attributes this to phenotypic

stunting. It is equally possible that the material from Westington Hill represents a dwarfed population.

The ontogeny, however, shows the clear development of a ptycholophe (see Pajaud 1966a, p. 618) whereas Rioultina is said never to get beyond the schizolophe (Pajaud 1966b). The problem therefore, appears to be one of definition; either one must accept that some moorellinids do have brachial lobes or these forms must be referred to a new genus. One hesitates to create further new genera until more is known about the relationship of the brachial with the pedicle valve. However, concerning the brachial valves of moorellinids it appears that the form of the brachial apparatus has a higher taxonomic value than the mere presence or absence of brachial lobes.

The presence of a ptycholophe in the genus poses the problem of its systematic position at family level, as the ptycholophe is regarded as a thecideid character. Owing to the difficulty of determining between post-forbesiform types and adults or even whether the ptycholophe is universally an adult character in the population its taxonomic significance can not yet be fully appreciated. However, the clear ability to develop a ptycholophe is regarded as being important, particularly in view of the phyletic relationships proposed by Rudwick (1968, p. 352) as it increases the probability that the simple ptycholophous thecideaceans have evolved from moorellinid stock.

Part B

Punctation mosaic.

SIGNIFICANCE OF THE PUNCTATION MOSAIC OF THE JURASSIC THECIDELLINID BRACHIOPOD MOORELLINA

Summary. Study of the punctation mosaics of Moorellina granulosa (Moore) and Moorellina ornata (Davidson), revealed by serial sectioning and stereoscan photomicrographs, shows that the apparent random distribution of punctae may be reconciled to two superimposed regular insertion patterns. Careful plotting of the endopunctae of M. granulosa from serial, cellulose acetate peels, reveals the presence of impersistent punctae. A new model is proposed, based on superimposed insertion patterns and offering an explanation for impersistence of punctae.

1. INTRODUCTION

Considerable attention has been paid to brachiopod punctation in recent years (De Haro, 1960; Kemezys, 1965; Cowen, 1966; Williams, 1956, 1965, 1966, 1968 a and b), but a really detailed account of the structure of caeca had not appeared until Owen & Williams's (1969) electron microscope studies. Study of the shells of living articulates confirms that endopunctae accommodate the caeca which originate in the outer lobe of the mantle and subsequently become enclosed within the shell as it is secreted.

Elliott (1953, 1955) arrived at the conclusion that all thecideidines are endopunctate, except possible Davidsonella. In M. granulosa and M. ornata caecal development would appear, from the position of endopunctae very close to the shell margin, to be typically terebratulide in the manner illustrated by Williams (1956). However, although the endopunctae are formed in the terebratulide manner, there is a difference in that the cup-shaped distal enlargements have not been seen. There is also, no evidence of the deflection of secondary fibres adjacent to the punctae. Forms such as M. ornata used for comparison purposes are typically endopunctate but also without the deflection of fibres adjacent to the punctae.

2. DISCUSSION OF EXISTING MODELS

Study of the punctae of M. granulosa shows the random distribution (Plate 1a) noted by Elliott (1955). Cowen (1966) in his criticism of Kemezys' (1965) models has shown that the apparent "rows" of punctae along growth lines are coincidental and has proposed a model based on De Haro (1960). However, in the light of Williams's work (1956, 1966, 1968a and b) on shell development it seems that the biological importance Kemezys attached to these rows is not without foundation. The evidence suggests that none of the models so far proposed, satisfactorily meets the requirements of the observed thecidellinid mosaic. Elliott, in his reference to the irregularity of pattern, apparently overlooked the remarkable constancy (about 45μ) of the separation between punctae in thecidellinids such as M. ornata. Plate 1b shows this regularity of spacing, a feature which must be more than accidental.

Williams (1956, p.247, fig. 2) has shown that terebratuloid caeca have their origin at the outer boundary of the outer mantle lobe, where the secretion of the primary layer begins. Sectioned moorellinid material shows that the caeca originated in thesame manner, as punctae clearly originate outside the boundary between the primary and secondary shell layers (Plate 1c). As punctae have their origin in the primary layer it is felt that their initiation must be related to the deposition of the primary layer. It is immaterial whether or how they are offset, for, if primary shell is deposited normal to the commissure, the order of appearance of punctae must be related either to growth lines (concentric) or to growth vectors (radial).

Work by De Haro (1960), indicating that the spacing of punctae might be functional and physiological, stimulated Cowen (1966) to advance the theory that the initiation of punctae may be expressed in terms of biological equipotential. Cowen's interpretative hypothesis suggests

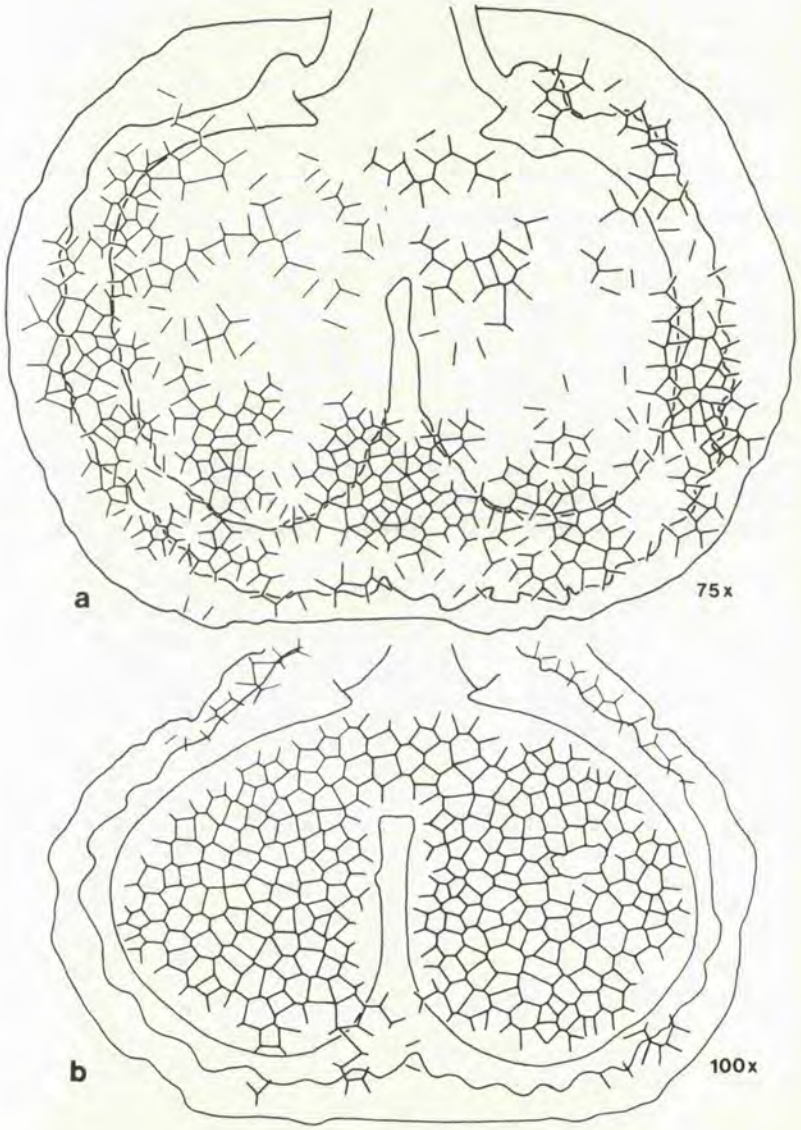


Fig. 1a. Reconstruction of the punctation mosaic (after Cowen, 1966) of a brachial valve of *Moorellina granulosa* (Moore) from sixteen superimposed, cellulose acetate peels. The outer boundary of the sub-peripheral rim (outlined) marks the approximate position of the boundary between the primary and secondary shell layers.

b. Reconstruction of the punctation mosaic of *Moorellina ornata* (Davidson) from a stereoscan photomicrograph of the interior of a brachial valve. Sub-peripheral rim (outlined).

that new punctae develop where the potential of previously formed punctae falls below a critical level. This ideally, would produce a hexagonal mosaic but variables such as shell curvature must be invoked to account for the actual polygonal mosaic observed in shells (Fig. 1a, b). Plots of punctae in areas of shells showing no convexity should therefore show a close approximation to the hexagonal pattern but this is found not to be the case. Also as a little experimentation will show, there is no reason why a hexagonal pattern should not find expression on a curved surface. It would appear, from the above, that the failure of the theoretical hexagonal pattern to find expression, except over small areas, is not to be correlated with shell curvature. However, Cowen's hypothesis of a potential gradient round each puncta (1966, p 272) is an attractive one and from a purely physiological point of view, one feels that puncta insertion must be initiated in this way.

Cowen stated that in non-ideal (polygonal mosaic) situations the "rows" of punctae cannot be maintained over more than small areas but made no attempt to explain why. In the present work attempts have been made to reconcile the observed punctation mosaic of M. granulosa with a workable model. If, as appears probable, there is some order regarding the insertion of punctae, one is forced to the conclusion that the regularity of insertion is masked in some way. As curvature is not critical, another answer must be sought. The theory of equipotential points appears sound but the appearance of punctae in the primary layer must be related to the deposition of that layer. Unfortunately, for Cowen's equipotential points to remain equidistant, it is required that growth be strictly linear. The growth of M. granulosa is radial (Baker 1970). A straight plot of equipotential points on a radial growth field produces a packing which, though remaining hexagonal, becomes increasingly distorted, as the equipotential points do not remain concentrically equidistant.

3. PROPOSED NEW MODEL

Correlating equipotential with equidistance of equipotential points, one finds that two superimposed fields emerge, a basic concentric (commissural) distribution which requires the presence of a linear (theoretical hexagonal) control to keep the equipotential points equidistant (Fig. 2). Where growth is essentially linear the two fields overlap but where growth vectors are divergent the fields also diverge or overlap to a greater or lesser extent. Where the fields show maximum divergence it is possible for one or other, or even both of the equipotential points to find expression in the initiation of punctae. Comparison of the divergent part of the fields in Fig. 2 with the plotted distribution in M. granulosa (Fig. 1a) shows a very close resemblance between the theoretical and observed distribution of punctae in thecidellinids. The apparent random distribution of punctae in thecidellinids and probably other brachipods also, may therefore, be the result of the superimposition of two essentially regular patterns of distribution.

4. OBSERVATIONS

The proposed model has several points in its favour. It satisfactorily explains why regular separation of punctae is not maintained over more than short distances and often coincides with a growth line. It shows how and why (by degree of divergence) the field varies from time to time and offers an explanation of the radial variation observed by Williams & Rowell (1965, H69). The model shows how apparently random mosaics may arise and throws important light on the distal coalescence (Cowen, 1966) and impersistence of punctae. Where the two fields are only slightly divergent, it is possible for two terminal discs to appear having an equipotential common to both fields (Fig. 2). In such a situation, coalescence to form a single puncta, or degeneration of one or other is not difficult to envisage.

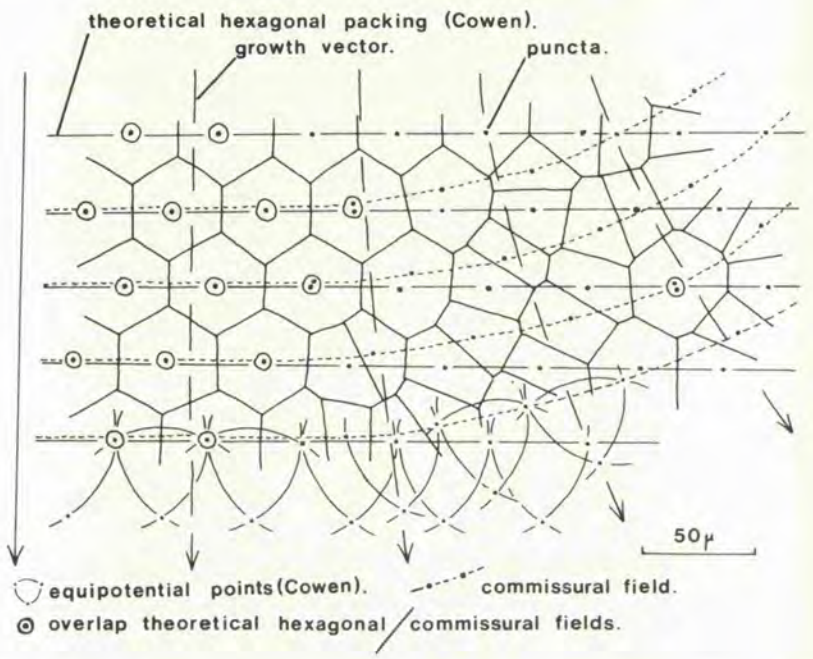


Fig. 2. Proposed new model superimposed upon the enlarged growth vector pattern from a stereoscan photomicrograph of the right antero-lateral sector of the exterior of a brachial valve of *M. granulosa*. The position of the commissure inferred by reference to growth lines.

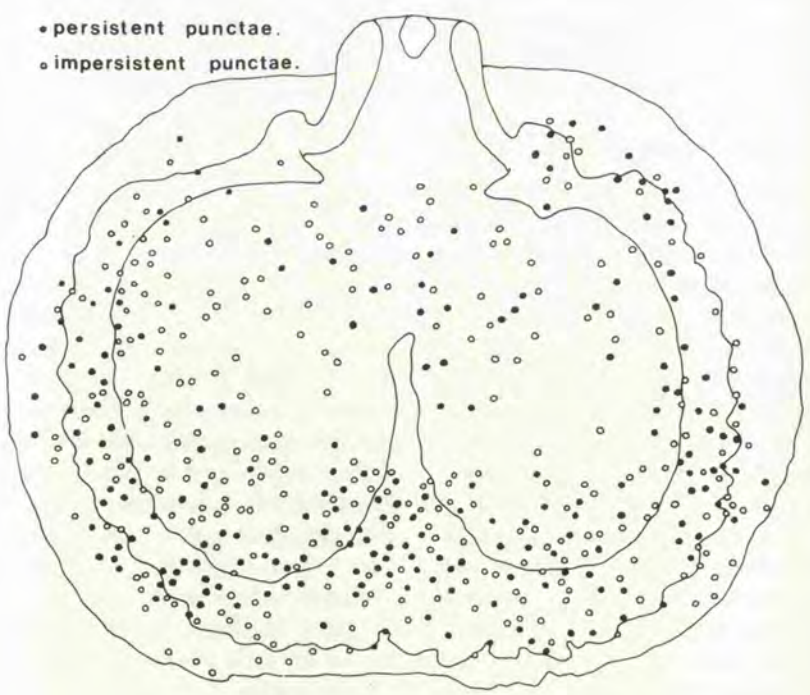
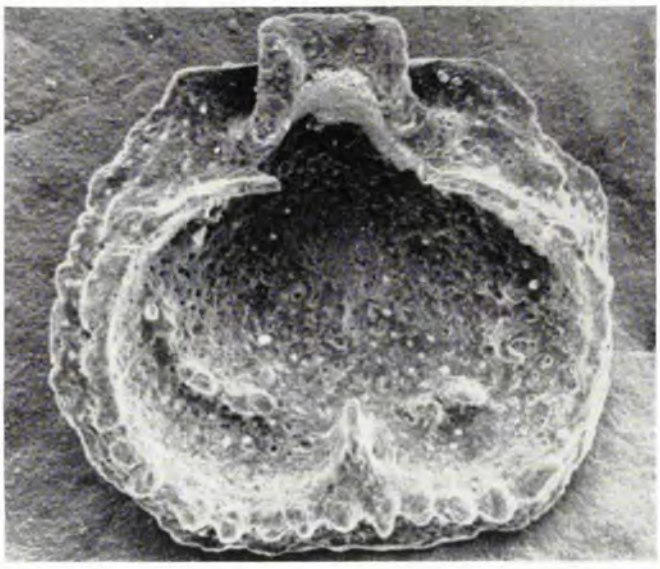


Fig. 3. Plot of persistent and impersistent punctae encountered during horizontal serial sectioning of a brachial valve of *M. granulosa*.

A mosaic approaching the theoretical hexagonal pattern will only be encountered where the growth vectors have a linear orientation. The greater degree of regularity of terebratuloids may therefore be a relative feature. The external surface area of an adult brachial valve of M. granulosa is in the order of 2.8 mm^2. Any zone of comparable size on the shell of even a fairly small terebratuloid, must show a much closer approximation to linear growth and, therefore, a corresponding increase in the regularity of the distribution of punctae. The apparent random punctation mosaic of M. granulosa may therefore be an attempt by the animal to reconcile its pronounced radial growth with the theoretically ideal distribution proposed by Cowen's model.

A plot of the endopunctae of M. granulosa from superimposed serial sections (Fig. 3, Plate 1d) shows a much higher density than ever appears on the internal surface of brachial valves (Plate 1e). Some may be concealed by matrix but the possibility that the punctae of M. granulosa are not typically persistent must be considered. Owen & Williams (1969, p. 189) suggested that coalescence of caecal bases may be caused by differential movement of epithelial cells. In the equipotential terms of superimposed punctation mosaic, the impersistent condition may be explained by suppression of one or other of adjacent punctae soon after their initiation. This is an interesting point when one appreciates that the only pre-requisite for the initial development of caeca in impunctate shells, or their degeneration in endopunctate shells, is the presence of secretory glands in the primary layer (Williams & Rowell, 1965).



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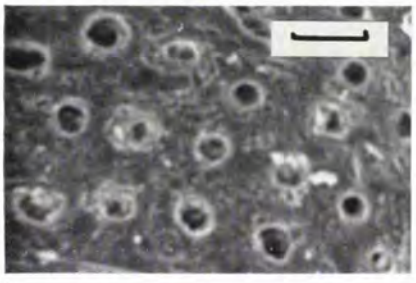

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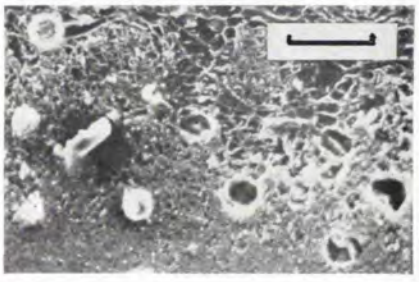

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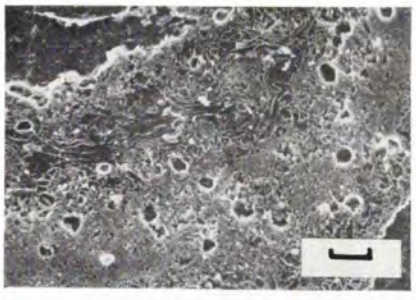

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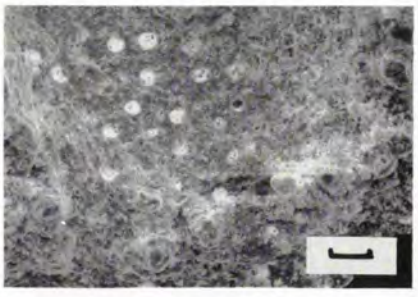

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EXPLANATION OF PLATES

1a. Stereoscan photomicrograph of the interior of a brachial valve of *Moorellina granulosa* (Moore) showing the appearance of endopunctae. x 50.
1b-e. Scale represents 45μ.
b. Stereoscan photomicrograph showing the spacing of punctae in the floor of a brachial cavity of *M. ornata.*
c. Stereoscan photomicrograph of an aluminium shadowed cellulose acetate peel of a horizontal section through a brachial valve of *M. granulosa* showing the occurrence of punctae in the primary layer (lower).
d. Stereoscan photomicrograph of an aluminium shadowed cellulose acetate peel of a horizontal section through a brachial valve of *M. granulosa* showing the distribution of punctae close to the external surface.
e. Stereoscan photomicrograph of the sector of the interior of the brachial valve figured in d, showing the decrease in the number of punctae at the inner surface of the shell.

Part C

Growth. Microstructure, Palaeoecology. Affinities.

THE GROWTH AND SHELL MICROSTRUCTURE OF THE THECIDEACEAN BRACHIOPOD MOORELLINA GRANULOSA (MOORE) FROM THE MIDDLE JURASSIC OF ENGLAND

ABSTRACT. Analysis of the growth habit of M. granulosa from a functional point of view has proved to be of value in the interpretation of shell microstructure. Serial sectioning of shells at 20μ intervals has revealed that fibre orientation may change suddenly at various levels within a shell. The paper notes the need for detailed information regarding the orientation and location of sections through shells, as study of M. granulosa indicates this may be of critical importance. The shell-structure differs markedly from that of Lacazella mediterranea (Risso), as the shells of some, if not all Inferior Oolite thecidellinids were differentiated into primary and secondary layers. Interpretation of the microstructure has taken into account the effects of shell resorption in the brachial valve and the development of crescentic tubercles in the pedicle valve. Some evidence has been obtained which indicates that the pedicle opening of M. granulosa occupied a supra-apical position. Despite the general spiriferoid appearance of the shell-structure, the detailed microstructure of various morphological features of the two valves, together with bulk morphological similarities, are thought to suggest strophomenoid affinity.

The microstructure outlined in this paper is based on combined evidence from serial sections and polished blocks prepared from fifty-three specimens, comprised of brachial valves, pedicle valves, and complete shells of Moorellina granulosa (Moore), from the Oolite Marl of Westington Hill Quarry in the Cotswolds. The stratigraphy and location of the quarry and the exact horizon from which the material was obtained have been described in a previous paper (Baker 1969). A further horizon has been located in the yellow-orange clay at the base of the Oolite Marl on the west face of the quarry but the material recovered was not sufficiently well-preserved for the study of shell microstructure.

In the material studied, many of the shells are recrystallized but some are well preserved. Partially recrystallized material is useful for comparing and contrasting the unaltered shell with diagenetic effects.

A discussion of the thecideacean environment and a detailed account of the morphology of the brachial valve (Pl. 18, fig. 1) is given in an earlier paper (Baker 1969).

The most prominent feature of thecideidines is the elaboration of the brachial apparatus. The inevitable result of interest in this structure is that in much of the published work the pedicle valve is neglected.

The pedicle valve of thecideaceans is subject to much less variation than the brachial valve and the pedicle valve of M. granulosa (Pl. 18, fig. 2) is morphologically very similar to that of Bifolium faringdonense (Dav.), described by Elliott (1948). Attachment to the substratum is by cementation and the shape of the pedicle valve is greatly influenced by the size of the scar of the area of attachment. Ontogenetic development of the valve concerns the appearance and development of crescentic tubercles, the change in position of the hinge teeth and the change in the relative proportion of the hemispondylium.

The shell of M. granulosa is endopunctate and shows the apparently random distribution noted by Elliott (1955). However, neither the models proposed by Kemezys (1965) nor Cowen(1966), satisfactorily explain the punctation mosaic and the proposal of a new model is to be published separately.

During analysis of the microstructure, particular care has been taken to attach significance only to structures seen in at least six different specimens. Occasional peculiar features are noted which may be important but occur so infrequently in the material studied that firm conclusions must not be drawn from them.

PREPARATION OF MATERIAL

A comprehensive account of the preparation of Oolite Marl material is given in Baker (1969) and the material studied in the present paper was obtained by the same method. For microstructure investigation however, it has been discovered that reduction of the etching time from ten seconds in 5% HCl, to eight seconds in 3% HCl yields better results. In addition it was found that fresh resin does not make a good bond with plain glass slides and blocks may become detached during sectioning. A more effective bond is obtained by the use of ground glass slides.

GROWTH AND DEVELOPMENT OF THE SHELL

General. The nature of shell growth is mixoperipheral, leading to a strophic condition (Rudwick 1959, p. 18), as, contrary to the belief of Elliott (1965), a small hypercline dorsal interarea (by definition, Williams 1965, H59) is present (Pl. 18, fig. 5). The lateral profile is obscured by the area of attachment but in forms with a small area of attachment, may be described as modified plano- to concavo-convex with a rectimarginate commissure. Certain differences in the development of structures in the brachial and pedicle valves have taxonomic significance and they will be discussed separately, following an account of the general shell growth.

A comprehensive account of shell deposition in living brachipods is given by Williams (1956, 1966, 1968a, b), Williams et al. (1965) and it is reasonable to suppose the shell of Moorellina granulosa (Moore) was deposited in the same manner. Evidence presented in this paper shows that Williams (1968a) is in error in regarding the single layered shell of Lacazella mediterranea (Risso) as typical of the thecideidine shell structure. M. granulosa clearly shows the development of primary and secondary shell layers.

As described in an earlier paper (Baker 1969) the brachial valve of M. granulosa is initially almost circular, later becoming broader than long. However, study of a number of specimens shows that the shape of the brachial valve is really controlled by the shape of the pedicle valve, which is itself strongly influenced by the size of the scar of the area of attachment. Williams (1956) has shown that although cell division occurs throughout the epithelium the enlargement of the brachiopod shell is controlled mainly by peripheral zones of growth.

Various aspects of the mode of shell growth have been defined by Rudwick (1959, p. 2). It is convenient for the purpose of demonstrating the mode of growth in M. granulosa to use his second interpretation, i.e. that the shell surface represents a series of sectors which were formed continuously by different arcs of the valve edge.

At a magnification of 250 x linear, the external surface of the shell of well-preserved specimens of M. granulosa is seen to be covered with small fibres. These fibres are inclined radially outwards from the umbo at a low angle from the shell surface and show an orientation normal to the growth-lines and commissure (Pl. 18, fig. 3). If one assumes that the fibres are associated with the deposition of primary shell, either mechanically or crystallographically, their orientation directions may be used as growth vectors for the determination of points of relatively rapid increase in various arcs of the commissure.

Rudwick has shown how growth at any point on the valve edge may be resolved into component growth rates. By assigning a value of one growth unit to an arbitrary surface area corresponding to Rudwick's growth points (1959, text-fig. 1a), provided that the growth vectors are known, different rates of growth in different sectors of a shell can be fairly accurately determined. To demonstrate this adequately in M. granulosa

EXPLANATION OF PLATE 18

Stereoscan photomicrographs of specimens of *Moorellina granulosa* (Moore) from the Oolite Marl, Westington Hill Quarry near Chipping Camden. All figures are of specimens coated with evaporated aluminium before photography.

Fig. 1. Interior view of a brachial valve (37512) showing the median septum and tuberculate sub-peripheral rim. Bridge and brachial apparatus broken. ×40.

Fig. 2. Interior view of a pedicle valve (37513) showing the teeth, supported hemispondylium and the sub-peripheral crescentic tubercles. Umbonal cavity filled by the broken cardinal process. ×40.

Fig. 3. External surface of a portion of the left postero-lateral region of a brachial valve (37512) showing the oriented fibres on the surface of the primary layer. Scale represents 30 μ.

Fig. 4. Lateral view of a complete specimen (37511) showing the growth habit and large free ventral anterior surface. ×50.

Fig. 5. Posterior view of specimen (37511) showing the large, ventral and small, dorsal interareas. Angle of incidence 40°. ×40.

Fig. 6. Profile view of an enlarged portion of specimen (37513) showing the supporting septum of the hemispondylium, with the dental ridges continuous with the outer edges of the hemispondylial plates. Angle of incidence 60°. ×65.

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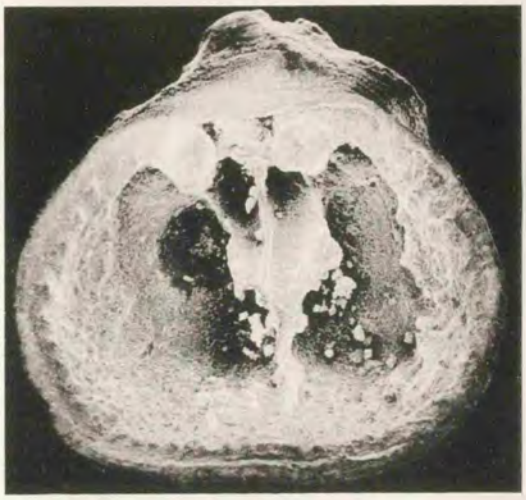

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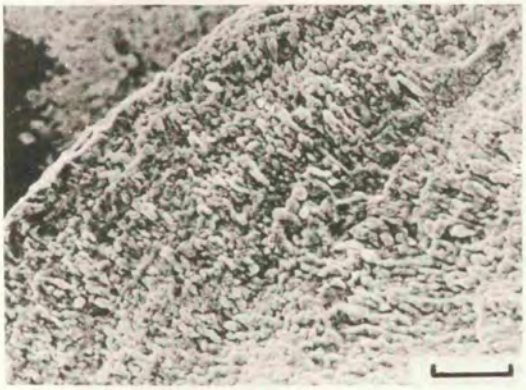

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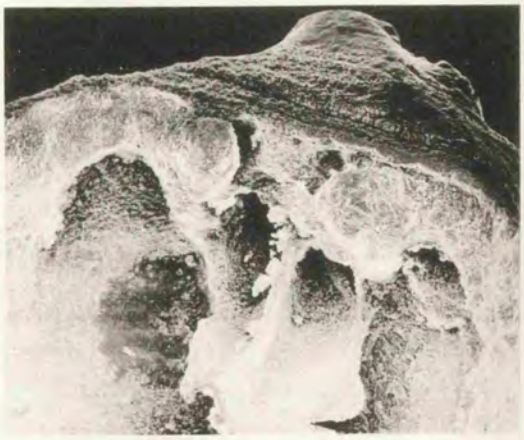

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BAKER, *Moorellina granulosa*

necessitates the introduction of additional "momentary" and "cumulative" terms. The growth vector may be regarded as the cumulative product of the arrangement of growth units normal to the mantle edge. The total number of growth units per growth vector may be represented as $d/\sqrt{x}$, where d represents the length of the vector and x represents the surface area of the growth unit. Proliferation points occur where the distance between two growth vectors has doubled and proliferation arcs are represented by lines joining series of new proliferation points. The growth rate in any sectors may be determined by the growth acceleration, v , which is represented by the number of proliferation arcs in any sector. The relative growth index may therefore be expressed as $v(d/\sqrt{x})$ for any sector of the valve. In Rudwick's terms, proliferation points and proliferation arcs are momentary and growth acceleration and relative growth index are cumulative.

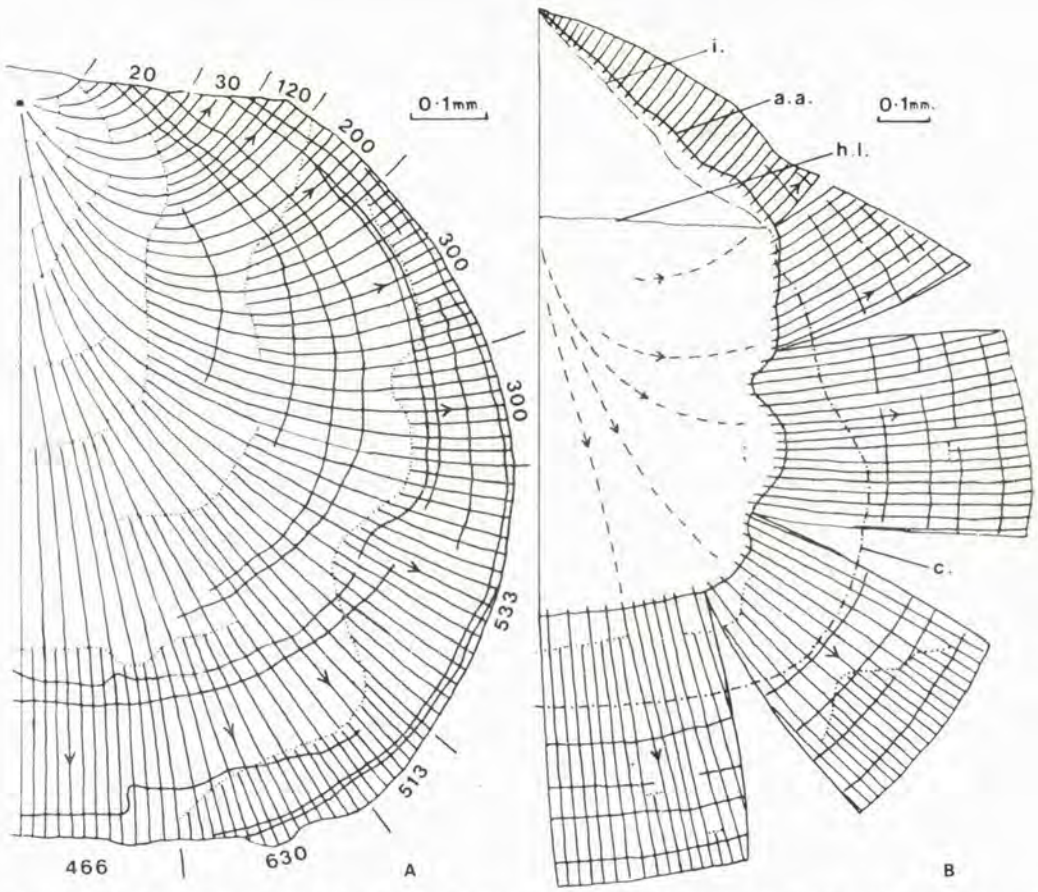
Brachial valve. The growth of the brachial valve of M. granulosa, when expressed in the manner outlined, shows a marked radial pattern with a high relative growth-rate anterolaterally (text-fig. 1A). For the reasons outlined in Williams and Wright (1963) it is considered that it is only necessary to plot the data for one-half of the valve.

The validity of the above interpretation obviously rests on the assumption that the proposed association of fibre orientation with deposition of the primary layer is correct. The author is alive to the possibility that in the material investigated, the growth vectors are not recorded from the exposed ends of primary fibres but from crystallites growing on their outer ends. However, the fibre orientation pattern shows a remarkable constancy in the thirty external brachial surfaces examined. Even if the development of the fibres is diagenetic, the constancy of their orientation pattern must be in some way connected with the microstructure of the primary layer, most probably the crystallographic orientation of the primary fibres themselves (Cloud 1942, p.24).

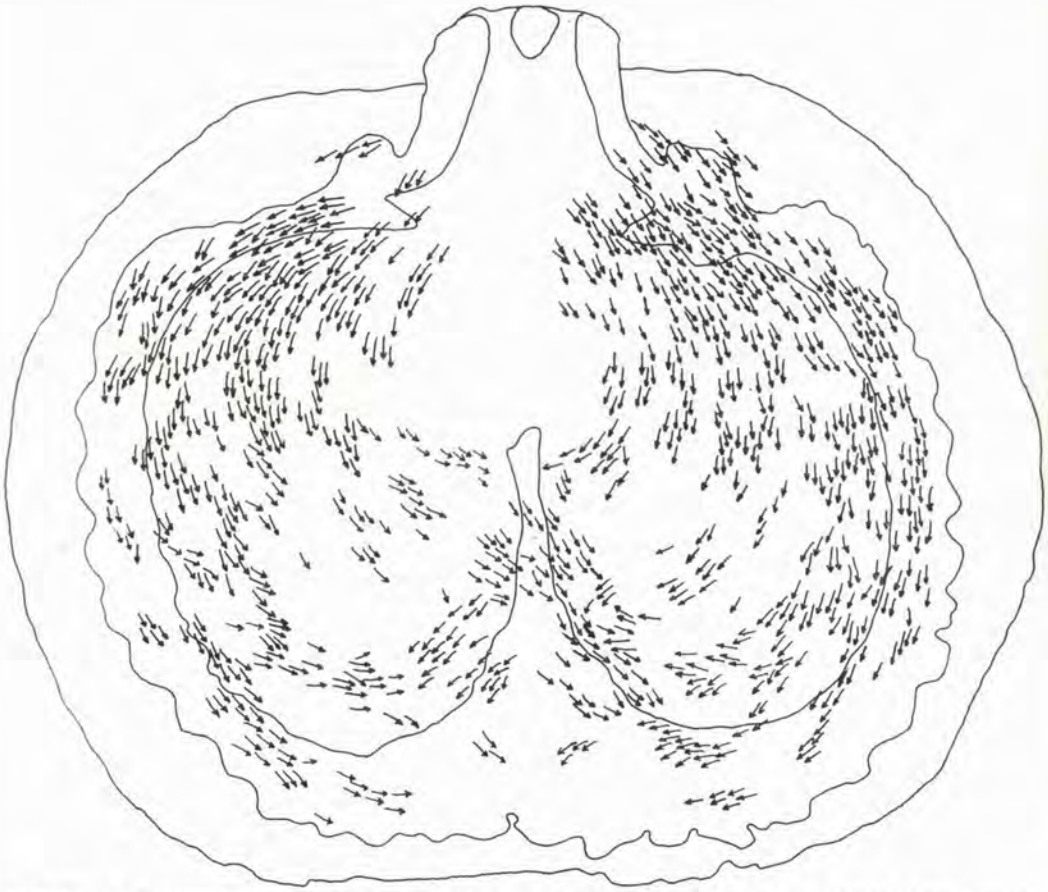
Pedicle valve. Analysis of the growth-lines of the pedicle valve of Thecidiopsis (Nekvasilová 1967) has enabled determination of the mode of development. Study of M. granulosa shows that the pedicle valve exhibits the same development régime, which, when advanced, produces an almost linear pattern masking the radial growth typical of brachial valves. After the development of the area of attachment and presumably in response to environmental influence, material is added to the anterior and anterolateral regions of the pedicle valve much more rapidly than in the other regions so that the angle between the plane of the commissure and the plane of the area of attachment changes rapidly and the anterior and antero-lateral regions of the shell develop rapidly without appreciably increasing the length of the commissure. This means that the deposition of the primary layer of the pedicle valve although remaining normal to the valve margin shows a distinctly linear growth orientation anteriorly (text-fig. 1B). In Rudwick's terms therefore, the growth of the shell of M. granulosa is characterized by a declining vertical component in the brachial valve and an increasing vertical component in the pedicle valve, a cumulative growth pattern which obviously serves to lift the anterior gape away from the substratum (Pl. 18, fig. 4).

Secondary layer. As shown by Williams the secondary shell consists essentially of fibres arranged with their long axes at a low inclination to the internal surface of the primary layer and overlapping to a greater or lesser extent according to the angle of inclination, usually about 10°. By plotting the orientation of the long axes of exposed parts of secondary fibres, Williams 1968a, pp. 10-15) has demonstrated a discernible lineation in several genera. Construction of a secondary growth mosaic for M. granulosa shows the existence of the same spiral arc arrangement in which there is a relatively constant deflexion of

the secondary fibres (text-fig. 2). The pattern is modified anteriorly in the brachial valve by the development of the relatively very thickened anterior of the median septum. There is no sign of peripheral reorientation normal to the shell edge but this may simply be the result of the disruptive influence of the tubercle cores. Williams (1966, p. 1148) notes the blurring of the pattern in areas of excessive calcite deposition in terebratuloids. In the pedicle valve also, the spiral arc pattern is modified anteriorly by the development of the crescentic tubercles. However, although Williams is able to demonstrate the bulk migration of the mantle in the direction of growth (1968a, p. 8) in order to account for the inclination of secondary fibres, the reason for the migration has not been explained. Study of his text-figure makes it apparent that it is impossible to extend the fibre series anteriorly or posteriorly without changing their inclination. The situation is further complicated by trying to impose the model on a convex shell. There is ample figured evidence, however, to show that his account of fibre shape must be correct. The solution to the problem must, therefore, lie in the orientation of the fibres themselves. The length of the fibres in any zone of the shell seems to remain fairly constant, suggesting that the cells of the epithelium secreting them have a standard life and secretory activity. Obviously the rate of cell division in the mantle groove must vary to account for the growth characteristics of the shell. If the organization of the cells is such that the calcite of the secondary fibres is secreted at a fairly constant rate, areas showing a relatively slow vectoral primary growth rate, i.e. postero-lateral sectors, must suffer from a build-up of secondary shell, unless the fibres are deflected away from the primary growth vectors in order to prevent the shell from becoming excessively thickened.



TEXT-FIG. 1. Reconstruction of the primary growth vectors of *M. granulosa*, plotted from oriented fibres. Proliferation arcs dotted. Concentric lines represent visible growth-lines. A. Right half of a brachial valve. Numbers indicate relative growth indices in different sectors. B. Right half of a pedicle valve. Broken lines within the area of attachment represent the vector mosaic inferred by the brachial valve. Commissure projected stereographically to allow plotting of the primary growth vectors. The relative position of a.a. edge of the area of attachment, c. commissure and i. edge of interarea, plotted from cellulose acetate peels. h.l. hinge-line.



TEXT-FIG. 2. Reconstruction of the secondary growth mosaic of *M. granulosa*, plotted from twenty-five superimposed peels. Solid outline represents the position of the sub-peripheral rim, median septum, and cardinal process.

Conversely the fibres may be deflected towards areas where thickening of the shell is taking place, such as the development of the median septum (text-fig. 2). This orientation deflexion of the secondary fibres away from sectors of relatively decelerated deposition of primary shell material would readily explain the forward migration of the secreting cells and the difference in orientation between the vectors of the primary and secondary layers (text-figs. 1A, 2).

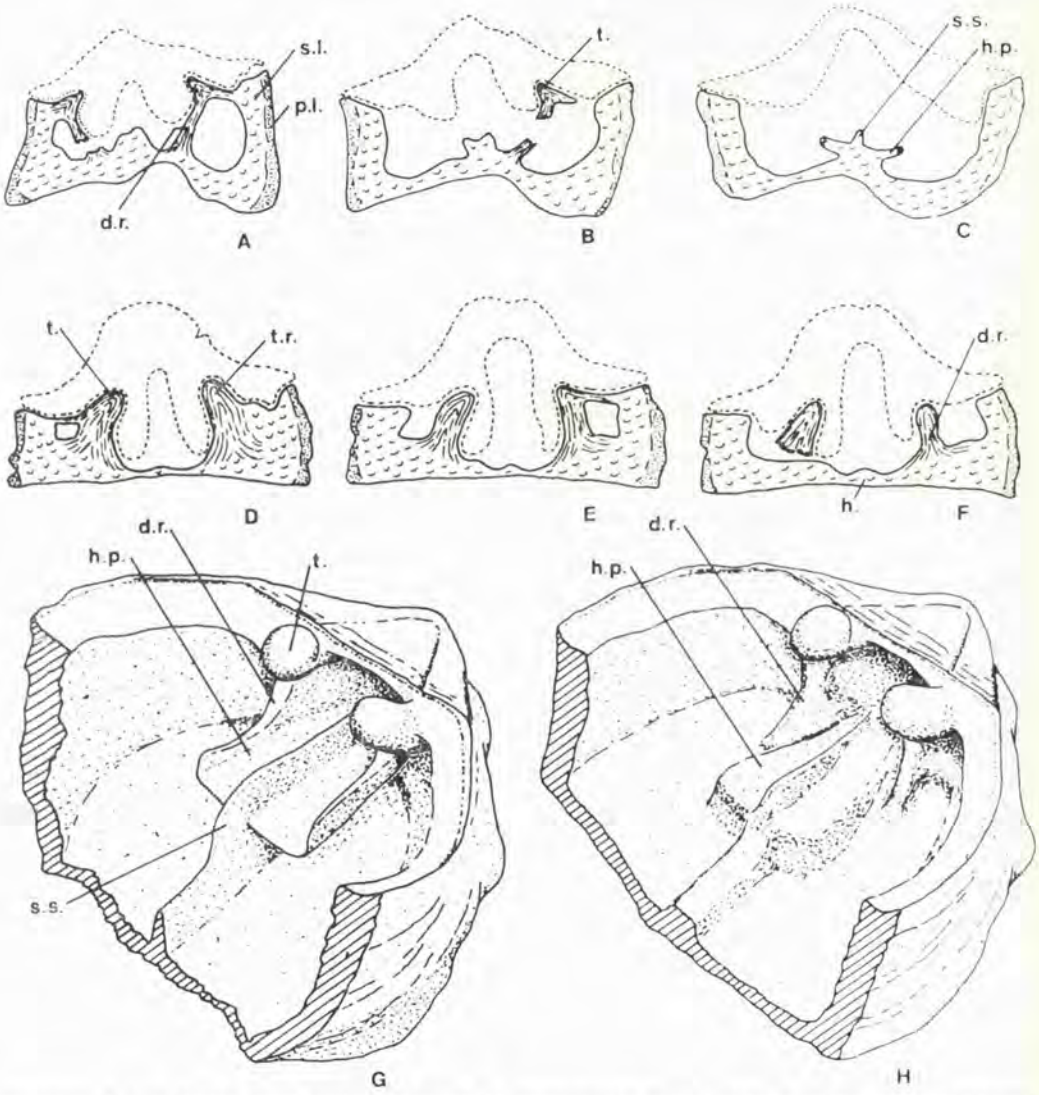
DEVELOPMENT OF SPECIFIC STRUCTURES

Development of the sub-peripheral rim. Very little progress regarding the determination of the microstructure of the brachial valve was made until the mode of development of the sub-peripheral rim was appreciated. Williams (1968a, p. 50) described local resorption in Lacazella and resorption is found to play an important role in M. granulosa. Ontogenetic studies (Baker 1969) show that the sub-peripheral rim appears at the preforbesiform stage of development and subsequently occupies the same position relative to the valve margin, irrespective of the size of the valve. As the sub-peripheral rim is too prominent to be submerged by subsequent secondary shell deposition, it must migrate outwards. Evidence that the migration is accomplished by development at the external margin of the rim and resorption along its inner margin will be presented later. The subperipheral rim is tuberculate and the generative zone of the tubercles appear to be where the secretory activity of the outer epithelial cells changes from the deposition of primary to the deposition of secondary fibres.

Development of the hemispondylium. Elliott (1948) noted the presence of a structure in the floor of the pedicle valve of Bifolium faringdonense (Davidson) to which he gave the name hemispondylium. In his opinion,

the structure was not formed by the fusion of dental plates. Elliott also noticed the presence of what might almost be called dental ridges, buttressing the hinge teeth internally but adopted the view that they played no part in the formation of the muscle supports (spondylium) as in other brachiopods, a view confirmed by the present work. Some specimens of M. granulosa however, show that the buttressing ridges which may represent rudimentary dental plates, are continuous with the upturned outer edges of the hemispondylial plates (Pl. 18, fig. 6). This arrangement is an interesting feature and may be homologous with the ankylosed median septum-dental ridge structure of the davidsoniacean Orthotetes.

Sectioned material enables resolution of the problem. Forms with a supporting septum have the appearance of possessing a spondylium simplex (text-fig. 3A-C, G). However, forms with a sessile hemispondylium show quite clearly that the dental ridges simply merge with the floor of the valve (text-fig. 3D-F, H). There can be no doubt therefore, that Elliott's interpretation is correct and that the hemispondylial plates are not formed by the fusion of dental plates but from secretion of secondary shell by the outer epithelium adjacent to the supporting septum. The dental ridges may or may not unite with them depending on the growth habit of the valve. In forms with well-developed dental ridges it is possible to obtain sections which are strikingly similar to sections through the umbonal region of pedicle valves of Derbyia (Williams et al. 1965, H404, fig. 261 D). As Nekvasilová (1964) has recorded in Lacazella (B) lacazelliformis (Elliott) and as Elliott has recorded in B. faringdonense, the hemispondylium is present in the smallest valves studied and may be sessile or supported by a median septum. Rare specimens may show the hemispondylial plates supported by a double septum anteriorly. A single specimen of M. granulosa shows the hemispondylial plates supported by three septa whilst another (Pl. 19, fig. 1) shows a reticulate support.



TEXT-FIG. 3. A–C. Three serial sections through *M. granulosa* to show the form of the supported hemispondylium. D–F. Three serial sections, showing the form of the sessile hemispondylium. G. Three-quarters profile reconstruction of a supported hemispondylium, showing the dental ridges continuous with the hemispondylial plates. H. Three-quarters profile reconstruction of a sessile hemispondylium, showing the dental ridges merging with the floor of the valve. Outline of brachial valve dotted. d.r. dental ridge, h. root of sessile hemispondylium, h.p. hemispondylial plate, p.l. primary layer, s.l. secondary layer, s.s. supporting septum, t. tooth, t.r. tooth ridge.

The form of the hemispondylium may be correlated with the form of the area of attachment and is apparently related to muscle efficiency (Elliott 1948, p. 20).

Development of the crescentic tubercles. Post-forbesiform and adult pedicle valves are characterized by the development of structures along the internal edge of the valve margin (Pl. 18, fig. 2; Pl. 19, fig. 2). which Elliott in B. faringdonense has called sub-pustulose marginal ornament. In M. granulosa these structures can be shown to be modified tubercles and are thought to be of considerable importance. As their shape is quite characteristic it is proposed to designate them crescentic tubercles. They appear to be most strongly developed in the anterior and antero-lateral sectors of the valve and show a development pattern entirely different from that of the tubercles of the subperipheral rim. Crescentic tubercles do not appear until the anterior of the pedicle valve begins to grow away from the attachment surface. They apparently grow simply by the incremental addition of material at their distal ends and the secreting cells must occupy an invagination of the outer epithelium so that the tubercle cores stay slightly in advance of adjacent outer epithelial secretory cells. Their relationship with adjacent secondary fibres would indicate that their long axes are not quite parallel with the internal shell surface but inclined dorsally inwards at an angle of about 2°. This development pattern of the crescentic tubercles is obviously related to the maintenance of a constant orientation relative to the tubercles of the sub-peripheral rim (text-fig. 6A, C).

DETAILED MICROSTRUCTURE

As already noted, Moorellina granulosa (Moore) offers conclusive proof that in some Jurassic thecidellinids at least, the shell was differentiated into primary and secondary layers. The primary layer is best seen in the

pedicle valve where it is relatively much thicker than in the brachial valve. It is possible that in some specimens the thin primary layer may occur only sporadically as in orthoids and strophomenoids where its absence is attributable to wear of a very thin layer. The possibility of the removal of the primary layer is important in the interpretation of occasional pitted structures, described later, occurring in the outer surface of some brachial valves.

The primary crystallite mat gives the typical fibrous, transverse (Pl. 19, fig. 3) and pitted, horizontal (Pl. 19, fig. 4) sections described by Williams, Transverse sections through secondary fibures show typical cross-sections (Williams 1968a, p. 9) with the exception that the lateral areas are much reduced so that a sub-hexagonal pattern is produced (Pl. 19, fig. 5). This standard shape appears to persist throughout the secondary layer of the pedicle valve but shows some modification in the brachial valve. Patches of fibres in the brachial valve show dorso-ventral flattening distally so that they develop flared ends (text-fig. 4C, D). The possibility that these were merely apparent transverse sections, produced by fibre reorientation was checked against horizontal longitudinal sections through fibres. The flared secondary fibres have a characteristic strap-like appearance and are up to three times (10-12μ) the width of normal fibres. It is possible that the modified fibres are associated with muscle scars but this could not be confirmed in the material studied. The location of the sections however, would suggest that the fibres occur in zones of the valve which were not areas likely to be associated with muscle attachment.

The variability of the fibres in section and the consequent possibility of misinterpretation of sections has been noted by Williams (1966, p. 1148). The present work has been hindered by the same rapid changes of fibre orientation. Studies indicate that orientation variation in the secondary

EXPLANATION OF PLATE 19

Stereoscan photomicrographs of specimens of *Moorellina granulosa* (Moore). Material of all figures coated with evaporated aluminium before photography.

Fig. 1. Interior view of a broken pedicle valve (37514) showing the hemispondylial plates supported by a reticulate structure. Umbonal region missing. × 40.

Fig. 2. Enlarged portion of the margin of pedicle valve (37515), showing the position and characteristic shape of the crescentic tubercles. × 170.

Fig. 3. Etched surface prepared from polished block (37516) showing the primary layer in transverse section, lower right, and detail of the junction with the secondary layer. Section orientation: vertical, longitudinal. Section location: pedicle valve, free anterior surface, close to the area of attachment. Scale represents 4 μ.

Fig. 4. Stereoscanned cellulose acetate peel (37518), showing the primary layer in horizontal section, lower right. Section orientation: perpendicular to the plane of the commissure at 75° to the long axis. Section location: pedicle valve, left postero-lateral sector. Scale represents 8 μ.

Fig. 5. Stereoscanned cellulose acetate peel (37518) showing transverse section through secondary fibres. Section orientation and location as fig. 4. Scale represents 5 μ.

Fig. 6. Interior of the brachial valve of a pre-forbesiform individual (37503) showing endopuncta and the exposed inner ends of secondary fibres on the floor of the left brachial cavity. Scale represents 5 μ.

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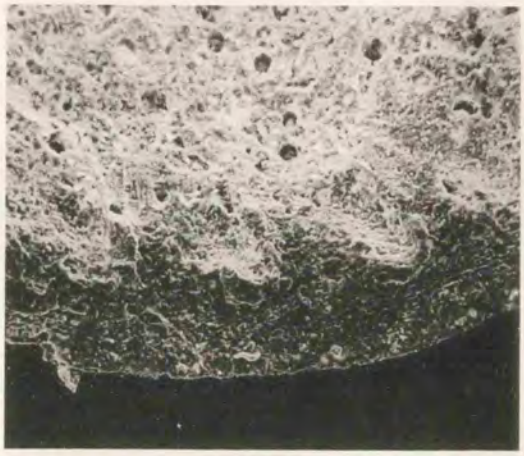

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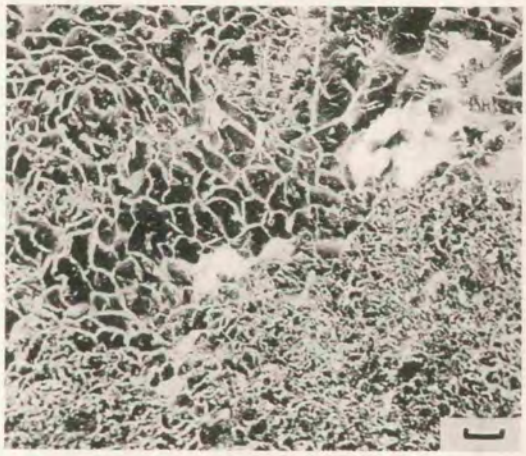

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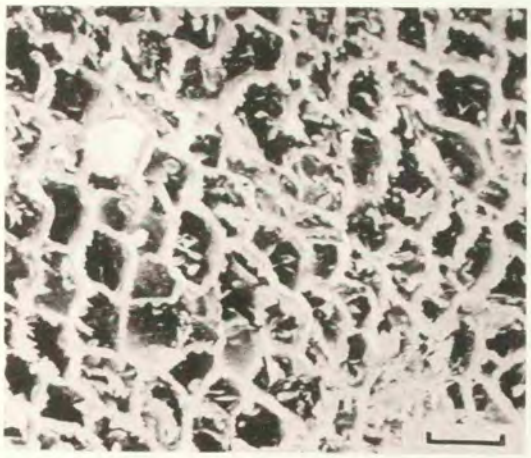

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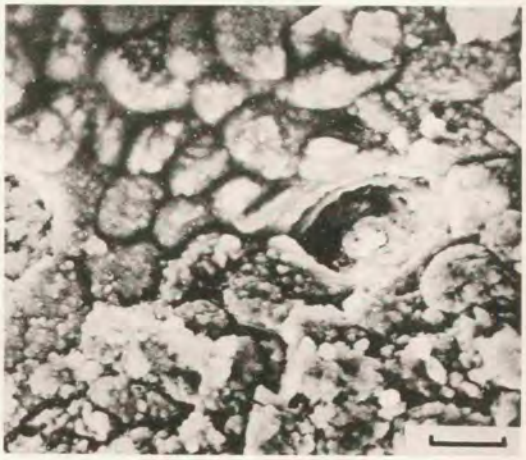

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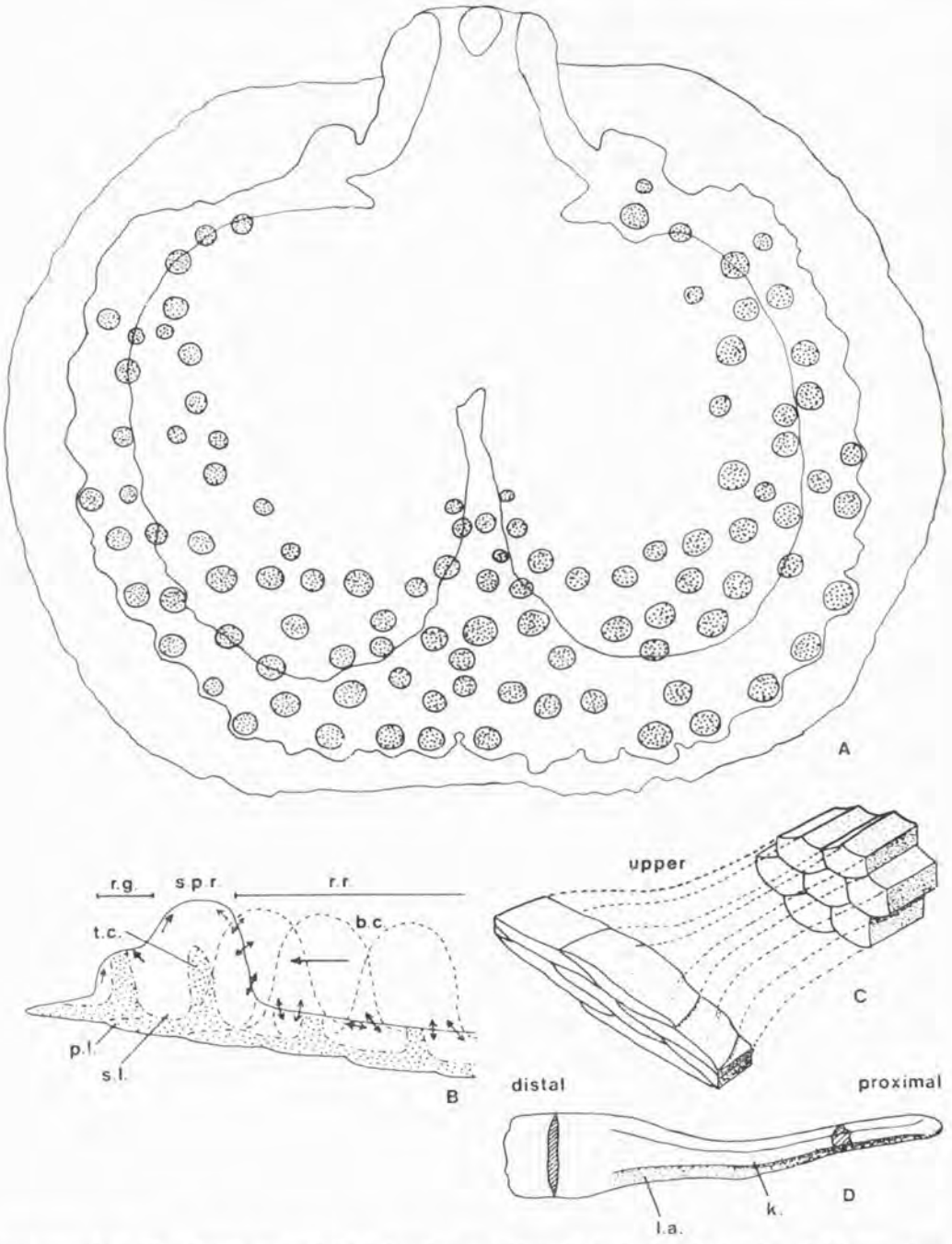
BAKER, *Moorellina granulosa*



TEXT-FIG. 4. A. The distribution of the tubercle cores (dotted) in the brachial valve of *M. granulosa*, plotted from twenty-five superimposed peels. The core distribution inside the sub-peripheral rim, outlined, indicates the areas of the brachial cavities where resorption has occurred. B. Diagrammatic representation of the probable mode of migration of the sub-peripheral rim during growth. C. Normal and flared transverse mosaics. D. Diagram to show the shape of an individual fibre. b.c. brachial cavity, k. keel, l.a. lateral area, p.l. primary layer, r.g. rim generation zone, r.r. rim resorption zone, s.l. secondary layer, s.p.r. sub-peripheral rim, t.c. tubercle core.

layer may occur at different depths, in different sectors of a valve, and that the microstructure of the brachial and pedicle valves of the same animal may show significant differences. For this reason it is felt that all future plate figures must be accompanied by accurate data concerning the orientation of sections through the specimen and the exact location of the section on the shell. The author has attempted to present such data in a concise form in the plate explanations, to enable other workers to avoid or duplicate these sections in subsequent investigations.

Relatively large areas of the brachial cavities of M. granulosa are formed by the progressive resorption of the sub-peripheral rim (text-fig. 4A, B). As a result of resorption in these areas, the fibre orientation persisting at the bases of former sub-peripheral rim tubercles is exposed on the internal surface of the valve, producing a very disturbed pattern (Pl. 20, figs. 1, 2). Once the significance of rim resorption had been appreciated, it was realized that undisturbed secondary mosaic would only be seen in areas which were not affected by shell resorption. This suggested three possible sites, (a) the border region outside the sub-peripheral rim, (b) the pedicle valve, and (c) the brachial cavities of pre-forbesiform (Baker 1969) individuals, where rim resorption had not yet begun. A detailed examination of brachial and pedicle valves was then undertaken with these considerations in mind. The border region has proved to consist entirely of primary shell and the mosaic on the inner surface of the pedicle valve is obscured by the development of crescentic tubercles. A pre-forbesiform brachial valve (37503) however, clearly shows traces of the internal mosaic of the secondary layer (Pl. 19, fig. 6).

The observed differences in the brachial and pedicle valves of M. granulosa have produced significant differences in microstructure and

render it necessary that the microstructure of the two valves be described separately.

Brachial valve. A thin primary and a disturbed secondary layer associated with the development and migration of the sub-peripheral rim are present.

A detailed investigation of the tubercles of the sub-peripheral rim was undertaken. If the concept of resorption is correct, it should be possible to distinguish the remains of tubercle cores in areas of the brachial cavity formerly occupied by the sub-peripheral rim. Horizontal, transverse, oblique, and longitudinal sections were prepared in order to establish their presence. Horizontal serial sections (Pl. 20, figs. 3 - 5) show that the tubercles are cored structures and that the tubercle cores are, in fact, continuous with the material of the primary layer (Pl. 20, fig. 5). The tubercle cores may be regarded therefore, as being composed of primary shell type material. The question of whether the primary layer has suffered diagenesis has little significance as the material of this layer and of the tubercle cores has the same characteristics and may logically be considered to have the same origin. The author envisages localized patches of outer epithelium continuing to secrete primary shell. It seems probable that the mechanism of development is similar to that which controls the initiation of punctae, as tubercles also are normally, but not universally, offset by one half-phase (Pl. 20, figs. 3, 5). A plot of the tubercle cores is superimposed serial sections through a brachial valve of M. granulosa shows that they persist through several sections and are intimately connected with the development of the sub-peripheral rim. They do not appear in zones of the shell which may be logically considered to have been deposited prior to the appearance of that structure (text-fig. 4A). Horizontal sections through the sub-peripheral rim (Pl. 20, fig. 3) confirms that the tubercle cores originate near the mantle edge, in fact at the outer boundary of the sub-peripheral rim itself,

and close to the point where the secretion of secondary shell begins. Subsequent isolation of eroded tubercle cores in the brachial cavities is brought about by the mode of development of the sub-peripheral rim during ontogeny (Pl. 20, fig. 4). Vertical sections (Pl. 20, fig. 6) shows that the tubercle cores are inclined at a high angle, almost normal to the external shell surface, with a slight outward deflection.

That the tubercle cores of the brachial valve are composed of primary shell material would appear to be confirmed by occasional curious pitted structures occurring on the external surface of valves. Although these occur in M. granulosa they are better preserved in the Upper Oxfordian, Moorellina ornata (Moore) (Pl. 20, figs. 7, 8). Each pit has a central granular mound and may possibly be interpreted as some form of exopuncta. However, in the light of observations regarding the thickness of the primary layer and the fact that the tubercle cores are shown to be continuous with it, it would appear that what is actually seen is the outer boundary of the secondary layer, exposed by the removal of primary shell. In which case, the apparent bands are the long axes of fibres and the central mounds of the pits are really weathered tubercle cores. This is supported by: (a) the orientation of the fibres is correct if they constitute part of a normal spiral arc, (b) they are the right thickness, about 4μ , (c) the granular nature of the central mound is the same as that of sectioned tubercle cores, (d) the diameter of the pits is the same as the diameter of tubercle cores in section, i.e. 25-30μ , and (e) they are too large to be normal punctae which have a diameter of only 8-10μ .

Pedicle valve. A well-developed primary and secondary layer are present. The primary layer thins posteriorly and the secondary layer shows modification anteriorly as a result of the growth habit of the valve.

Attempts to reconstruct a secondary mosaic in the manner described above, failed to produce a decipherable pattern because the secondary layer

of the pedicle valve of M. granulosa is itself composed of two regions with regard to fibre orientation. There is an outer, essentially normal, spiral arc orientation and an inner layer in which the fibre orientation is intimately bound up with the development of the crescentic tubercles (Pl. 21, figs. 1, 2). In the lateral and postero-lateral sectors of the valve, the secondary fibres show a normal spiral arc arrangement. In the zones of the anterior surface adjacent to the area of attachment, the orientation of the fibres of both regions of the secondary layer appears to follow the primary growth vectors and longitudinal sections produce typical longitudinal sections through fibres (Pl. 21, fig. 3). However, as growth of the pedicle valve proceeds away from the substratum, the secondary layer is differentiated into outer and inner regions. The orientation of the fibres in the outer region changes in such a way that they come to lie almost parallel with the commissure. Longitudinal sections through these zones produce almost transverse sections through the fibres of this outer layer (Pl. 21, fig. 4).

With this information available the growth mosaics of the two regions were fairly easily reconstructed by plotting the fibres of the outer and inner regions separately. This was achieved by plotting the primary/secondary layer junctions of serial sections, together with the orientation direction of the fibres adjacent to the junctions. The mosaic produced (text-fig. 5A) was interpreted as representing the growth mosaic of the outer region of the secondary layer of the anterior surface of the pedicle valve. Similarly, a re-plot of the remaining fibre orientation on each serial section, i.e. omitting those plotted in text-fig. 5A, was interpreted as representing the growth mosaic of the inner region of the secondary layer (text-fig. 5B). A suggested explanation for this anterior differentiation is offered later, as it can be shown not to be present throughout the whole of the secondary layer.

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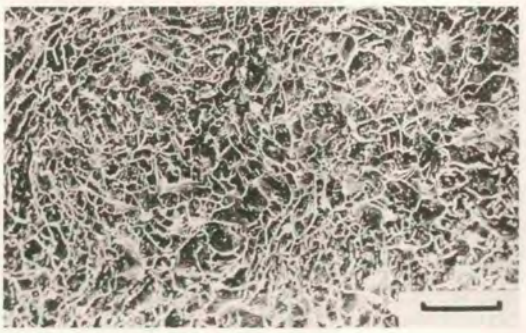

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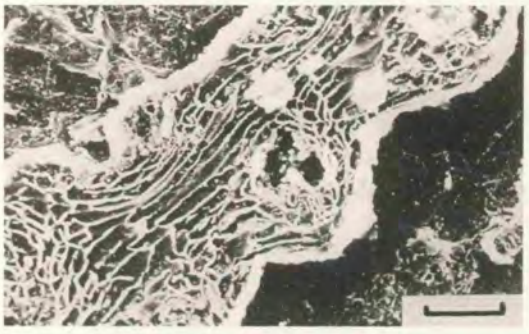

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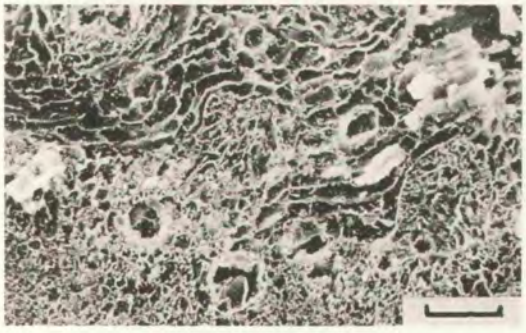

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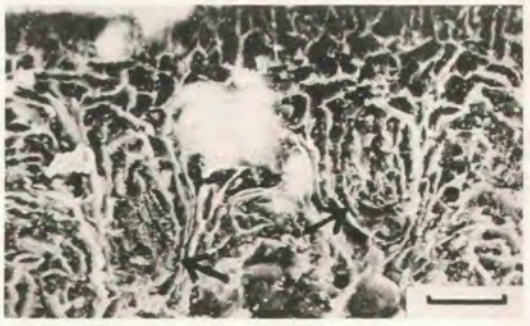

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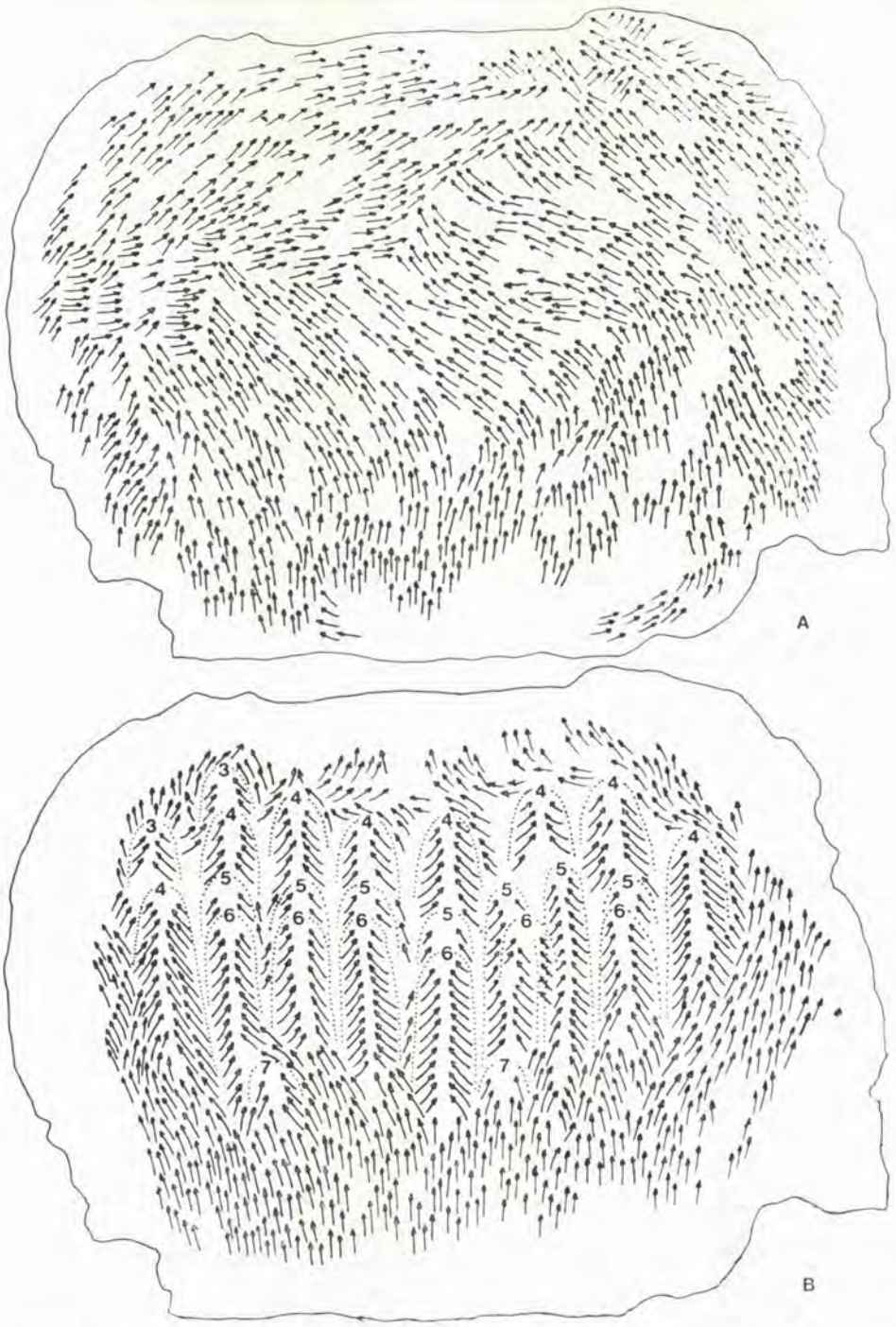
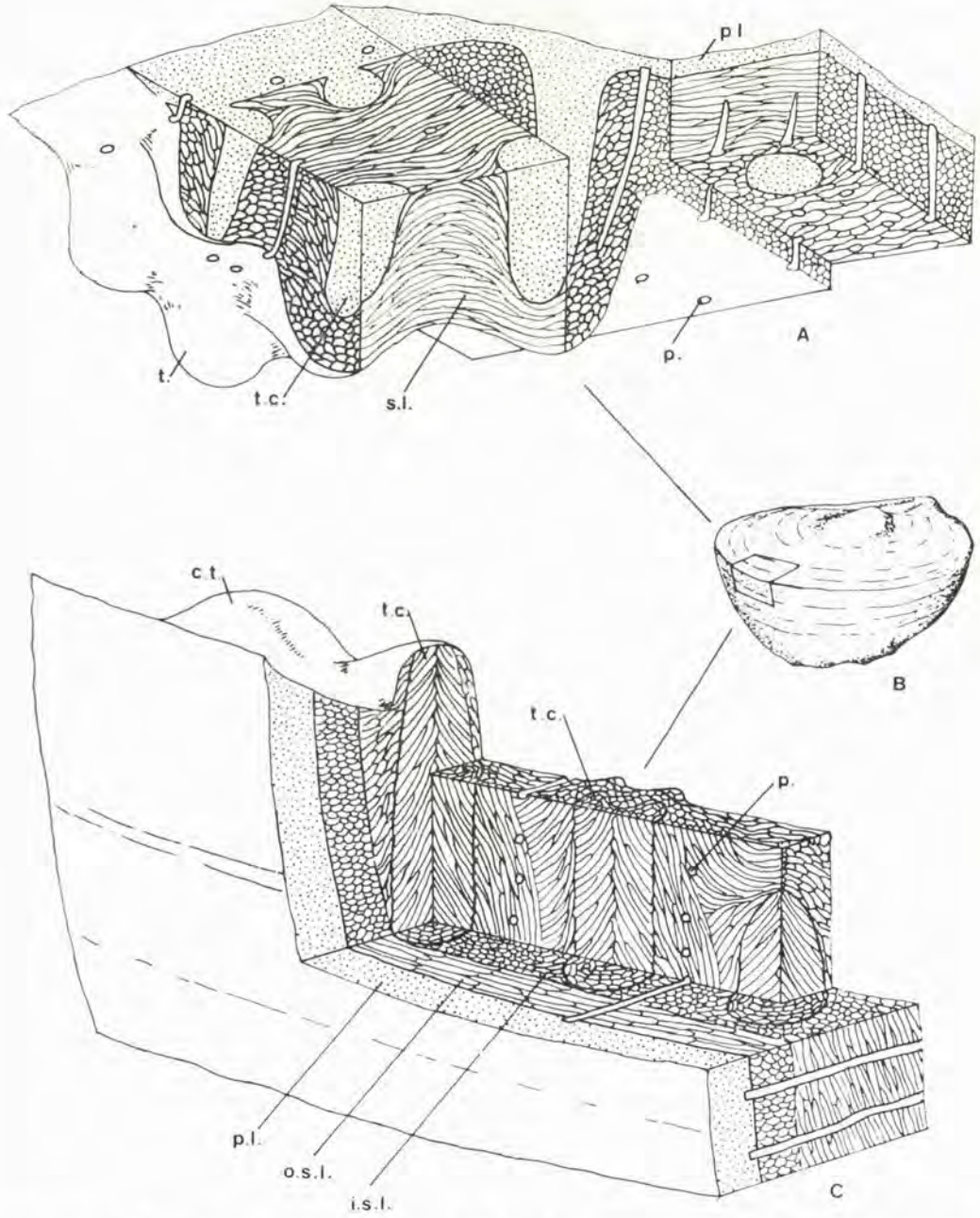
BAKER, *Moorellina granulosa*



TEXT-FIG. 5. Reconstruction of the fibre orientation of the outer and inner regions of the secondary layer of the free anterior of the pedicle valve of *M. granulosa*, from eight superimposed peels. A. Fibre orientation of the outer region. B. Fibre orientation and tubercle cores of the inner region. Numbers indicate the position of the tubercles in successive peels, from the internal surface of the valve.



TEXT-FIG. 6. Diagrammatic reconstruction of the shell microstructure of *Moorellina granulosa* (Moore). A. Block diagram showing the microstructure of the brachial valve. B. Complete specimen showing relative position of the reconstructed segments. C. Block diagram showing the microstructure of the pedicle valve. c.t. crescentic tubercle, i.s.l. inner secondary layer, o.s.l. outer secondary layer, p. puncta, p.l. primary layer, s.l. secondary layer, t. tubercle, t.c. tubercle core.

As in the brachial valve, the structure of the crescentic tubercles was investigated with the aid of transverse, horizontal, oblique, and longitudinal serial sections. In longitudinal sections the tubercles are seen to be composed entirely of fibrous cones (Pl. 21, figs. 2, 5) deflecting the other fibres adjacent to them. In transverse section (Pl. 21, fig. 1) the tubercles exhibit a characteristic reniform shape. The presence of these structures may be of profound significance and their implication is discussed later.

Compilation of the features exhibited by serial sections at various orientations allows reconstruction of the microstructure of the shell of M. granulosa (text-fig. 6A-C).

The pseudodeltidium and pedicle sheath. Study of Lacazella (Williams et al. 1965) indicates that neither the pedicle nor its muscle system is developed. The structure of the strophomenoid pseudodeltidium is still imperfectly known but it is now generally agreed that it consists of primary and secondary material and was secreted between the teeth ridges by the outer epithelium. Ventral umbonal regions of well-preserved specimens of M. granulosa were carefully sectioned in an attempt to resolve the problem of the fate of the pedicle opening in Jurassic thecidellinids. Owing to the mode of growth of the area and the minute proportions of the structures involved, it was difficult to distinguish the pseudodeltidium at all. Of the limited number of specimens in which it could be recognised, only three showed any discernible microstructure. In these specimens, transverse sections close to the ventral umbo show the presence of a minute pore 50 μ in diameter and apparently plugged by calcite having a different orientation from that of the pseudodeltidium (Pl. 21, figs. 7, 8). The pore appears at about 0.06 mm. from the posterior of the pedicle valve and close to the area of attachment (text-fig. 7C) in what must

be regarded as a supra-apical position (text-fig. 7H). It appears to be surrounded laterally and dorsally by a collar or ring of material in which the fibres show a concentric orientation in the plane of section. The dorsal surface of the ring is exposed externally and is obviously the structure interpreted as a pseudodeltidium. In subsequent sections the pore migrates dorsally away from the area of attachment and the ring increases in size, still maintaining its dorsally exposed surface (text-fig. 7C-F). Continuity of thestructure through several sections reveals that it is really a calcareous tube, which, if the plugged pore represents the site of the atrophied pedicle opening, may be regarded as a form of pedicle sheath which initially closed the delthyrium. At about 0.14 mm. from the umbo the structure terminates (text-fig. 7G) and is replaced by the ventral umbonal cavity, housing the posterior tip of the cardinal process. The space between the tooth ridges is now occupied by a plate of more normal pseudodeltidial appearance. Unfortunately, at the moment there is no evidence to show whether this is a discrete plate or whether it is the product of over-growth by the outer epithelium at the anterior termination of the calcareous tube. Atrophy of the pedicle would explain why the tube ceased to develop and only closes the posterior part of the delthyrium, an operation subsequently taken over by the outer epithelium.

EXPLANATION OF PLATE 21

Stereoscan photomicrographs of specimens of *Moorellina granulosa* (Moore). Material of all figures coated with evaporated aluminium before photography.

Fig. 1. Stereoscanned cellulose acetate peel (37520). Transverse section through a pedicle valve showing the orientation of the outer fibres of the secondary layer and the reniform tubercle cores. Section orientation: parallel with the plane of the commissure. Section location: left antero-lateral sector, 0·4 mm. from the distal ends of the tubercles. Scale represents 50 μ.

Fig. 2. Stereoscanned cellulose acetate peel (37521). Section through the secondary layer showing fibres deflected by the crescentic tubercles. Section orientation: parallel with the anterior surface. Section location: pedicle valve, anterior surface, 0·168 mm. from the external surface. Scale represents 20 μ.

Figs. 3, 4. Etched surface prepared from polished block (37516). Section orientation and location as in fig. 3 (Pl. 19). Fig. 3 shows the primary layer, bottom and detail of the secondary fibres in longitudinal section. Fig. 4 shows reorientation of the fibres of the outer region of the secondary layer to give almost transverse section. The elongate fibres (oblique section), upper left, represent a tubercle core sectioned near the axis. Scale represents 10 μ.

Fig. 5. Stereoscanned cellulose acetate peel (37521). Section through the secondary layer showing the fibrous cores of the crescentic tubercles. Section orientation and location as in fig. 2, but 0·096 mm. from the external surface. Scale represents 50 μ.

Fig. 6. Interior view of the anterior surface of a pedicle valve (37515) showing the arrangement of the punctae in rows relative to the crescentic tubercles. × 50.

Fig. 7. Stereoscanned cellulose acetate peel (37523). Transverse section through the ventral umbonal region showing the plugged pedicle opening and dorsally exposed pedicle sheath. Section location: 0·08 mm. from the umbo. Scale represents 50 μ.

Fig. 8. Retouched photomicrograph of fig. 7.

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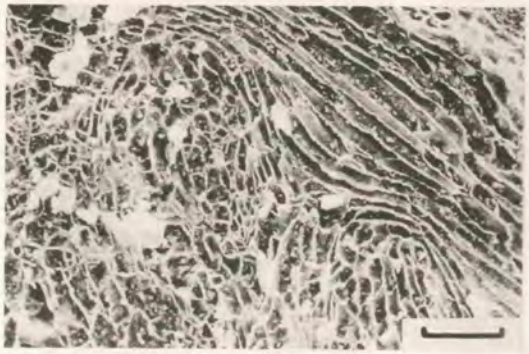

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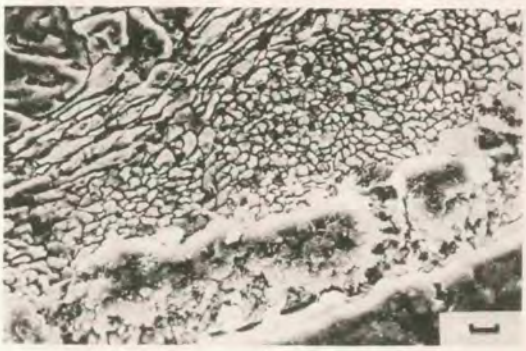

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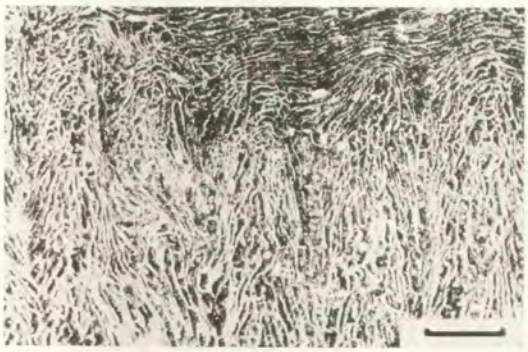

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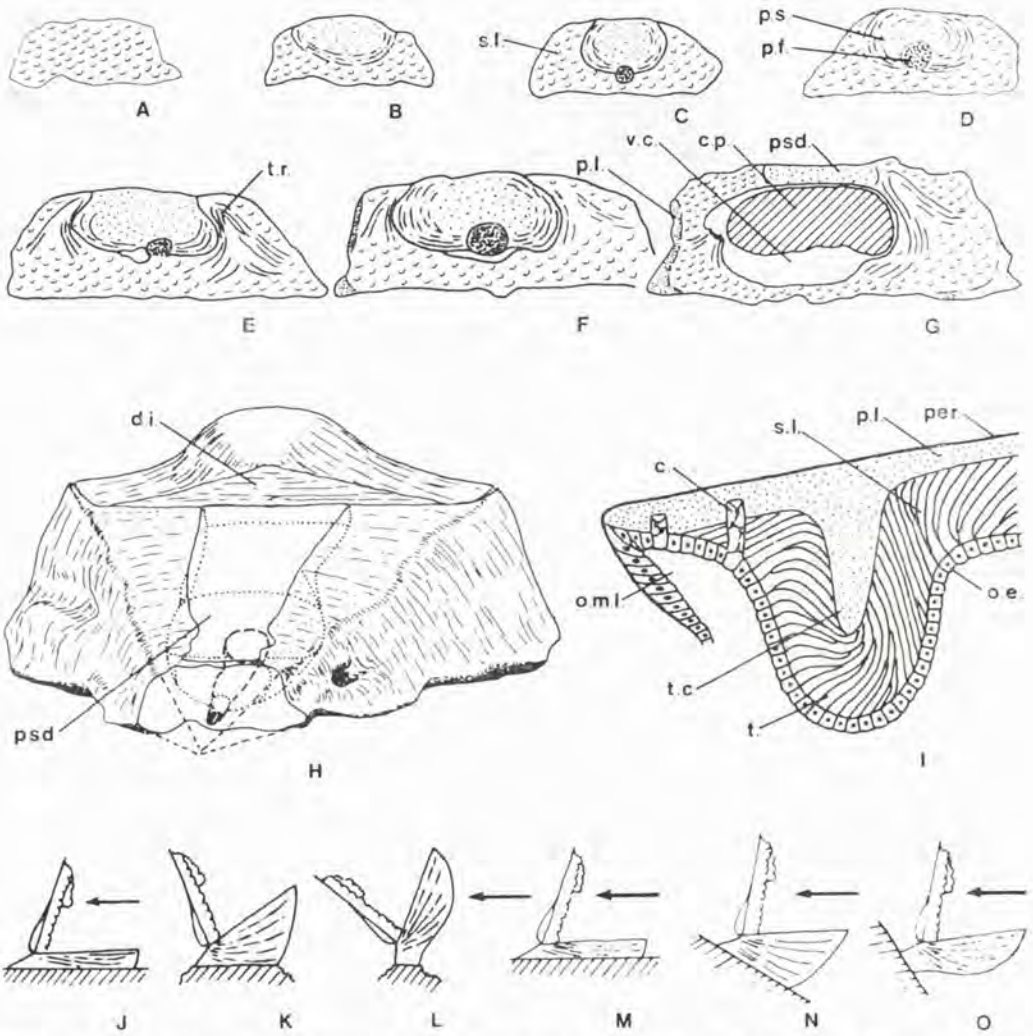
BAKER, *Moorellina granulosa*



TEXT-FIG. 7. A–G. Drawings prepared from cellulose acetate peels of serial transverse sections through the ventral umbonal region of *M. granulosa* showing the continuity and anterior termination of the pedicle sheath and the plugged pedicle foramen. H. Reconstruction of the ventral umbonal region from thirteen superimposed peels. Outline of the pedicle sheath dotted and the pedicle opening, broken line. Position of umbo projected by dotted lines. I. Diagrammatic section through the sub-peripheral rim to show the difference in the development of endopunctae and tubercle cores. J–O. Series of six diagrams to show the orientation of the brachial apparatus relative to a prevailing current, arrowed. J–L, constant growth position with variable size of the attachment surface. M–O, constant orientation at various growth positions. c. caecum, c.p. cardinal process, d.i. dorsal interarea, o.e. outer epithelium, o.m.l. outer mantle lobe, per. periostracum, psd. pseudodeltidium, p.f. pedicle foramen, p.l. primary layer, p.s. pedicle sheath, s.l. secondary layer, t. tooth, t.c. tubercle core, t.r. tooth ridge, v.c. ventral umbonal cavity.

SIGNIFICANCE OF THE OBSERVED GROWTH AND MICROSTRUCTURE

Growth orientation. Obviously there must be some genetic control of the proliferation of epithelial cells in the mantle fold and it is not possible to show absolute growth in M. granulosa. However, the use of a system of growth units makes it possible, providing one knows the primary growth orientation, to determine areas of rapid proliferation of cells and, therefore, relatively rapid increase in size. The observed external fibre orientation is clearly a topological expression of shell growth. There is a very close resemblance between the distribution of primary costae in Rhipidomella oblata (Hall) and the external fibre orientation of M. granulosa but this is to be expected if addition of material is normal to the commissure with mixoperipheral growth. This would clearly suggest that the radial ornament of the dalmanellaceids (Williams and Wright 1963, p. 22) is topological also. Work on the orientation pattern of M. granulosa would therefore appear to confirm their view that dalmanellaceid ornamentation patterns of "progressive" species of Watsella (Bancroft 1945, p. 190) have no supra-specific taxonomic status.

The anteriorly modified spiral arc of the pedicle valve of M. granulosa, producing a secondary layer differentiated into two regions can only be clearly demonstrated in valves having a large free anterior surface. If one considers the thecideacean environment (Ager 1965, 1967; Nekvasilová 1967; Baker 1969) this anterior differentiation of the secondary layer is readily explained. Forms with a large free anterior surface (small area of attachment) would have relatively more of the pedicle valve exposed to the rigours of the environment. Development of crescentic tubercles would produce a structure which would secure the commissure (interlocking effect)

but at the same time produce an exposed anterior surface which could be more easily breached at the relatively weak junctions between adjacent tubercles (Pl. 21, fig. 5). Differentiation of the secondary layer anteriorly into what might be described as a cross-laminate structure would greatly increase its strength. The above seems a logical explanation for the observed micro-structure of the pedicle valve of M. granulosa and the relationship between fibre orientation and micro-structure of other attached brachiopods is well worth investigating. Strophomenides, for example, may have solved the problem by the modification of fibres to produce laminae (Williams 1968a, p. 37). The fibres with flared ends noted in the brachial valve of M. granulosa may represent an attempt in this direction.

Ecology and functional morphology. Consideration of the growth habit of the pedicle valve in ecological terms is interesting. If the cumulative growth pattern is designed to lift the anterior gape away from the substratum, it is difficult to see why the characteristic is suppressed in forms with a large area of attachment. It seems probable that it is the degree of inclination, rather than the size of the surface to which the animal attaches itself, which is the major control. Elliott's (1948) paper would suggest that the relatively enormous gape (Rudwick 1968) of the thecideidines is associated with orientation of the brachial apparatus relative to the "prevailing" environment, probably represented by a persistent current direction. The above relationship seems entirely probable and supports the author's argument. Individuals attaching themselves to surfaces of suitable inclination already have their commissures in the "ideal" orientation position from an ecological standpoint. Such individuals would have no need to develop elaborate anterior surfaces, although development of even the relatively small anterior surface encountered in these specimens must inevitably require the cumulative growth pattern postulated.

There seems to be a correlation between size of animal and degree of elaboration of the brachial apparatus (Elliott 1948), interpreted as being related to the animal's food-gathering ability in a competitive sense. This may partially explain the onset of the development changes which lead to the freeing of the anterior of the pedicle valve from attachment to the substratum. Size of the animal is obviously critical where small size of the attachment surface is concerned but observations indicate that size may be critical independently. Attainment of a certain size might render necessary a change in organisation, to effectively meet theincreasing nutritional demands.

There are obviously other factors to be considered such as accommodation of the brachial apparatus and the developing sub-peripheral rim, the relative efficiency of the lophophore and the ecological niche (Rudwick 1962) occupied by any particular individual. However, if, as there would appear to be, there is any order associated with the growth habit, it is easier to reconcile this, in ecological terms, with the attainment of a certain orientation position of the gape (text-fig. 7J - O) rather than the size of the surface to which the animal was attached. One feels that the orientation of the gape, in terms of functional efficiency of the brachial apparatus, is the more satisfactory explanation for the variable growth habit observed in the pedicle valves of thecidellinids.

As M. granulosa is a member of the surf-zone fauna, the interlocking tubercles of the two valves on such cemented forms may have acted as accessory teeth and sockets to help secure the brachial valve in position during adverse conditions. The preponderance of brachial valves in any collection may be a measure of the relative vulnerability that the abnormally wide gape exposed in the existing hinge.

Microstructure. Williams, in his work on Lacazella (1968a, b) apparently abandons his earlier interpretation (1955, 1956, 1965) that a secondary layer is present, in favour of a shell composed only of primary material. The three earlier accounts are essentially similar. The 1955 paper records the present of fibre bundles almost perpendicular to the "lamellar" layer, producing the appearance of pseudopunctae but, in the absence of a non-fibrous core, unrelated to the strophomenid spicules. These core bundles are figured in the rather vague reconstruction of the shell of Lacazella mediterranea (Risso) in 1965, H67), but their orientation is apparently in the wrong direction. Attention is, however, drawn to the similarity of this type of shell structure and that of the terebratellaceid Mergerlina lamarkiana (Dav.). The 1956 paper records the same fibrous cores in thecidaceids but offers no information as to which were studied. It is felt that the structures described must be referred to the microstructure of the crescentic tubercles of M. granulosa (Pl. 21, figs. 2, 5, text-fig. 6C).

The absence of a secondary layer in Lacazella is interpreted as being the result of neotenous suppression (Williams 1968a). Although changes in the secretory habit of the epithelial cells in M. granulosa appear to follow a normal pattern, the stability of the thickness of the primary layer does not appear to be quite as constant as Williams has suggested and it is possible to see groups of secondary fibres apparently embedded in primary shell. This irregularity of deposition of the secondary layer in M. granulosa may be the first expression of its ultimate suppression.

Although M. granulosa is not costellate, it is worth noting that the external expression of the crescentic tubercles on the inner edge of the margin of the pedicle valve, bears a strong resemblance to the follicular eminences and embayments of the Recent Terebratulina and also

fossil enteletacean (Williams and Wright 1963, p. 19; Williams and Rowell 1965, H81) brachiopods and may have served a similar purpose. Similar structures are seen in the cemented inarticulate Crania anomala (Müller) where they are not associated with setae but control the distribution of punctae. In M. granulosa, the crescentic tubercles appear to exercise a similar control over the distribution of punctate (Pl. 21, fig. 6).

Elliott (1953, 1955) has arrived at the conclusion that all thecideidines are endopunctate with the possible exception of Davidsonella. Study of M. granulosa and M. ornata shows that although the endopunctae are formed in a terebratuloid manner, the cup-shaped distal enlargements and the deflexion of secondary fibres have not been seen.

Deeper issues are at stake with regard to the implication of the described tubercle structure. They occur together with endopunctae and the initiation of punctae and tubercle cores seems to follow the same pattern. Upon consideration of their structure, the question arises whether the tubercles are homologous with pseudopunctae. Tubercle cores must arise in a very different manner from endopunctae (text-fig. 7I), and therefore if homologous with pseudopunctae, pseudopunctae and endopunctae must be totally unrelated.

Williams (1965, H72) has stated that taleolae are comparable in texture with the terebratuloid primary layer. Sections parallel with the plane of the commissure through M. granulosa have shown that the tubercle cores of the brachial valve are in fact continuous with the primary layer and as far as can be ascertained, represent imperfectly developed primary shell, secreted by persistent patches of columnar epithelium, surviving from the tip of the outer mantle lobe.

Williams (1965) has shown that pseudopunctae are markedly asymmetrical in longitudinal section, with their apices directed inwardly and anteriorly to protrude from the internal surfaces of both valves as

tubercles. The orientation of the tubercles in the brachial valve of M. granulosa shows this approximate pattern. In the pedicle valve, it only requires a slight exaggeration of this trend to produce, in M. granulosa, tubercle cores running almost parallel with the plane of the valve in such a way that they emerge as tubercles along the inner edge of the anterior margin. In which case, they may be regarded as homologous with the pseudopunctae of davidsoniaceans such as Derbyia, which consist of fibrous cones of the type shown to exist in the pedicle valve of M. granulosa (text-figs. 5B, 6C, Pl. 21, fig. 5).

The suspected close relationship between pseudopunctae with and without taleolae is confirmed by the presence of both types in a single animal. A careful sectioning technique, supported by the fact that the structures are located in different valves, enables one to show that the tubercles of the brachial valve have cores, whilst those of the pedicle valve are without cores. If one considers the pure mechanics of this arrangement it would appear to be quite logical. In the brachial valve where orientation of the tubercle axis is near perpendicular to the surface of the valve, the development of the primary core in the manner suggested is the simplest way of bringing about an invagination of the outer epithelium. On the other hand, in the pedicle valve, where by virtue of the growth habit, the orientation of the tubercles must necessarily be nearly parallel with the valve inner surface, a primary core would become very attenuated. In this situation it would be far easier to produce a tubercle core by a slight change in the orientation of secondary fibres.

If one considers the tubercles in terms of this functional requirement, they may be regarded as the modified counterpart of strophomenoid pseudopunctae. They deflect secondary fibres in the same way and the similarity of the disposition of the fibres presumably indicates a similar pattern of development.

AFFINITIES

The affinities of the Thecideidina have been a subject of interest and speculation for a number of years, Elliott (1948, 1953, 1958), Rudwick (1968), and Williams (1965, 1968a, b) being notable among the later works. Demonstration of a primary and secondary shell layer in M. granulosa invalidates only Williams's (1968a, b) conclusion that Lacazella is a typical model of the thecideidine shell and in no way impairs his line of descent. If, as Williams's work suggests, the secondary layer of Lacazella has been neotenously suppressed to the point of exclusion, M. granulosa occupies an attractive position, as Jurassic forms in which this process might just be beginning, represent an important contribution to our knowledge. One feels that the diversity of shell microstructure encountered in a single specimen of M. granulosa, must represent a genetic disturbance which could quite easily result in the ultimate suppression of the secondary layer. The banded shell of Lacazella might in environmental terms, more easily satisfy the requirements for a reinforced shell and render the structurally reinforced secondary layer of M. granulosa obsolete, thus accounting for its disappearance. The secondary shell mosaic seems closer to terebratulide or spiriferide than any other. However, the shape of the fibres is different and also variable within an individual, so that one may see fibres with flared outer ends reminiscent of the laminae of plectambonitaceans. Still other features of the microstructure may be reconciled with davidsoniaceans.

The value of functional analysis of morphology, demonstrated by Rudwick (1968) and the significant correlation between the modification of the microstructure of M. granulosa and environmental influence, unlerlines an advance in our knowledge of taxonomic technique. Obviously, not only structures but also their significance in environmental terms

must be critically examined before assigning a species to a particular systematic position, as convergence may be encountered at the micro-structure level. It is felt therefore, that the taxonomic importance of some aspects of shell microstructure should not, as has happened frequently in the past on discovery of a character, be overestimated.

The value of shell microstructure from a taxonomic point of view has been discussed by Williams (1956, 1968a, b), Rudwick (1968), and Gauri and Boucot (1968). As the present investigations have shown, there are important differences between the microstructure of the brachial and pedicle valves of M. granulosa. That this is not a feature peculiar to thecidellinids has been demonstrated by Gauri and Boucot (1968) who record that in the pentamerids Antirhynchonella, Clorinda, and Zdimir, the prismatic layer is absent from the brachial valve. Their study of pentameraceans and the gulf which exists between Williams's (1968a) thecideidine model and the observed microstructure of M. granulosa indicates that the state of our knowledge of shell microstructure in brachiopods is not yet sufficiently advanced to allow anything other than a tentative taxonomic significance to be ascribed to it.

With regard to the fate of the pedicle, it appears unlikely that M. granulosa will yield the quality of evidence to enable one to make categoric statements concerning the microstructure of the pedicle opening. Evidence yielded by Lacazella mediterranea (Risso) must remain suspect in view of the neotenous modification of this species. The main hope seems to lie in the discovery of well-preserved, larger thecideidines from other horizons. Only limited significance should therefore be attached to the pseudodeltidium of M. granulosa until the evidence has been strengthened. If a pedicle sheath does arise supra-apically, then it is possible to equate this with the strophomenoid pseudodeltidium. Arber (1942) has recorded a very similar solid pseudodeltidium, fused

with the floor of the pedicle valve in the Orthotetinae and Rafinesquinae. However, Williams (1956) has noted an imperforate delthyrial cover in Eospirifer. The indication that the pseudodeltidium of M. granulosa was deposited by the ventral edge of the capsule of a pedicle undergoing atrophy, appears to confirm the views of Arber (1942) and Williams (1956) regarding the form of the pseudodeltidium of Lacazella.

Although it appears that the thecideacean pseudodeltidium is homologous with the pseudodeltidium of strophomenoids, Williams and Rowell (1965, H188) regard the similarity between strophomenoids and thecideaceans as an expression of convergence and derive the thecideidines from possible suessiacean ancestors. One must agree that the secondary mosaic is very similar to Cyrtina but encounters the same time-gap objection raised by Williams (1956) to the affinity proposed by Kozlowski (1929) for the lophophore platforms of some plectambonitaceids and thecidaceids.

Structurally there appears to be no significant difference between strophomenoid pseudopunctae and the tubercles of M. granulosa. The similarity between them and pseudopunctae of the davidsoniacean Derbyia is even closer. On this basis, it would not be unreasonable to conclude that the tubercles of thecidellinids are homologous with strophomenoid pseudopunctae, functionally modified.

Elimination of obscure similarities, plectambonitaceid, enteletacean, terebratellacean, etc., leaves one with the basic problem of whether the thecideidines show strophomenide or spiriferide affinity. An analysis of the literature shows that the systematic position of Thecospira is of critical importance as far as the thecideidines are concerned. It seems strange that Williams (1968a), after lengthly discussion of the low

taxonomic value of a limited number of characters, should re-assign the genus to the Spiriferida solely on the basis of its shell structure and admitted non-spiriferoid calcareous spires. If one considers the points of similarity between M. granulosa and Thecospira they are most striking. Both are strophic and show the same lateral profile. Thecospira shows punctate and obscurely pseudopunctate representatives. M. granulosa is endopunctate but probably independently from terebratuloid endopunctation (Williams 1968c, p. 489). The similarity in Thecospira and M. granulosa, of the cardinal process, the hinge articulation, the sub-marginal structures, the coalesced punctae and lateral shift of the main adductor muscles is thought to be more than coincidental. Differences such as the lack of costellate ornament may not be profound, as radially arranged fibres have been recognized in M. granulosa. As spiral brachidia apparently evolved twice among the Spiriferida, there is no reason why similar brachidia should not evolve in non-spiriferide forms, e.g. Thecospira and Cadomella (Cowen and Rudwick (1966) whose epithelia had the ability to resorb material. If one bears in mind the neotenous origin of the thecideidines and extends the posterior horns of the brachial lobes of M. granulosa (Baker 1969, text-fig. 3F) back to unite with the bridge extensions, one may derive or 'lose' a simple spiral brachidium as a result of the demonstrated resorptive activity taking place in the brachial cavities.

Rudwick (1968) has put forward a reasoned argument for the assignment of the Thecideacea to the Strophomenida, close to, but distinct from the Davidsoniacea. As outlined in the discussion of possible environmental influence, the possibility of a convergent origin of the davidsoniacean characters of M. granulosa must not be overlooked but the similarity between Moorellina granulosa (Moore), the spire-bearing Thecospira and known davidsoniaceans such as Derbyia and Orthotetes is

thought to be much too close to be merely convergent. The weight of evidence now accumulated would suggest that the thecideidines show affinity closer to the davidsoniaceans than any other group. The author must agree with Rudwick, that on the basis of our present knowledge the Thecideacea should be assigned to the Strophomenida.

Appendix Section 1 - Moorellina granulosa (Moore)

An important development following the somewhat hasty conclusions of Termier. Termier and Pajaud (1966) has been the publication of the reasoned arguments of Cooper and Grant (1969) concerning the true taxonomic position of Cooperina inexpectata. The distinctly thecideidine morphological aspect of the brachial valve of this almost micromorphic productoid must now raise serious doubts whether the morphological similarity between Thecospira and Moorellina (Baker, 1970, p 98) is the result of convergent evolution rather than an indication of genetic affinity.

Grant (1970, personal communication) has had the opportunity to observe Thecidellina in its native habitat on a Pacific atoll. It was not found shallower than about 20.5 m. but was abundant down to a diving limit depth of 40 m. and has been dredged from much deeper. The specimens observed occupied crannies and niches on the underside of whatever medium they were attached to and with the hinge pointing in any random direction. The inference is that it was living at depths where the currents had little influence, that it hung upside down and that the wide gape thus effectively placed the entire lophophore outside the shell cavity. However, it may be argued that if Thecidellina has colonised an environment without current influence the adoption of this attitude may be essential for its survival.

More recent works by Jackson, Goreau and Hartman (1971) demonstrates the close association of Thecidellina barretti (Davidson), T. congregata Cooper and Lacazella mediterranea (Risso) with the cryptic habitats (well-shaded to dark, semienclosed surfaces) of Recent coral reefs. Their distribution appears to be correlated with low light intensity as the population density increases with depth. Lacazella is more characteristic

of the more open areas whilst T. barretti predominates in the darker regions. The depth range - 15 to - 80 m. conforms well with Grant's observations. Jackson et al. postulate that elevation of the thecideidine commissure is adaptive in providing some protection against overgrowth by encrusting sponges. Also, that the life situation of the species described (roof and higher walls of cavities) is attributable to intolerance of sedimentation, as they are commonly absent from the lower walls and floors of caves with muddy or silty bottoms. The coincidence between the appearance of the first true coral reefs characteristic of the framework corals and the rapid radiation of the thecideidines in the Middle Jurassic is a persuasive argument for the successful colonisation of a new ecological niche, comparatively free from competition with many common reef taxa. The problem of determining the habitat of the ancestral forms which were able to successfully invade this new environment still remains however. The investigations carried out by Nekasilová and the apparently reinforced shell of Moorellina indicate life in a turbulent environment. The observed loss of reinforcement structures in Lacazella may in fact be explained by adaptation away from a turbulent environment. In addition, elevation of the commissure seems to be a facility enjoyed by the earliest of the Middle Jurassic thecideidines, before this competitive association with encrusting sponges could have been well established.

Section 2 - *Zellania davidsoni* Moore

Introduction

During the collection of the thecidellinid material occasional specimens of this rare micromorphic genus were obtained. Eventually, over a long period, the collection became sufficiently large to allow study using destructive techniques, which in turn enabled determination of the morphology and microstructure.

THE MORPHOLOGY AND MICROSTRUCTURE OF ZELLANIA DAVIDSONI MOORE (BRACHIOPODA), FROM THE MIDDLE JURASSIC OF ENGLAND

ABSTRACT. Investigation of Oolite Marl samples from the mid Cotswolds has yielded occasional minute brachiopods which are undoubtedly specimens of the little-known species Zellania davidsoni Moore 1855. The material studied has enabled determination of the correct orientation, growth, development, and microstructure of the shells and provides the first record of the internal morphology of the pedicle valve. Adolescent and adult shells may be recognized, which enables the mode of development of certain internal structures to be determined. Sectioned material shows that the shell of Z. davidsoni is differentiated into primary and secondary layers of a type which, although unusual, may be reconciled with the shell of primitive terebratulides. Although Z. davidsoni occurs together with thecidellinids the form of the shell is thought to be indicative of a sheltered environment. Microstructural features exhibited by shells support the view that Zellania is of terebratellacean affinity. The paper records the probable location of Moore's type specimens, missing since before 1927.

Zellania is a rare, little-known micromorphic brachiopod genus of undertain affinities, which occurs in the Jurassic of England. Material of the species Z. davidsoni (Moore 1855) has been obtained during a study of the brachiopod fauna of the Oolite Marl (Upper Aalenian, murchisonae zone) of the Cotswolds, South England.

Information on Z. davidsoni is singularly lacking. The account in the Treatise on Brachiopoda has perpetuated a misinterpretation of the type material by Moore in his original description.

Of the specimens of Z. davidsoni figured in the Treatise (fig. 741, 1a-c, H857) and presumably, in the absence of the types, taken from Moore (1855), 1a is in fact a pedicle valve and 1b figures the exterior

of a brachial valve.

The type specimens of Z. davidsoni were found to be missing from the Moore collection, held in Bath City Reference Library, when it was catalogued by Dr. Wallis in 1927. The only zellaniid material in the collection was a tube containing three specimens identified as types of Zellania oolitica Moore, ref. no. M3036. Study of these specimens reveals that they bear little resemblance to any of the published figures (Moore 1860, Davidson 1874) of Z. oolitica but are certainly specimens of Z. davidsoni bearing a very close resemblance to Moore's figured types. The author is of the opinion therefore, that it is the type material of Z. oolitica which is missing and inadvertently represented by the specimens of Z. davidsoni (M3036) which should be reinstated as the types of Z. davidsoni.

The rarity of Z. davidsoni in the Oolite Marl is indicated by the fact that the collection of specimens over a period of more than four years has yielded only two complete pedicle valves, four complete brachial valves and twenty-eight complete specimens, together with numerous brachial and a few pedicle valve fragments. It is possible that the rarity of the species may be, in part, an artefact of the fragility of the shell. The rarity of the pedicle valve is undoubtedly due to its form and lack of the strengthening effect of structures such as the ridge and septum which occur in the brachial valve. The weakness of the pedicle valve may be gauged by the fact that it is often crushed into the brachial valve during compaction of the sediment. The observations contained in this paper are therefore based on a very small collection. However, the uniformity of character exhibited by the material studied indicates that the observations are nevertheless valid.

PREPARATION OF MATERIAL

The material studied was obtained during the collection of thecidellinids from the Oolite Marl. A detailed account of the preparation of Oolite Marl residues and the investigation techniques employed, is given in Baker (1969) with minor amendments in Baker (1970).

Early attempts to section Z. davidsoni by the methods employed for M. granulosa were unsuccessful because peculiarities of the microstructure of the shell allowed blocks of shell to be lifted away during the production of cellulose acetate peels. This, combined with the relatively very thin zellaniid shell and poorly consolidated matrix led to rapid disaggregation of the shell layers. Vacuum embedding was tried with considerable success but some difficulty with peel bubbling was still encountered owing to the porous matrix. This can be eliminated by running hot paraffin wax on to the specimen prior to each successive stage of sectioning. The wax soaks into the matrix and solidifies. The wax overlying the shell material is, of course, removed as the block is ground preparatory to re-etching but sufficient wax remains in the matrix to act as an effective sealant.

MORPHOLOGY

Information concerning the morphology of Zellania davidsoni is limited. The accounts in Moore (1855) and in the Treatise on Brachiopoda (1965) concern only the brachial valve and need some amplification. Detailed examination of the internal ridges (Moore 1855) (inner ridges Treatise) of the brachial valve in serial transverse section (Pl. 120, fig. 7) shows that they are structurally ridges (by definition, Williams 1965, H152), though appearing more in the manner of outwardly inclined flanges (Pl. 118, fig. 7; text-figs. 1B, 2K-P). They occupy a position

similar to that of the sub-peripheral rim of the thecidellinids (Baker 1969) but arise in a different manner (Baker 1970) and apparently performed a function similar to the lophophore platform of the plectambonitacean Leptellina. There is no evidence that the structure seen in the brachial valve of Z. davidsoni is any way related to the lophophore platform of Leptellina. It is by definition not a flange. It performed a function different from that of the thecidellinid sub-peripheral rim. In order to avoid confusion therefore, it is proposed to refer to the structure as a sub-marginal ridge.

Figures of the interior of the brachial valve in Moore, C. (1855) and Elliott (in Moore, R. C. 1965) indicate a depression at the end of the median septum (clearly visible in specimen M3036). Studies show that the septum is a hollow structure for much of its length (Pl. 119, figs. 1-3, text-figs. 1B, 2P-R) and that the floor of the cavity is endopunctate in the normal manner (Pl. 119, fig. 1). It is proposed to refer to this cavity as an intra-septal cavity. Counterparts of the sub-marginal ridge and median septum are found in the pedicle valve and it is proposed to term them lateral ancillary ridges and ancillary septum respectively.

Growth and external morphology. Z. davidsoni (Pl. 118, figs. 1-4) is very small form. The growth is mixoperipheral, leading to a strophic condition, with a rectimarginate commissure. The width : length ratio of the shell is in the order of 1·2 : 1 and specimens rarely exceed 1·3 mm. in length. Specimens in which the protegulum (Pl. 118, fig. 4) and growth-lines are visible, show that the width:length ratio does not change appreciably throughout the life of the animal. Small forms, here correlated with adolescents (Pl. 118, fig. 6), are almost biconvex. During growth the pedicle valve retains its convexity but

the brachial valve shows a declining vertical growth component (Rudwick 1959) so that adults have a characteristic plano-convex lateral profile (Pl. 118, fig. 2). The adult shell outline is typically shield-shaped (Pl. 118, fig. 1) but subject to some variation, adolescents particularly having a more rounded outline (Pl. 118, fig. 5). The interareas are anacline and relatively well developed, the dorsal interarea being only slightly smaller than that of the pedicle valve. The pedicle opening (Pl. 118, fig. 4), as stated in the Treatise on Brachiopoda, is amphithyridid and it is relatively very large. Stereoscan photomicrographs reveal that the feeble striate ornamentation of shells is in fact a series of radially arranged fissures (Pl. 119, figs. 7, 8) penetrating the primary shell but not extending down into the secondary shell layer. At X250 magnification incipient striae are found to be present on smooth shells also.

Z. davidsoni is unusual in that the umbo of the brachial valve projects posteriorly to a greater degree than the umbo of the pedicle valve and gives the appearance of being a pedicle valve, probably accounting for the error in the Treatise (Elliott, in Moore 1965, H857). The significance of this arrangement in terms of life-attitude will be discussed later.

Interior. Brachial valve. The adult brachial valve (Pl. 118, fig. 7) is regularly endopunctate, with a large notothyrium. Its internal morphology is dominated by the sub-marginal ridge and a hollow median septum. These structures were present in the valves of all sizes studied, although degree of development was found to vary. In smaller specimens the ridge terminates in the lateral zones of the shell. The cardinal process is very small and transversely concave in a manner similar to that of thecidellinids (Baker 1969, text-fig. 2B) but not contributing to the formation of socket ridges (Pl. 119, fig. 1; text-fig. 2A-D). The muscle pattern is not known but two depressions

EXPLANATION OF PLATE 118

Stereoscan photomicrographs of *Zellania davidsoni* Moore, from the Oolite Marl, Westington Hill Quarry near Chipping Campden. All specimens coated with evaporated aluminium before photography.

Figs. 1–4. Brachial, lateral, anterior and posterior views of an adult specimen (37530), showing the shield-shaped outline, fig. 1; the posterior extension of the brachial umbo and plano-convex lateral profile, fig. 2 (tilt angle 88°); the rectimarginate commissure, fig. 3; the interareas, protegula and large amphithyridid pedicle opening, fig. 4. ×60.

Fig. 5. Pedicle view of an adolescent shell (37531) showing the rounded profile. Shell surface coated with crystallites. ×66.

Fig. 6. Near lateral view of an adolescent shell (37532) showing the relatively more biconvex lateral profile. ×60.

Fig. 7. Interior view of an adult brachial valve (37533) showing the cardinal process, sockets, and the sub-marginal ridge and hollow median septum with denticulate anteriors. ×55.

Fig. 8. Interior view of an adolescent brachial valve (37534) showing the short sub-marginal ridge and short median septum with no intra-septal cavity. ×60.

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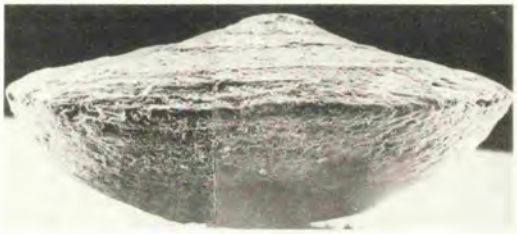

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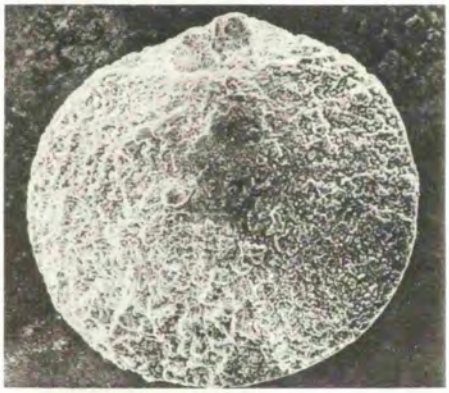

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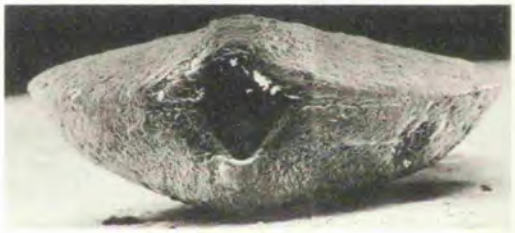

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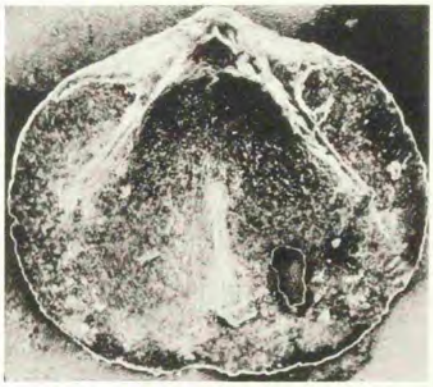

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at the base of the cardinal process may represent diductor muscle scars. The socket ridges are very prominent (Pl. 119, fig. 2) and in fact bound the notothyrium, the outer socket ridge being represented by the edge of the dorsal interarea. In none of the stereoscanned material has the granulation described by Moore (1855) been seen. Certain shells however, show the development of crystallites on the internal surface and it is possible that it is to these that Moore was referring. If, in fact, the specimens M3036 are the types of Z. davidsoni this speculation becomes virtual certaintly. The interior of the brachial valve represented has this crystallite covered surface and has been coated with glue, obviously for the purpose of repairing the damaged median septum. The optical effect of the glue-coated crystallites is to produce an apparently granular interior. The presence of this septum is important as Davidson (1874, p. 113), states that in Z. oolitica there is no indication of the presence of a septum in either valve.

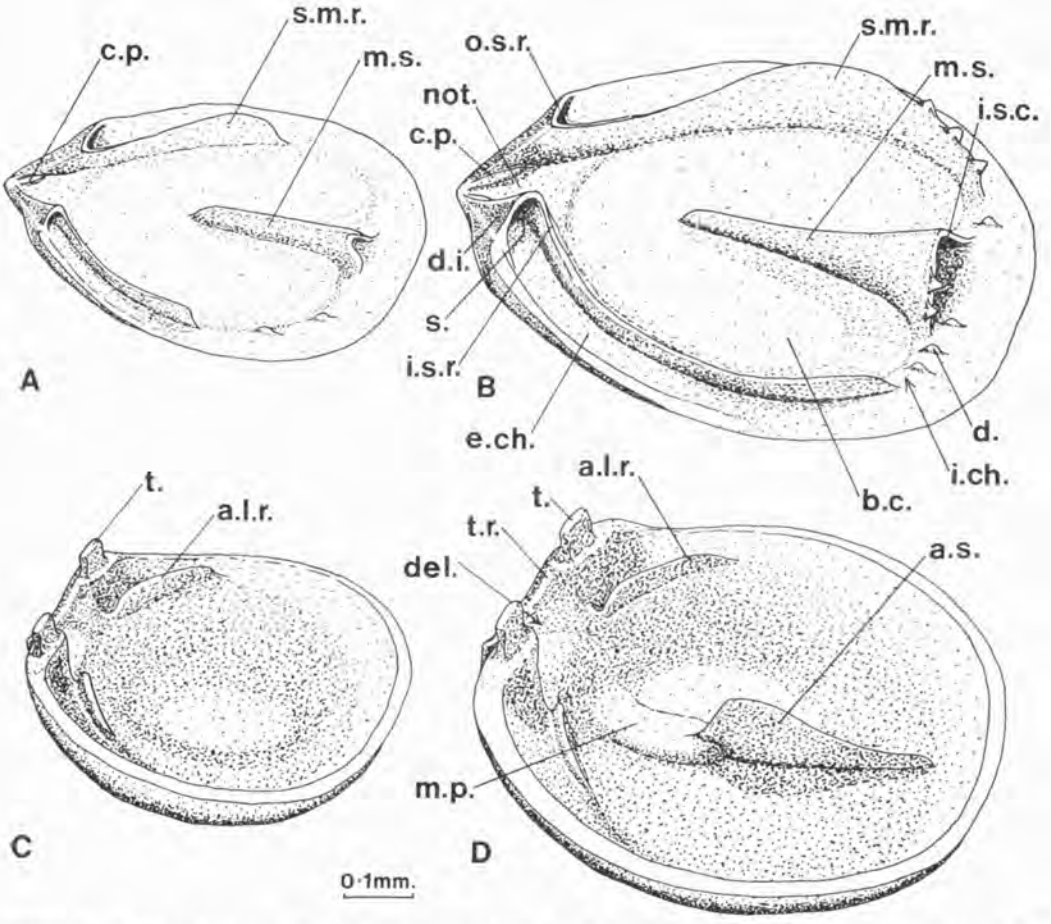
Interior. Pedicle valve. The pedicle valve (Pl. 119, figs. 4, 5) is con~~cave~~vex, endopunctate, with a large open delthyrium bounded by what may presumably be regarded as tooth ridges although the teeth themselves are very weakly developed. They appear as two posteriorly arching flaps, almost indistinguishable from the secondary shell material of the ventral interarea and invariably broken in separated valves. The apex of the delthyrium is occupied by a concave plate, lying between the tooth ridges on the floor of the valve in the position of a pedicle collar. Serial sections show the development of a small ridge, the lateral ancillary ridge (text-fig. 2I-N) also sub-marginal in position and situated in the postero-lateral and lateral zones of the shell (Pl. 119, fig. 6). The orientation of these ridges is such that they abut against the edge of the sub-marginal ridge when the valves are closed. There are no visible muscle scars but transverse sections of

shells show a callus on the floor of the valve which may have been the site of muscle scars. From the anterior of this thickened region, a thin blade-like septum extends almost to the anterior of the valve (text-fig. 1D) and is almost in contact with the median septum when the valves are closed.

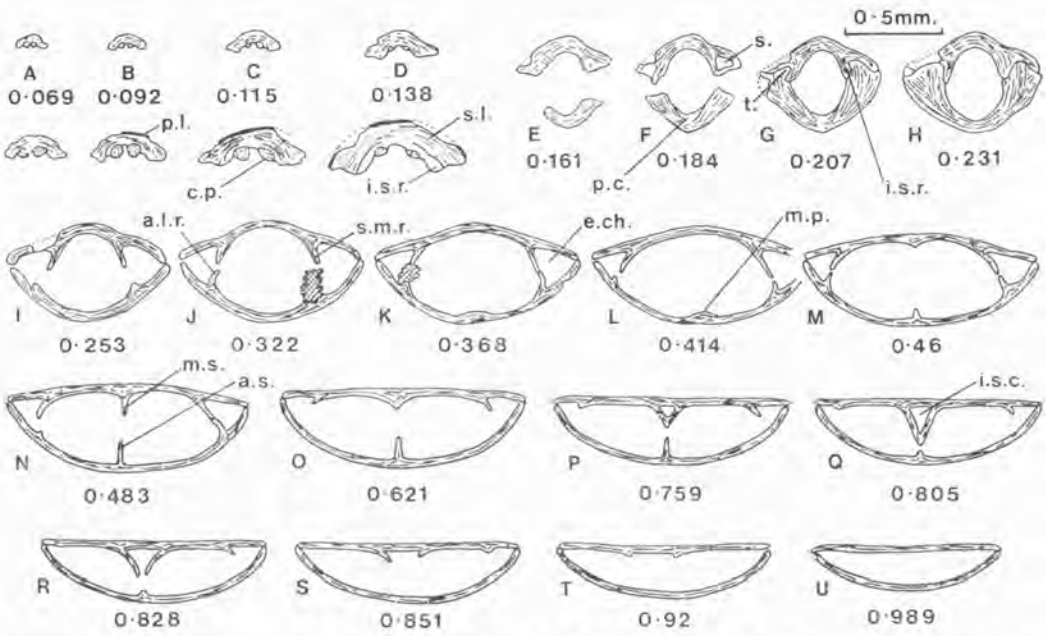
Development of structures. On the basis of faunal analyses conducted for other studies, Z. davidsoni may be regarded as comprising approximately 0.04% of the brachiopod fauna of the Oolite Marl in Westington Hill quarry (Baker 1969); and even if the number of specimens is drastically reduced by fragmentation it is indeed a rare species. Any attempt at detailed ontogenetic studies would therefore be fruitless. Owing to the delicate nature of the shell, valves are usually fragmented but sufficient material has been recovered to enable determination of the mode of development of various structures and the recognition of certain growth stages (text-fig. 1A-D).

It is possible to distinguish specimens which, by their invariably smaller size, although morphologically similar to the larger shells, may be regarded as adolescent forms. The largest shells do not exceed a length of 1.4 mm. and the argument that they represent adults is essentially that outlined in earlier studies (Baker 1969). The primitive aspect of the cardinalia and the small size, together with the form of the pedicle opening and probable form of the lophophore, suggests that, like the thecidellinids, Zellania is the product of neotenous modification.

Development of the sub-marginal ridge and median septum. Existing accounts state that the inner ridges (sub-marginal ridge) are reflexed anteriorly into a posteriorly directed septum. In fact, adolescent brachial valves show that the sub-marginal ridge and median septum arise separately (Pl. 118, fig. 8), and are extended anteriorly as growth proceeds. At this adolescent stage of development the sub-



TEXT-FIG. 1. Three-quarter profile reconstructions from photomicrographs and serial sections to illustrate the internal morphology of the determinable growth stages of *Z. davidsoni*. A, B adolescent and adult brachial valves. C, D adolescent and adult pedicle valves. a.l.r. ancillary lateral ridge, a.s. ancillary septum, b.c. brachial cavity, c.p. cardinal process, d. denticle, del. delthyrium, d.i. dorsal interarea, e.ch. exhalent channel, i.ch. inhalent channel, i.s.c. intra-septal cavity, i.s.r. inner socket ridge, m.p. muscle platform, m.s. median septum, not. notothyrium, o.s.r. outer socket ridge, s. socket, s.m.r. sub-marginal ridge, t. tooth, t.r. tooth ridge.



TEXT-FIG. 2. Drawings prepared from microprojected cellulose acetate peels of serial transverse sections through *Z. davidsoni* showing the morphological features in section. Number indicates distance o section in mm. from the brachial umbo. A–D reproduced at ×2 scale to show microstructure. Apparently thick pedicle valve, F–H due to obliquity of valve posteriorly relative to the plane of section (see Westbroek 1969). Recrystallization shaded. a.l.r. ancillary lateral ridge, a.s. ancillary septum, c.p. cardinal process, e.ch. exhalent channel, i.s.c. intra-septal cavity, i.s.r. inner socket ridge, m.p. muscle platform, m.s. median septum, p.c. pedicle collar, p.l. primary layer, s. dental socket, s.l. secondary layer, s.m.r. sub-marginal ridge, t. tooth.

marginal ridge extends little more than half the length of the valve and the median septum is a low structure, extending from near the anterior margin, posteriorly, about half-way to the cardinal process. It is only hollow at the extreme anterior end.

In adult brachial valves the sub-marginal ridge extends almost to the anterior margin and may extend in the direction of the median septum as a row of denticles (Pl. 118, fig. 7). The posterior termination of the median septum however, maintains a constant position relative to the socket ridges and cardinal process (Pl. 118, figs, 7, 8). Increase in the size of the structure must therefore, be achieved by addition of material at the anterior end and, as the walls diverge, so the intra-septal cavity increases in size.

Serial sections (Pl. 120, fig. 7; text-fig. 2K-P) show that the ridge, on the evidence of the orientation of fibres, develops from the floor of the valve. Therefore, both the ridge and median septum, in terebratuloid terms, represent ascending elements, a point of significance in consideration of affinities. The ridge increases in size by the simple incremental addition of secondary material. Exactly how this occurs is not clear, but the development of denticles may be an initial feature of the anterior extension of the sub-marginal ridge and also the median septum (Pl. 119, fig. 3). Posteriorly the sub-marginal ridge forms the inner socket ridges, and the dental sockets are obviously much deepened as the ridge develops.

The sub-marginal ridge is not vertical but directed outwards (Pl. 119, fig. 2; text-fig. 2 K-P). As material is added at the summit therefore, the size of the brachial cavities must be increased. A similar trend is exhibited by the median septum. As it increases in height, the walls become more divergent (Pl. 119, figs. 1-3; text-figs. 1B, 2 P-R) so that the intra-septal cavity increases in size. The result of this development pattern is the development of

a border morphologically similar to that of certain thecidellinids (Baker 1969) but differing structurally and with no migration as encountered in the sub-peripheral rim of Moorellina granulosa (Moore) (Baker 1970).

Development of the pedicle valve. The two complete pedicle valves discovered, judging from their small size, apparently belonged to adolescent individuals. The teeth are missing but the only discernable difference between these and the valves of serially sectioned larger forms appears to be a relative decrease in the prominence of the lateral ancillary ridges as the sub-marginal ridge of the brachial valve becomes more well developed. The development of the callus on the valve floor and the development of the thin ancillary septum are apparently late ontogenetic features as they are not seen in adolescent valves of the size studied.

MICROSTRUCTURE

The material studied shows that in Z. davidsoni the endopunctate shell, although very thin, was clearly differentiated into primary and secondary layers (Pl. 119, fig. 8; Pl. 120, fig. 2). Although the punctae deflect the secondary fibres in a normal (Williams (1968a) terebratulide manner (Pl. 210, figs. 5, 6), the microstructure of the layers themselves differs from the normal terebratulide pattern.

Primary layer. The zellaniid primary layer is thin and apparently of an unusual type. Reference has already been made to the radially arranged fissures in the primary shell (Pl. 119, figs. 7, 8; Pl. 120, fig. 1). In transverse sections (Pl. 119, fig. 8) the shell material is seen to be of crystalline type and without the normal pitted appearance described by Williams (1968a). The persistence of the radial arrangement of the fissures and their failure to penetrate the secondary layer must indicate a more than coincidental relationship with the primary

EXPLANATION OF PLATE 119

Stereoscan photomicrographs of specimens of *Zellania davidsoni* Moore. Material of all figures coated with evaporated aluminium before photography.

Fig. 1. Interior view of a brachial valve fragment (37535) showing the endopunctation and cardinal process. The left dental socket is damaged and the hollow anterior region of the median septum has been broken away to reveal the endopunctate floor of the intra-septal cavity. ×60.

Fig. 2. Profile view of specimen (37535) to show the relative prominence of the inner socket ridges bounding the notothyrium, the inclined sub-marginal ridge, left, and the divergent anterior of the median septum. Angle of tilt 70°. ×65.

Fig. 3. Enlarged view of specimen (37533) to show detail of the denticulate anterior of the hollow median septum and sub-marginal ridge. ×110.

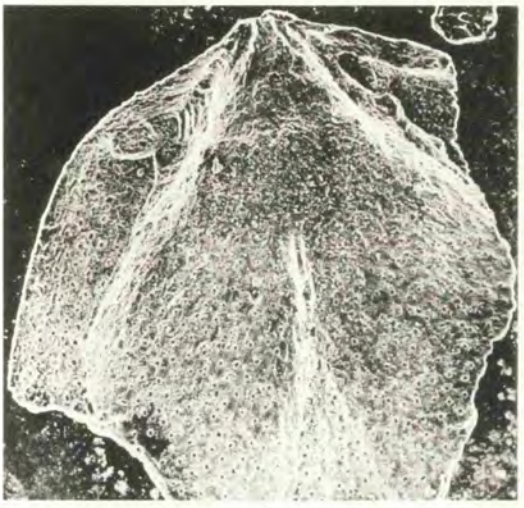
Fig. 4. Interior view of an adolescent pedicle valve (37536). Detail obscured by a heavy coating of crystallites but the left lateral ancillary ridge is just visible, upper left. Teeth missing. ×58.

Fig. 5. Posterior view of specimen (37536) showing the delthyrium bounded by tooth ridges. Angle of tilt 57°. ×70.

Fig. 6. Profile view of the interior of a fragment of an adolescent pedicle valve (37537) showing the lateral ancillary ridge, centre-left. Angle of tilt 70°. ×150.

Fig. 7. Enlarged portion of the exterior of the brachial valve of specimen (37538) showing the radial fissuring of the primary shell layer. ×400.

Fig. 8. Stereoscan photomicrograph of a cellulose acetate peel of a transverse section through the shell of specimen (37543) showing the fissures in the prismatic primary layer, upper, and the fibrous secondary layer. Section location: Pedicle valve, right antero-lateral sector. ×1080.



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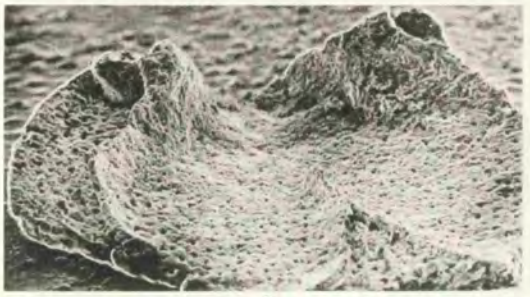

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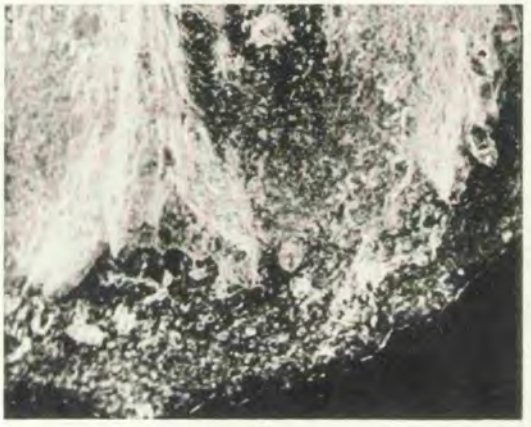

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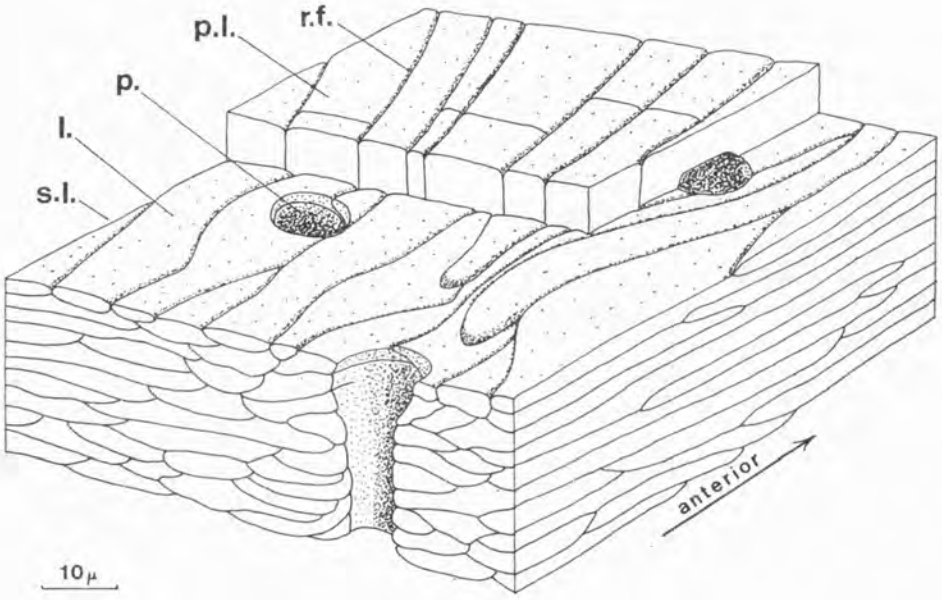

TEXT-FIG. 3. Block reconstruction of the shell of *Z. davidsoni* from photomicrographs of cellulose acetate peels, to show the form of the primary layer and the orientation and variability of the fibres of the secondary layer. l. lamina, p. puncta, p.l. primary layer, r.f. radial fissure, s.l. secondary layer.

shell material. The radial pattern is relieved at intervals by cross-joints so that the primary layer in effect, consists of a series of sub-rectangular blocks of prismatic calcite (text-fig. 3). The primary layer is usually poorly preserved because the physical characteristics described contribute to its easy removal mechanically, as evidenced by the difficulties encountered during the preparation of cellulose acetate peels.

Secondary layer. Stereoscan photomicrographs of etched secondary shell surfaces and investigation by horizontal, transverse, and longitudinal serial sections, shows that the secondary shell mosaic also is of rather unusual type. Even the most careful orientation of sectioned material has failed to produce anything approaching a typical (Williams 1968a) terebratulide or spiriferide transverse mosaic except at the base of the teeth (horizontal sections). Horizontal (Pl. 120, fig. 4) and transverse (Pl. 120, fig. 5) sections show that the secondary shell material appears typically as a series of sheets or very broad (20-30 µm. wide) laminae which are, in longitudinal section, disposed with normal (Williams 1956, 1966, 1968a) secondary orientation relative to the primary layer (Pl. 120, fig. 8). Horizontal sections show that the orientation of laminae changes rapidly, so that, in places, a zigzag rather than a spiral arc (Williams 1968a) secondary growth mosaic is produced.

General observations. At present the origin and purpose of the radial fissuring is unknown, but it may represent the diagenetic expression of some peculiarity in the mode of deposition of the primary shell material. The uncertainty of whether the fissures are of primary or diagenetic origin is obviously a point of considerable importance because, if primary, the features indicate in Zellania the existence of a new type of primary shell material. Owing to the rarity of material resolution

EXPLANATION OF PLATE 120

Stereoscan photomicrographs of *Zellania davidsoni* Moore. Material of all figures coated with evaporated aluminium before photography and all, with the exception of fig. 3, taken from cellulose acetate peels.

Fig. 1. Horizontal section through the primary shell layer of specimen (37540) showing the radially arranged fissures and block-like nature of the primary shell. Section location: Brachial valve, anterior sector. ×1200.

Fig. 2. Horizontal section through the shell of specimen (37541) showing the primary/secondary layer junction, broken line. Shell partially recrystallized. Section location: Brachial valve, left antero-lateral sector. ×1200.

Fig. 3. External surface of specimen (37542) from which the primary layer has been removed, showing detail of the fibre mosaic at the external surface of the secondary shell layer. Normal proximal, centre right, and laminar distal, centre, regions of fibres are visible. Figure location: Brachial valve, left antero-lateral sector. ×900.

Fig. 4. Oblique section through the secondary shell layer showing endopunctae and the secondary fibres arranged as overlapping laminae. Section location. Brachial valve, right lateral sector. Section orientation: Parallel with the plane of the commissure. ×550.

Fig. 5–7. Transverse sections through specimen (37543).

Fig. 5 shows the primary layer, upper and the fibres of the secondary layer deflected by punctae. Section location: Brachial valve, right antero-lateral sector. ×540.

Fig. 6. Enlarged section to show detail of an endopuncta and deflected secondary fibres. Section location as Fig. 5. ×2000.

Fig. 7. Transverse section through the sub-marginal ridge showing the orientation of the secondary fibres. Section location. Brachial valve, right lateral sector. ×400.

Fig. 8. Longitudinal section through specimen (37544) showing the orientation of the secondary fibres relative to the primary shell layer, lower. Section location: Pedicle valve, 0·086 mm. to the left of the mid-line. ×1000.

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PLATE 120

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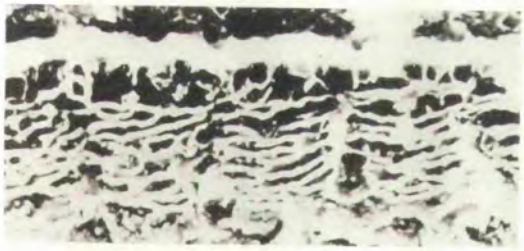

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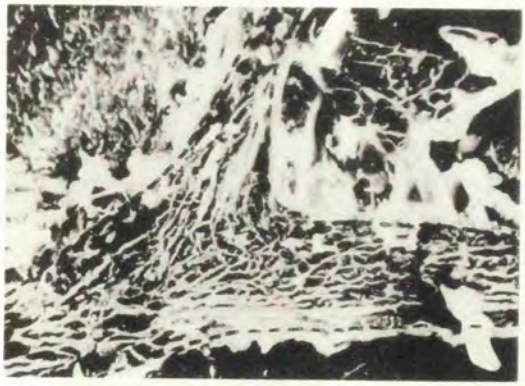

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of the problem will be difficult. A certain amount of indirect evidence is available: (a) shells coated with crystallites, and in which some recrystallization has obviously occurred, show obliteration of the fissuring effect, (b) the fissures are most clearly seen in the best-preserved material, (c) they are a pronounced feature of all horizontal sections through the primary layer and (d) it is difficult to envisage a diagenetic process which would, universally, affect the primary layer to such an extent, with no apparent effect on the secondary layer. Williams (1968b) suggests that the finely crystalline covering of Billingsella represents the recrystallized primary layer. Similar recrystallization may have occurred in Zellania, but it is odd that the line of demarcation between recrystallized and unaltered material should be so abrupt, and also that the structure is present in all sections involving primary shell. Williams (1968a, p. 31) states that the primary layer of all specimens of Spiriferina walcotti (Sow.) examined is recrystallized but that the secondary shell is normally well preserved. He notes a strong lineation in the primary layer (Williams 1968a, Pl. 11, fig. 5) normal to the shell surface and is of the opinion that this lineation may represent an original fabric. The evidence available, therefore, indicates that the microstructure of the zellanid primary layer is of secretory rather than diagenetic origin. Some transverse sections of secondary shell (Pl. 120, fig. 6) are very similar to the re-crystallized secondary mosaic of Nisusia ferganensis (Williams 1968b, p. 487). However, if re-crystallization in Zellania extended below the primary layer, so that some of the secondary fibres have been re-crystallized whilst retaining their morphological characteristics, the observed features of the primary layer may also be regarded as original.

The zellaniid laminae are curiously like the flared fibres of Moorellina granulosa (Moore) described in Baker (1970, p.84). In

M. granulosa, only the distal ends of the fibres are affected but in Z. davidsoni this expansion has a tachygenetic expression and affects all but the extreme proximal end of the fibre. The unmodified proximal ends of some secondary fibres (Pl. 120, fig. 3) are similar to the secondary fibres (Williams 1968a, pl. 7, fig. 4) of Terebratulina caput-serpentis (Linne). However, the microsructure of the shell as a whole most closely resembles that of the stringocephalacean Mutationella podolica (Siemiradzki), illustrated in Williams (1968a, pl. 11, figs. 1-3).

PALAEOECOLOGY

Z. davidsoni occurs together with thecidellinids and other, larger, brachiopods; the probable environment of the thecidellinids is discussed in Baker (1969). It may be argued that Zellania, by association, occupied the same environment. The close morphological similarity between certain internal characters of Zellania and thecidellinids has been noted, but it has been clearly shown that the structures arise in different ways and probably performed different functions. Morphological similarity produced by convergent evolution is to be expected if the animals did occupy a similar environment. However, there are certain features of the organization of Z. davidsoni which render the above argument hazardous.

Analysis of the microstructure of the thecidellinid Moorellina granulosa in functional terms (Baker 1970) reveals the development of a reinforced shell which is entirely in agreement with the turbulent environment suggested by Ager, Baker, and Nekvasilová (in Baker 1969). The pedicle opening of Z. davidsoni is disproportionately large relative to the size of the animal. Moorellina is a cemented form and it is possible that Zellania required a large pedicle for anchorage. However,

the shells of the two genera are in direct contrast. In M. granulosa the shell is thick and reinforced. In Z. davidsoni the shell is thin and very brittle; so brittle in fact that shells are often crushed by a degree of compaction of sediment which does not deform Moorellina at all. Such a shell could not survive in anything other than a sheltered environment. Dr. J.D. Hudson (personal communication) has suggested that Zellania may have occupied a sheltered micro-environment, e.g. protected cavities under large shells (Ostrea, etc.). This would afford protection whilst the animal was alive but when the pedicle decayed the shell would be liberated into the turbulent general environment. The cardinal process and teeth of M. granulosa are strongly developed. The cardinal process of Zellania is small and the teeth are very fragile so that unless transportation of the shell occurred before the musculature of the animal decayed, the valves would almost certainly become dis-articulated. It seems likely that the musculature would decay before the pedicle, thus allowing separation of the valves. Of the material collected however, complete specimens are the most common although the broken teeth of the pedicle valves and perforations in some brachial valves (Pl. 118, figs. 7, 8) do indicate a degree of abrasion consistent with some transportation.

There exists therefore, the apparent anomaly of a strong pedicle and a weak shell. Analysis of the shell characters of Z. davidsoni in environmental terms is indicative of a sub-littoral mud-grade environment (Ager 1965) into which the thecidellinids, the organodetrital remains and the peri-reefal brachiopods (Baker 1969) were drifted. It is possible to reconcile a large (rather than strong) pedicle with this view, as it would afford anchorage in a soft substratum, although the anatomy of the pedicle itself is unlikely ever to be described.

The association of micromorphic brachiopods with shell debris is noted by Swedmark (1967) who records the occurrence of Gwynia capsula

(Jeffreys) in a sub-tidal mineral sand containing a high proportion of fine broken shell. In this environment the animal apparently seeks the shelter of serpulid tube fragments.

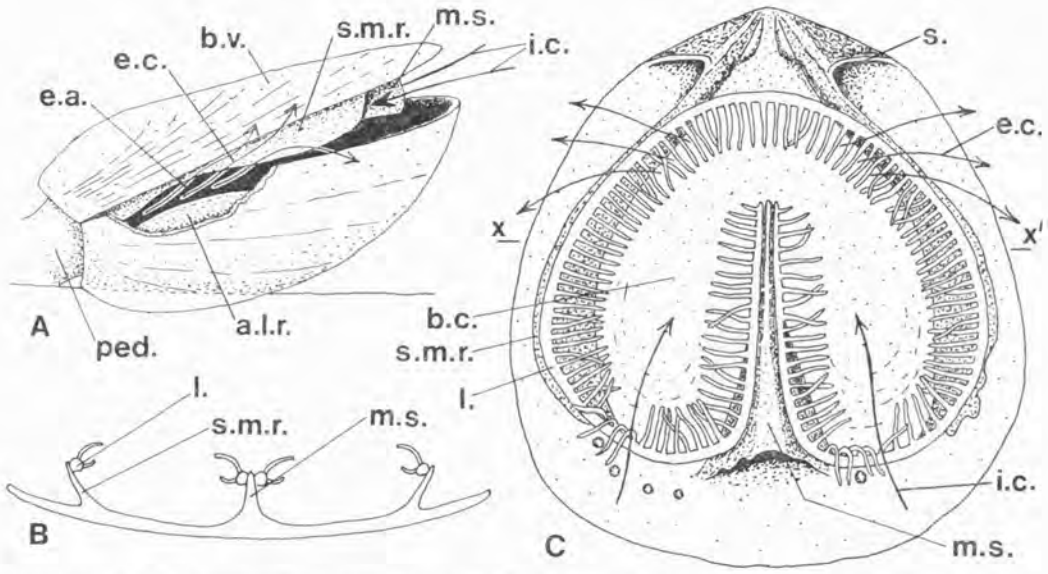
Circumstantial evidence is provided by speculation concerning the life-attitude and the functional significance of the internal structures of Zellania. Analysis of the growth habit of M. granulosa indicates a growth pattern designed to lift the brachial apparatus away from the attachment surface (Baker 1970). This growth habit requires that the brachial valve be uppermost in position. The posteriorly projecting brachial umbo of Z. davidsoni may indicate similar orientation. The convex pedicle valve, possibly partially buried in the sediment, would enable the dorsally oriented, relatively plate-like brachial valve to be lifted clear of the sub-stratum (text-fig. 4A). This hypothesis is supported by a consideration of the functional significance of the sub-marginal ridge and ancillary structures. From a consideration of the thecidellinid brachial apparatus it is probable that the inner surface of the sub-marginal ridge and the sides of the median septum (text-figs. 4B, C) supported a simple schizolophe (Rudwick 1968). Study of brachiopod feeding mechanisms (Rudwick 1965, H206) indicates that in schizolophous forms the valves gape fairly widely and the filaments form a bell-like inhalent chamber. If Zellania occupied a mud-grade environment it is possible that under certain conditions, e.g. high turbidity, the valves did not gape as widely as normal. The denticulate anterior of the brachial valve (text-fig. 1B) may, therefore, represent the point of entry of the inhalent current when the valves were almost closed (text-figs. 4A, C). In this case it is thought that the exhalent apertures were situated postero-laterally in the zones occupied by the lateral ancillary ridges. The current flow would now be influenced by the degree of gape of the valves, as the exhalent apertures

would be closed as the sub-marginal ridge and lateral ancillary ridges came together (text-fig. 4A). The virtual compartmentation of the shell (text-fig. 2) must have some significance and may be an expression of the lack of turbulence in the water, thus assisting in the separation of the inhalent and exhalent currents produced by the filaments of the lophophore.

These arguments, of course, apply equally well to occupation of a sheltered micro-environment but it is considered that the sum of the morphological and microstructural features of Z. davidsoni favours the postulated mud-grade environment.

AFFINITIES

The close morphological similarity between the internal characters of Zellania and thecidellinids has been noted, but it has been clearly shown that the structures arise in different ways, and therefore contradict Moore's (1855) view that thecideaceans and Zellania are related. In the Treatise, Zellania is tentatively linked with the terebratellaceans. The material studied shows all degress of preservation but there is little doubt that the secondary mosaic is of modified terebratulide or spiriferide type. The similarity between some secondary fibres of Z. davidsoni and secondary fibres of Terebratulina caput-serpentis (Linne), and the similarity between the primary shell of Zellania and Spiriferina walcotti (Sow.),has been noted. The sub-marginal ridge is very like the loop of stringocephalids such as Rensselandia johanni (Hall) in a sessile position. However, the shell microstructure of Z. davidsoni appears to most closely resemble that of the Lower Devonian stringocephalacean Mutationella podolica (Siemiradzki). Studies strongly indicate that the secondary shell mosaics of even distantly related brachipods may show a similar initial development pattern, although subsequently diverging. The evidence



TEXT-FIG. 4. A. Diagrammatic reconstruction of the possible life-attitude of *Z. davidsoni* with the valves gaping slightly. A small portion of the pedicle valve is omitted to show the postulated exhalent aperture. B. Transverse section through X–X′, fig. C. to show the postulated position of the schizolophe relative to the sub-marginal ridge and median septum. C. Diagrammatic representation of the interior of a brachial valve of *Z. davidsoni* showing the probable form and position of the lophophore and inhalent and exhalent apertures. a.l.r. ancillary lateral ridge, b.c. brachial cavity, b.v. brachial valve, e.a. exhalent aperture, e.c. exhalent current, i.c. inhalent current, l. lophophore, m.s. median septum, ped. pedicle, s. socket, s.m.r. sub-marginal ridge.

presented in the present paper, although not solving the problem of immediate affinity, indicates that the microstructure of Zellania may partially recapitulate the phylogeny of the genus. It is generally accepted that recapitulation in organisms can occur, although its value as an evolutionary criterion is open to criticism. If it is possible for the secretory régime of the secondary fibres to recapitulate phylogeny, accompanied by tachygenesis, the process may be arrested and the evidence thus preserved in neotenous forms such as Zellania. The dorsal cardinalia are of billingsellacean type, i.e. primitive, and work in progress, on very young terebratulides, shows that the initial development of the cardinal process of Moorellina, Zellania, and terebratulides follows the same pattern and supports the hypothesis of recapitulation.

Stehli (in Moore 1965, H739) derives both the Terebratulidina and Terebratellidina from mutationellin ancestors. The shell of Zellania shows mutationellin affinities. Owing to the enormous time-gap it would be ambitious to suggest that Zellania is descended from a stringocephalacean ancestor. However, consideration of features such as the recapitulatory nature of secondary fibre secretion, the development of the submarginal ridge from ascending elements and the typical endopunctation certainly suggest that Z. davidsoni may be closely related to terebratellacean stock.

Section 3. Nannirhynchia longirostra sp. nov.

A NEW MICROMORPHIC RHYNCHONELLIDE BRACHIOPOD FROM THE MIDDLE JURASSIC OF ENGLAND

Abstract. Recent work on micromorphic brachiopod faunas from the Inferior Oolite reveals the presence of a new rhynchonellide species attributable to Nannirhynchia Buckman but with diagnostic beak characters. The new species N. longirostra is proposed. Although the presence of a pedicle collar has not previously been recorded in the Norellinae, the form of the shell, the definitely arcuifer crura and the way in which they curve ventrally into the pedicle valve are thought to justify its inclusion in the sub-family. Juveniles are easily recognizable but no characteristic transition to adult form is noted. Investigation of the shell microstructure leads to the conclusion that deltidial plates are not invariably developed. The possibility of synonymy with Spiriferina? minima Moore, is discussed.

The species investigated was recovered from the Oolite Marl, a weakly coherent interbedded marl and biomicrite (Folk 1959) of Upper Aalenian age occurring in the Inferior Oolite of the mid-Cotswolds. Organo-detrital residue obtained from treated marl yields numerous other brachiopod micromorphs, notably Moorellina granulosa (Moore) juveniles of terebratulides such as Zeilleria leckenbyi (Walker) and 'Terebratula' whitakeri Walker, Ms., also rare specimens of Zellania davidsoni Moore. A detailed account of the techniques adopted for preparation of the material for study may be found in Baker (1969; 1970).

Although the detail of separated valves is well preserved, the interior of uncrushed complete shells is invariably coated with minute crystals which makes determination of the form of the crura difficult. Fortunately, the strong beak resists diagenesis very well and its internal characters may be easily ascertained by serial sectioning.

Order RHYNCHONELLIDA Kühn 1949
Family DIMERELLIDAE Buckman 1918
Genus NANNIRHYNCHIA Buckman 1918

Nannirhynchia longirostra sp. nov.
Plates 135-137; text-figs. 1, 2.

Diagnosis. Very small, biconvex Nannirhynchia, up to about 2.5 mm in length, 2.0 mm. in width, and 1.0 mm. in thickness. Pyriform in outline with well-developed intraplicate anterior commissure. Rostrate. Radial striae clearly seen on specimens in which the primary shell layer is weathered.

Type specimens. Holotype and nine topotypes to be housed in the British Museum (Natural History), register number BB 45820-45829.

Distribution. Geographic distribution unknown. All the material studied was collected from Westington Hill Quarry, grid ref. SP142368, near Chipping Campden in Gloucestershire.

Stratigraphically the species is so far known only from a single horizon in the lower Inferior Oolite (Upper Aalenian, Murchisonae Zone), notably at the base (Baker 1970) of the Oolite Marl, where it is associated with other micromorphic brachiopods such as Moorellina granulosa (Moore) and Zellania davidsoni Moore.

Dimensions of Holotype. Length 2.3 mm., width 1.8 mm., thickness 1.0 mm.

Description. External Characters. Study of 39 specimens and numerous shell fragments shows that the recorded dimensions of the holotype are very close to the maximum for the species and that the beak characteristics are stable throughout the material studied. The arguments advanced previously (Baker 1969), in favour of regarding the associated micromorphic brachiopods as adults, are equally applicable to this study. Ontogenetic stages are available which show that adults are characterized by a well-developed, rounded, central plication with complementary sulci on either side and occasionally a single, low, lateral costa on each side.

The shell is typically non-strophic sensu Rudwick and is biconvex throughout growth. In young forms, both the brachial and pedicle valves have a median sulcus and thus a ligate form. The central plication is

produced by bifurcation of the brachial sulcus and subsequent deepening of the thus formed complementary sulci. Therefore as Ager (1967) has shown for N. pygmaea the plication in N. longirostra also is a consequence of the development of the sulci and thus intraplicate sensu Buckman, rather than uniplicate with lateral sulci. Striae when visible are a diagenetic development.

The beak is strong, sharp, projecting, and slightly incurved with narrow palintropes. The delthyrium is open, hypothyridid, and bounded by strongly developed tooth ridges, with or without narrow deltidial plates.

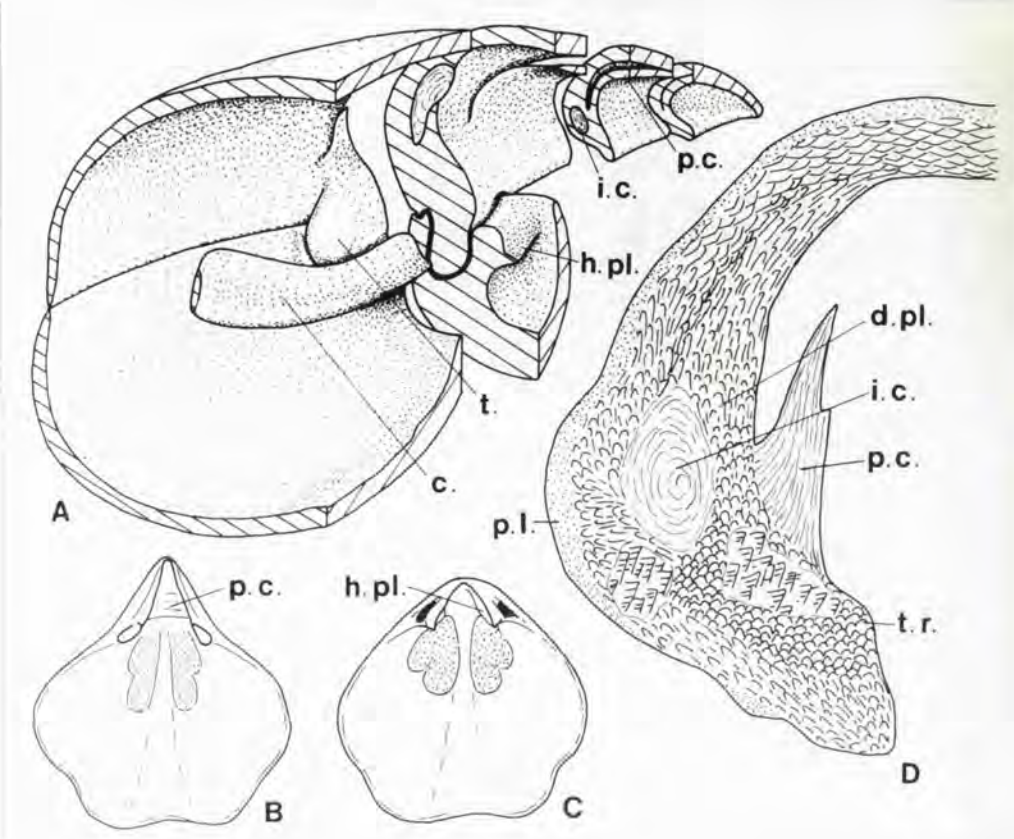
Internal Characters: Pedicle valve. The most characteristic feature of the pedicle valve is the well-developed, almost sessile pedicle collar with its clearly defined growth lines (Pl. 136, fig. 1). The hinge teeth of this species are relatively large.

Dental plates are present. These are inclined and show a strong lateral deflection so that the lateral umbonal cavities remain very small (Pl. 137, figs. 3, 4, text-fig. 2). The dental plates are easily overlooked in adult shells as the lateral umbonal cavities quickly become filled with subsequently deposited secondary shell so that the dental plates appear to form part of the umbonal wall (Pl. 136, fig. 1).

In young forms the dental plates are sometimes visible and the partially infilled lateral umbonal cavities appear as small perforations (Pl. 136, fig. 2).

The delthyrium is bounded by narrow widely disjunct structures usually interpreted as deltidial plates. Reference to these structures will be made later.

Small denticula are present, clearly visible on separated valves (Pl. 135, fig. 10; Pl. 136, fig. 2) but not well defined in transverse sections.



TEXT-FIG. 1. A. Block reconstruction of the posterior region of the right half of the shell of N. longirostra, based on superimposed cellulose acetate peels. The anterior faces of the block segments correlate with peels 37549/43, 26, 12, and 8 respectively, X 60 approx. B, C. Impressions of the ventral (B) and dorsal (C) muscle fields (stippled) of N. longirostra reconstructed from visible boundaries and the distribution of terminally pitted secondary fibres, X 17. D. Trace of a stereoscan montage X 225, of part of peel 37549/15 showing the orientation of the secondary shell fibres in the various structures depicted. c. ventrally deflected arcuifer crus, d.pl. dental plate, h.pl. hinge plate, i.c. infilled lateral umbonal cavity, p.c. pedicle collar, p.l. primary layer, t. hinge tooth, t.r. tooth ridge. Patches of recrystallised shell cross-hatched.

EXPLANATION OF PLATE 135

Stereoscan photomicrographs of specimens of Nannirhynchia longirostra sp. nov. Material of all figures coated with evaporated aluminium before photography.

Figs. 1 - 3. Brachial, anterior, and lateral views of the holotype 37550, X 30.

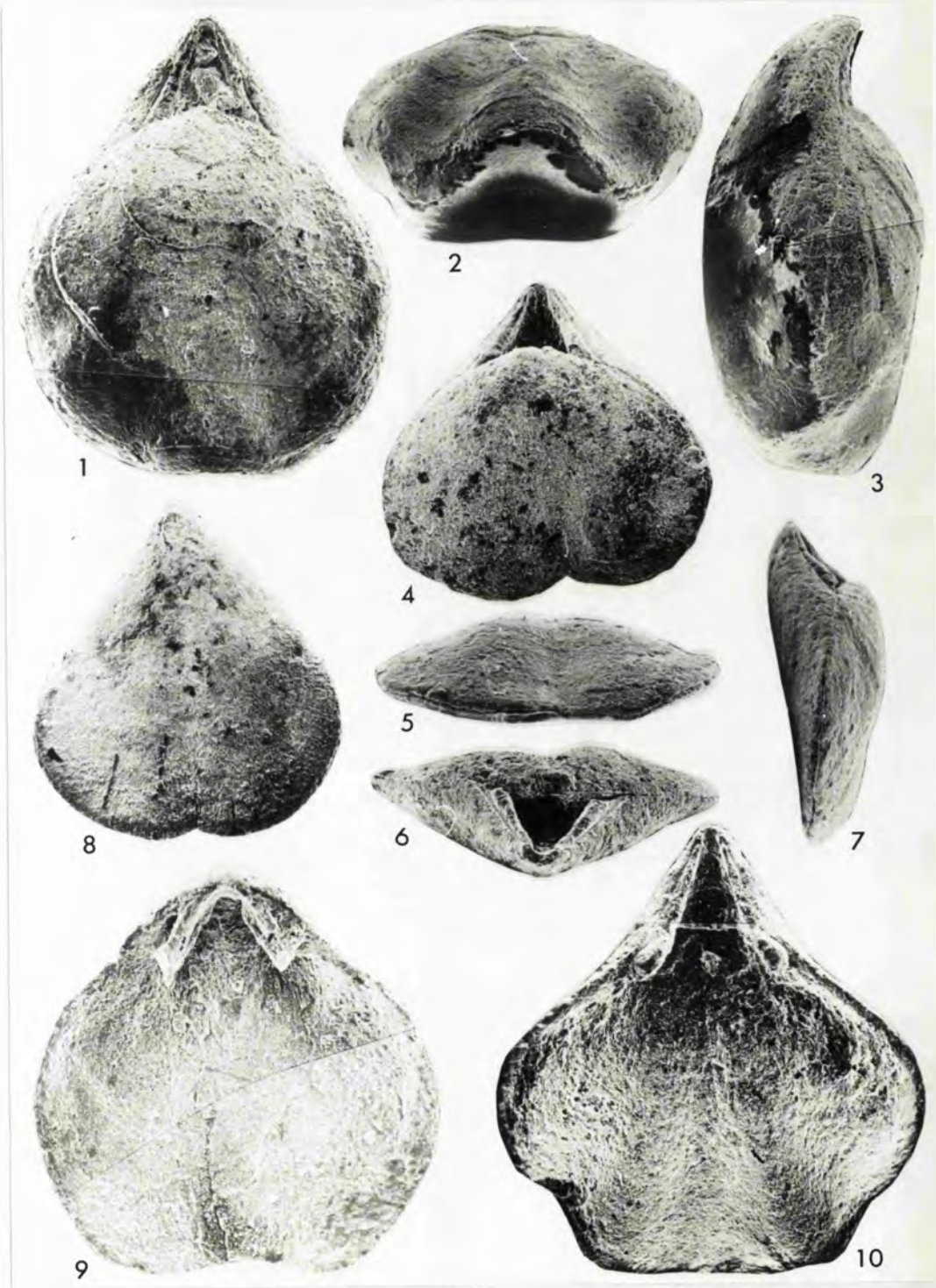
Figs. 4 - 7. Brachial, anterior, posterior, and lateral views of a juvenile 37551. The posterior view (fig. 6) shows the tooth ridges surmounted by small deltidial plates, X 40.

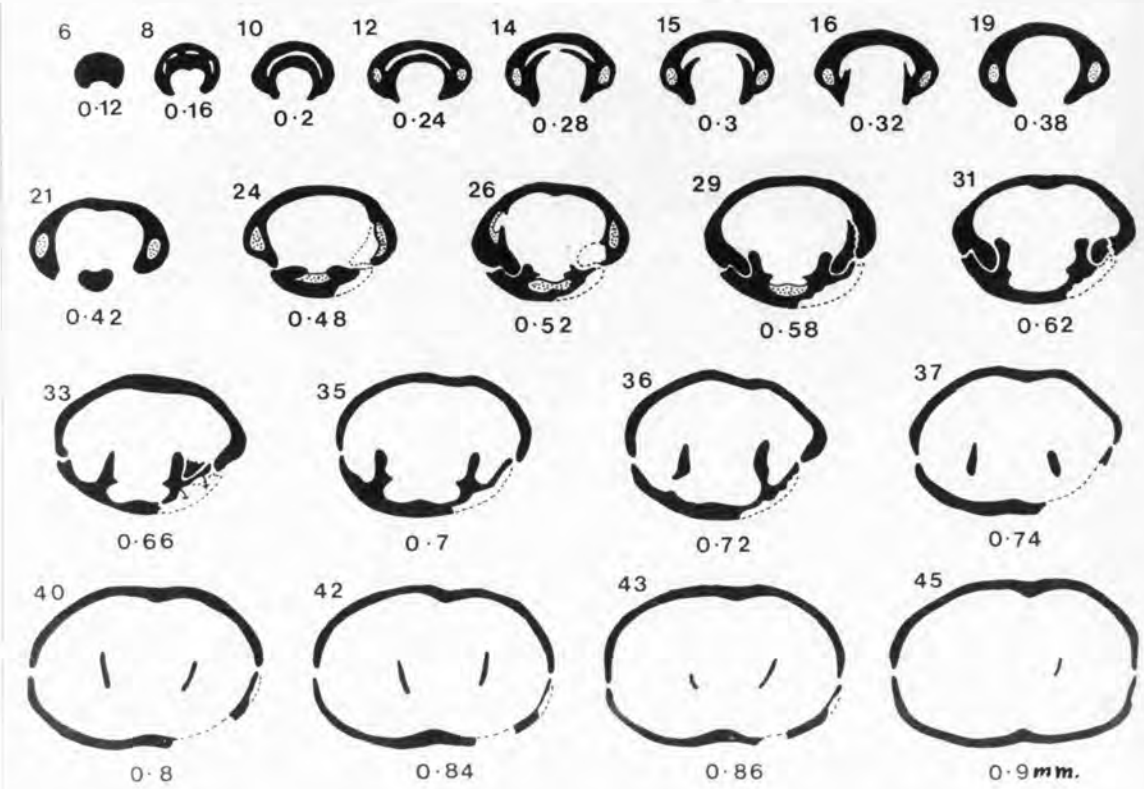
Fig. 8. Pedicle view of a juvenile 37552, showing the laterally deflected beak and radial striae, X 30.

Fig. 9. Interior of a brachial valve 37558, showing the hinge plates and the absence of a cardinal process and median septum. Crura broken, X 32.

Fig. 10. Interior of a pedicle valve 37546, showing the pedicle collar, hinge teeth, and denticula, X 32.

PLATE 135





TEXT-FIG. 2. Nannirhynchia longirostra sp. nov., series of 21 serial transverse sections through specimen 37549, drawn from cellulose acetate peels, showing all the features of the species. Numbers refer to specific peels illustrated (top left) and the distance from the beak. Subsequent shell deposition stippled. All x20.

Owing to the effects of diagenesis on the internal surface of shells it has not been possible to determine the true configuration of the muscle scars. The interior of separated valves, however, often shows impressions of the muscle fields and diagenesis has not completely obliterated the stellate pitting on the terminal faces of the secondary fibres lying within these areas (Pl. 136, fig. 7). The form of the muscle fields is shown in text-fig. 1B, C.

Brachial Valve. There is no cardinal process but the posterior end of the valve protrudes into the delthyrial cavity. Hinge plates are present (Pl. 135, fig. 9; Pl. 136, fig. 4) but not well developed and in the material examined they are horizontal and not fused posteriorly so that there is nothing approaching a septalium and no median septum (text-figs. 1A, 2). Crural bases arise dorsally from the hinge plates (Pl. 137, fig. 7) and give rise to ventrally deflected, arcuifer crura (Pl. 137, figs. 5, 6, 8). Outer socket ridges are present but as in the case of the denticula they are only clear in separated valves (Pl. 136, fig. 4).

Microstructure. The microstructure of shells is characteristically rhynchonellide (Williams 1968). The primary layer and the terminal faces of secondary fibres often show some effects of diagenesis but the fabric of the secondary layer itself is generally remarkably well preserved (Pl. 136, figs. 6, 8; Pl. 137, figs. 1, 2). Individual fibres are very long, often extending from the junction with the primary layer, right through the secondary layer to its internal boundary. This produces a rather weak shell and half valves, fractured longitudinally are most common. Secondary fibres often show well-defined growth lines representing stages in the repeated advance of the terminal face during fibre growth (Pl. 137, fig. 2). The overall impression is that the secondary fibres are relatively flatter and much larger than in many other brachiopods. They do not show any marked decrease in size in the muscle

fields but exhibit the curious stellate pitting of myotest fibres (Pl. 136, fig. 7). Williams (personal communication) suggests that these pits may represent differential diagenetic solution but in the author's opinion their regularity indicates a fundamental property of the underlying fibre. In section the fibres show the characteristic blurring of outline (Pl. 136, fig. 8) and at high magnification, the minute trails associated with myotest.

Ontogeny. Complete juveniles (Pl. 135, figs. 4-8) are apparently much more common than complete adults but there is no difficulty in assigning these to the same species owing to the fact that their typical morphology can easily be seen in the early growth lines of adult shells (Pl. 135, fig. 1). The pedicle collar as may be anticipated from its growth lines, is present in even the smallest pedicle valves studied. Brachial valves of a complementary size show broken crura so that the development of crura also is a very early feature. No characteristic ontogenetic stages are therefore present and the only significant change during growth is the rapid transition from opposite to alternate folding. Buckman (1918, p. 81) used the term pliciligate for the change from opposite to alternate folding by the formation of a fold within the dorsal sulcus. However, pliciligate as defined by Williams and Rowell (1965, H150) implies only a low folding in the brachial valve. The amplitude of the folding in N. longirostra is symmetrical through the plane of the commissure. As the distinction between intraplicate and pliciligate sensu Buckman is not clear and in order to avoid confusion, the term intraplicate adopted by Ager (1967, p. 139) is adhered to.

Remarks. Attention has been paid to the radial striae of Nannirhynchia (Buckman 1918, p. 67; Ager 1967, p. 139). Stereoscan photomicrographs of N. longirostra (Pl. 136, figs. 5, 6) show that the appearance of

EXPLANATION OF PLATE 136

Stereoscan photomicrographs (except fig. 8) of specimens of N. longirostra. Material of all figures coated with evaporated aluminium before photography.

Fig. 1. Interior of a pedicle valve 37546, tilted to show the relatively large hinge teeth and the pedicle collar with its characteristic growth lines. The dental plates are apparently merged with the shell wall owing to infilling of the lateral umbonal cavities. Deltidial plates not developed. Tilt angle 68°, X 75.

Fig. 2. Interior of a juvenile pedicle valve 37559, tilted to show the denticulum and the hinge tooth supported by a dental plate with the relic of the left lateral umbonal cavity (arrowed). Tilt angle 65°, X 165.

Fig. 3. Enlarged view of the umbonal region of specimen 37551, showing the concave terminal face of each deltidial plate, X 100.

Fig. 4. Enlarged view of the umbonal region of the interior of a brachial valve 37547, showing the inner and outer socket ridges, the crura, broken, the small hinge plates, and the absence of a cardinal process and median septum, X 95.

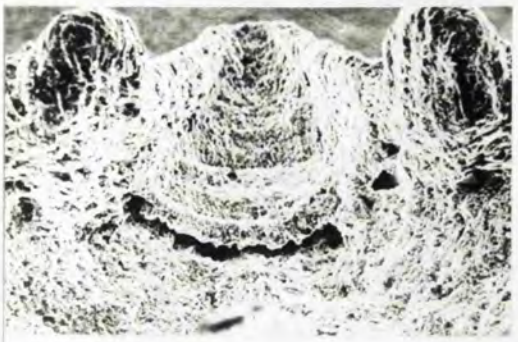
Fig. 5. Enlarged view of the striae on the external surface of the shell of specimen 37552 to show that they are an expression of the diagenesis of the primary shell layer, X 1000.

Fig. 6. Junction of the primary and secondary layers in an exfoliated shell 37564, showing the well-preserved secondary mosaic, left, and the primary shell with independently aligned striae, X 1000.

Fig. 7. Enlarged view of a portion of specimen 37562 showing the stellate pitting of the fibres lying in the depressed areas interpreted as muscle fields. Location of section, floor of the brachial valve approaching the mid-line, X 4500.

Fig. 8. Electron micrograph of a two-stage replica of an oblique section through the shell underlying a muscle field, showing the characteristic blurring of the outline of fibres associated with myotest. Location of section, approximately as in Fig. 7, X 2200.

PLATE 136



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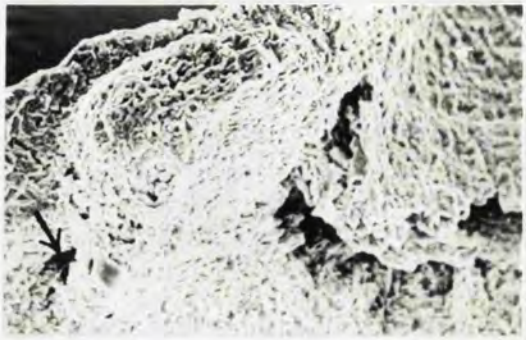

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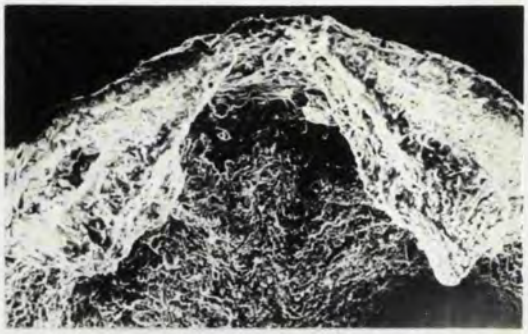

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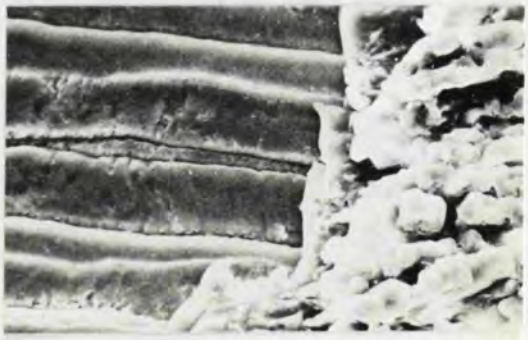

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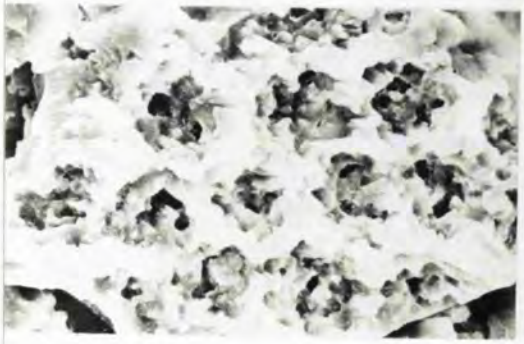

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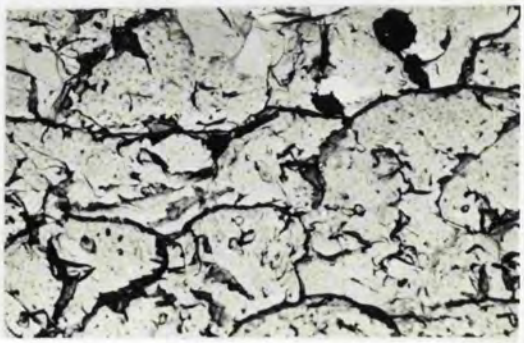

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striae is an expression of diagenesis of the primary shell, which may but does not normally, reflect the orientation of the secondary fibres.

Work in progress, on the origin and growth of deltidial plates shows that they arise from the dorsal surface of the tooth ridges. In numerous instances in N. longirostra and probably many of the other micromorphic forms with so-called very narrow deltidial plates, the epithelium responsible for initiating the development of the deltidial plates never received the necessary stimulus and the deltidial plates failed to develop. In which case the narrow ridges bounding the delthyrium and having the appearance of deltidial plates are in fact the exposed dorsal surfaces of the tooth ridges. Where deltidial plates are present (size of the animal seems to be no criterion) their development parallels the anterior extension of the teeth (Pl. 135, fig. 6) and they show a characteristic concave terminal face (Pl. 136, fig. 3).

The separation of the pedicle collar from the shell wall closely resembles that described by Copper (1965, p. 363, text-fig. 3A) in the atrypoid Mimatrypa insquamosa (Schnur.). Unfortunately, although the absence of lateral umbonal cavities is noted, the text-figure does not include a key to the shell-material type so it is not possible to determine whether they are secondarily infilled.

In Ager (1967) five nominal species have been previously recognized as belonging to the genus Nannirhynchia. These are N. milvina Buckman, N. ? minima (Moore), N. ? moorei (Davidson), N. pygmaea (Morris) and N. subpygmaea Buckman. N. milvina may be distinguished from N. longirostra by its shorter beak, episulcate folding, and later occurrence (U. Bajocian). The original of Spiriferina? moorei is apparently lost and Davidson was

probably correct in assuming that it was a juvenile Spiriferina. Ager (1967) discusses the possibility that the specimen might have been a stunted adult and states that there is no particular reason for attributing it to Nannirhynchia as suggested by Buckman (1918). Distinction between N. pygmaea and N. subpygmaea is not indisputably established but Ager prefers to keep them taxonomically separate in view of the present lack of knowledge of N. subpygmaea and its later occurrence (N. pygmaea, U. Lias, N. subpygmaea, U. Bajocian). Both species may be easily distinguished from N. longirostra by their beak characters.

It is probable that the species is very closely related to the form described by Moore (1861, p. 190, pl. 2, figs. 19, 20) as Spiriferina? minima and the specimen illustrated in fig. 19 undoubtedly shows great similarity with the holotype of N. longirostra. However, significant differences exist between N. longirostra and the illustration of S? minima in Davidson (1874, Suppl. pl. 11, fig. 17a) which in the context of the sentence (Davidson 1874, p. 103) purports to be a careful drawing of one of Moore's specimens. Davidson illustrates a correctly defined (Williams and Rowell 1965, H145) hinge line. His figure implies the presence of an interarea and therefore a strophic shell (Rudwick 1959, p. 19) differing from the non-strophic shell of N. longirostra. Moore himself states that the area is broad and flattened and refers to a broad hinge-line but figures what is essentially a cardinal margin similar to that of N. longirostra. An interesting feature is the way Moore (1861, pl. 2, fig. 20) illustrates a lateral deflection of the beak. This character is commonly observed in young forms of N. longirostra in the material collected from Westington Hill quarry (Pl. 135, fig. 8). Buckman (1918, p. 68) noted the similarity between S? minima and N. subpygmaea (Walker) but also commented on the large beak and apparently straight hinge line depicted by Davidson. Later (p. 74) Buckman assigns

these characters to the genus Rectirhynchia and suggests both Moore and Davidson may have unwittingly combined details from more than one specimen, i.e. combined the characters of two species.

Both Moore and Davidson refer to the presence of a triangular deltidium yet none of the figures clearly shows the structure. Davidson's figure shows a constriction at the anterior of the delthyrial region, very similar to the disjunct deltidial plates of certain young terebratulides, whilst Moore (1861) figures either an open delthyrium bounded by very narrow deltidial plates or has shaded to indicate a concave plate. Reference to their accounts of other micromorphic forms precludes the possibility that both authors could be mistaken with regard to the presence of a plate situated in the delthyrium. The conclusion must therefore be that S? minima possessed a concave plate within the delthyrium, identifiable with the pedicle collar of N. longirostra.

Unfortunately a careful search through the micromorphic brachiopods in the Moore collection has failed to reveal the types of S? minima. They were not listed by Dr. Wallis when he catalogued the collection in 1927 so it appears that the originals are lost. The degree of affinity between N. longirostra and S? minima must therefore remain a matter of speculation. Demonstration of the close similarity between the two forms introduces the possibility that we are here, simply recording the discovery of S? minima in a new locality, and raises the question of the validity of the new species. In view of the very limited knowledge of S? minima and in view of the absence of the original types, it is felt that there is justification in the erection of a new species to include the Westington Hill material.

Reference numbers quoted in the plate figures refer to stereoscan negatives of figured specimens which are to be retained in the negative library of the Department of Geology, University of Leicester.

EXPLANATION OF PLATE 137

Stereoscan photomicrographs (except figs. 5, 6) of N. longirostra. Material of all figures coated with evaporated aluminium before photography.

Fig. 1. Portion of an exfoliated shell showing the extension of individual secondary fibres from the outer to the inner (upper left) boundary of the secondary layer, X 200.

Fig. 2. Surface of an exfoliated secondary fibre showing growth lines, X 2200.

Fig. 3. Enlarged portion of peel 37549/15 showing the dental plate and subsequently infilled lateral umbonal cavity. T.S. X 150.

Fig. 4. Enlarged portion of peel 37576/19 showing the pedicle collar developed from the inner surface of the dental plate and the very small infilled lateral umbonal cavity, close to its posterior termination. T.S. X 150.

Fig. 5. Photomicrograph, reflected light. Transverse section through specimen 37549 showing the crystallite coated interior of the shell and the crystallite encrusted, arcuifer crura, X 40.

Fig. 6. Retouched copy fig. 5.

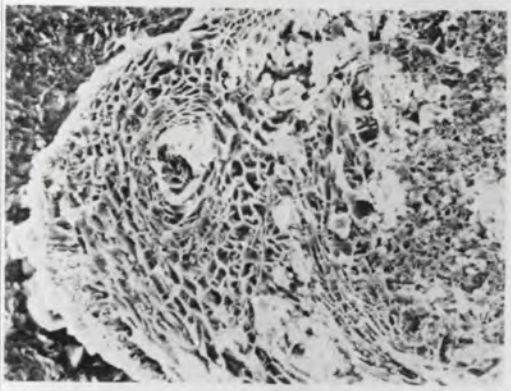
Fig. 7. Enlarged portion of peel 37576/26, showing the crural base (c.b.) adjacent to the inner socket ridge and arising from the dorsal surface of the hinge plate (h.p.). T.S. X 150.

Fig. 8. Horizontal section through specimen 37587 showing the form of the left crus, X 175.

PLATE 137

1

2



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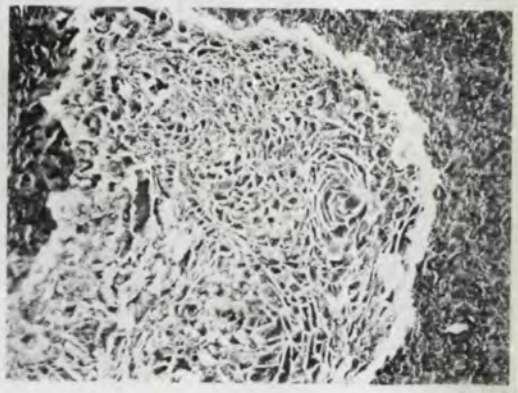

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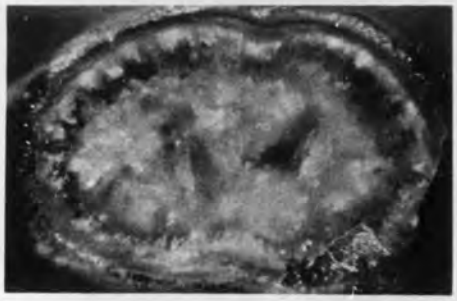

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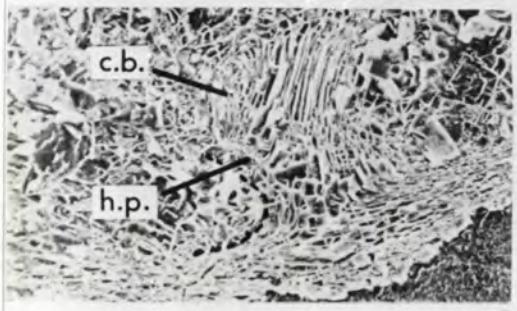
6



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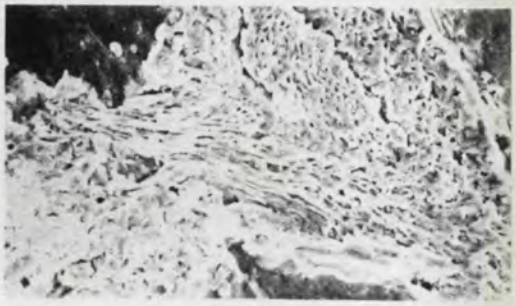


8

Section 4. Zeilleria leckenbyi (Dav.)

Introduction

During the search for micromorphic brachiopods in Oolite Marl residues, forms which were obviously juvenile terebratulides were noticed. Eventually a collection of some 250 shells was obtained, ranging from 0.4 - 14.0 mm. in length. The collection did not seem to be of any great value as several terebratulides occur at this horizon (Appendix list 1) and there seemed little hope of successfully correlating the juveniles with their respective adults. However, the potential of the material was soon appreciated when it was realised that only a single zeilleriid was represented among the adults present. The terebratulide juveniles are so similar in shape that variations in L/W and L/Ht. ratios fall well within the range of intra-specific variation. Accordingly, the collection was analysed on the basis of 27 morphological characters (Appendix fig. 3, table 1, 2) and separated into two clearly defined groups (Appendix Pl. 3, fig. 3-6), one of which could be correlated with the adult Z. leckenbyi. Sectioning of representative juveniles from this group confirmed that they were indeed juvenile long-looped forms and by inference, juvenile zeilleriids.

The excellent preservation of some of the juveniles encouraged an attempt to describe the actual growth of the developing loop, based on microstructural evidence. The section is presented in the form of the manuscript which has been accepted for publication in Palaeontology, 15, part 3.

THE DEVELOPMENT OF THE LOOP IN THE JURASSIC BRACHIOPOD ZEILLERIA LECKENBYI.

ABSTRACT. An ontogenetic series of Z. leckenbyi has been obtained from a locality in the mid-Cotswolds. Serial sectioning has enabled determination of the microstructure and development régime of the loop. The work reveals that a loop of adult character is formed by the time the brachial valve is about 4.0 mm. long, confirming Elliott's suspicion that in zeilleriids the early stages of loop development were passed through very quickly. During early development phases the loop is connected to a septal pillar rising from the floor of the brachial valve. The general pattern of loop development appears to combine terebratellid and dallinid characters. It is found that the descending elements play only a subsidiary role during loop development. That they become relatively massive fairly early appears to be due to the fact that they are required to support the ascending complex after resorption of the connection with the median septum has occurred. The growth pattern of the median septum indicates that it may be regarded as a secondary character and therefore makes only a very limited contribution to loop development in the Zeilleriidae. Attention is focussed on the gross inadequacy of our knowledge of the actual growth of juvenile loops during the recognised stages passed through during ontogeny. Analysis of the development régime illustrates some of the dangers of recording growth stages which are essentially momentary phenomena in what must necessarily be a cumulative process. The current work indicates that a cryptacanthiinin of Glossothyropsis type may be ancestral to the Zeilleriidae. It is concluded that the microstructure of developing loops will provide the key to the solution of the complex phylogeny of the Terebratulida and that the possession of spinose ascending and descending elements is a more important ancestral character than the absence of a median septum.

INTRODUCTION. The loop ontogeny of Terebratulides is not well known and even the more recent interpretations (Dagis 1958, 59, Babanova 1964) rely heavily on the work of Elliott (1948, 53). Undoubtedly the main reason for the lack of information is the scarcity of juveniles of representative genera. It is surprising therefore, that despite our general lack of data, high taxonomic significance is attributed to the loop ontogeny of terebratulides. It appears that microstructural analysis of loop elements will enable some of the gaps in our knowledge to be bridged and that bulk sampling may reveal the presence of very small juveniles previously overlooked.

The material used in these investigations was recovered during the search for micromorphic brachiopod faunas in the Oolite Marl. This deposit is a weakly-coherent interbedded marl and biomicrite of Upper Aalenian (murchisonae zone) age occurring in the Inferior Oolite of the mid-Cotswolds around Cheltenham. The two best remaining exposures are at Cleeve Cloud SO 984261 and Westington Hill Quarry SP 142368 from which locality the current material was obtained. The stratigraphy of the Oolite Marl and the horizon from which collections have been made are outlined in Baker (1969, p. 388). A third, excellent exposure in the old cutting at Notgrove Railway Station SP 094213 is now unfortunately, no longer available as the area has been taken over for site development.

In addition to a rich organo-detrital residue and micromorphic brachiopods (Baker 1969) the Oolite Marl yields juvenile rhynchonellides and terebratulides and adults assigned to the species Globirhynchia subobsoleta (Dav.), Epithyris submaxillata (Morris), Plectothyris fimbria (Sow.), "Terebratula" whitakeri Walker MS and Zeilleria leckenbyi (Davidson ex Walker MS).

A collection of 250 juvenile terebratulides, ranging in size from 0.6 - 14.0 mm. in length, was analysed on the basis of 27 morphological characteristics. The data obtained from this analysis is too voluminous to be included in the present work and is to be published later. Briefly it may be stated that the larger juveniles may be readily correlated with their adult counterparts and on the basis of character evaluation may also be correlated with progressively smaller juveniles. Fortunately, Zeilleria leckenbyi is the only long-looped species present so the possibility of error is greatly reduced.

Thirty specimens ranging from 0.8 - 25.6 mm. in length were selected, which, on the basis of the results obtained from morphological analysis, were anticipated to be juveniles and adults of Z. leckenbyi (Pl. A, Fig. 1 - 12). These specimens were serially sectioned and the results obtained are summarised in Table 1. The external morphological characters of all the specimens anticipated to be Z. leckenbyi were supported, with only two exceptions, by zeilleriid internal characters. The obvious developmental "progression" leaves little room for doubt that the remaining 28 shells represent the ontogenetic stages of a single species.

Fundamental to all thinking regarding the interpretation of secondary shell fabric must be the realisation that the smaller the unit considered, the closer it must approach Rudwick's (1959) "momentary" conception of growth and the larger the unit, the closer it approaches his "cumulative" conception. This means that the various parts of the developing loop are the cumulative product of a series of momentary units. As Westbrek (1967 p.29) has pointed out, increase in size of internal structures is the result of deposition of shell at their distal ends but thickening is usually

the result of shell deposition proximally i.e. in posterior zones of the shell where structures arise apically. It follows therefore, that in the apical region of a shell, early growth stages will only be preserved (where no resorption of material has taken place) as cores buried in the shell material of subsequently enlarged structures. Added to this is the problem that growth of the valve must necessarily bring about a change in the orientation of an early structure relative to the commissural plane. As the early growth phases of the pedicle valve are eliminated by resorption in Z. leckenbyi, attempts to trace continuity of structures must be based on the study of brachial valves. A consideration of critical importance (Westbroek, 1969), apparently largely ignored by many workers, is that owing to the change in orientation of structures during growth, the orientation of the plane of section must be adjusted accordingly if "buried" structures are to be clearly identifiable in sections of larger shells. For instance, transverse sections through units of the very early cardinalia will be encountered in near horizontal sections through adult shells.

In view of the need for accurate correlation between specimens in different size ranges, trios of specimens were selected which were as near identical as possible, morphologically and in size. Of these, one was retained as a reference, one was sectioned, normal, transverse and the third specimen was sectioned growth oriented according to the normal transversely sectioned specimen of the preceeding size range. In the text therefore, horizontal sections refer to the orientation of the plane of section relative to the loop rather than to the orientation of the shell, which is usually low oblique. Orientation can not be exact because the loop is obviously not visible but critical sections may be correlated to a greater extent using this method. There can be

no hard and fast correlation between size of animal and stage of loop development, for at a given size, loop development will be either precocious or retarded according to the momentary point which has been adopted as the mean. The closest approach to such a correlation, must therefore, lie in the relation of development phases to approximate size categories (Table 1.).

Owing to the very small size of the early juveniles and the delicate nature of their loop elements, it was virtually impossible to recognise loop elements in transverse section. This became particularly apparent where the infilling matrix was not of uniform texture. Most of the work was therefore based on horizontal sections. This orientation offered the greatest chance of success as the component fibres of the elements would be more or less length-sectioned and therefore, more easily visible in the matrix. Traces of transverse sections through specimens are included (text fig. 7A - C) to conform with the accepted method of illustrating serially sectioned brachiopod loops. However, at this early stage of development the various elements may be only 3 - 4 fibres thick and do not respond well to photography. For recording loop development photographically, horizontal sections showing length-sectioned fibres yield far better results. Accordingly the evidence provided by horizontal sections has played an important part in the reconstruction of early loops. Those sections which are regarded as critical are also figured (Pl. C fig. 1 - 12).

Acknowledgements. The author is indebted to Dr. J. D. Hudson, Department of Geology, The University of Leicester, for discussion during the preparation of this paper. Thanks are due to Mr. G. McTurk for preparation of the stereoscan negatives and to Professor Sylvester-Bradley for use of the research facilities of the Department of Geology, The University of Leicester.

Registration of Material. The material figured in this paper, together with original and duplicate peels, is to be housed in the Museum collection of the Department of Geology, University of Leicester under the catalogue numbers quoted.

TECHNIQUES AND PREPARATION OF MATERIAL

A comprehensive account of the preparation of Oolite Marl material is given in Baker (1969) and the material studied in the present paper was obtained by the same method. The smaller specimens up to 4.0 mm. in length were investigated using the techniques developed for the study of the micromorphic thecidellinid Moorellina granulosa (Moore) (Baker 1970). The larger specimens were studied using the techniques developed by Hendry et. al. (1963).

It has not been possible to locate a separated juvenile brachial valve in which the loop is complete although the bifid appearance of the ascending lamellae is quite common (Pl. A, Fig. 16 - 18).

NOMENCLATURAL PROBLEMS

This and other studies show that the differences, discussed later, between dallinid and terebratellid loop ontogenies are often very subtle. Although all the changes are variants of two common plans they are complicated by precocious or retarded development and by changes in the relative proportions of the same structures in successive growth stages of a single genus also as a result of changes in the relative proportions of different parts of the loop in different genera. From an evolutionary point of view it is obvious that loop development within the sub-order Terebratellidina forms a fairly intimate complex and it would therefore, be wrong to introduce an entirely new nomenclature for zeilleriid loop ontogeny. New terms

must be introduced with due regard for their probable affinity with comparable structures in other forms.

Great care has been taken to avoid the use of the term median septum in description of ontogenetic stages as it can be shown that the median septum as observed in the adult Z. leckenbyi plays no part in the development of the ascending elements of the loop. Whether the structure plays a valid role in the development of the loops of other terebratellidines is not yet clear.

Muir-Wood (1934) noted that in the Zeilleriidae the septalium is formed by two plates, the septalial plates, which converge and fuse together to form a septum. She states (1934, p. 529) that the septum appears to be distinct from the true median septum in many species. In very young specimens of Z. leckenbyi there is no septalium and the plates extending from the crural bases to the floor of the valve (Pl. A, fig. 14, 15) should, according to the Treatise definition (Williams et. al. 1965) be regarded as crural plates. Muir-Wood also noted that in Digonella the dorsal end of the median septum appears to be inserted in the wall of the brachial valve. Study of oriented valves of Z. leckenbyi indicates that both the above structures are represented by the sessile bundle of secondary fibres which give rise to the septal pillar of this species, in which case the median septum as observed in adult shells is a bi-component subsequent valve element It post-dates the septal pillar, as the remnant of this structure (Pl. D, fig. 1, 2) is enveloped as the septum is extended anteriorly. In Z. leckenbyi therefore, the median septum sensu latu, makes only a limited, if any, contribution to the development of the ascending elements.

Elliott (1953, p. 263) refers to the often pillar-like upgrowth from the valve floor which constitutes the precursor of the ascending

elements in the Terebratellidina. The use of Elliott's term, septal pillar, being most apt, is adopted to describe the almost cylindrical structure arising from the valve floor and leaning anteriorly in a characteristic terebratellid (Elliott 1953, p. 267) manner.

Following the appearance of the pillar the ascending elements develop rapidly and as a number of components appear almost simultaneously the term ascending complex is introduced (text Fig. 1C, D). It is felt that this term is required to describe structures which are the precursors of the ascending elements proper (ascending branches and transverse bar) and also those which regulate the early location and anterior extension of the descending branches. The component parts of the ~~axial~~ ascending complex in order of appearance are as follows:-

Posteriorly arching spurs. Posteriorly directed outgrowths from the sides of the septal pillar near its distal end. The descending elements unite with them and grow along their ventral edge to fuse with the material of the ascending lamellae which lies between the anterior spurs (text Fig. 1A, B, 6A. Pl. B, Fig. 2, 3).

Ascending septum. Small, vertical, axially aligned plate, developed on top of the septal pillar and replacing the dallinid hood which is sometimes preserved as a rudiment on the posterior edge (text Fig. 1C, D).

Ascending lamellae. A pair of diverging plates which arise from the anterior edge of the ascending septum and are subsequently extended along its ventral edge. These lamellae are the precursors of the ascending branches. As they increase in size they give rise to horns of material posteriorly, which are deflected towards the mid-line until they unite to form the transverse bar (text fig. 6B - D, Pl. B, fig. 6).

Anterior spurs. A pair of prismatic calcite spurs developed from the base of each ascending lamella. They regulate the position of the descending branches relative to the ascending branches and become ensheathed in secondary fibres as the decending branches are extended anteriorly (text fig. 1E, F, 3, 4, Pl. B, fig. 1, 8).

From the host of modifications described by Elliott (1953, 1960) and Muir-Wood et. al. (1965) it becomes clear that terms such as campagiform and frenuliform must not be applied too rigidly. Also the use of the term stage is deplored. It is thought that the term stage is likely to lead to inflexibility as it implies a growth attainment of a momentary nature (Rudwick 1959). Accordingly the author proposes to use the term phase as this suggests the more real, cumulative growth pattern of the loop.

While the ascending complex is developing it shows a close resemblance to the modified magadiniform type seen in Australiarcula artesiana Elliott and Bouchardia rosea (Mawe) (Elliott 1960). As the microstructure of the magadiniform loop is unknown, the term paramagadiniform will be used to describe the loop of Z. leckenbyi during this growth phase.

Differences of opinion exist (Thomson 1927, Elliott 1947, 1953) with regard to the correct definition of the campagiform loop but all specify the presence of a hood. Therefore, by definition Z. leckenbyi does not possess a campagiform stage because the hood even if present is never more than a rudiment. However, the growth phase succeeding the paramagadiniform culminates in a structure resembling the campagiform loop but arrived at by a different development sequence. Therefore, the phase of development succeeding the paramagadiniform phase will be termed syncampagiform to describe the loop of campagiform appearance which arises without the involvement of a hood.

ZEILLERIID DEVELOPMENT PHASES

The developing loop of Z. leckenbyi passes through seven recognisable phases of growth, which, on the basis of experience may be anticipated to coincide with certain approximate size ranges.

Phase 1. Pre-paramagadiniform. Shell length < 1.8 mm.

It seems probable that the floor of the brachial valve is at first featureless. The precursor of the ascending elements of the loop appears very early as a bundle of fibres, longitudinally arranged, lying almost parallel with the floor of the valve (Pl. B, fig. 11). Growth increments are added to the ventral surface of this bundle, as might logically be expected from the position it occupies on the valve floor. An abrupt change in this growth pattern occurs when the animal is about 1.3 mm. long. The bundle of fibres becomes re-oriented to rise as a septal pillar projecting from the valve floor (text fig. 1A, B, Pl. A, fig. 13 - 15). This change in fibre orientation is accompanied by a change in growth pattern as the new growth increments are now added anteriorly i.e. on the originally dorsal surface of the fibre bundle (Pl. B, fig. 9, 10). The explanation for this change is obvious, for the new development régime will carry the developing loop anteriorly.

Soon after the formation of the septal pillar, two ribbons of calcite, arched posteriorly, arise laterally at a point close to its distal end (Pl. B Fig. 2, 3, 5, text fig. 1A, B, 6A). The descending elements at this time are very short. Before the shell reaches a length of 1.8 mm. a further development phase begins.

Phase 2. Paramagadiniform. Shell length 1.8 - 2.5 mm.

The distal end of the septal pillar becomes laterally flattened and rises vertically as an ascending septum (text fig. 1C, D, 6B).

The descending elements become more strongly developed and there is a proportionate increase in the size of the posteriorly arching spurs, so that the two soon unite. A swelling appears about half way up the posterior edge of the septum. On occasional specimens this may be seen to develop into a low ring-like collar at its distal end. The structure actually plays no part in the formation of the loop but may be interpreted as a rudimentary hood of the type found in Australiarcula artesiana Elliott. At the same time two divergent lamellae, the ascending lamellae, develop at the anterior edge of the ascending septum (Pl. A, fig. 18, Pl. B, fig. 6, text fig. 6B, C). During this phase of development the crural plates become raised above the floor of the valve. In the mid-line they become turned down to form a shallow septalium (Pl. A, fig. 17) and extend as an overlay of secondary fibres above and one either side of the earlier deposited fibre bundle which represents the sessile portion of the septal pillar (Pl. B, fig. 11). The divergent lamellae are of the utmost importance for they represent the precursors of the whole of the subsequently developed loop. Within each lamella arise the proximal ends of a pair of spurs which herald what is fundamentally the most important phase of development of the entire loop.

Phase 3. Syncampagiform. Shell length 2.5 - 3.5 mm.

No direct evidence is available but it is believed that the ascending lamellae extend up the anterior edge of the ascending septum and along its ventral edge, at first diverging and subsequently converging posteriorly to form the rudiment of the transverse bar of the adult loop (text. fig. 6B - D). This mode of origin is favoured because the campagiform hood is never more than a rudiment and the transverse connection when first formed is always thread-like.

Following the initiation of the spurs (occasionally three on each lamella) their development proceeds rapidly and is accompanied by thickening of the distal ends of the descending branches and broadening of the ascending lamellae so that the loop becomes relatively massive (text fig. 1E, F, 6D). Investigation shows that the anterior spurs are composed of prismatic calcite (Pl. B, fig. 4, text fig. 3, 4). As they are extended anteriorly, they are responsible for controlling and facilitating the location of the descending branches (Pl. B, fig. 1, 8). The spurs act as girders for the anterior extension of the descending branches, becoming at first partially, then completely enveloped by secondary fibres as the descending elements are extended (text fig. 3, 4). The culmination of this development phase is the development of a structure which morphologically bears a close resemblance to the dallinid campagiform stage. At the moment however, there is no data on the dallinid type to show whether the two forms are microstructural equivalents.

Subsequently deposited material continues to accumulate posteriorly in the mid-line of the valve to form a recognisable median septum which is extended anteriorly so that the septal pillar itself becomes partially enveloped (Pl. B, fig. 11, text fig. 3, 4). Although this has a strengthening effect on the pillar the primary objective appears to be the provision of a base for the attachment of adductor muscles.

Development through the three phases described, may be regarded as being aimed at the attainment of a basic skeletal structure which is capable of being translated into a loop able to support a plectolophe. Metamorphosis of this existing framework is necessary to elaborate and alter the relative proportions of the various loop elements produced by the initial development régime. Shell resorption, until now, not a prerequisite of loop development, quite suddenly assumes a critical

role in current and all subsequent development.

Phase 4. Frenuliform. Shell length 3.5 - 4.0 mm.

Although this phase of development probably does not reflect any change in the form of the lophophere it does illustrate that important physiological changes are taking place. Whilst the anterior of the loop is developing in the manner described above, resorptive activity begins at the posterior of the ascending complex. Two lacunae appear close to the point of divergence of the ascending lamellae (text fig. 1G, H, 6E).

Phase 5. Terebrataliiform. Shell length 4.0 - 7.2 mm.

As the lacunae increase in size the distal portion of the pillar is also resorbed so that the loop becomes freed from its connection with the septal pillar (text fig. 2A, B, 6F). None of the material sectioned showed the retention of a connection between the descending branches and the septal pillar so that a form corresponding to the true terebrataliiform stage of the dallinids has not been seen in Z. leckenbyi. However, if the mechanics of resorption are considered it seems probable that the delicate strips of material posterior to the lacunae would be lost before the descending branch connections and it is therefore logical to assume a short terebrataliiform phase. It is the intimate relationship between the processes of accretion and resorption which during this phase sculpture the approximate configuration of the adult loop.

The anterior spurs have by now apparently fulfilled their purpose as they cease to develop although their remnants are still visible (Pl. D, fig. 3, text fig. 6F) and these continue to regulate the development of the descending branches. Apparently, the posterior end of the lower spur of each lamella is resorbed more slowly as forms passing through this phase of development normally show a small,

posteriorly pointing projection, posterior to the point of union of the lamella with the descending elements.

Resorption, after it has begun, apparently proceeds rapidly as the transition from syncampagiform to late terebrataliiform is accomplished quickly and as far as can be ascertained, during the time that the shell is between 3.5 and 7.2 mm. in length.

The median septum continues to extend anteriorly after resorption of the connection of the septal pillar with the ascending elements has occurred. The pillar remnant, enveloped by subsequently deposited fibres, can be clearly seen in horizontal sections through young shells, some distance from the anterior termination of the median septum (Pl. D, fig. 1, 2). The median septum therefore, as seen in zeilleriids must be regarded as a median septum sensu latu.

Phase 6. Dalliniform. Shell length 7.2 - 19.0 mm.

The dalliniform phase of development is essentially concerned with smoothing out the irregularities of the crudely adult loop development during the preceeding development phase. The loop thus formed (text fig. 2C, D, 6G) although quite symmetrical is still relatively heavy and the anterior of the ascending branches still has a plate-like aspect.

Phase 7. Zeilleriiform. Shell length >19.0 mm.

The culmination of the accretion-resorption régime produces an adult loop in which all the elements are comparatively slender and ribbon-like (Ager 1956) with the descending branches often densely spinose (text fig. 5A, B). The growth and resorption zones of the adult loop show the same basic pattern as that illustrated by Williams (1968, p 25) in Magellania flavescens (Lamarck). The main difference lies in the fact that the spinose zones of the descending branches of the adult loop of Z. leckenbyi consist of a double ribbon of shell material (Pl. D, fig. 4, 6). The spines develop in the same manner

as the anterior spurs and show a similar fibre enveloped prismatic core (Pl. D, fig. 5).

DEVELOPMENT OF SPINES

Occasional spines appear on the descending elements even during the syncampagiform phase but they only become numerous during the late dalliniform phase. The development of spines is considered by Elliott to be indicative of some power of secretion of calcite by cirri. In Z. leckenbyi the spines can be shown to be a fundamental part of the loop. At first it was thought that the spines might be "unused" anteriors of spurs which had become isolated by resorption and owed their orientation to rotation of the loop axis during growth. Later it was realised that the spurs always lie relatively close to the mid-line of the valve and could in no way migrate to the observed position of the spines on the descending elements. It appears therefore, that the spines and spurs follow the same pattern of development. The implication of this will be discussed later.

FUNCTION OF THE LOOP

From a consideration of Rudwick's work (1962) on filter-feeding mechanisms in brachiopods. It seems certain that during the pre-paramagadiniform growth phase the brachial apparatus supported a schizolophe and that during the paramagadiniform phase it supported a zygolophe. As the ascending lamellae diverged and the transverse bar appeared, the zygolophe would develop into a plectolophe.

At the beginning of the syncampagiform phase material is added rapidly to the descending elements so that the descending branches become relatively massive. It seems that the posterior projections from the ascending complex provide an initial framework for the accelerated development of the descending elements i.e. they act as

"formers" to enable the descending elements to progress rapidly but the directive control over the morphology of the anterior of the loop is exercised by the ascending elements.

Elliott (1953) suggests that selection pressure is directed towards the development of a more efficient lophophore and the fact that most terebratulide loops are believed to have supported a plectolophe indicates that this form of organisation was in some way advantageous to the animal. Elliott further maintains that any mutation favouring the earlier attainment of an adult pattern of lophophore would be selected and correlates this with the advantages conferred by earlier attainment of an adult loop. As in Z. leckenbyi the anterior spurs and spines follow the same development pattern it seems probable that they appeared as undifferentiated structures on the descending and ascending elements of ancestral forms. At some point in time, possibly under the influence of strong selection pressure certain spines on the ascending elements could be "fortuitously" utilised for the extension of the descending branches and therefore, for the increase in size of the loop. The importance of a mutation which enabled the animal to utilise the anterior spines in a locating role, as a means for rapidly extending the anterior portion of the loop, will be readily appreciated.

Elliott (1948) regards the peak of brachial evolution, expressed by the Terebratellidina, to be intraregressional and coinciding with the radiation of the relatively more mobile Bivalvia. The arguments advanced appear logical and the zeilleriids, which developed adult-pattern (in the terebratellid sense) loops very early should have remained dominant. In fact they were the first to die out during the Lower Cretaceous, although other terebratellidine Forms, e.g. Kingena, Trigonellina and Zittelina, having juvenile loops in the zeilleriid

sense but presumed to be adults, appear later and have loops capable of supporting a small plectolophe. The Zeilleriacea are largely replaced by the Terebratellidae and the later representatives of the Dallinidae and Terebratulidina. It is felt that it is incorrect to correlate density of population with elaboration of loop as there is no evidence to suggest that competition was any less severe in terebratulidine colonies where forms with short loops appear to be no less successful. Indeed, the terebratulacean Terebratulina with its very strong fused loop with heavy anterior spiculation is probably one of the most successful of all Mesozoic - Recent brachiopods. The advantage therefore, appears to lie in the possession of a plectolophe and it appears that selection pressure was geared to the early attainment of this organ however it may be arrived at. A view of this sort is necessary to explain the continuance of short and long-looped forms and also the various apparently neotenous forms which co-exist with them.

With regard to loop form it seems probable that long loops have evolved several times. Williams and Wright (1961) regard the enteletacean Tropidoleptus as a homeomorph of the juvenile terebratellacean loop. However, the development pattern of zeilleriid, dallinid and terebratellid loops displays such community of character that it seems likely that they are very closely related. All patterns of loop can be accounted for by differing degree and time of onset of calcification during development of the same type of lophophore. The unifying theme is apparently the early attainment of an ascending complex from an outgrowth from the floor of the brachial valve.

INTER-RELATIONSHIPS OF MESOZOIC LONG LOOPED TEREBRATULIDA

Phylogenetic aspects of brachiopod microstructure have been studied previously by Baker (1970), Williams (1968, 70). Elliott (1953) considers the median septum fundamental to the Terebratellacea, for in modern

short-looped forms the septum is absent and there are various extinct long-looped forms, not terebratelloids, where, so far as is known, the septum played little part in the development of the loop. Therefore, it seems that the demonstration that the median septum sensu latu may be relieved of its role as a loop former in zeilleriids, may be important in a phylogenetic sense.

It has been demonstrated that the early phases in the development of the zeilleriid loop have terebratellid counterparts whilst the later phases have a dallinid aspect. At present there is no information as to whether the same similarities exist at the microstructure level. However, it seems probable, as divergence of the anterior of the lower edges of the campagiform hood to produce long spurs is well known in dallinids (Elliott 1953). In addition Elliott noted that in growth stages of higher genera and when first attained in adult terebrataliiform genera, the terebrataliiform stage is somewhat angular, often with short spines at the anterior points of recurvature of the descending and ascending branches. It appears therefore, that when the ontogeny of the loops of other spinose forms is studied more critically, the role that the anterior spurs play in the extension of the descending elements will prove to be a character not unique to Z. leckenbyi.

Asymmetry of loop development is described by Fischer and Oehlert (1892) and in several juveniles of Z. leckenbyi, the right ascending lamella was found to be more strongly developed.

Investigation by Babanova (1965) of Aulacothyris pala (Buch) and A. karabugasensis Moisseiv, confirmed the presence of a connection between the loop and the median septum early in ontogeny. Babanova proposed that the genus Aulacothyris Douville be removed from the Zeilleriidae and together with several similar forms should be placed in a new tribe

Aulacothyrini assigned to the Dallinidae. The basis for this argument is that the Zeilleriidae are characterised by the absence of a connection between the loop and the median septum even in the earliest stages of ontogeny. This view, propounded by Stehli (1956b), Dagis (1958, 1959) if carried to its conclusion, will in the light of the present discovery necessitate the removal of typical zeilleriids from the Zeilleriidae.

Z. leckenbyi may be shown to pass through a connected phase quickly and very early in ontogeny i.e. size range 2.00 - 4.00 mm. length. Similar phases of development are seen in Aulacothyris karabugasensis and A. pala but over a much larger size range i.e. 4.00 - 9.5 mm. length. In A. karabugasensis the campagiform stage (Babanova 1965, fig. 3a) has a short broad loop, not deeply dissected into two lobes anteriorly. The general morphology and absence of spurs indicates that the early development régime of the aulacothyrid loop differs from that of Z. leckenbyi. However, the late terebrataliiform loop of Z. leckenbyi, particularly the morphology of the ascending elements closely resembles the terebrataliiform stage of A. karabugasensis.

The specimens studied by Stehli and Dagis are also significantly larger than the early growth phases recorded in Z. leckenbyi. Stehli (1956b) studied specimens of an unnamed terebratellacean from Peru which were 7.5 mm. in length. This was subsequently named Eodallina peruviana Elliott (1959) although its systematic position remains uncertain (Muir-Wood et. al. 1965, H844). Dagis (1958) described the development of Zeilleria agechbokensis Moiss. through a size range 5.2 - 8.7 mm. length. The loop of this species is very similar to the syncampagiform loop of Z. leckenbyi, though not actually united with the median septum in the material studied. In 1959, Dagis published a further paper on the development of Aulacothyropsis reflexa (Bittner) and Pseudorugitela pulchella (Bittner). The actual dimensions of the specimens are not

listed but the distance from the umbo to the end of the loop is 5.6 mm. and 10.00 mm. respectively. As Z. leckenbyi appears to be closely related to ornithellids it is probable that a similar ontogeny will be present in that genus also. Obviously the early juveniles of Z. leckenbyi represent some of the smallest zeilleriid material as yet available for study. In view of the evidence therefore, it seems that possession of a connection with the median septum during the early phases of development is not valid justification for the removal of genera from the Zeilleriidae. It is hoped that early juveniles of other genera will eventually become available, together with data on the development régimes of other known ontogenies. It is felt that a basic pattern of loop development in dallinids and related forms exists. Correlation of the various development régimes will enable the systematic position of the Zeilleriidae to be fixed more accurately.

With regard to the systematic position of the Zeilleriidae relative to that of the Terebratellacea it is necessary to review the criterion for separation of the Dallinidae and Terebratellidae. This criterion at present lies in the dallinid hood and the terebratellid ring and the mode of development of the descending branches of the loop. The difference between the hood and the ring may not be as fundamental as it appears. Elliott (1960) has described an Upper Cretaceous terebratellid, Australiarcula artesiana sp. nov. which possesses a primitive magadiniform loop with well developed descending branches and also a rudimentary hood. The same type of structure has been noted in some paramagadiniform specimens of Z. leckenbyi, the entire ascending complex during this phase of development bearing a striking resemblance to the loop of Bouchardia rosea (Mawe). There is also a resemblance between the early ascending lamellae of Z. leckenbyi and the two divergent plates which constitute the early development of the loop of Kraussina. However, it is unlikely

that these forms are derived neotenously from the zeilleriid type as all three genera are without the dental plates which are invariably present in Z. leckenbyi, even in the earliest juveniles it has been possible to isolate (0.8 - 0.9 mm. long).

Elliott also noted (1953) the spiny nature of many mature and immature dallinid loops and the almost complete absence of spines in the terebratellids. In view of the latter point it appears that the bulk of the development pattern of the loop of Z. leckenbyi, despite its early terebratellid aspect, is much closer to that of the Dallinidae. It is hoped that the present paper will stimulate research into the continuous growth phases of the juvenile loops of other forms, for critical investigation of the fabric of the developing loop must provide the solution to many of the systematic problems posed by the varied assemblage of genera at present comprising the Jurassic Terebratellidina.

The evidence now available shows that some terebratellid forms exist which possess a rudimentary hood characteristic of the dallinids. Also, that zeilleriids pass through a development phase comparable with these terebratellid types. The inference being therefore, that by varying the degree and/or order of expression of the elements of the ascending complex, zeilleriid stock is potentially ancestral to both the Dallinidae and the Terebratellidae. Suppression of the posteriorly arching spurs and accelerated development of the hood would initiate a dallinid line, whereas elimination of the hood would consolidate a terebratellid line.

AFFINITIES WITH PALAEOZOIC TEREBRATULIDES

The concept of investigating developing loops at the microstructure level is quite novel and work in the first instance therefore, must be largely descriptive. However, there is some merit in attempting to analyse the results from an evolutionary point of view.

It is clear that if the septal pillar is disregarded, the anterior of the ascending complex of Z. leckenbyi during the paramagadiniform phase of development has a distinct affinity with the divided septum of certain Lower Carboniferous centronelliform types e.g. Gacina (Stehli 1956a, p. 197). It is generally agreed by most workers that selection pressure favoured rapid attainment of a larger lophophere and presumably a larger loop. The most obvious advantage of a terebratellid loop is that it allows loop development to proceed from two points, i.e. the median septum and the dorsal cardinalia. It has been demonstrated that in Z. leckenbyi the ascending elements can arise from a septal pillar without the involvement of a median septum sensu latu. All that is needed therefore, to derive the zeilleriid ascending complex from Carboniferous centronelliform types, is a slight change of organisation to allow the ascending complex to be supported by a septal pillar. However, as previously mentioned, the presence of spines on the ascending elements appears to be a very important ancestral character for these appear to be the mechanism by which rapid anterior advancement of the loop was attained. Dental plates, being the first internal structures to appear, are also presumed to be important.

It seems therefore, that in evolution the zeilleriid loop progressed via a modified centronelliform type through a cryptonelliform type in which the ascending and descending elements were marginally spinose e.g. Glossothyropsis type.

The characters, dental plates, cardinal plate (supported by median septum or unsupported) primitively centronelliform and spinose cryptonelliform loop are to be found in cryptacanthiinin centronellidines, allowing a Gacina-Glossothyropsis type trend. Spinose cryptonelliform loops, dental plates and a supported or unsupported cardinal plate are however, also found in cryptonellacean genera such as Heterelasma.

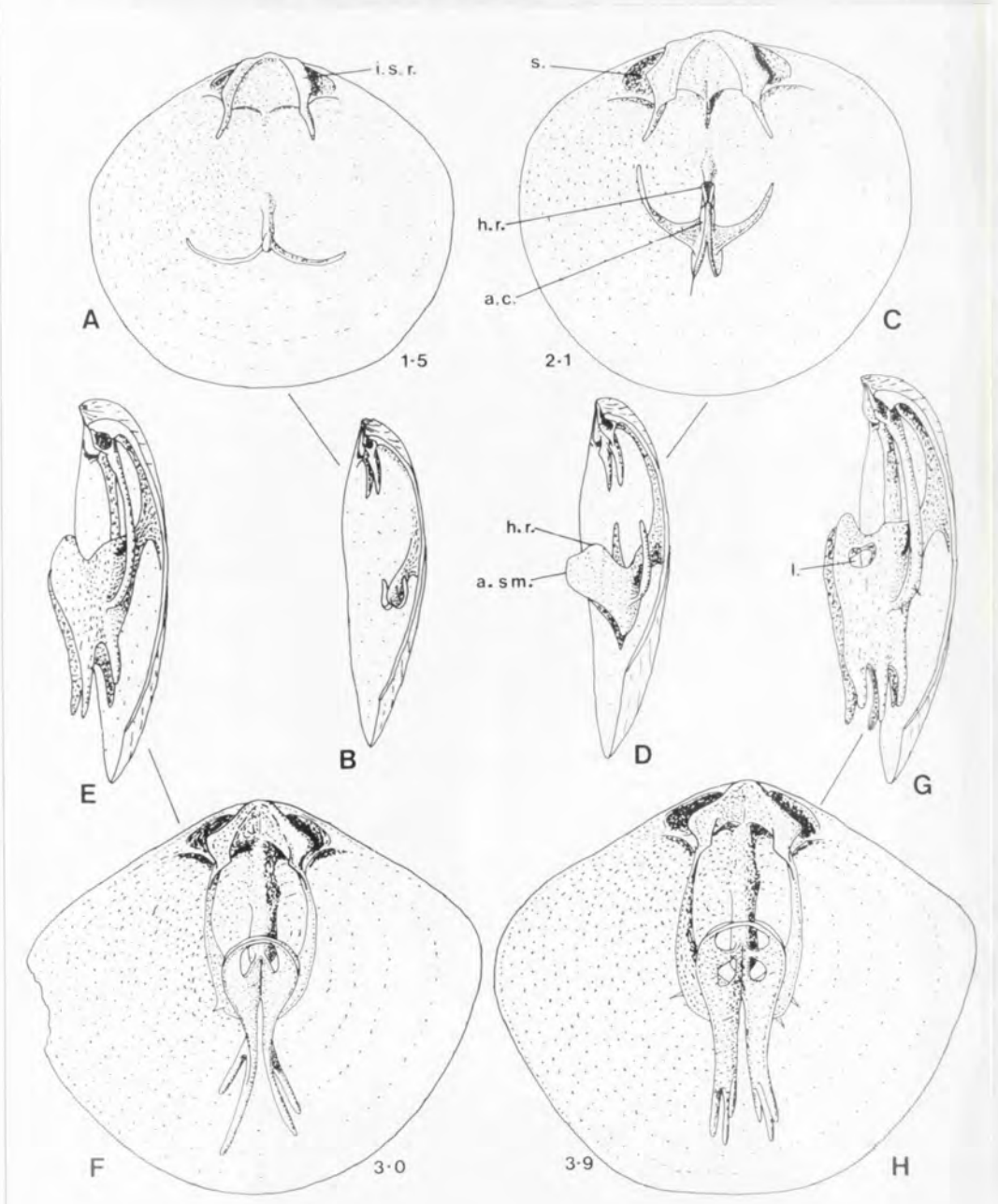
Unfortunately information on the early ontogeny of cryptonelliform loops is not at present available and passage through a modified centronelliform phase of development cannot be demonstrated.

The zeilleriid median septum sensu latu, being a subsequent development need not be regarded as a critical factor when considering ancestry and appears to be antedated by the cardinal plate. The one basic problem remaining therefore, whether the zeilleriid loop be derived from centronellidine or cryptonellid stock, is the appearance and resorption of the septal pillar. A great deal more work is necessary but having brought the importance of the median septum into perspective, initial studies indicate that the origin of the Zeilleriidae may be found in cryptacanthiinin stock of Glossothyropsis type and that zeilleriid and cryptonellid loops may have arisen independently. The cryptonellacean loop has a degree of symmetry which suggests that it may itself be the end product of an evolutionary trend. Probably the most important single contribution made by this paper is the demonstration that in attempting to trace the origin of the Zeilleriidae the presence of spinose ascending and descending elements is likely to be of more significance than the absence of a median septum.

EXPLANATION OF TEXT-FIG 1A - H

Reconstructions of early juvenile brachial valves of Zeilleria leckenbyi (Davidson). Sequence of interior and lateral views to show the morphology of the developing loop and its prominence relative to the plane of the commissure. The figures are based essentially, on data obtained from stereoscanned cellulose acetate peels but the evidence was reinforced by polished sections and separated valves. A, B. Preparamagadiniform phase (37589/7). A. Brachial view, crural plates sloping down to unite with valve floor. B. Lateral view showing the relatively low pillar with an anterior inclination. C, D. Paramagadiniform phase (37589/3). C. Brachial view showing the form of the ascending complex. Median septum still not properly developed but the anteriors of the crural plates are separating from the valve floor and beginning to form a septalium. D. Lateral view showing the increased development of the descending elements and the ascending complex much higher relative to the commissural plane. E, F. Syncampagiform phase (37570/1). Lateral and brachial views showing the well developed ascending lamellae, anterior spurs and transverse bar. Descending branches now united with the sides of the ascending lamellae. Septalium formed and septal pillar enlarged. G, H. Frenuliform phase (37580). Lateral and brachial views showing the location of the lacunae. a.c. ascending complex, a.sm. ascending septum, h.r. hood rudiment, i.s.r. inner socket ridge, l. lacuna, s. dental socket. Numbers refer to the length of the shell in mm. from which the peels were obtained.

TEXT-FIG. 1

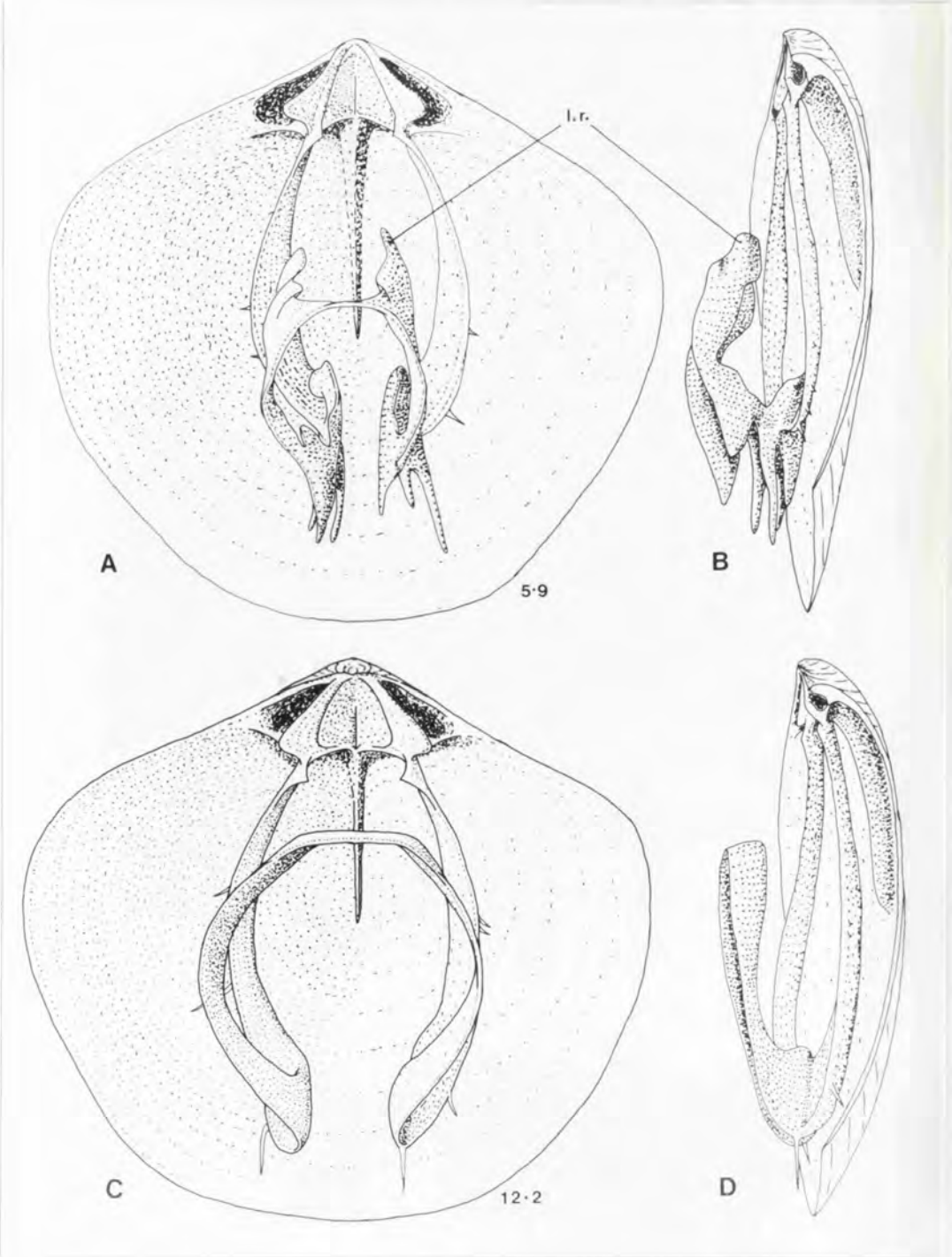


EXPLANATION OF TEXT-FIG. 2A - D

Reconstructions of juvenile brachial valves of Z. leckenbyi. The figures are based essentially on data obtained from stereoscanned cellulose acetate peels but the evidence was reinforced by polished sections and separated valves.

A, B. Brachial and lateral views of a late terebrataliiform shell (37582). All connections with the septal pillar have been resorbed. The descending branches are relatively massive and the ascending branches and transverse bar are differentiated. The ascending lamellae are now only represented by unresorbed lamella remnants, l.r. The loop rises very high above the commissural plane, almost touching the floor of the pedicle valve. The septalium is fully developed and the median septum is formed by the rapid extension of the septalial plates to envelop and extend beyond the remains of the septal pillar. C, D. Brachial and lateral views of a typically dalliniform early adult loop (37664). The descending branches, ascending branches and transverse bar are of relatively massive proportion. The anterior spurs have by now been eliminated by resorption. The anterior extension of the median septum is relatively slower and the lateral profile of the loop is becoming flatter. Numbers indicate the length in mm. of the shell from which the peels were obtained.

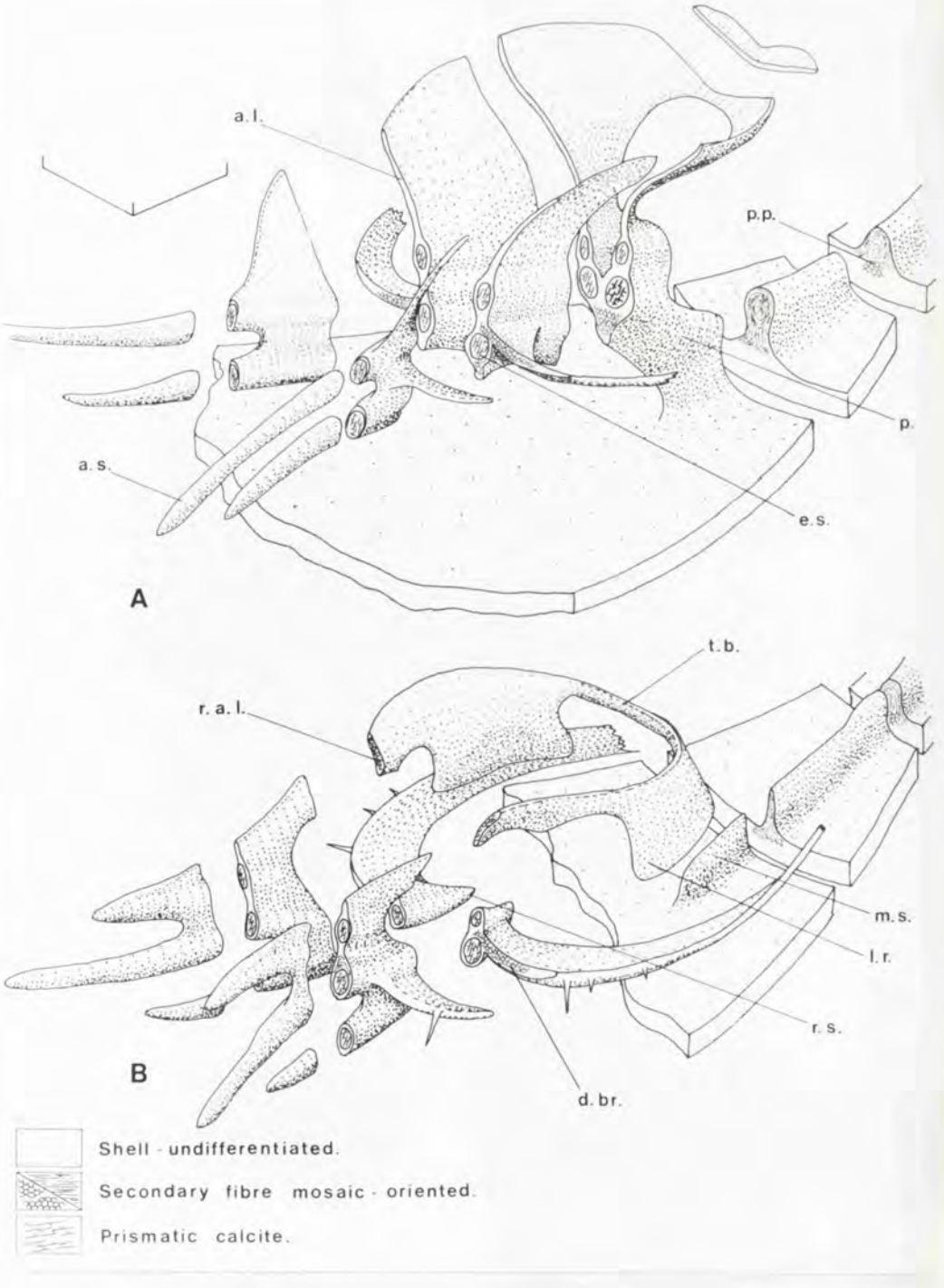
TEXT-FIG. 2



EXPLANATION OF TEXT-FIG. 3

Serial block reconstructions to show the microstructure of the loop of Z. leckenbyi as it appears in transverse section during the syncampagiform, A, and terebrataliiform, B, phases of development. For the purposes of clarity only the distal portions of the descending branches are included. a.l. ascending lamella, a.s. anterior spur, d.br. descending branch, e.s. enveloped spur, l.r. lamella remnant, m.s. median septum, p. septal pillar, p.p. pillar precursor, r.a.l. resorbed ascending lamella, r.s. resorbed spur, t.b. transverse bar. Scale represents 0.2 mm.

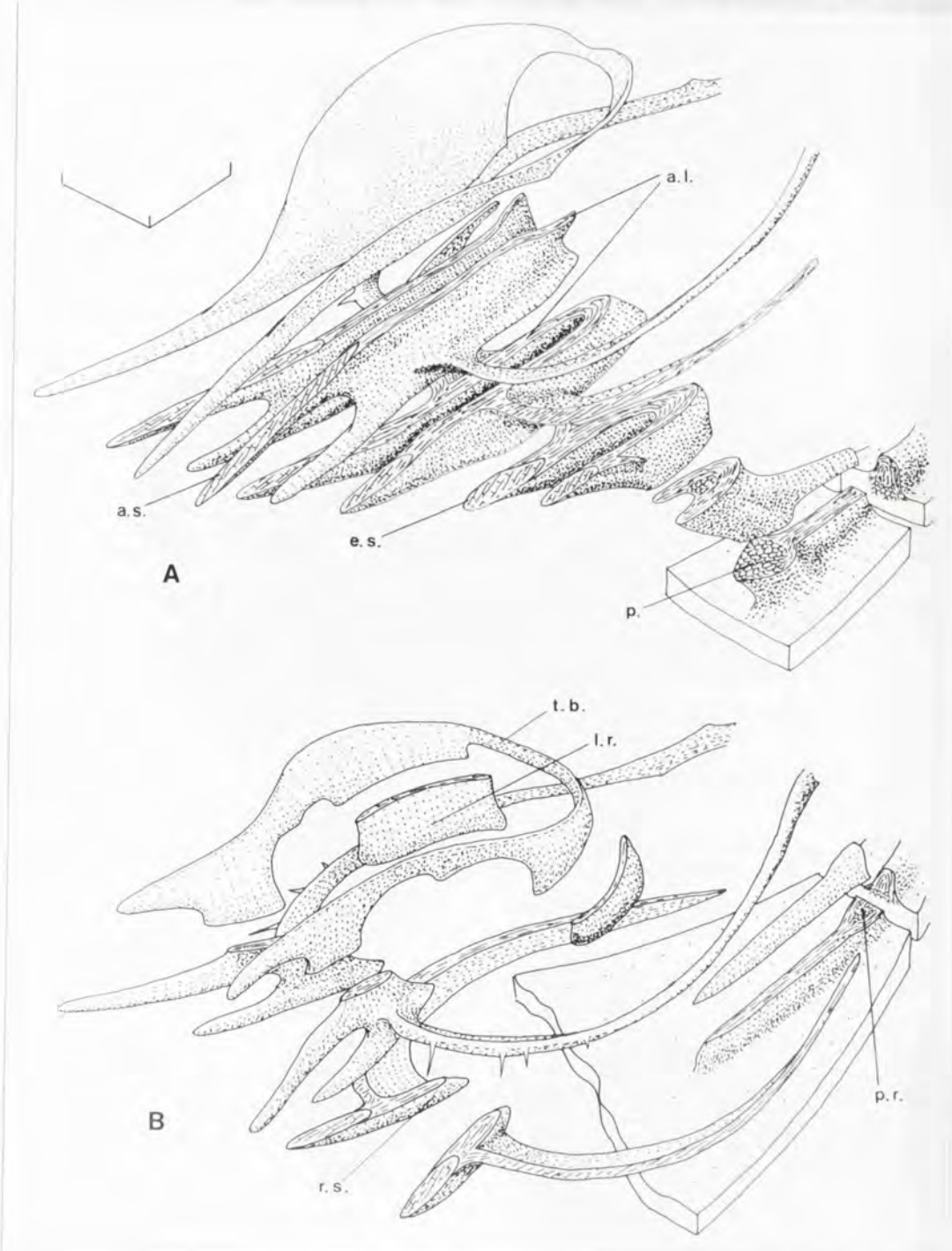
TEXT-FIG. 3


a.l.
p.p.
p.
a.s.
e.s.
A
t.b.
r.a.l.
m.s.
l.r.
r.s.
B
d.br.
Shell - undifferentiated.
Secondary fibre mosaic - oriented.
Prismatic calcite.

EXPLANATION OF TEXT-FIG. 4

Serial block reconstructions to show the microstructure of the loop of Z. leckenbyi as it appears in horizontal section during the syncampagiform, A, and terebrataliiform, B, phases of development. Lettering as in FIG. 3 except p.r. pillar remnant. Scale represents 0.2 mm.

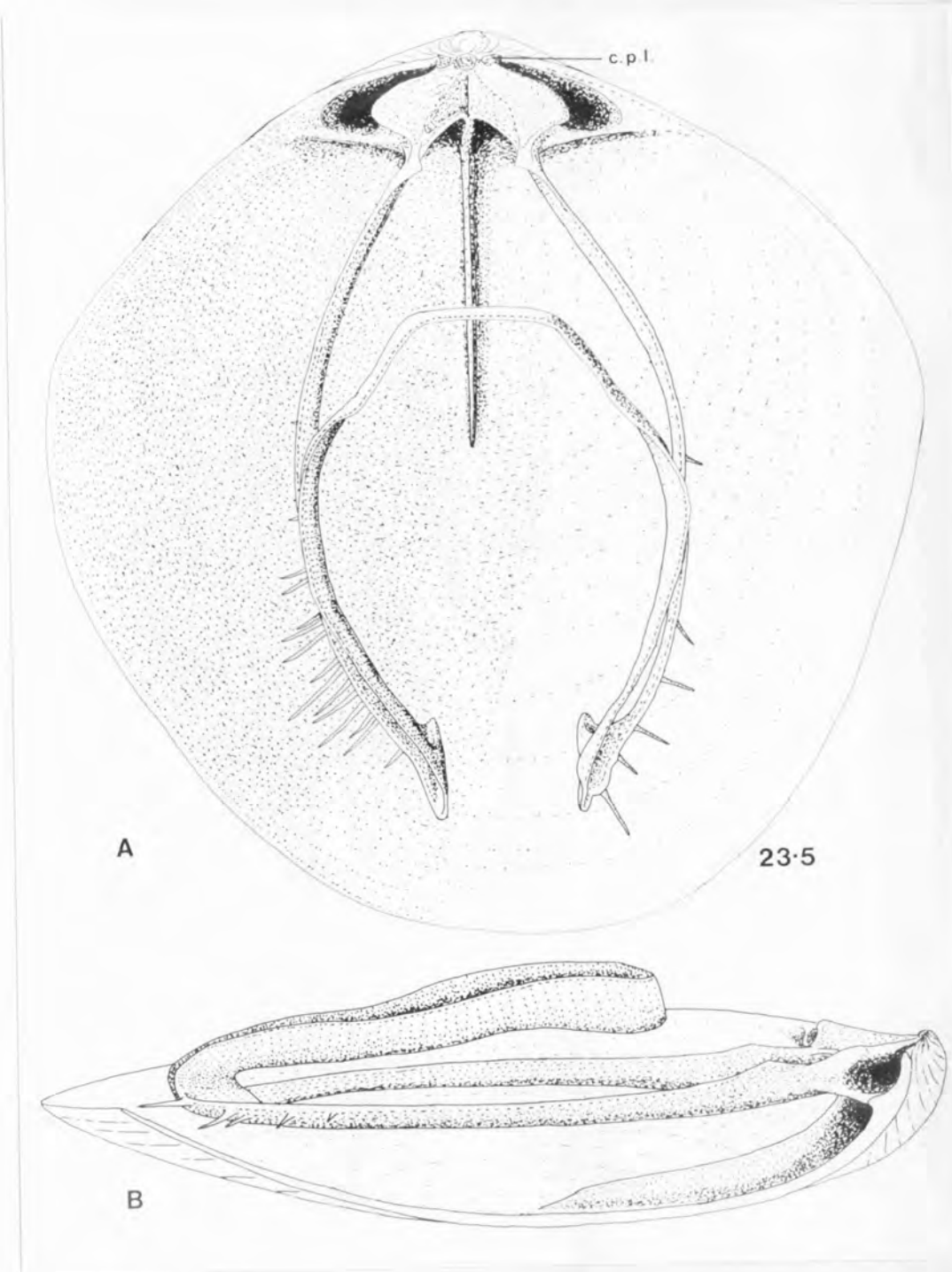
TEXT-FIG. 4



EXPLANATION OF TEXT-FIG. 5 A, B

Brachial and lateral reconstructions of the adult (zeilleriiform) loop of Z. leckenbyi (37661). Loop long, with spinose descending branches. It may be distinguished from the dalliniform type by its more slender descending branches and ribbon-like ascending branches and transverse bar. c.p.l. cardinal process lobe. Number refers to the length in mm. of the shell from which peels were obtained.

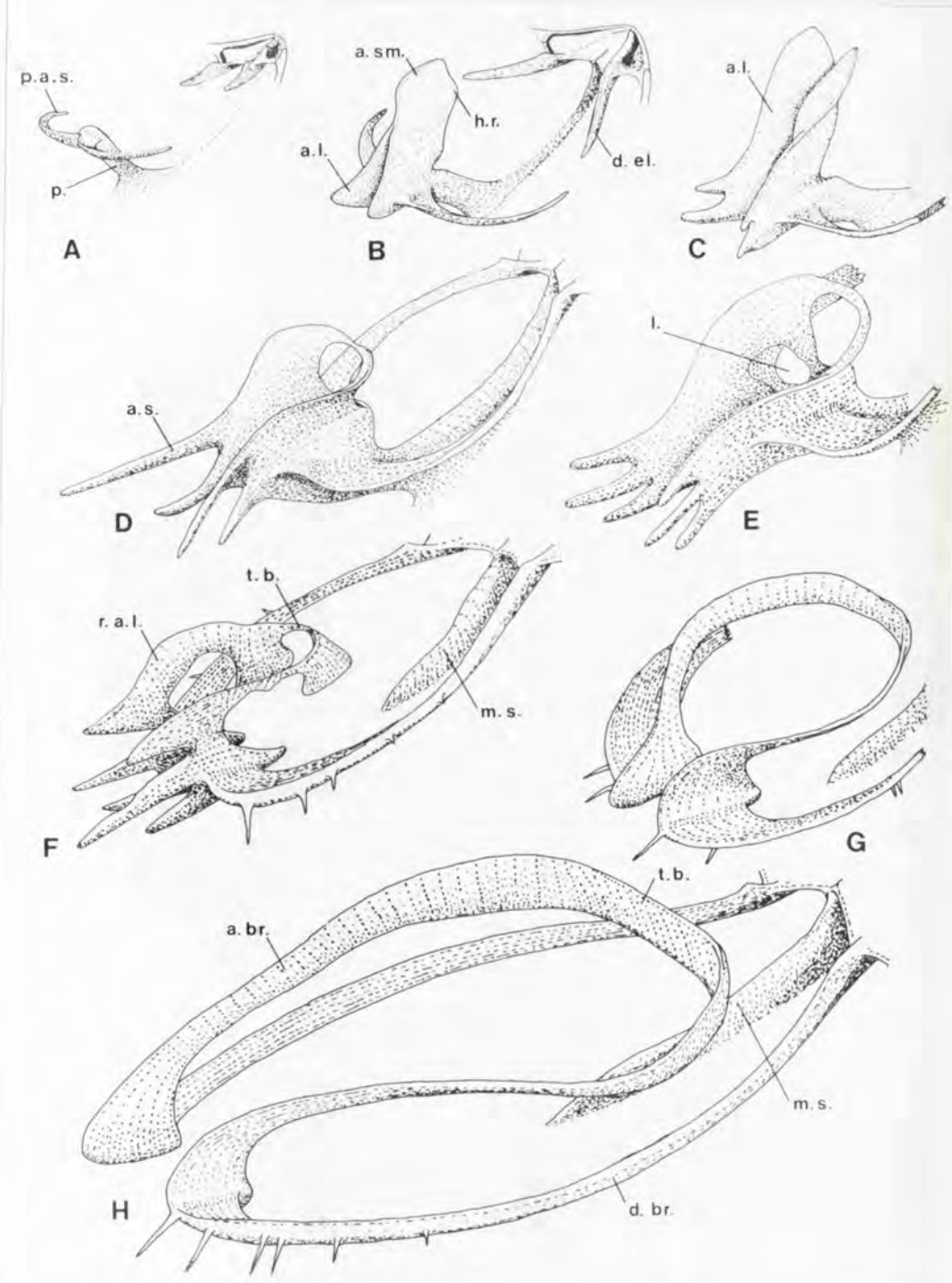
TEXT-FIG. 5



EXPLANATION OF TEXT-FIG. 6

Series of threequarters profile reconstructions (not to scale) of the loop of Z. leckenbyi showing the various elements in the complete development sequence. A. Preparamagadiniform. B, C. Early and late magadiniform. D. syncampagiform. E. Frenuliform. F. Terebrataliiform. G. Dalliniform. H. Zeilleriiform. Figs. C, E, G show only the distal portions of the descending branches. a. br. ascending branch, a.l. ascending lamella, a.s. anterior spur, a. sm. ascending septum, d.br. descending branch, d.el. descending element, h.r. hood rudiment, l. lacuna, m.s. median septum, p. septal pillar, p.a.s. posteriorly arching spur, r.a.l. resorbed ascending lamella, t.b. transverse bar.

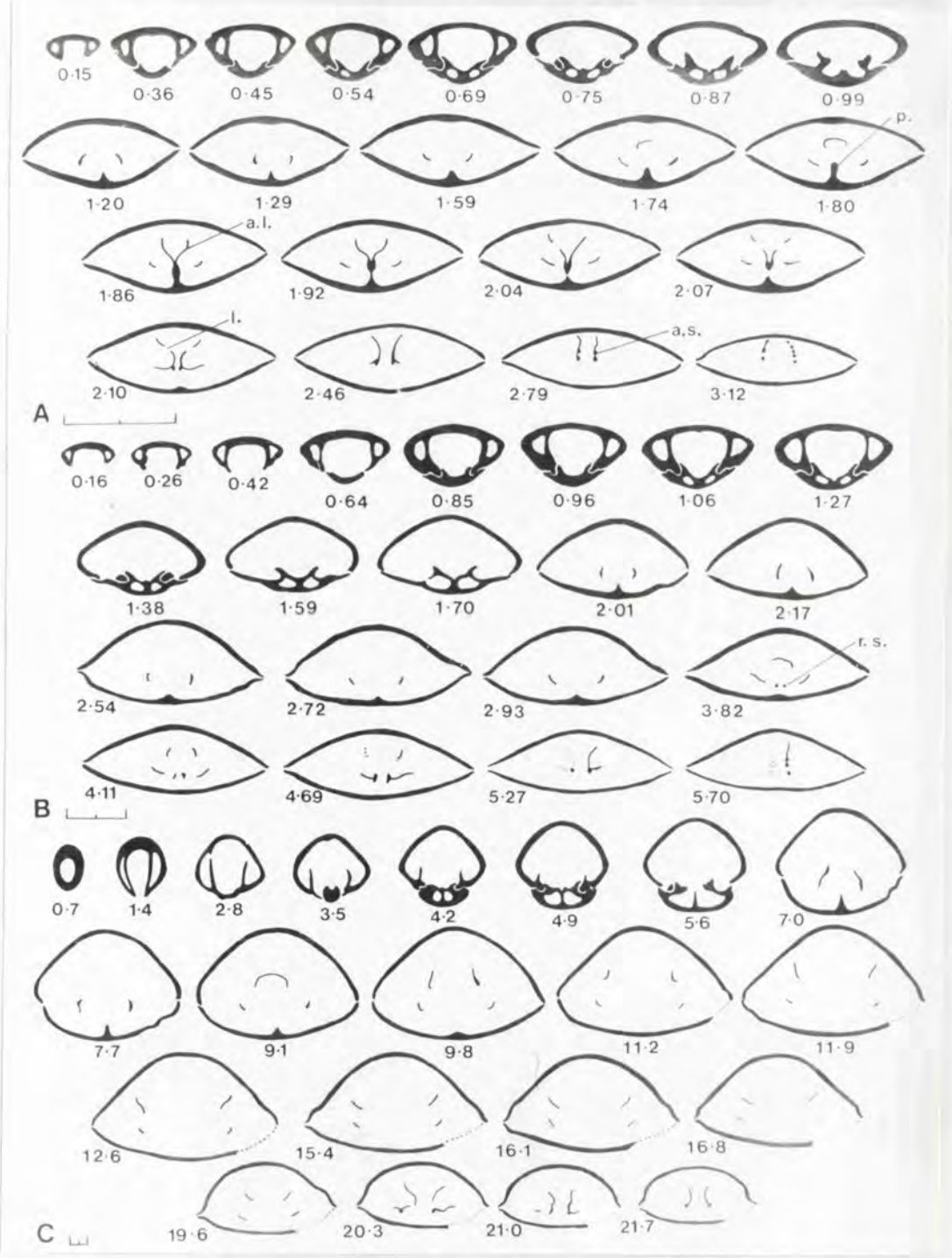
TEXT-FIG. 6



EXPLANATION OF TEXT-FIG. 7A - C

Series of serial transverse sections through specimens of Z. leckenbyi, drawn from microprojected cellulose acetate peels, showing features of the species during different phases of development. A. Frenuliform specimen (37580). B. Terebrataliiform specimen (37583). C. Adult specimen (37666). Numbers refer to the distance of the sections from the beak. Lettering as Fig. 3, 6. Scale represents 2.0 mm.

TEXT-FIG. 7


0·15
0·36
0·45
0·54
0·69
0·75
0·87
0·99
p.
1·20
1·29
1·59
1·74
1·80
a.l.
1·86
1·92
2·04
2·07
l.
2·10
2·46
a.s.
2·79
3·12
A
0·16
0·26
0·42
0·64
0·85
0·96
1·06
1·27
1·38
1·59
1·70
2·01
2·17
r. s.
2·54
2·72
2·93
3·82
4·11
4·69
5·27
5·70
B
0·7
1·4
2·8
3·5
4·2
4·9
5·6
7·0
7·7
9·1
9·8
11·2
11·9
12·6
15·4
16·1
16·8
19·6
20·3
21·0
21·7
C

EXPLANATION OF TABLE 1

Tabulation of the structures present in 28 specimens of *Z. leckenbyi* out of a sample of 30 shells anticipated to belong to that species. Of the remaining two shells, one, 1.0 mm. long showed no dental plates, the other, 9.0 mm. long and having a damaged beak, proved to be a short looped form.

TABLE 1

Table I.

Specimen	Dimensions mm.			Orientation	Internal characters present																Developmnt. phase represented
									Asc. elements							Desc. elts.					
	L.	W.	Th.		Dental plates	Crural plates	Septalium	Median septum	Septal pillar	Postr. arching spurs	Asc. lamellae	Anterior spurs	Connection with median septum	Lacunae	Asc. branches with spur remnants	Desc. branches	Asc. and desc. elements united	Spinose	Loop of adult form	
37628/23	0·8	0·7	0·28	H.S.	+																Pre paramagad-iniform
37629/29	0·9	0·8	0·3	H.S.	+																
37630/19	1·2	1·0	0·35	H.S.	+																
37629/9	1·2	1·1	0·4	H.S.	+	+															
37629/4	1·3	1·3	0·4	H.S.	+	+			+												
37629/10	1·3	1·1	0·4	H.S.	+	+															
37629	1·3	1·1	0·4	H.S.	+	+			+												
37589/7	1·5	1·5	0·5	H.S.	+	+			+	+						+					
37630/28	1·7	1·6	0·6	H.S.	+	+		+	+	+	+					+					
37589/3	2·1	2·1	0·7	H.S.	+	+	+	+	+	+	+	+				+					Paramagad-iniform
37556	2·5	2·4	1·1	T.S.	+	+	+	+	+		+	+	+			+					
37570/1	3·0	3·0	1·2	H.S.	+	+	+	+	+		+	+	+				+	+			Syncampag-iform
37580	3·9	3·4	1·4	T.S.	+	+	+	+	+		+	+	+	+			+	?			Frenuliform
37581	5·0	5·0	1·7	T.S.	+	+	+	+			+	+			+		+	+			Terebratal-iiform
37617	5·4	5·2	1·8	H.S.	+	+	+	+			+				+			?	+		
37582	5·9	5·4	2·4	H.S.	+	+	+	+			+				+			+	+		
37583	6·5	6·0	2·5	T.S.	+	+	+	+			+				+			+	+		
37622	7·2	7·0	3·0	H.S.	+	+	+	+			+				+			+	+		
37663	10·5	10·4	4·1	H.S.	+	+	+	+										?	+		Dalliniform
37664	12·2	12·5	5·5	H.S.	+	+	+	+										+	+		
37665	14·5	14·5	7·3	T.S.	+	+	+	+										+	+		
37667	17·2	18·5	7·5	T.S.	+	+	+	+										+	+		
37660	17·5	16·7	8·2	H.S.	+	+	+	+										+	+		
37657	19·0	18·0	8·0	T.S.	+	+	+	+										+	+		
37658	19·0	19·0	9·0	H.S.	+	+	+	+										+	+		
37659	21·0	20·0	9·0	H.S.	+	+	+	+										+	+		Zeilleriiform
37661	23·5	20·0	11·0	H.S.	+	+	+	+										+	+		
37666	25·6	22·0	13·0	T.S.	+	+	+	+										+	+		

EXPLANATION OF PLATE A

Stereoscan photomicrographs, except figs. 10 - 12, of various specimens of Z. leckenbyi (Davidson) from the Oolite Marl, Westington Hill Quarry near Chipping Campden, showing the general morphology during ontogeny. Figures are of specimens coated with evaporated aluminium before photography.

Fig. 1 - 3. Brachial, anterior and lateral views of a preparamagadiniform juvenile (37629). Note the rounded appearance of the brachial valve and the beginning of apical resorption of the delthyrium during this phase of development. X 35.

Fig. 4 - 6. Lateral, brachial and anterior views of a syncampagiform juvenile (37530). Apical resorption is now advanced and a low anterior sulcus is present. X 15.

Fig. 7 - 9. Anterior, brachial and lateral views of a terebrataliiform juvenile (37581). Brachial valve now becoming more elliptical. X 8.

Fig. 10 - 12. Brachial, lateral and anterior views of an adult (37668) for comparison purposes. X 1.

Fig. 13. Interior of a brachial valve (37671) during the preparamagadiniform phase of development, showing the septal pillar rudiment in the floor of the valve prior to the formation of the median septum. X318.

Fig. 14. Threequarters profile view of specimen (37671) showing the septal pillar rudiment and crural plate (arrowed) descending to the valve floor. X 50.

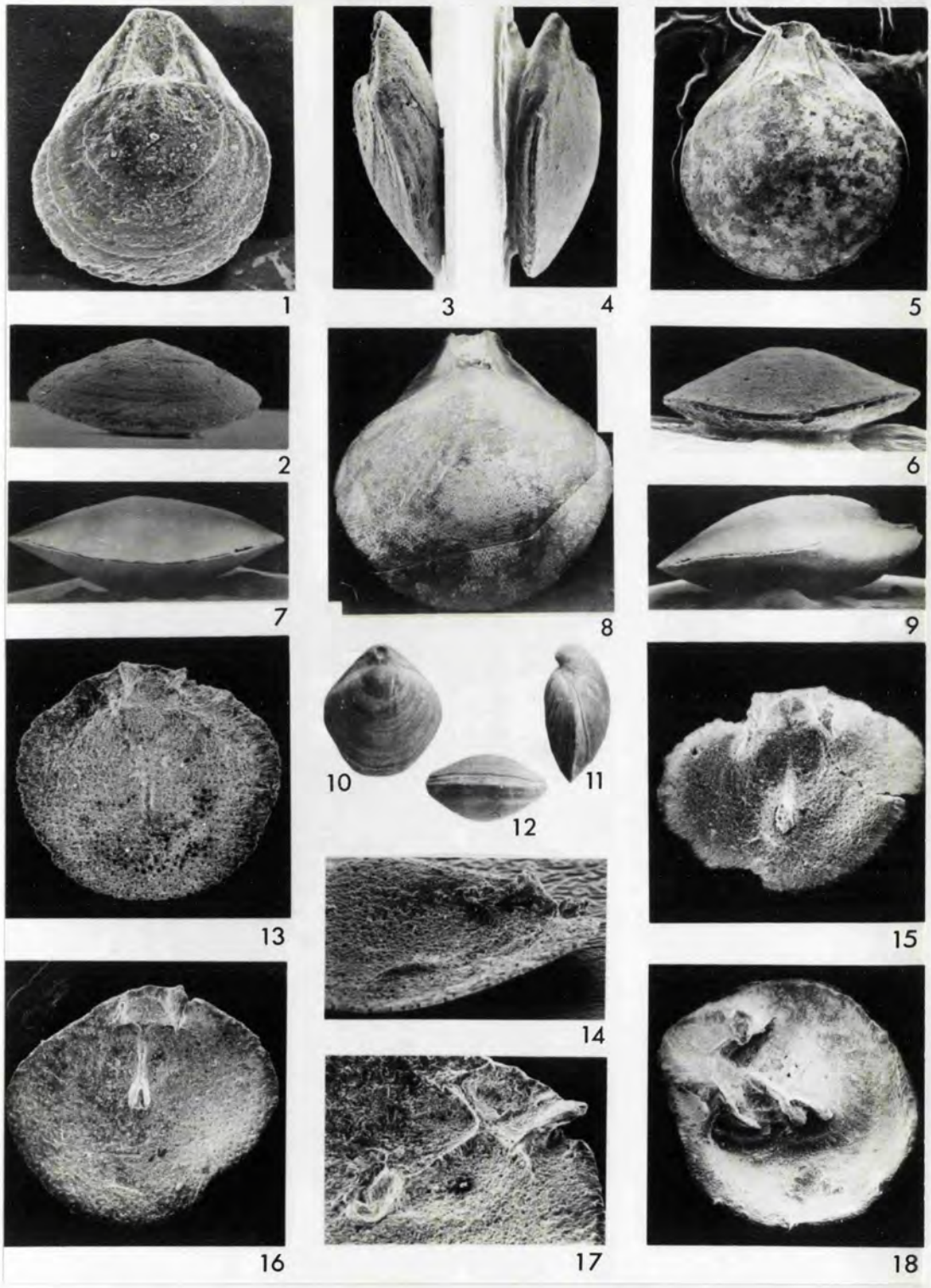
Fig. 15. Interior of a brachial valve (37672) showing the septal pillar rising from the valve floor. The crural plates are more well developed but still united with the valve floor. X 20.

Fig. 16. Interior of a brachial valve (37669) showing the median septum and septal pillar with divergent ascending lamellae. X 18.

Fig. 17. Threequarters profile view of specimen (37669) showing the crural plates now raised above the floor of the valve and forming a shallow septalium. X 45.

Fig. 18. High incidence profile view of specimen (37584) showing the ascending lamellae. The loop of this specimen is clearly damaged and was probably syncampagiform or frenuliform. X 12.

PLATE A



EXPLANATION OF PLATE B

Stereoscan photomicrographs of specimens of Z. leckenbyi. Material for all figures except figs. 2, 3 obtained from cellulose acetate peels coated with evaporated aluminium before photography.

Fig. 1. Montage of a horizontal section through a syncampagiform ascending lamella (37570/1, 12) showing the anterior spur, a.s., ensheathed in secondary fibres posteriorly and "locating" the fibres of the descending element (arrowed) X. 500.

Fig. 2. Photomicrograph, reflected light, of a horizontal section through a polished specimen (37589/3 showing the posteriorly arching spurs arising from the septal pillar. X. 40.

Fig. 3. Retouched copy of fig. 2.

Fig. 4. Transverse section through an anterior spur of a frenuliform specimen (37580/102) showing the prismatic calcite core. X. 525.

Fig. 5. Micrograph of a peel obtained from the etched surface of specimen (37589/3) fig. 2. above, enlarged to show detail of the junction of the posteriorly arching spurs with the septal pillar. X. 180.

Fig. 6. Horizontal section through a paramagadiniform specimen (37589/11) showing the ascending septum and divergent ascending lamellae arising from its anterior edge. X. 70.

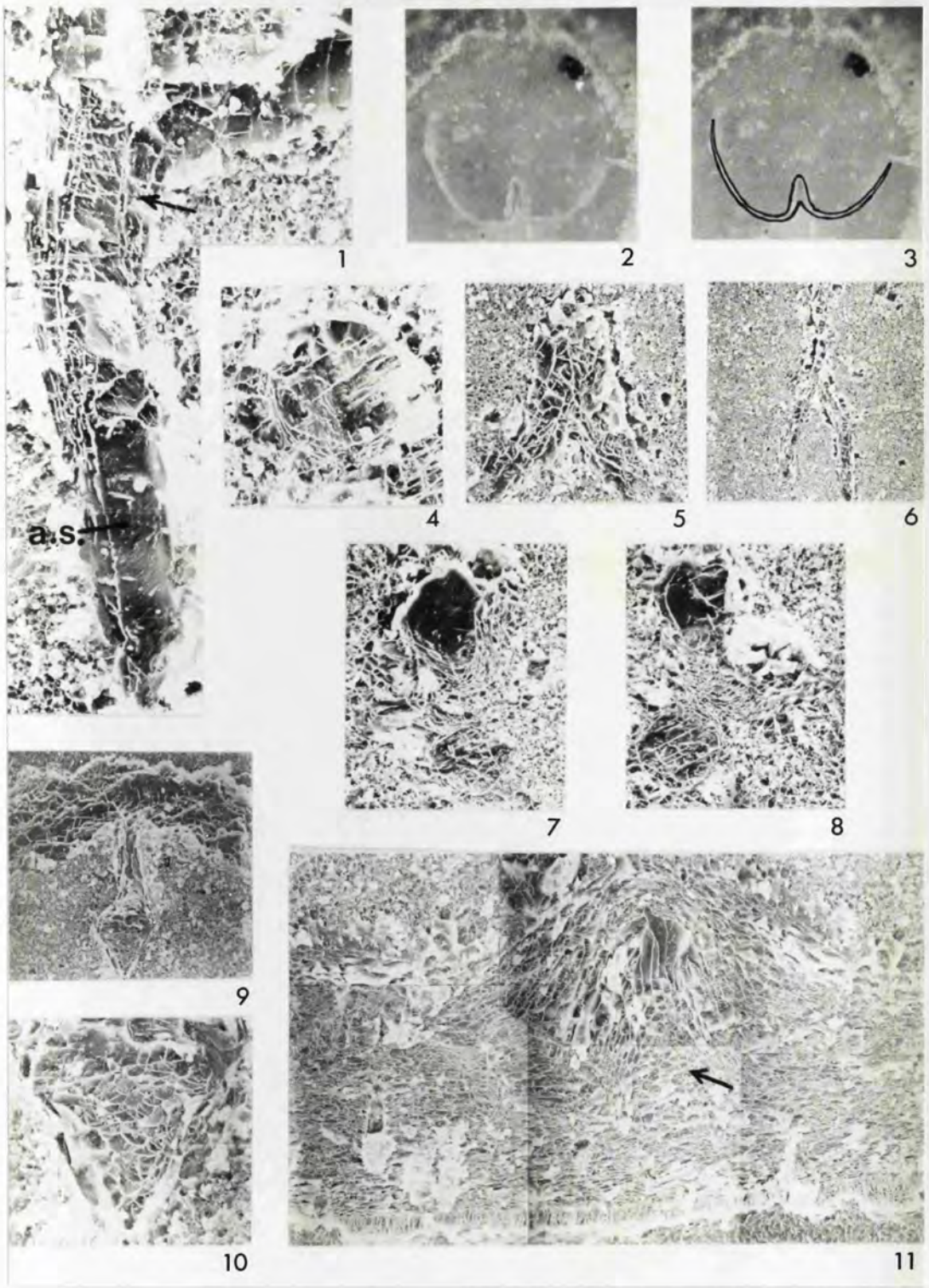
Fig. 7, 8. Transverse sections through the anterior spurs of the left, fig. 7 and right, fig. 8, ascending lamellae of specimen (37580) showing the enveloped prismatic cores and their controlling influence of the location of the descending branches, fig. 8, centre. X. 200. The actual separation between the left and right lamellae at this magnification would be approximately 65 mm.

Fig. 9. Horizontal section through a syncampagiform specimen (37570/1, 7) showing the septal pillar in near transverse section with the change in the orientation of the secondary fibres anteriorly. X. 100.

Fig. 10. Enlarged view of the anterior portion of the septal pillar shown in fig. 9, to show detail of the fibre mosaic. X. 275.

Fig. 11. Montage of a transverse section through a frenuliform specimen (37580/48) showing the septal pillar precursor fibre bundle (arrowed) overlain by secondary fibres as a result of the anterior extension of the median septum. X. 300.

PLATE B



EXPLANATION OF PLATE C

Stereoscan photomicrographs of specimens of Z. leckenbyi. Material of all figures coated with evaporated aluminium before photography.

Fig. 1 - 12. Cellulose acetate peels of selected horizontal serial sections through a juvenile (37570/1) showing the various elements of the syncampagiform loop. Peel interval 20 μ .

Fig. 1. Ascending lamellae and connection with the dorsal edge of the descending branches. Peel 10, X. 40.

Fig. 2. Enlarged view of the ascending complex shown in fig. 1. X. 120.

Fig. 3, 4. Ascending lamellae with the anterior spurs beginning to develop. Peel 11, original and re-touched copy, X. 110.

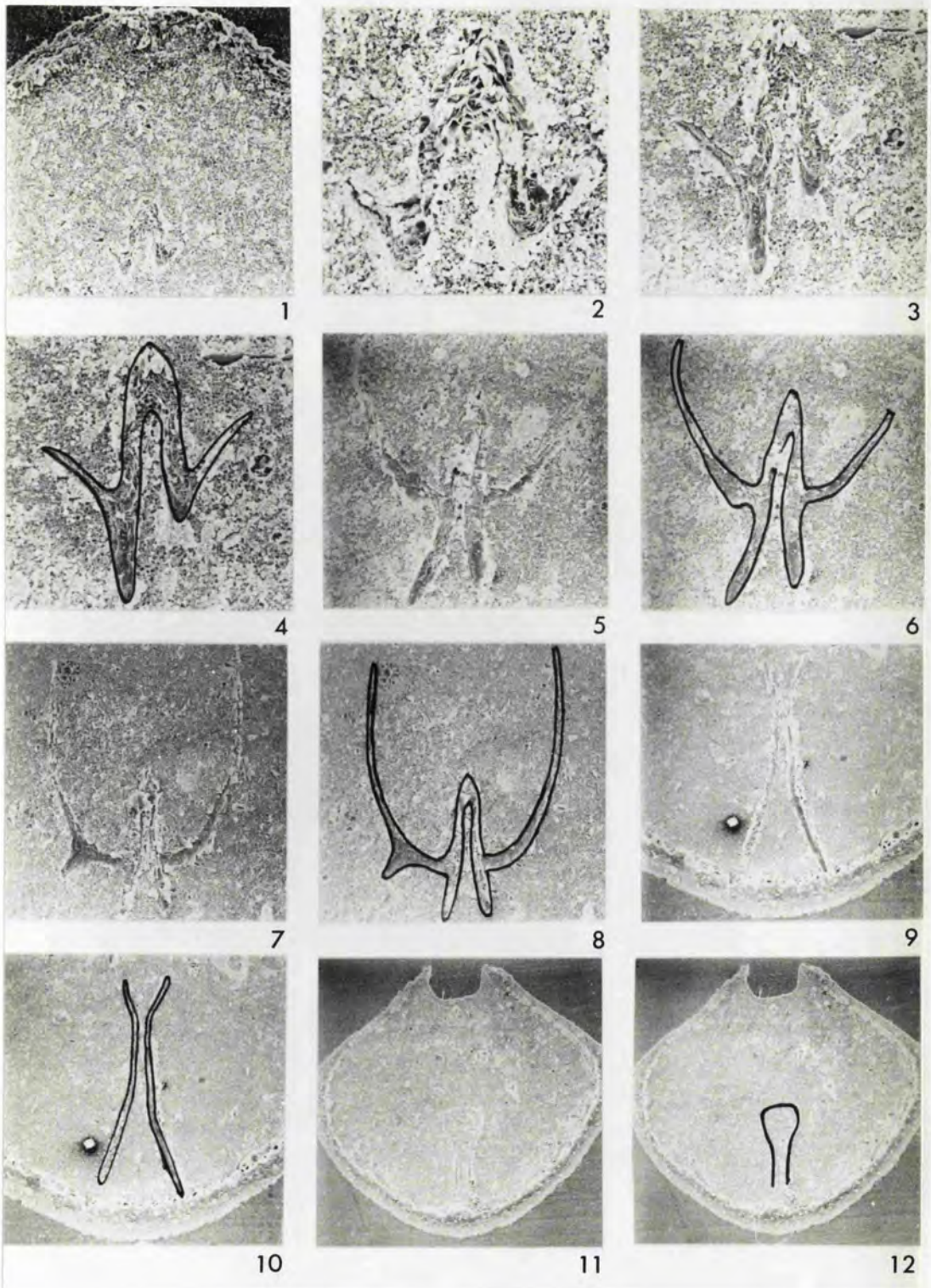
Fig. 5, 6. Ascending lamellae with the lower anterior spurs and descending branches. Peel 12, original and re-touched copy, X. 70.

Fig. 7, 8. Descending branches (left one with spine) beginning to extend along the spurs. Peel 14, original and re-touched copy, X. 50.

Fig. 9, 10. Ascending lamellae separated, with the upper anterior spurs almost reaching the anterior margin of the shell. Peel 25, original and re-touched copy, X. 36.

Fig. 11, 12. Ascending lamellae united posteriorly to form the transverse bar. Peel 32, original and re-touched copy, X. 20.

PLATE C



EXPLANATION OF PLATE D

Stereoscan photomicrographs of Z. leckenbyi. Material for all figures obtained from cellulose acetate peels coated with evaporated aluminium before photography.

Fig. 1. Horizontal section through the median septum of an early terebrataliiform specimen (37617/7). X. 45.

Fig. 2. Montage of an enlarged portion of the proximal end of the septum shown in fig. 1, to show the pillar remnant enveloped by the development of the septum. X. 260.

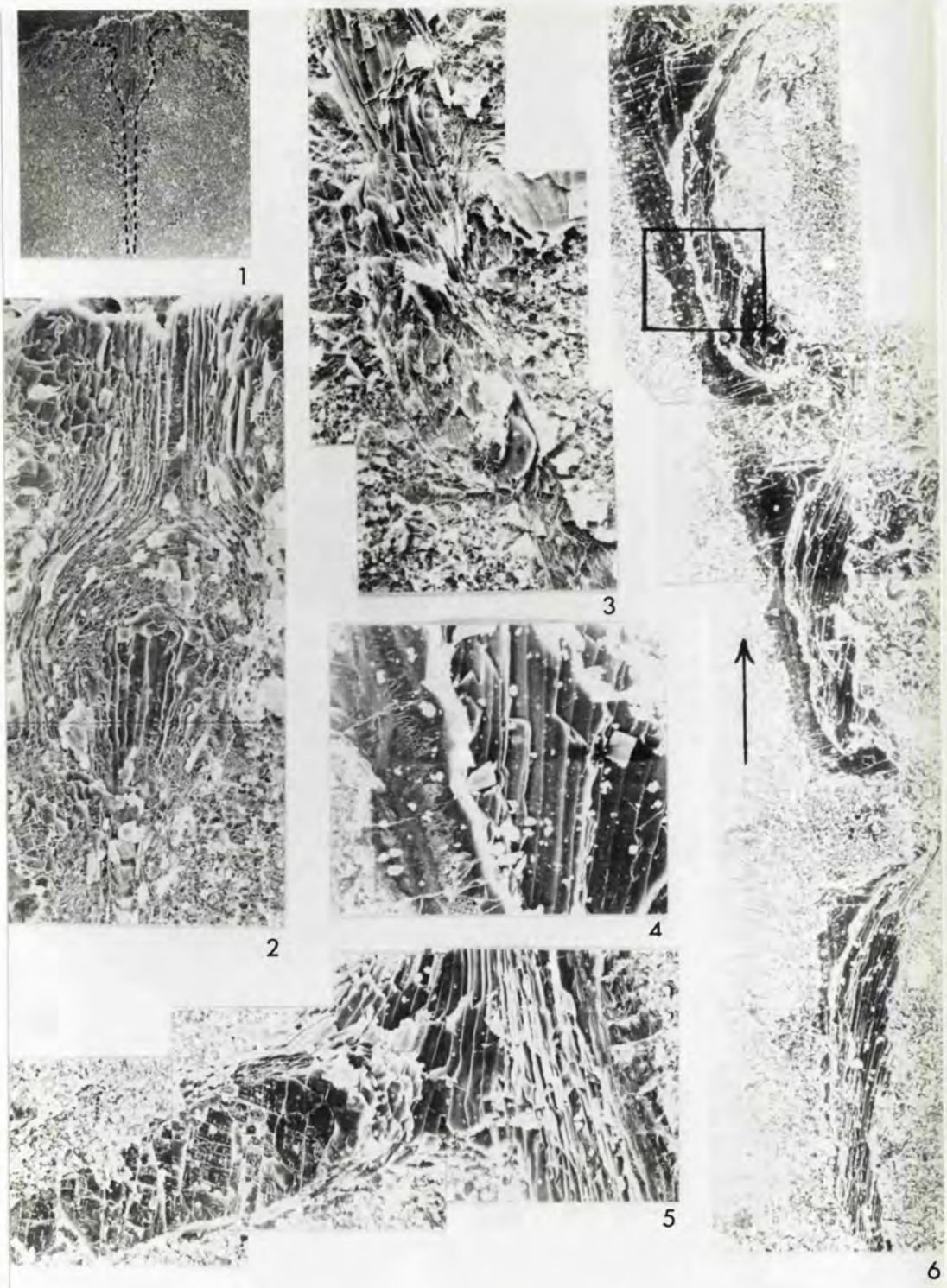
Fig. 3. Montage of the point of union between the ascending and descending elements, upper right, of a late terebrataliiform specimen (37582/25) showing the remnant of the anterior spur, lower centre. Horizontal section. X. 275.

Fig. 4. Enlarged portion of fig. 6. showing the detail of the prismatic inner, left, and fibrous outer, right, double ribbon of the descending braches of the loop. X. 265.

Fig. 5. Montage of a horizontal section through a portion of a descending branch of an adult loop (37661/13) showing the prismatic core of a spine sectioned obliquely. X. 260.

Fig. 6. Montage of a horizontal section through a portion of the distal end of a descending branch of an adult loop (37661/11) showing the prismatic inner ribbon repeatedly deflecting the outer fibrous ribbon to form cored spines. Arrow indicates anterior of loop. X. 105.

PLATE D



Appendix Section 4 - Zeilleria leckenbyi

Publication of Owen's (1970) Revision of the brachiopod sub-family Kingeninae Elliott, reveals a close resemblance between frenuliform and terebrataliiform juveniles of Z. leckenbyi and kingenids such as K. concinna, M. Cenomanian and K. lima, U. Chalk.

SUMMARY OF CONCLUSIONS

Convergent homoeomorphy with its attendant problems of morphological similarity is quite common and apparently repetetive e.g. Cooperina (Permian productoid) and Moorellina also Thecospira (Triassic spiriferide) and Moorellina.

The very close resemblance between the median and lateral ridges of Cooperina and the median septum and peripheral rim of Moorellina, even to the presence of node/tubercle ornament (Compare Cooper and Grant 1969, Pl. 3, fig. 26 with Appendix Pl. 2 fig. 1.) demonstrates how intense environmental pressure may be in the 'selection' of favourable mutations. It appears that the ecological niche vacated by Cooperina became occupied by the thecideidines which were subsequently 'moulded' to the form ideal for that particular niche and therefore inevitably would become facsimiles of the previous occupants. A situation of this type might lead to systematic groupings contrary to those envisaged by Cowen and Rudwick (1967). Westbroek (1967) and Sass and Munroe (1967) have shown how fibre orientation may change rapidly at different levels within the shell. Gauri and Boucot (1968, 1970) have demonstrated differences in the microstructure of the brachial and pedicle valves in pentamerids and the spiriferide Cryptothyrella. The important differences in the microstructure of the brachial and pedicle valves of M. granulosa indicate that taxonomic inferences may be misleading unless a fairly extensive knowledge of the microstructure of the whole shell of a species is available.

Rousselle(1967) has published a comprehensive study of intraspecific variation in Goniothyris buckmaniana. (Walker-Davidson). In Moorellina the importance of the size and shape of the scar of attachment in determination of the form of the ventral interarea has been adequately demonstrated. Bassett(1970) cites examples of environmentally induced

intraspecific variation in the orthacean Ptychopleurella. However, the forms in which no cardinal process was apparently developed may be the result of a genetic deficiency similar to that which is thought to be responsible for the non-development of deltidial plates in some specimens of Nannirhynchia longirostra. Occasional deficiency in shell resorption or secretion mechanisms is clearly shown by some juvenile terebratulides (Appendix Pl. 2, fig. 2 - 4, Pl. 3, fig. 1, 2) although it seems doubtful that such abnormalities lived for any length of time.

These observations together with Rudwick's (1971) publication and Williams' electron microscope studies really reinforce the argument that analysis of structure in terms of functional morphology must play an important part in determining the systematic position of convergent homoeomorphs. Also, it has become quite clear from the investigation of the juvenile zeilleriids, that analysis of the component microstructures of various morphological features may provide important data with regard to the phylogeny of the group.

Finally, the relative abundance of micromorphic and early juvenile brachiopods in the Oolite Marl indicates that they are more common than is generally realised but owing to their small size, remain largely overlooked.

APPENDICES

Appendix List 1.	Faunal List - Brachiopoda.	p 152
Appendix Table 1.	Population Analysis - Characters.	p 154
" Table 2.	Summary of analysed characters.	p 155
Appendix Fig. 1.	Geological Map - Westington Hill Quarry.	p 156
" Fig. 2.	Stratigraphical succession - Westington Hill Quarry	p 157
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Proposed future investigations.		p 165

APPENDIX LIST 1

Brachiopoda from the Oolite Marl.

Westington Hill Quarry (SP 142368)

Epithyris submaxillata (Morris)

Flabellirhynchia lycettii (Davidson)

Globirhynchia subobsoleta (Davidson)

Moorellina granulosa (Moore)

Moorellina c.f. ornata (Moore)

Moorellina sp. nov.

Nannirhynchia longirostra sp. nov.

Plectothyris fimbria (Sowerby)

"Terebratula" whitakeri Davidson ex Walker Ms

Zeilleria leckenbyi (Davidson ex Walker Ms)

Zellania davidsoni Moore

Catsbrain Quarry, Painswick (SO 869117)

Plectothyris fimbria

Globirhynchia subobsoleta

Cleeve Cloud, Cheltenham (SO 984261)

Epithyris submaxillata

Flabellirhynchia lycettii

Globirhynchia subobsoleta

Granulirhynchia granulata (Upton)

Moorellina granulosa

Plectothyris fimbria

Plectothyris sp. nov.?

Plectoidothyris polyplecta Buckman

Pseudoglossothyris leckhamptonensis (Rollier)

"Terebratula" whitakeri

Zeilleria leckenbyi

Notgrove Railway Station (SP 094213)

Epithyris submaxillata

Globirhynchia subobsoleta

Granulirhynchia granulata

Moorellina c.f. ornata

Plectothyris fimbria

Pseudoglossothyris leckhamptonensis

Zeilleria leckenbyi

APPENDIX TABLE 1

Characters selected for population analysis.

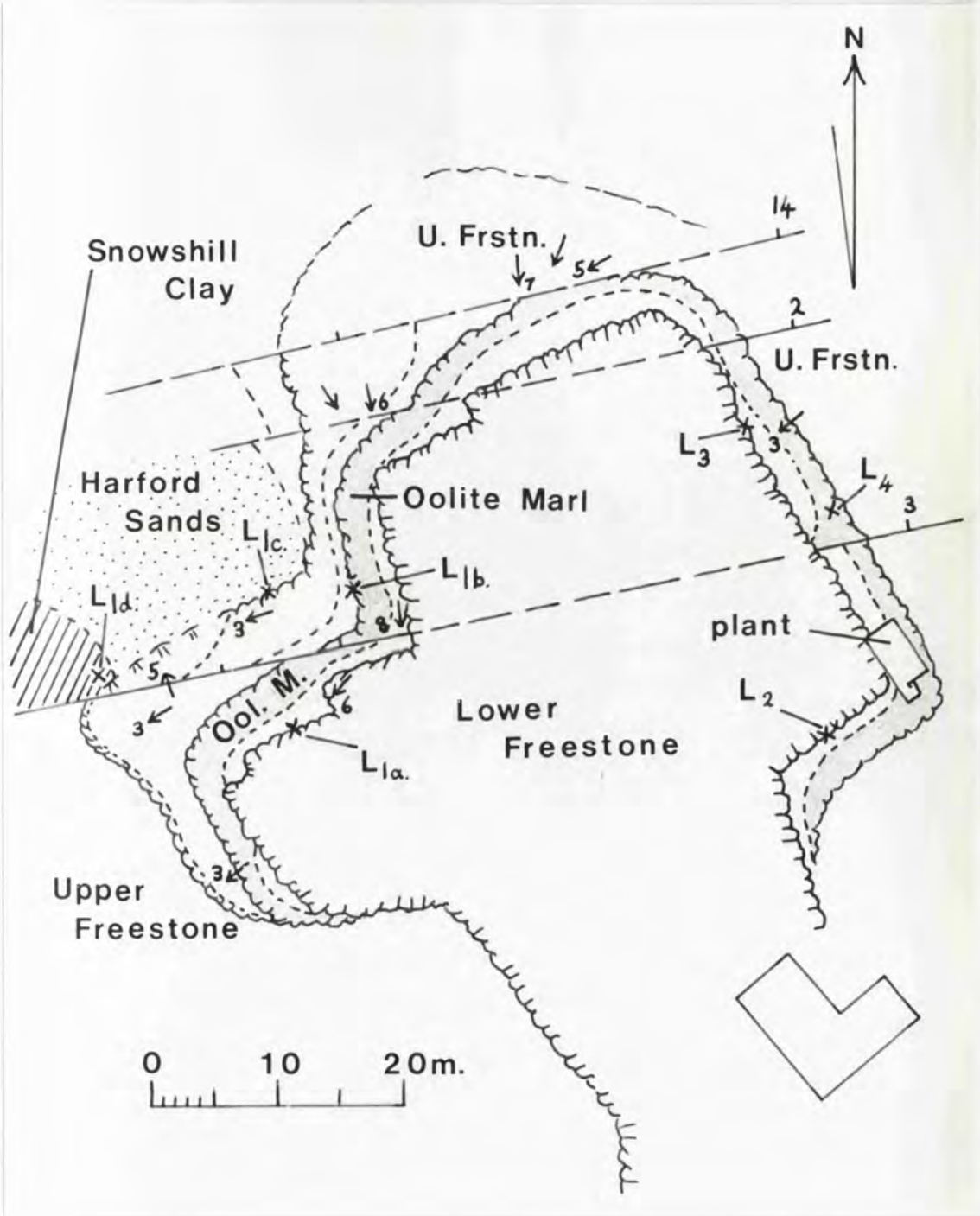
Cardinal margin	1	Convex
	2	Sinuate
Brachial valve	3	Sub-circular
	4	Elliptical to sub-pentagonal
	5	Elongate
	6	Anterior sulcus
Area	7	Strophic
	8	Non strophic
Beak	9	Curved
	10	Beak ridges well defined
Pedicle opening	11	Hypothyridid
	12	Submesothyridid
	13	Mesothyridid
Delthyrium	14	Triangular
	15	Parallel sided
	16	Deltidial plates
Pedicle collar	17	Present
Brachial umbo termination in delthyrial region	18	Flat
	19	Concave
	20	Convex
Tooth ridges	21	Projecting
	22	Concordant
Visible median septum	23	Present
Pedicle resorption	24	Present
Convexity of brachial valve in transverse profile	25	Strong
	26	Medium
	27	Low

APPENDIX TABLE 2

Summary of character analysis based on the data contained in Appendix Fig. 3.

Group I c.f. Z. leckenbyi	Group II incl. 'T' whitakeri
1. Important up to 4.0 - 5.00 mm. length	All
2. Replaces 1 at 4.0 - 5.0 mm. length	Rare
3. Up to about 3.0 mm. then replaced by 4	Majority
4. After about 3.0 mm. length	More common in adults
5. Intermittently	None
6. Begins to develop at about 2.8 mm. length, then characteristic	Rare
7. Character often supported up to 2.8 mm.	Supported up to 5.5 mm.
8. Replaces 7 at about 2.8 mm. length	Replaces 7 at about 6.0 mm.
9. Important after about 3.6 mm.	Important after 2.00 mm.
10. Majority through all size ranges	Rounded after 3.0 mm.
11. Normally supported up to 1.5 mm. Intermittent to 4.0 mm.	)
12. Intermittently supported 1.5 - 5.0 mm.	) As group 1
13. Usually after 5.0 mm. length	)
14. Present up to about 3.0 mm.	Present up to 4.0 mm
15. Intermittent 2.0 - 7.0 mm.	Similar
16. Present above 1.8 mm. length	Present above about 2.0 mm
17. Character not supported	Character supported
18. Intermittently up to 5.0 mm. length	Rare
19. " " " 3.0 mm. length	Usually
20. " " " 3.0 mm. length and almost always after	Rare
21. Often up to 4.0 mm. length	Similar
22. Not important	Similar
23. Depends on the state of the primary layer	Character never supported
24. According to 12, 13.	Similar
25. Not often	Not often
26.) About even distribution through	Not often
27.) all size ranges	Usually

APPENDIX FIG. 1



Geological map of the enlarged quarry at Westington Hill including recent excavations up to October 1971. L_{1a-d}, composite section, Appendix Fig. 2B. L_2, hard, brown-weathering band 0.35 m. thick developed below the grey marl, corresponds to the "ironstone" of Richardson. L_3, fresh face grey marl not well marked. L_4, patch reef development. Throw of faults in feet.

Explanation of Appendix Fig. 2

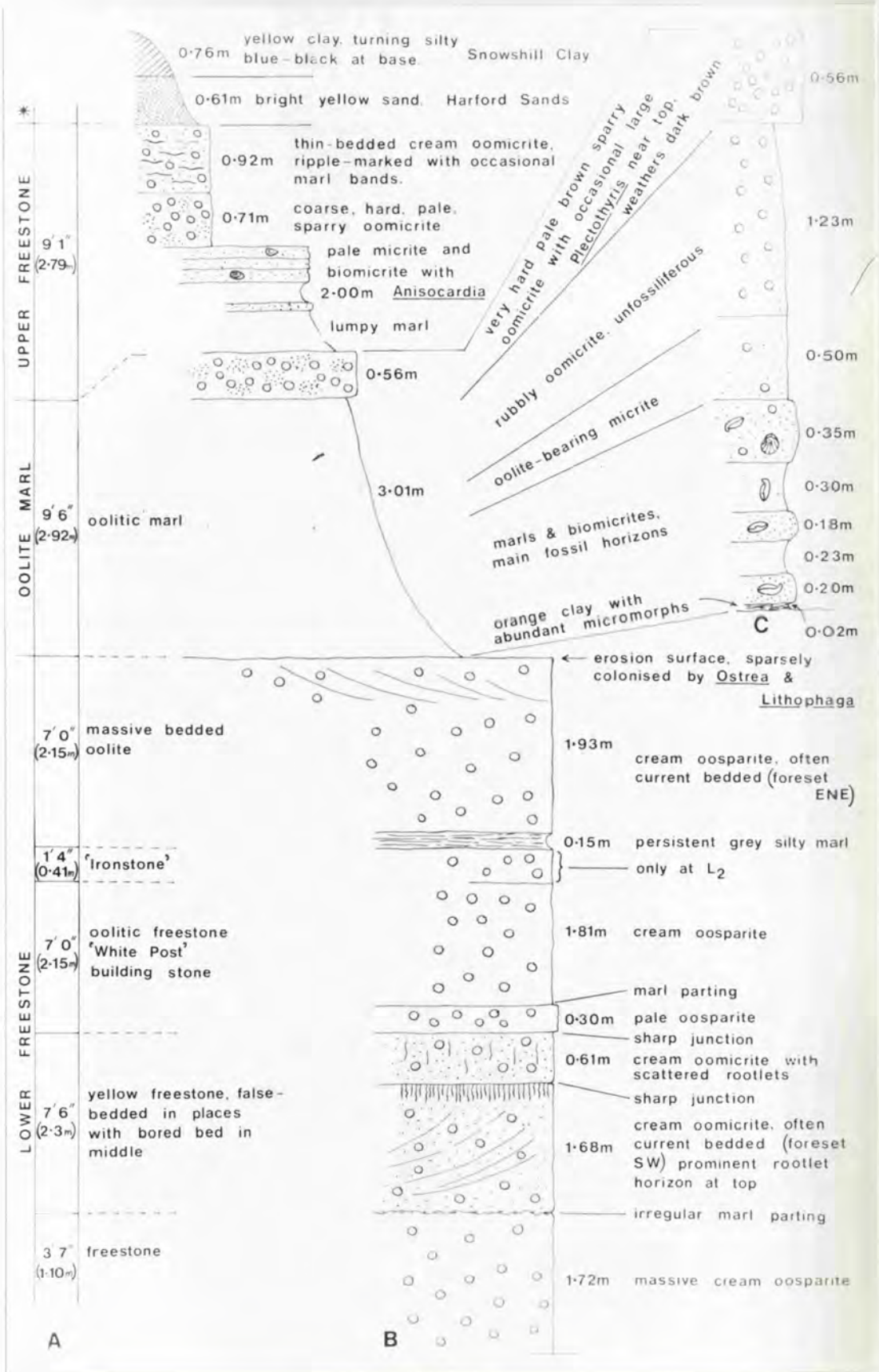
A. Succession in Westington Hill Quarry described by Richardson 1929

*Harford Sands described by Woodward 1894, mentioned but not seen by Richardson.

B. Measured succession, October, 1971. A composite section (based on locality numbers 1a-d on the accompanying map) to show the various lithological units exposed in the quarry and their correlation with Richardson's succession.

C. An enlarged succession to show the Oolite Marl in greater detail. The highest bed, included in the Upper Freestone by Richardson, is here, on lithological and faunal grounds, correlated with the Oolite Marl.

APPENDIX FIG. 2



Explanation of Appendix Fig. 3

Figs. A-D. Graphical representation of the occurrence of the characters selected for the analysis of the collection of terebratulide shells obtained from Westington Hill Quarry.

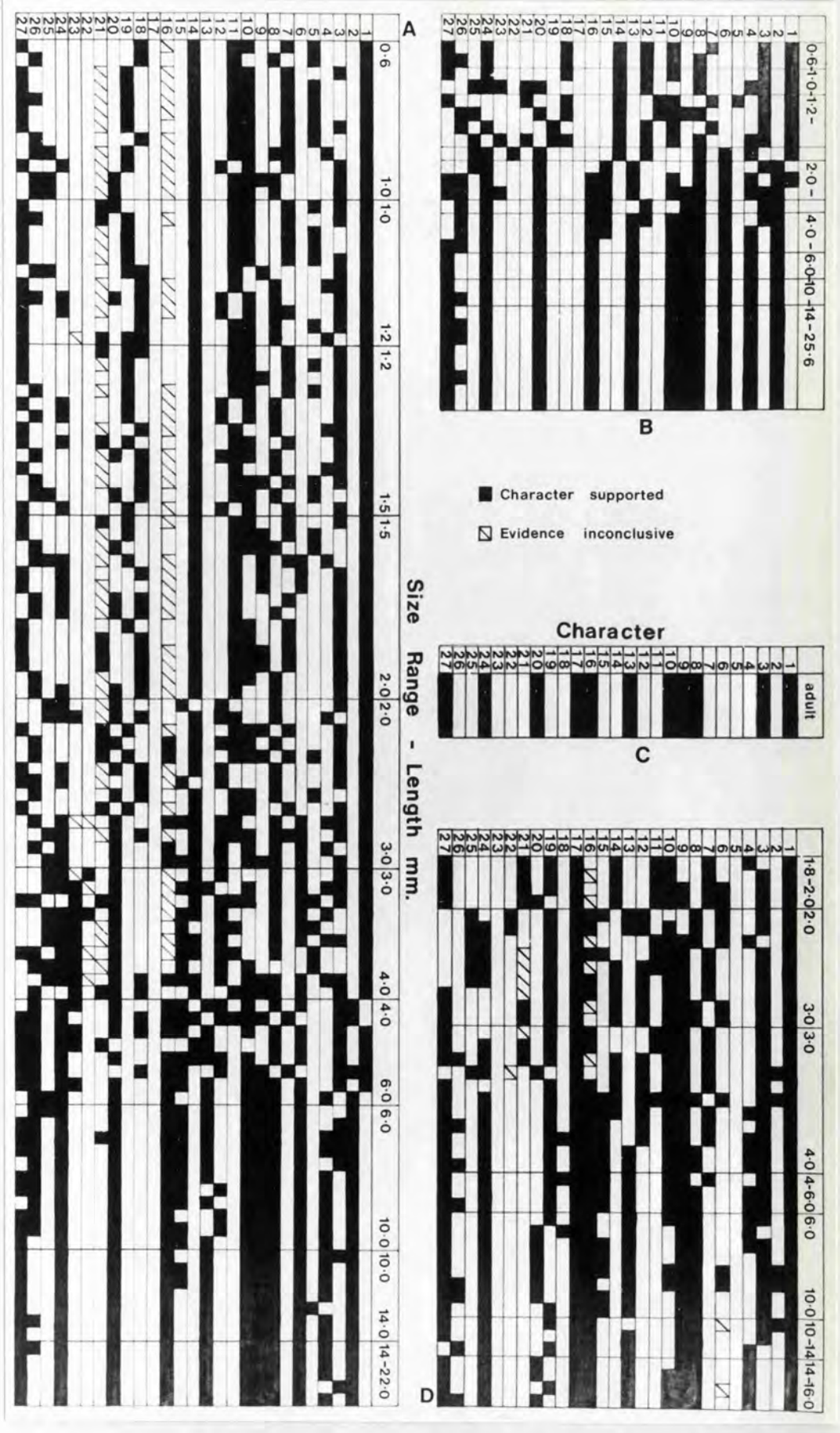
A. Analysis of 104 shells ranging from 0.6 - 22.0 mm. in length, in which character 17 (pedicle collar) is absent.

B. Analysis of the 28 shells, proved by sectioning to be long-looped forms (thesis, section 4, Zeilleria leckenbyi, Table 1.) ranging from 0.6 - 25.6 mm. in length. The distribution of characters represents a condensed version of fig. A.

C. Characters of an adult "Terebratula" whitakeri for comparison with Fig. D and the 14 - 25.6 mm. range of Fig. B.

D. Analysis of the 42 shells ranging from 1.8 - 16.0 mm. in length, isolated from population A on the basis that character 17 (pedicle collar) is supported. This feature excepted, the distribution of the remaining characters produces a pattern which is generally dissimilar to those of Figs. A and B, indicating the presence of two groups of juveniles and adults in the initial sample.

APPENDIX FIG. 3



SUPERIMPOSITION OF SERIAL SECTIONS

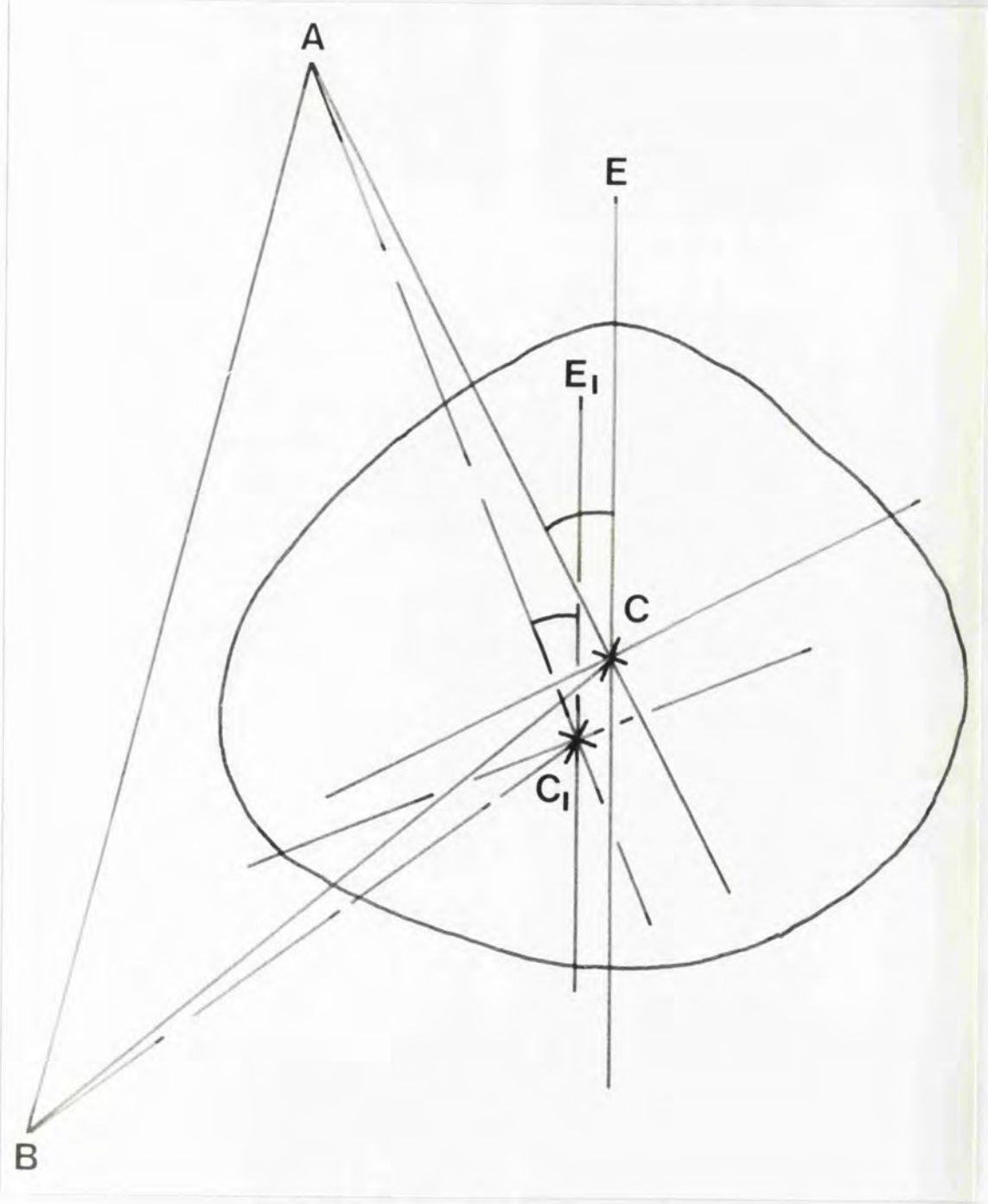
Working with such small specimens requires that cellulose acetate peels are superimposed with a very high degree of accuracy if reliable information concerning relative changes in the position of structures is to be obtained. To study this material, the following technique has been adopted, in which the inherent error is not likely to exceed 1%. Reference points A and B are marked on the block with a specially sharpened needle prior to taking the acetate peels (care must be taken to ensure frequent re-marking so that the reference points are not ground away). Each peel is mounted with, preferably, the long axis of the specimen vertical and the point to be enlarged centred in a position which will ensure its appearance in the field of view at high magnification. The peel is then projected at a magnification which enables the reference points A and B to be seen, e.g. x 20 and the specimen outline is drawn in. Reference axes are constructed intersecting at right angles and centred on the point to be enlarged in such a way that A lies on one axis. Measure the deviation ($\angle$ACE) of the axis AD from the vertical. Construction of the triangle ABC locates the position of point C relative to points A and B and fixes the orientation of the peel (Appendix Fig. 4).

As the reference points A and B are incorporated into the peel from the block surface the base-line AB must be standard through successive peels. Therefore changes in the relative position of features of the sectioned specimen both with regard to the reference points and to each other can be ascertained by the changing values of $\angle$ BCA.

Superimposition of microprojected structures in which the

reference points are not visible requires that the true position of A and B outside the field of view be known. After the initial procedure described above, the peel is microprojected at the magnification required, e.g. x 200, with care being taken not to disturb its orientation. The reference axes are superimposed on the microprojected image with the same orientation relative to the vertical ($\angle$ACE) as at x 20. The triangle ABC is reconstructed at the original x 20 (or conveniently enlarged) scale, thus locating the reference points A and B relative to the specimen but now within the field of view. As these points remain fixed, subsequent peels may be superimposed by adjusting the $\angle$'s ACE and BCA. Where absolute accuracy is required the procedure must be adopted for each peel. However, where an anatomical trend is established, only each third or fourth peel needs to be treated unless a significant departure from the trend is noted.

APPENDIX FIG. 4

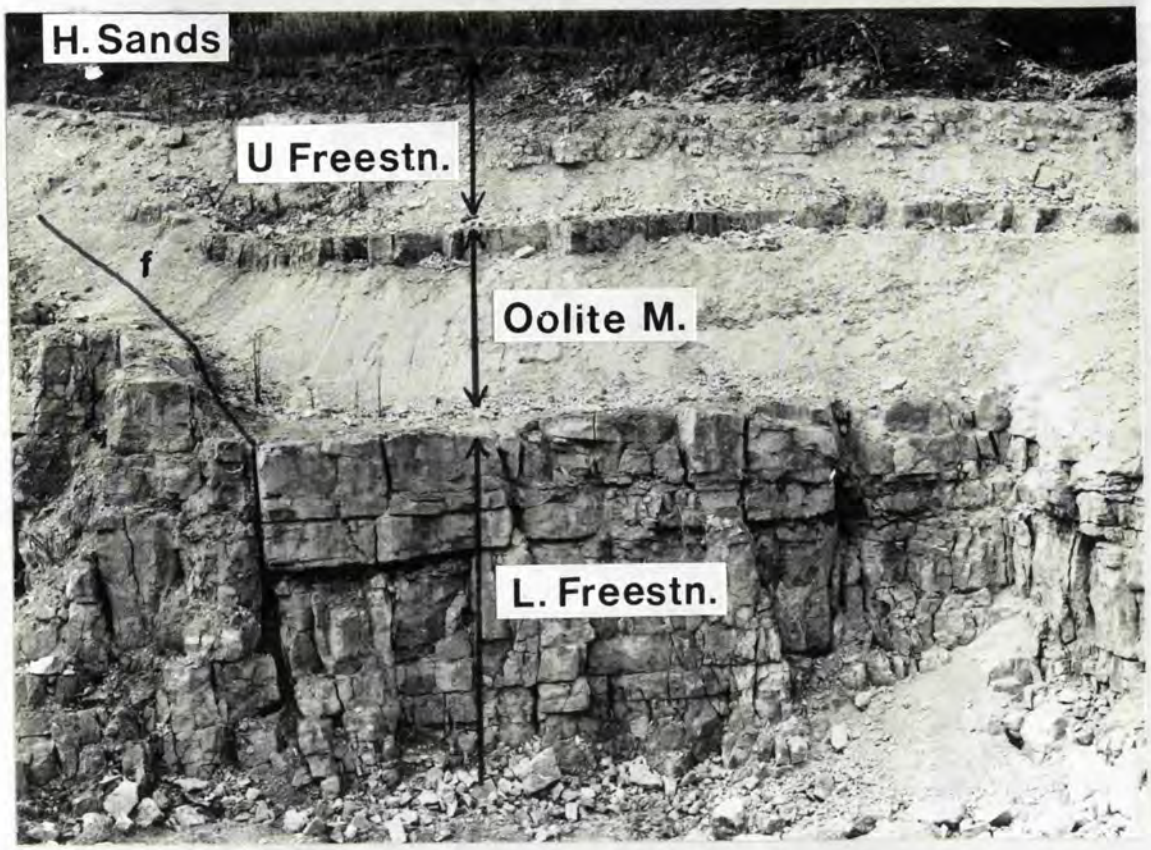


Model of the technique adopted to enable recognition of changes in the relative position of structures (C, C^1) with regard to the shell profile and the reference base-line A-B in microprojected serial cellulose acetate peels of horizontal sections through zeilleriid juveniles.

Explanation of Appendix Plate 1

Fig. 1. A section of the west face of Westington Hill Quarry showing the persistent oosparite at the top of the Oolite Marl and the effect that the small fault has on its outcrop.

Fig. 2. A section through the Oolite Marl exposed in the N.W. face of the Quarry. For explanation of the horizons marked see Appendix Fig. 2C.



1

2

Explanation of Appendix Plate 2

Stereoscan photomicrographs of specimens coated with evaporated aluminium before photography.

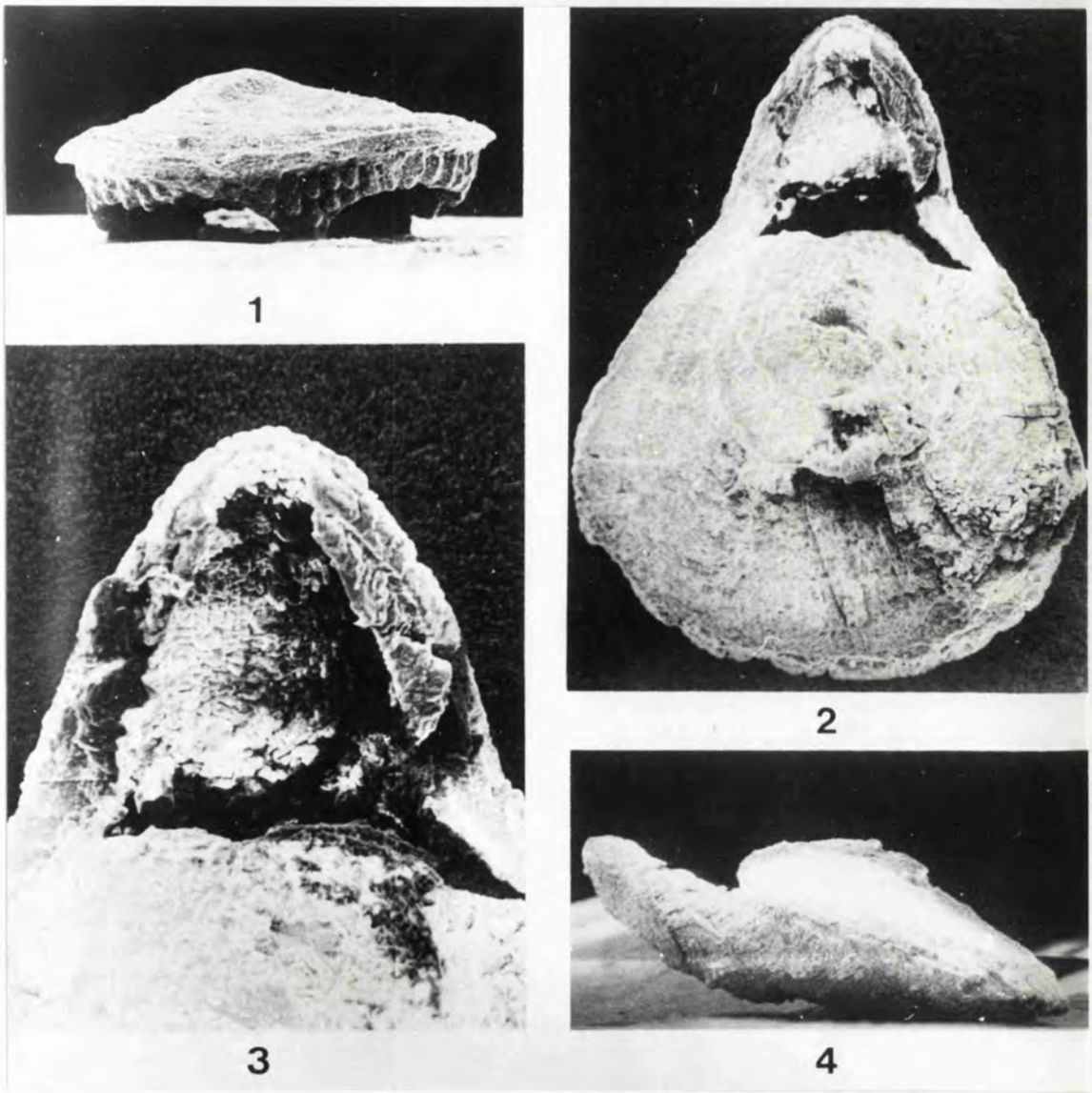
Fig. 1. Anterior view of a brachial valve of Moorellina granulosa (37526) to show the similarity between the tuberculate moorellinid subperipheral rim and the anterior slopes of the brachial valves of Cooperina. 40 X.

Fig. 2. Brachial view of an early juvenile zerilleriid (37630/25) showing the enlargement of the delthyrium resulting from the failure of the beak resorption stimulus. 80 X.

Fig. 3. Enlarged view of a portion of fig. 2 to show detail of the deformed beak and the delthyrium with the sporadic development of deltidial plates, upper right. 160 X.

Fig. 4. Lateral view of specimen 37630/25 to show how failure of the resorption mechanism results in the disproportionate size of the early beak. 56 X.

APPENDIX PLATE 2



Explanation of Appendix Plate 3

Stereoscan photomicrographs of specimens coated with evaporated aluminium before photography.

Fig. 1. Brachial view of a juvenile zeilleriid (37570/2) showing how normal beak resorption, accompanied by retarded development of the deltidial plates produces a greatly enlarged delthyrium. 20 X.

Fig. 2. Enlarged view of a portion of fig. 1 to show detail of the enlarged delthyrium. 50 X.

Fig. 3. Brachial view of a juvenile zeilleriid (37570) showing the normal development of the deltidial plates and normal beak resorption. 17 X.

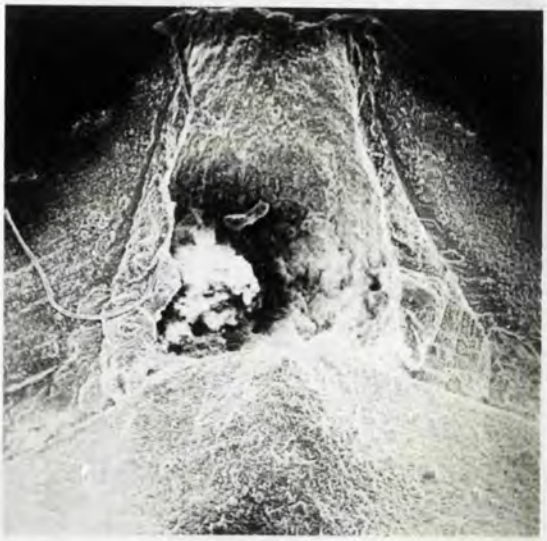
Fig. 4. Enlarged view of fig. 3 showing the deltidial plates, the resorbed beak and the convex brachial umbo termination in the delthyrial region. 90 X.

Fig. 5. Brachial view of a short-looped juvenile c.f. "Terebratula" whitakeri. 52 X.

Fig. 6. Enlarged view of fig. 5 showing detail of the pedicle collar, the deltidial plates and the concave brachial umbo termination in the delthyrial region. 170 X.

APPENDIX PLATE 3

1



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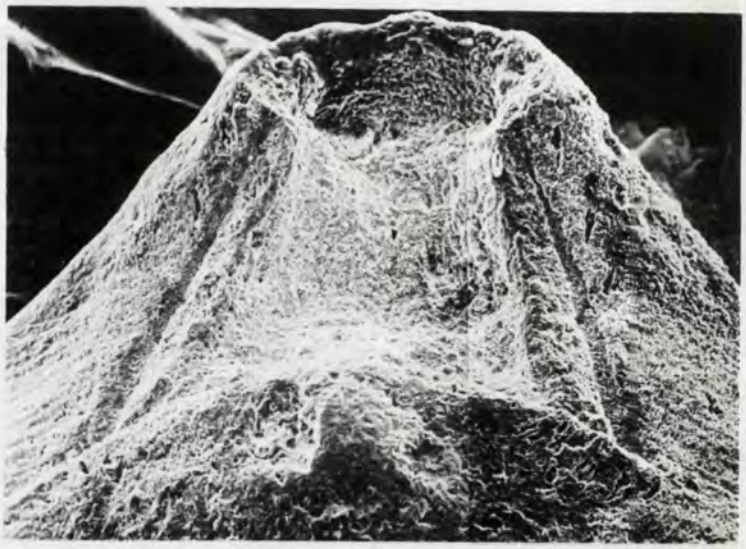

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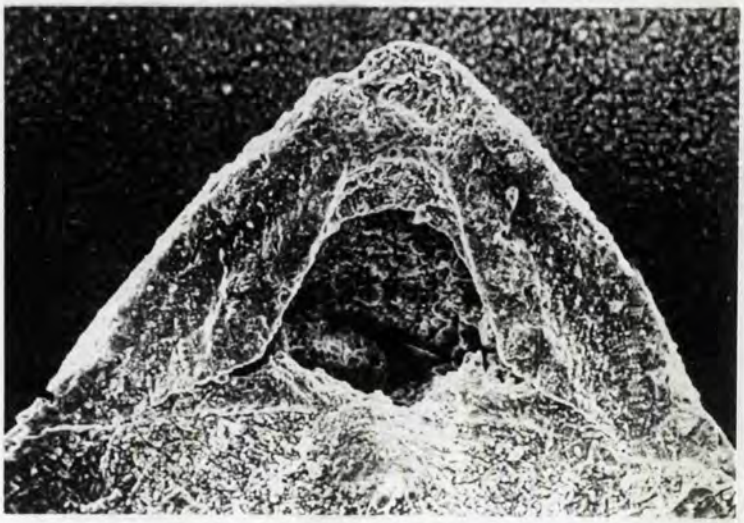

6

PROPOSED FUTURE INVESTIGATIONS

1. Revision of the thecidellinids assigned to the genus Moorellina.
2. Determination of the geographical and stratigraphical range of Moorellina in the Cotswolds and other areas.
3. Investigation of the origin and development of the cardinalia in the early juveniles of the long and short looped brachiopods from the Oolite Marl.
4. Subject to availability of material, investigation of the microstructure of developing dallinid loops.

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The ontogeny of the thecideacean brachiopod *Moorellina granulosa* (Moore) from the Middle Jurassic of England

BY

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THE ONTOGENY OF THE THECIDEACEAN BRACHIOPOD MOORELLINA GRANULOSA (MOORE) FROM THE MIDDLE JURASSIC OF ENGLAND

by P. G. BAKER

ABSTRACT. Investigation of fifty-five brachial valves and several sectioned shells from a new locality has led to the conclusion that in *Moorellina granulosa* the brachial apparatus shows progressive elaboration from simple tubercles to very delicate convoluted lobes which are in the form of a ptycholophe. Also that *Thecidium forbesi* Moore (1855) should be regarded as an early pre-brachial lobe stage of *M. granulosa*.

Five ontogenetic stages are described. The argument for an ontogenetic series is strengthened by the changes occurring in the cardinal process, coincident with the development of the brachial apparatus. Reference is made to the improbability of finding detached brachial valves showing adult characteristics. It is considered that the generic distinction between *Moorellina* Elliott (1953) and *Rioultina* Pajaud (1966) should be based on the form of the brachial lobes and not merely on their presence or absence. Specific determination based on the morphology of the brachial valve is considered unsatisfactory and a technique has been developed for the study of the internal characters of complete specimens.

THE paper records the occurrence of thecidellinids in the Oolite Marl of the Mid-Cotswolds. The deposit is rather variable and outcrops at a number of localities. It is well developed on Cleeve Cloud near Cheltenham where it attains a thickness of over 4 m. The Marl is typically a pale, cream-coloured marl, relatively harder and more oolitic in the upper layers, softer and with the ooliths more scattered towards the base. It thins in a north-easterly direction towards Chipping Campden and changes lithologically in a south-westerly direction, becoming indurated south from Painswick until it is indistinguishable from the overlying limestone.

Stratigraphically the Oolite Marl was placed by Arkell in the Lower Inferior Oolite (Upper Aalenian, *murchisonae* zone). It rests on a clearly recognizable bored surface of Lower Freestone but cannot be structurally separated from the overlying Upper Freestone, into which it passes laterally in the vicinity of Stroud.

The material described in this paper was obtained from the northernmost outcrop of the Oolite Marl two miles to the south of Chipping Campden at Westington Hill quarry, grid. ref. SP 142368. The Marl occurs at the top of the quarry which exposes almost 8 m. of Lower Freestone. The collection was made from a bed of soft, pale marl 30 cm. thick, which occurs in the north face of the quarry between two harder bands and about 60 cm. above the top of the Lower Freestone.

The thecidellinids from this locality occur together with a variety of organo-detrital remains which are recorded in tabular form in the text. This fauna is essentially similar to the surf-zone fauna recorded by Nekvasilová (1967) (Nekvasilová *in* Ager 1965, p. 146). The occasional large brachiopods which occur are forms which are anatomically characteristic (Ager 1965) of peri-reefal deposits.

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Registration of Material. The specimens figured and referred to in this paper are to be deposited in the museum collection of the Department of Geology, University of Leicester. The specimen numbers quoted refer to their catalogue numbers.

TABLE 1

Residue retained on sieve mesh

Residue type	2mm. mesh		422μ. mesh		152μ. mesh	
	Av. ten 5gm.samps.	Av. % sample	Av. ten 5gm.samps	Av. % sample	Av. ten 1gm.samps.	Av. % sample
Oolite fragments	3·8	4·7	40·8	0·78	–	–
Ooliths	–	–	1198·8	22·9	148·8	0·8
Brachiopod shell fragments	69·9	84·3	3555·0	68·0	17064·0	98·4
Bivalve shell fragments	3·8	4·7	45·0	0·84		
Echinoderm debris	1·8	2·2	214·8	4·1	64·5	0·3
Gastropods	–	–	0·3	0·006	–	–
Thecidellinids	0·2	0·24	14·4	0·27	2·6	0·01
Other brachiopods	1·4	1·6	13·8	0·26	5·7	0·03
Ostracods	–	–	8·4	0·16	38·9	0·2
Polyzoa fragments	1·7	2·0	112·2	2·1	2·0	0·01
Annelid worms	0·4	0·48	19·1	0·36	3·5	0·01
Total	83·0		5222·6		17330·0	

PREPARATION OF MATERIAL

Weathered marl samples were dried and crumbled through a 6-mm. sieve to remove large fragments. The sieved material was immersed in water and cleaned for ten minutes in a Dison electrosonic cleaner, marketed by Headland Engineering Developments Ltd. The samples were then washed until a clean residue was obtained. This was dried and passed through 2-mm., 422-μ, and 152-μ sieves, each residue size being analysed for faunal content (Table 1). Experience has shown that only the material retained on the 422-μ mesh is likely to yield thecidellinids. The cleaned residue was hand-picked under a binocular microscope and the brachiopods transferred to glass tubes for further cleaning. The individual tubes were replaced in the cleaner for periods of 10–20 seconds until the matrix had been removed. The shells were examined at each phase of cleaning

to determine whether the treatment should be continued. It should be emphasised that this is a very slow method of collecting as the thecidellinid content of the residue is approximately 0·3%. The collection of 172 specimens is comprised as follows:

Brachial valves	55
Pedicle valves	16
Complete specimens	43
Broken valves with significant detail	58
	172

Complete specimens selected for sectioning were cemented to glass slides, using a mixture of Lakeside cement (obtainable from Cutrock Engineering Co.) and chloroform. This remains plastic for sufficient length of time to allow correct orientation of the specimen under a binocular microscope. When the cement has hardened, the orientation of the specimen is checked and a plasticine mould is built round it. The mould is then filled with Ceemar cold setting resin, which, when hardened, allows the block (attached to the slide) to be serial sectioned on a Croft parallel grinder (see Hendry *et al.* (1963) for other methods). Although the theory of sectioning such small specimens at 0·02 mm. intervals is sound it is found to be inaccurate in practice. Better results are obtained if acetate peels are taken after a standard number of 30–50 revolutions (depending on the area of the block face). The length of the specimen is divided by the number of peels obtained, thus averaging out any error.

ANALYSIS OF RESIDUE

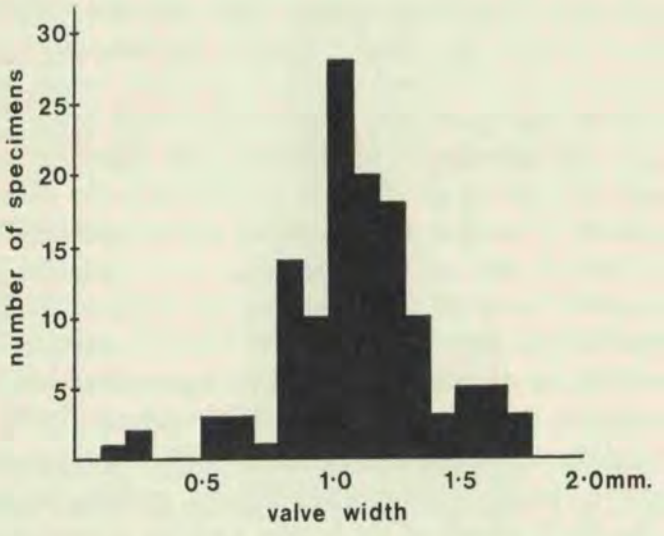
Residue obtained by the method described was found to constitute approximately 40% of the Oolite Marl from the Westington Locality. An analysis of the composition and faunal content of the cleaned residue is shown in Table 1.

In all size ranges, the bulk of the residue is composed of brachiopod shell fragments which may be identified as rhynchonellid and terebratuloid. Occasional specimens of *Globirhynchia subobsoleta* (Dav.), *Epithyris submaxillata* (Morris), and *Plectothyris fimbria* (Sow.) occur in the coarse residue and it is probable that the shell debris was formed from the remains of these species. The bivalve shell fragments may be identified as *Ostrea* and *Lopha* species. The echinoderm debris consists of unidentified echinoid spines and plates, crinoid ossicles of *Pentacrinus* type, unidentified ophiuroid plates and vertebrae. Three very small gastropods of *Nerinea* type were recovered from the 422–μ sample. The polyzoa fragments have been identified by Dr. A. W. Medd as *Actinopora* sp., *Berenecea* sp., *Meliceritites* sp., and *Spiropora* sp. The ostracods are *Bairdia* sp., *Cytherella* sp., and several unidentified cytheracean genera.

The analysis probably shows a bias towards brachiopod shell fragments as the true nature of the shell type was frequently obscured by adherent matrix. It is possible therefore, that some fragments included in the brachiopod count may in fact have been bivalve material. In addition, quite large echinoid spines appear in the 422-μ sample as their diameter is the critical factor. In the 152-μ size range it was not possible to distinguish between brachiopod and bivalve shell material with any degree of accuracy and

they are therefore grouped. However, as the proportion of brachiopod shell material is so large it is considered that the probable error is of no significance. Analysis of the brachiopod content was very critical and it is unlikely that any specimens escaped attention, even in the 152-μ samples. Although the number of ostracods shows a marked rise in this size range, they still represent approximately the same percentage of the sample.

The thecidellinid material shows the same ranges of variation of shell shape noted by Elliott (1948) during his study of *Bifolium* and by Nekvasilová (1967) during her study of *Thecidiopsis*. It appears to be correlated with the size of the area of attachment



TEXT-FIG. 1. Histogram to show the size distribution of 126 brachial valves of *Moorellina granulosa* (Moore) from Westington Hill Quarry. Number of individuals plotted against width of the brachial valve.

and is almost certainly the result of environmental influence (Rudwick 1962). The dangers of using a single character are evident but for the purpose of expressing size distribution (text-fig. 1) width of the brachial valve is used, as this appears to be one of the least variable growth characteristics. This feature is particularly useful as over half the material consists of complete or broken brachial valves.

Scars of the area of attachment on the pedicle valve occasionally show portions missing and occasionally, the pedicle valves are still cemented to shell fragments. Nekvasilová (1967) has shown that the form of the area of attachment is consistent with *Thecidiopsis* being attached, either to the valves of living oysters (liberated on the decay of conchiolin), or settled directly to some firm rocky substratum. The author is in agreement with her views on the ecology of *Thecidiopsis* and the evidence suggests that *Moorellina* occupied a similar environment, that is, belonged to the epifauna of the inner sub-littoral zone. This opinion is further supported by their association with peri-reefal brachiopods and the nature of the organo-detrital remains with which they are deposited (ref. Table 1).

A consideration of the evidence indicates that the collection represents a transported death assemblage, the size-frequency distribution (text-fig. 1), showing moderate positive skewness. This may be regarded as the product of a normal growth-mortality

rate if compared with the histograms plotted by Hallam (1967) in his work on molluscan death assemblages.

The fragmentation of thecidellinids, other brachiopods, bivalves, and Polyzoa indicates that the debris was formed in a turbulent environment. However, the lack of abrasion of the fragments together with the persistence of occasional bridges and brachial lobes in detached brachial valves of thecidellinids would suggest that the organo-detrital remains were transported only a short distance. Reference to Table 1 will show that thecidellinids are most common in the 422-μ size range whereas ostracods are most common in the 152-μ size range. Brachiopod shell fragments represent a high percentage of the material in all size ranges. These data and arguments advanced by Hallam (1967) suggest that no significant sorting of the population has occurred. The absence of appreciable numbers of small thecidellinids which would reflect the normally expected high juvenile mortality rate may simply be the result of selective shell breakage (Hallam 1967, p. 35). The presence of brachiopod shell fragments in excess of 2 mm. diameter, the absence of large thecidellinids and particularly the absence of large thecidellinid shell fragments, is considered to indicate that thecidellinids with a brachial valve width of more than 2 mm. are not represented in the population. Sedimentation factors are not thought to have affected the upper size limit as ooliths larger than the largest complete thecidellinid shells are common in the 422-μ sample. Clearly, therefore, the larger size-distributions of the sample may be regarded as adult shells. This is a much smaller population than that studied by Nekvasilová (1967) but the ratio of brachial valves to pedicle valves and complete shells within the sample is similar.

The material shows a number of progressive changes, such as, the development of the cardinal process, the development of the border and the appearance and progressive elaboration of the sub-peripheral rim. The brachial apparatus develops in the same manner and, in the tuberculate stages, forms with from one to five pairs of brachial tubercles are present. For reasons to be described later it is thought that some of these latter are damaged adults. All the structures, with the exception of the adult brachial lobes, show varying degrees of development in the material studied. This shows the presence of an intimate relationship between the progressive development of the various growth features with general size increase.

The collection of the material from one sample from a single bed, the size distribution and the close parallel between the growth stages of *Moorellina* and the ontogenetic development of *Bifolium* (Elliott 1948), *Lacazella* (*B.*) *lacazelliforme* (Elliott) (Nekvasilová 1964), and *Thecidiopsis* (Nekvasilová 1967) leaves little room for doubt that the material from Westington Hill quarry represents the ontogenetic stages of a single species.

Comparison of the forms having a single pair of brachial tubercles with *Thecidium forbesi* Moore 1855 indicates that there is no valid basis for the separation of *T. forbesi* from *Moorellina granulosa*. It is proposed, therefore, that the adolescent growth stages showing this degree of development of the brachial apparatus should be designated forbesiform. It is considered that five ontogenetic stages may be recognized, each marked by the appearance of a characteristic feature (text-fig. 3A–F). The dimensions recorded are those of the specimens figured in Plate 73 and are intended to indicate only the general size relationship, the stages represented being obviously subject to natural size variation.

	Length mm.	*Width mm.*	*Thickness mm.*
A. Brephic valve	0·47	0·5	0·2
Pre-forbesiform stage	0·9	1·0	0·3
C. Early forbesiform stage	1·0	1·2	0·35
D. Late forbesiform stage	1·2	1·6	0·35
E. Post-forbesiform stage	1·4	1·7	0·4
F. Adult valve	1·1	1·3	0·4

MORPHOLOGY

The present paper is concerned only with the morphology of the interior of the brachial valve (text-fig. 2A) but it is felt that some attempt should be made to reconcile the interpretations of Elliott (1948) and Pajaud (1963) with the glossary laid out in the *Treatise on Brachiopoda* but without adding to the existing confusion. Briefly the new morphological terms and the justification for their introduction are as follows:

Border. The term is introduced to define the flat region of the valve between the sub-peripheral rim and the periphery of the valve. This unites the limbe-marginal and bord frontal of Pajaud and enables the distinction between anterior, lateral, and postero-lateral regions to be made. It is felt that this is necessary as it is noted that the postero-lateral border is the first to appear during the pre-forbesiform stage of development (text-fig. 3B).

Brachial shelf. The term is introduced to define the raised flat areas, within the lophophorian area, from which the brachial tubercles develop. The inner boundary of the shelf is occasionally raised to form low ridges which may correspond, in part, to the ridge extensions described by Elliott (1948) during the early ontogeny of *Bifolium faringdonense* (Davidson).

Brachial tubercle. The dotted brachial ridge (Elliott) is not thought to be sufficiently explicit. The rounded dots (Elliott 1948, p. 9) are by definition tubercles (Williams 1965, H154) and the term brachial tubercle is introduced as these structures are of considerable importance in the development of the brachial apparatus.

Socket ridges. As defined in the glossary, inner and outer socket ridges are present (Pl. 74, fig. 3).

The recommendation of the glossary (op. cit. H148) that the term marginal flange should be replaced by sub-peripheral rim is adopted but it is noted that this has a postero-lateral extension demarcating the outer boundary of the cardinal area. The term brachial lobe introduced by Pajaud (1966*b*) for the establishment of the genus *Rioultina* is adopted, particularly as lobes are referred to in Moore's original description of *Moorellina granulosa* (Moore 1855). One must recognise however, that the brachial lobes of *M. granulosa* are convoluted and not as in *Rioultina*, auriform.

Ontogenetic stages recognized. The brephic valve (text-fig. 3A; Pl. 73, fig. 1) is the first stage represented and is 0·5 mm. wide. The valve is almost circular, thick, and cap-like. The cardinal margin is almost straight and approximately two-thirds of the width of the valve. The cardinal process is the only recognizable thecidellinid feature, being low

and broad, occupying a little more than half the hinge-line and projecting slightly beyond the cardinal margin (text-fig. 2B). There is no median septum but the postero-lateral border is just discernible. The dental sockets are poorly developed but clearly bounded anteriorly by the lateral divergence of the sides of the cardinal process, forming inner socket ridges where they turn down to unite with the posterior margin of the valve. No sub-peripheral rim is present at this stage. Three valves show this stage of development.

Stage two is marked by the appearance of the median septum which is considered to be a neanic feature (text-fig. 3B; Pl. 73, fig. 2). The valve is still nearly circular, relatively thick, markedly convex, and in the specimen figured, 1 mm. wide. The cardinal margin is slightly curved and somewhat less than half the width of the valve. The cardinal process is more strongly developed (text-fig. 2C) and turns down sharply into the floor of the valve anteriorly. The postero-lateral border is now clearly defined, also the dental sockets. The sub-peripheral rim is represented by a row of denticles which, posteriorly, mark the inner boundary of the postero-lateral border, not, as in Elliott (1948), trending inwards to form the sides of the cardinal process. Laterally the denticulate rim is almost peripheral so that there is no noticeable border. It will be noticed that the bridge extensions do not unite with the inner socket ridges and that they merge laterally with the sub-peripheral rim. The median septum is fairly thick, developing from the anterior margin and extending posteriorly, the posterior portion being free from the floor of the valve. This stage is designated pre-forbesiform by virtue of the fact that the brachial tubercles of *T. forbesi* Moore (1855) are not yet developed. Six valves show this stage of development.

The two stages described correspond closely with the first two ontogenetic stages of *Bifolium faringdonense* (Davidson) described by Elliott (1948) but the subsequent stages showing the development of the brachial apparatus are quite different.

Stage three is marked by the appearance of the brachial tubercles characteristic of *T. forbesi* and is accordingly designated the forbesiform stage, early and late features being distinguishable (text-fig. 3C, D; Pl. 73, figs. 3, 4).The valve is now slightly wider than long. The cardinal margin is well-defined, slightly curved, and just less than half the width of the valve. The cardinal process is by now a prominent feature, projecting markedly beyond the cardinal margin. The dental sockets are deep and the postero-lateral border inclined to the plane of the valve. The sub-peripheral rim is well developed so that the lateral and anterior portions of the border are now visible. At this stage the

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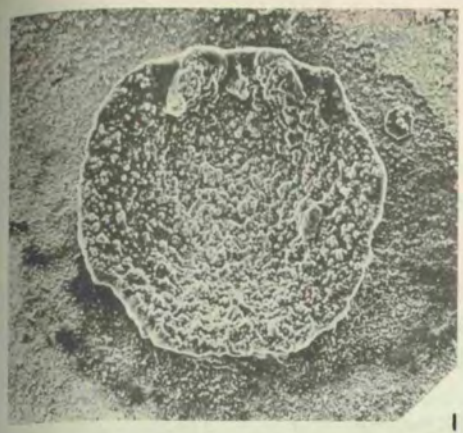
EXPLANATION OF PLATE 73

Figs. 1–6. Stereoscan photomicrographs of brachial valves of *Moorellina granulosa* (Moore) collected from the Oolite Marl, Westington Hill Quarry near Chipping Campden. All the figures are interior views of specimens coated with evaporated aluminium before photography. The bridge is broken on specimens fig. 3–5. 1. Brephic valve (37500), shell recrystallized. ×75. 2. Pre-forbesiform stage of development (37503) showing the development of the median septum. Cardinal process slightly damaged. ×50. 3. Early forbesiform stage (37505) showing the brachial shelf and appearance of the first pair of brachial tubercles. ×50. 4. Late forbesiform stage (37507) showing four pairs of brachial tubercles, well defined sub-peripheral rim and border. ×50. 5. Post-forbesiform stage (37508) showing the expanded brachial tubercles, uniting posteriorly to form arches. Cardinal process slightly damaged. ×50. 6. Adult valve (37509) showing the form of the right brachial lobe. Cardinal process slightly damaged. ×50.



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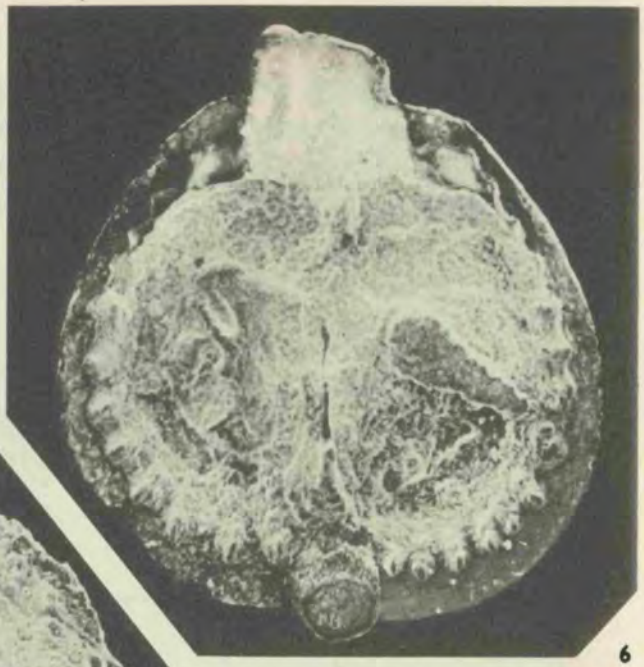

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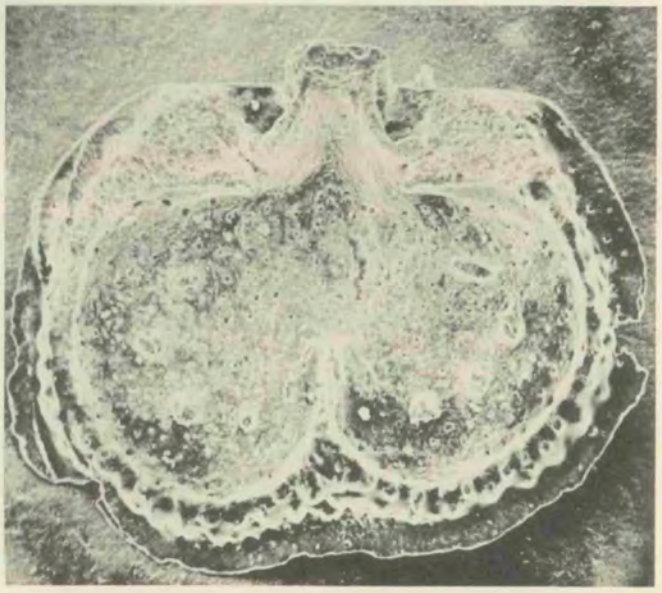

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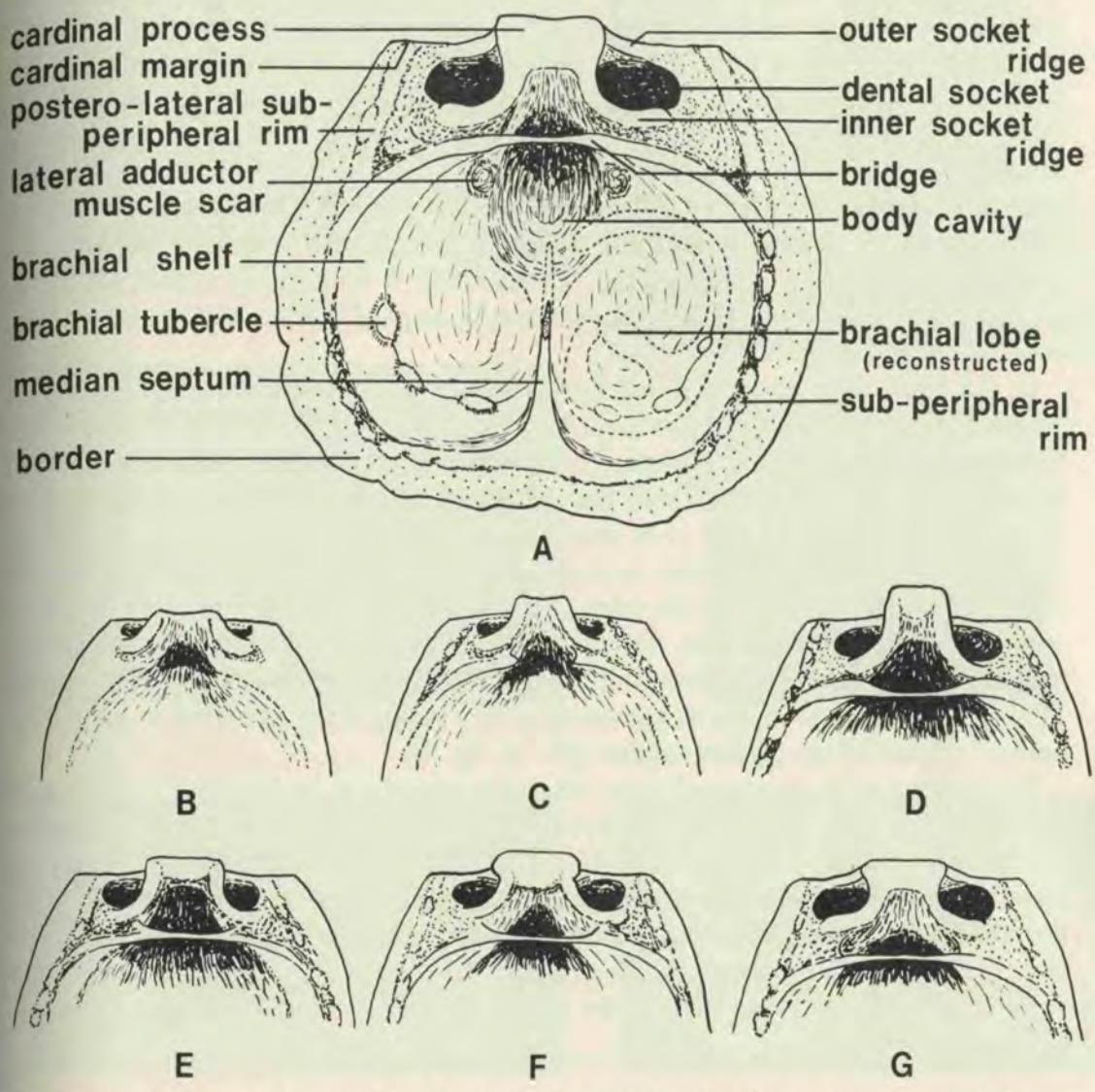
BAKER, *Moorellina granulosa*

bridge is usually complete (broken in the specimen figured during cleaning) but without the marsupial notch (Elliott 1948). The posterior portion of the median septum is quite clearly free from the floor of the valve and is usually slightly larger than that shown. The floor of the valve is now characterized by two raised areas (brachial shelf), along



TEXT-FIG. 2. A. Composite drawing from brachial valves 37509 and 37510 to show the morphological features of the interior of the adult valve. Brachial lobe and median septum reconstructed from specimen 37510. B–G. Drawings to show the form and modification of the cardinal process during ontogeny, together with the development of the inner and outer socket ridges. B, brephic 37500. C, preforbesiform 37503. D, E. early forbesiform 37505, 37506. F, late forbesiform 37507. G, post forbesiform 37508.

the inner boundary of which the brachial tubercles develop, usually appearing in pairs. Valves with one or two pairs of tubercles are said to constitute an early forbesiform stage, whilst those with four to five pairs are said to constitute a late forbesiform stage. Attention is drawn to the fact that the tubercles are regularly arranged and without the random distribution figured by Pajaud (1966*b*) in his work on material from the

Inferior Oolite of Dundry. During the early forbesiform stage the cardinal process begins to lose its concavity posteriorly (text-fig. 2D, E) eventually forming a flattened region which gives rise to the outer socket ridges during the late forbesiform stage (text-fig. 2F; Pl. 74, fig. 3). The bulk of the valves show this stage of development.

The beginning of stage four may be recognized by the fact that the distal ends of the brachial tubercles expand and develop projections which ultimately unite with those of adjacent tubercles to form delicate arches. This degree of organisation is taken to represent a post-forbesiform stage (text-fig. 3E; Pl. 74, fig. 1) The cardinal margin is, by definition, a hinge line. The outer socket ridges, developed from the posterior of the cardinal process are now clearly visible (text-fig. 2G; Pl. 73, fig. 5). The median septum extends back almost as far as the edge of the body cavity. The floor of the valve is characterized by expanded brachial tubercles showing the development of arches and inward pointing projections. The brachial shelf is now hardly visible, its decline probably to be correlated with the higher development of the brachial apparatus. Five valves show this stage of development.

In the adult state, stage five, the arches of the post-forbesiform stage are united, thickened, and extended to form convoluted lobes (text-fig. 3F). Two specimens were found at this stage of development, 37509 with the right brachial lobe intact (Pl. 73, fig. 6; Pl. 74, fig. 2) and 37510 with the left brachial lobe intact. The brachial lobes of both specimens could be seen to be joined to brachial tubercles anteriorly. An attempt to clean specimen 37510 in order to provide conclusive evidence for the view that the brachial lobes are attached to the valve solely by brachial tubercles, resulted in the loss of the remaining brachial lobe. Specimen 37509 has therefore been subjected only to partial cleaning, this in itself being sufficiently destructive to remove part of the bridge. This specimen is remarkable in possessing a very young form cemented to its anterior border in front of the median septum (Pl. 74, fig. 4).

For reasons to be mentioned later, very little appears to be known about the adult brachial valve of *M. granulosa*. The above specimens are almost certainly examples of the type referred to by Davidson (1874, p. 110) in Moore's collection from Dundry and almost identical with Moore's type specimens, M2850, Nos. 2, 5, and 6 held in the basement of the City of Bath Reference Library. The Westington Hill specimens are smaller than the examples of *M. granulosa* held at the British Museum. These have a brachial valve width of 2·5–3·5 mm. whereas the largest specimens from Westington Hill have a

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EXPLANATION OF PLATE 74

Figs. 1–8. *Moorellina granulosa* (Moore) 1. Stereoscan photomicrograph (37508) showing the brachial arches. Postero-lateral view, angle of incidence 48° to the plane of the valve. ×250. 2. Stereoscan photomicrograph (37509) showing the brachial lobe free from the floor of the valve. X indicates the point of attachment to one brachial tubercle. Antero-lateral view, angle of incidence 36° to the plane of the valve. ×100. 3. Stereoscan photomicrograph (37507) normal to the plane of the valve showing the cardinal process with inner and outer socket ridges. ×100. 4. Very young form cemented to the anterior border of specimen 37509. ×250. 5. Photomicrograph, reflected light. Vertical transverse section through specimen (37511) showing the posterior extensions of the brachial lobes and median septum. ×46. 6. Retouched copy of fig. 5. 7, 8. Photomicrographs prepared from acetate peels of vertical transverse sections of specimen (37511) at 0·68 and 0·7 mm. from the umbo, showing the form of the brachial lobes and their attachment to the floor of the valve by brachial tubercles. ×50.

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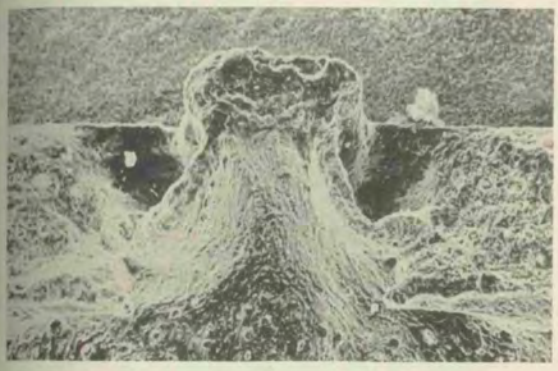

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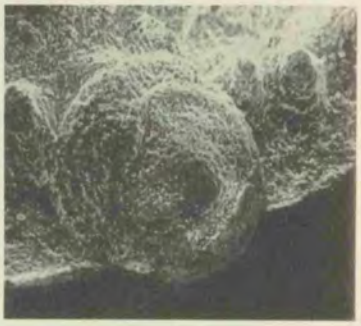

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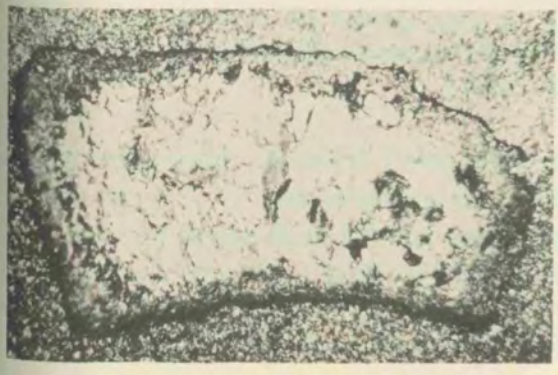

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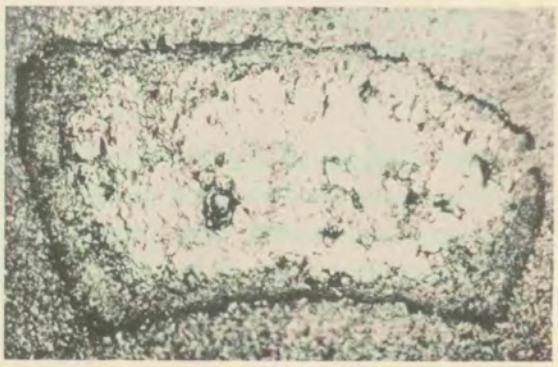

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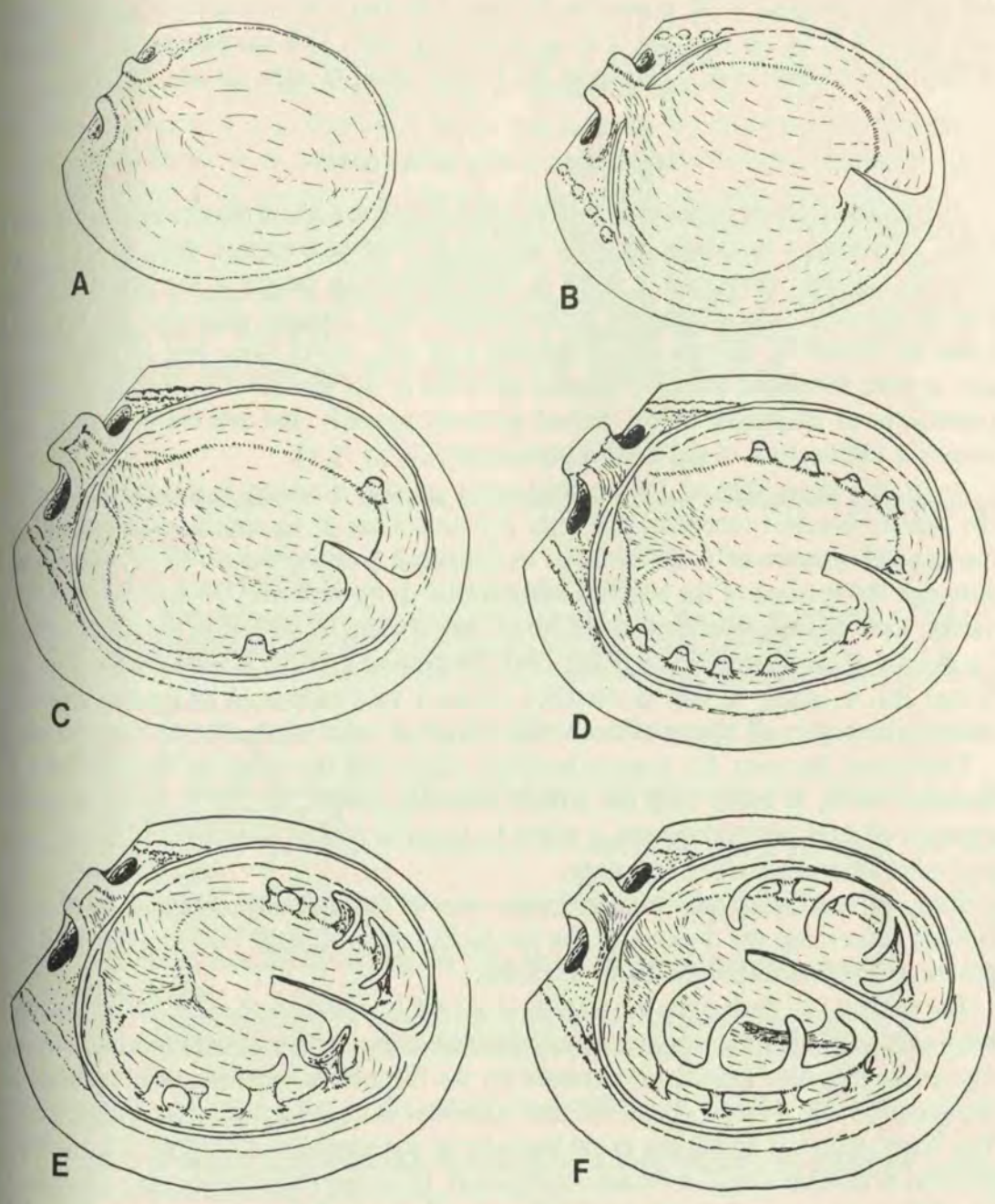
BAKER, *Moorellina granulosa*



TEXT-FIG. 3. Series of three-quarter profile drawings to show the development of the morphological features of the interior of the brachial valve of *Moorellina granulosa* (Moore) during ontogeny. A. brephic valve, B. pre-forbesiform stage, C. early forbesiform, D. late forbesiform, E. post-forbesiform F. adult valve.

brachial valve width of only 1·7 mm. (Moore's types 1·2–1·8 mm.). In addition, the posterior region of the sub-peripheral rim is different, the rim being inclined posteriorly in the majority of the large Dundry specimens and forming quite pronounced angles where it turns to unite with the bridge. In the Westington Hill and Moore's type material the rim remains vertical in this posterior region (Pl. 73, figs. 3–6). It is felt, therefore, that re-study of the larger forms must be undertaken in order to ascertain whether they

are properly assigned to *M. granulosa*. Although the stages show a general size increase, size is found to be no criterion of stage of development. This morphological variation is judged by Elliott (1948, p. 24) to be the natural result of intra-specific variation.

GENERAL OBSERVATIONS

As it appears almost impossible to clean brachial valves without destroying the brachial lobes, if present, a technique for serial sectioning oriented complete shells at 0·02 mm. intervals has been developed in order to discover the true nature of the brachial lobes and the nature of their attachment to the brachial valve. Sections show that the brachial lobes are extremely delicate (approximately 0·03 mm. thick) when first formed. They are, in fact, developed from the brachial tubercles in the manner described and extend posteriorly as crescentic horns, turned inwards, towards, but not uniting with, the posterior termination of the median septum (Pl. 74, fig. 5–8).

As, in the forms studied, the brachial lobes are only attached to the valve floor by the slender brachial tubercles, one feels that this must surely be the explanation for the general absence of brachial lobes in detached brachial valves of *M. granulosa*, although the remains of the brachial tubercles are quite common. On separation of the valves, such delicate structures could hardly be expected to survive in the accepted environment of the thecidellinids (Ager 1965, Nekvasilová 1967). It is probable that the bridge also is usually broken in detached valves, a view supported by the fact that the bridge is present in all sectioned shells with a brachial valve width of more than 0·8 mm.

Distinction between the post-forbesiform stage and the adult is not possible in brachial valves, in which only the broken tubercles remain. As size is found to be no criterion of stage of development, it might be better at present to include all forms with expanded tubercles in the adult stage.

Study of the Oolite Marl material may resolve the difficulty observed by Pajaud (1966*b*) concerning the division of the sub-family *Moorellininae* Pajaud 1966 into the genera *Moorellina* Elliott 1953 and *Rioultina*.

The criterion of distinction between these genera is said to be the absence of brachial lobes (*Moorellina*) or the presence of well established auriform brachial lobes (*Rioultina*). The genus *Elliottina* Pajaud 1963 created on the form of the area is wisely reduced to sub-generic rank. Pajaud maintains that *Rioultina* is evolved from *Moorellina* stock. The Westington Hill specimens might logically be considered to occupy an intermediate position in time (*Moorellina*, Rhaetic to Bajocian, *Rioultina*, Pliensbachian to Oxfordian). Careful comparison of the thecidellinid material of the British Museum and the Institute of Geological Sciences with that collected from Westington Hill shows a range of features in the Westington material which grade from moorellinid to rioultinid so that the only real difference is that of size. Rudwick (1962, p. 334) notes the occurrence of typically adult shells of *Terebratella inconspicua* (Sowerby) which are much below the normal size and attributes this to phenotypic stunting. It is equally possible that the material from Westington Hill represents a dwarfed population.

The ontogeny, however, shows the clear development of a ptycholophe (see Pajaud 1966*a*, p. 618) whereas *Rioultina* is said never to get beyond the schizolophe (Pajaud 1966*b*). The problem therefore, appears to be one of definition; either one must accept that some moorellinids do have brachial lobes or these forms must be referred to

a new genus. One hesitates to create further new genera until more is known about the relationship of the brachial with the pedicle valve. However, concerning the brachial valves of moorellinids it appears that the form of the brachial apparatus has a higher taxonomic value than the mere presence or absence of brachial lobes.

The presence of a ptycholophe in the genus poses the problem of its systematic position at family level, as the ptycholophe is regarded as a thecideid character. Owing to the difficulty of determining between post-forbesiform types and adults or even whether the ptycholophe is universally an adult character in the population its taxonomic significance can not yet be fully appreciated. However, the clear ability to develop a ptycholophe is regarded as being important, particularly in view of the phyletic relationships proposed by Rudwick (1968, p. 352) as it increases the probability that the simple ptycholophous thecideaceans have evolved from moorellinid stock.

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Significance of the punctation mosaic of the Jurassic thecidellinid brachiopod *Moorellina*

P. G. BAKER

(Plate 1)

Summary. Study of the punctation mosaics of *Moorellina granulosa* (Moore) and *Moorellina ornata* (Davidson), revealed by serial sectioning and stereoscan photomicrographs, shows that the apparent random distribution of punctae may be reconciled to two superimposed regular insertion patterns. Careful plotting of the endopunctae of *M. granulosa* from serial, cellulose acetate peels, reveals the presence of impersistent punctae. A new model is proposed, based on superimposed insertion patterns and offering an explanation for impersistence of punctae.

1. INTRODUCTION

Considerable attention has been paid to brachiopod punctation in recent years (De Haro, 1960; Kemezys, 1965; Cowen, 1966; Williams, 1956, 1965, 1966, 1968 a and b), but a really detailed account of the structure of caeca had not appeared until Owen & Williams's (1969) electron microscope studies. Study of the shells of living articulates confirms that endopunctae accommodate the caeca which originate in the outer lobe of the mantle and subsequently become enclosed within the shell as it is secreted.

Elliott (1953, 1955) arrived at the conclusion that all thecideidines are endopunctate, except possibly *Davidsonella.* In *M. granulosa* and *M. ornata* caecal development would appear, from the position of endopunctae very close to the shell margin, to be typically terebratulide in the manner illustrated by Williams (1956). However, although the endopunctae are formed in the terebratulide manner, there is a difference in that the cup-shaped distal enlargements have not been seen. There is also, no evidence of the deflection of secondary fibres adjacent to the punctae. Forms such as *M. ornata* used for comparison purposes are typically endopunctate but also without the deflection of fibres adjacent to the punctae.

2. DISCUSSION OF EXISTING MODELS

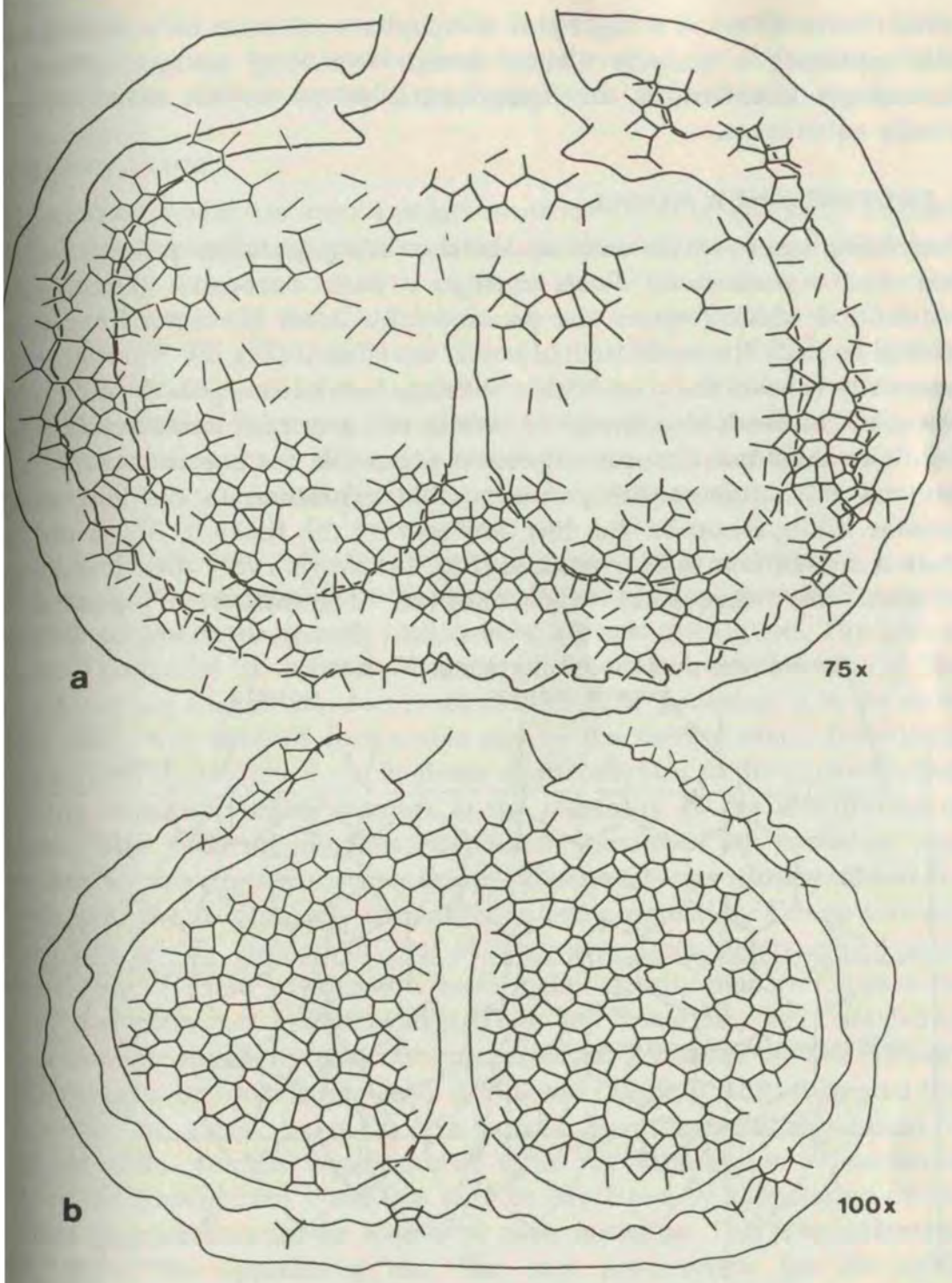
Study of the punctae of *M. granulosa* shows the random distribution (Plate 1a) noted by Elliott (1955). Cowen (1966) in his criticism of Kemezys' (1965) models has shown that the apparent 'rows' of punctae along growth lines are coincidental and has proposed a model based on De Haro (1960). However, in the light of Williams's work (1956, 1966, 1968a and b) on shell development it seems that the biological importance Kemezys attached to these rows is not without foundation. The evidence suggests that none of the models so far pro-

posed, satisfactorily meets the requirements of the observed thecidellinid mosaic. Elliott, in his reference to the irregularity of pattern, apparently overlooked the remarkable constancy (about 45μ) of the separation between punctae in thecidellinids such as *M. ornata*. Plate 1b shows this regularity of spacing, a feature which must be more than accidental.

Williams (1956, p.247, fig. 2) has shown that terebratuloid caeca have their origin at the outer boundary of the outer mantle lobe, where the secretion of the primary layer begins. Sectioned moorellinid material shows that the caeca originated in the same manner, as punctae clearly originate outside the boundary between the primary and secondary shell layers (Plate 1c). As punctae have their origin in the primary layer it is felt that their initiation must be related to the deposition of the primary layer. It is immaterial whether or how they are offset, for, if primary shell is deposited normal to the commissure, the order of appearance of punctae must be related either to growth lines (concentric) or to growth vectors (radial).

Work by De Haro (1960), indicating that the spacing of punctae might be functional and physiological, stimulated Cowen 1966) to advance the theory that the initiation of punctae may be expressed in terms of biological equipotential. Cowen's interpretative hypothesis suggests that new punctae develop where the potential of previously formed punctae falls below a critical level. This ideally, would produce a hexagonal mosaic but variables such as shell curvature must be invoked to account for the actual polygonal mosaic observed in shells (Fig. 1a, b). Plots of punctae in areas of shells showing no convexity should therefore show a close approximation to the hexagonal pattern but this is found not to be the case. Also, as a little experimentation will show, there is no reason why a hexagonal pattern should not find expression on a curved surface. It would appear, from the above, that the failure of the theoretical hexagonal pattern to find expression, except over small areas, is not to be correlated with shell curvature. However, Cowen's hypothesis of a potential gradient round each puncta (1966, p. 272) is an attractive one and from a purely physiological point of view, one feels that puncta insertion must be initiated in this way.

Cowen stated that in non-ideal (polygonal mosaic) situations the 'rows' of punctae cannot be maintained over more than small areas but made no attempt to explain why. In the present work attempts have been made to reconcile the observed punctation mosaic of *M. granulosa* with a workable model. If, as appears probable, there is some order regarding the insertion of punctae, one is forced to the conclusion that the regularity of insertion is masked in some way. As curvature is not critical, another answer must be sought. The theory of equipotential points appears sound but the appearance of punctae in the primary layer must be related to the deposition of that layer. Unfortunately, for Cowen's equipotential points to remain equidistant, it is required that growth be strictly linear. The growth of *M. granulosa* is



g. 1a. Reconstruction of the punctation mosaic (after Cowen, 1966) of a brachial valve *Moorellina granulosa* (Moore) from sixteen superimposed, cellulose acetate peels. The ter boundary of the sub-peripheral rim (outlined) marks the approximate position of e boundary between the primary and secondary shell layers.

Reconstruction of the punctation mosaic of *Moorellina ornata* (Davidson) from tereoscan photomicrograph of the interior of a brachial valve. Sub-peripheral rim (out-ed).

radial (Baker 1970). A straight plot of equipotential points on a radial growth field produces a packing which, though remaining hexagonal, becomes increasingly distorted, as the equipotential points do not remain concentrically equidistant.

3. PROPOSED NEW MODEL

Correlating equipotential with equidistance of equipotential points, one finds that two superimposed fields emerge, a basic concentric (commissural) distribution which requires the presence of a linear (theoretical hexagonal) control to keep the equipotential points equidistant (Fig. 2). Where growth is essentially linear the two fields overlap but where growth vectors are divergent the fields also diverge or overlap to a greater or lesser extent. Where the fields show maximum divergence it is possible for one or other, or even both of the equipotential points to find expression in the initiation of punctae. Comparison of the divergent part of the fields in Fig. 2 with the plotted distribution in *M. granulosa* (Fig. 1a) shows a very close resemblance between the theoretical and observed distribution of punctae in

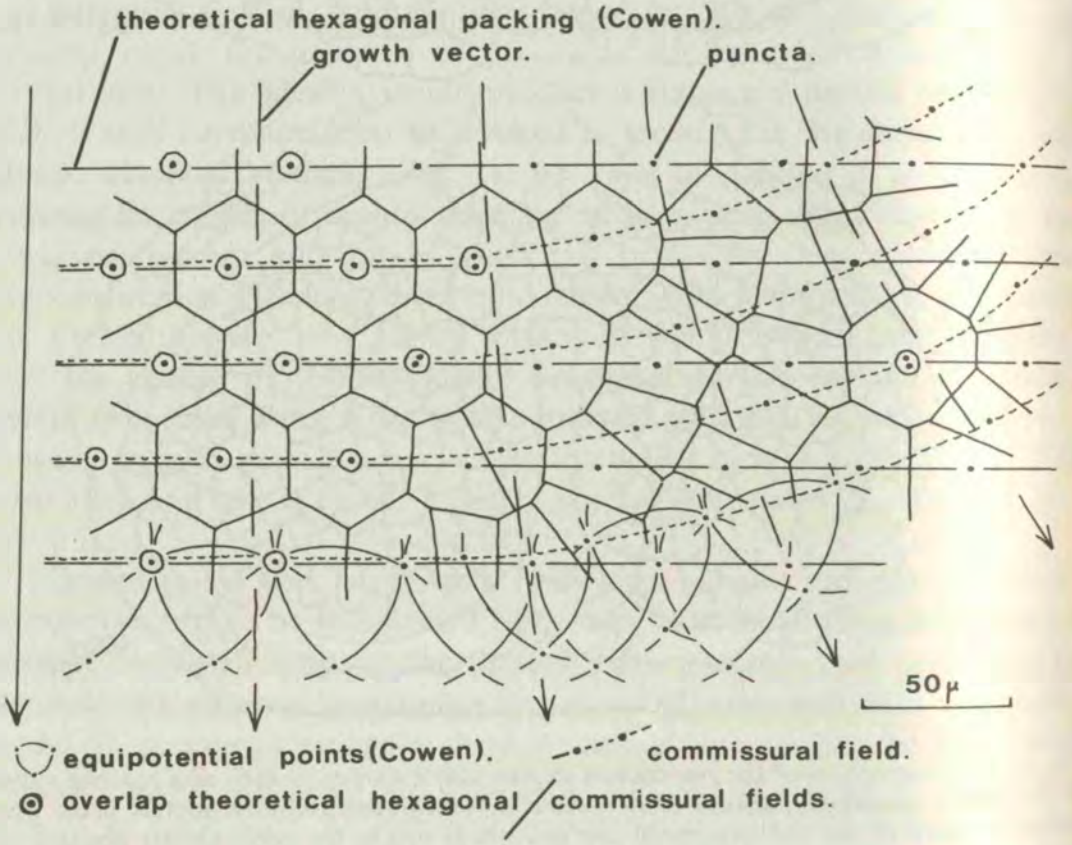


Fig. 2. Proposed new model superimposed upon the enlarged growth vector pattern from a stereoscan photomicrograph of the right antero-lateral sector of the exterior of a brachial valve of *M. granulosa*. The position of the commissure inferred by reference to growth lines.

ecidellinids. The apparent random distribution of punctae in thecidellinids d probably other brachiopods also, may therefore, be the result of the perimposition of two essentially regular patterns of distribution.

OBSERVATIONS

ıe proposed model has several points in its favour. It satisfactorily explains ıy regular separation of punctae is not maintained over more than short stances and often coincides with a growth line. It shows how and why (by gree of divergence) the field varies from time to time and offers an planation of the radial variation observed by Williams & Rowell (1965, 69). The model shows how apparently random mosaics may arise and rows important light on the distal coalescence (Cowen, 1966) and npersistence of punctae. Where the two fields are only slightly divergent, it possible for two terminal discs to appear having an equipotential common both fields (Fig. 2). In such a situation, coalescence to form a single ıncta, or degeneration of one or other is not difficult to envisage.

A mosaic approaching the theoretical hexagonal pattern will only be ıcountered where the growth vectors have a linear orientation. The greater gree of regularity of terebratuloids may therefore be a relative feature. The ternal surface area of an adult brachial valve of *M. granulosa* is in the order f 2.8 mm^2. Any zone of comparable size on the shell of even a fairly small rebratuloid, must show a much closer approximation to linear growth and, ierefore, a corresponding increase in the regularity of the distribution of unctae. The apparent random punctation mosaic of *M. granulosa* may ierefore be an attempt by the animal to reconcile its pronounced radial owth with the theoretically ideal distribution proposed by Cowen's model.

A plot of the endopunctae of *M. granulosa* from superimposed serial ctions (Fig. 3, Plate 1d) shows a much higher density than ever appears on ıe internal surface of brachial valves (Plate 1e). Some may be concealed by ıatrix but the possibility that the punctae of *M. granulosa* are not typically ersistent must be considered. Owen & Williams (1969, p. 189) suggested that oalescence of caecal bases may be caused by differential movement of pithelial cells. In the equipotential terms of superimposed punctation ıosaic, the impersistent condition may be explained by suppression of one r other of adjacent punctae soon after their initiation. This is an interesting oint when one appreciates that the only pre-requisite for the initial evelopment of caeca in impunctate shells, or their degeneration in ndopunctate shells, is the presence of secretory glands in the primary layer Williams & Rowell, 1965).

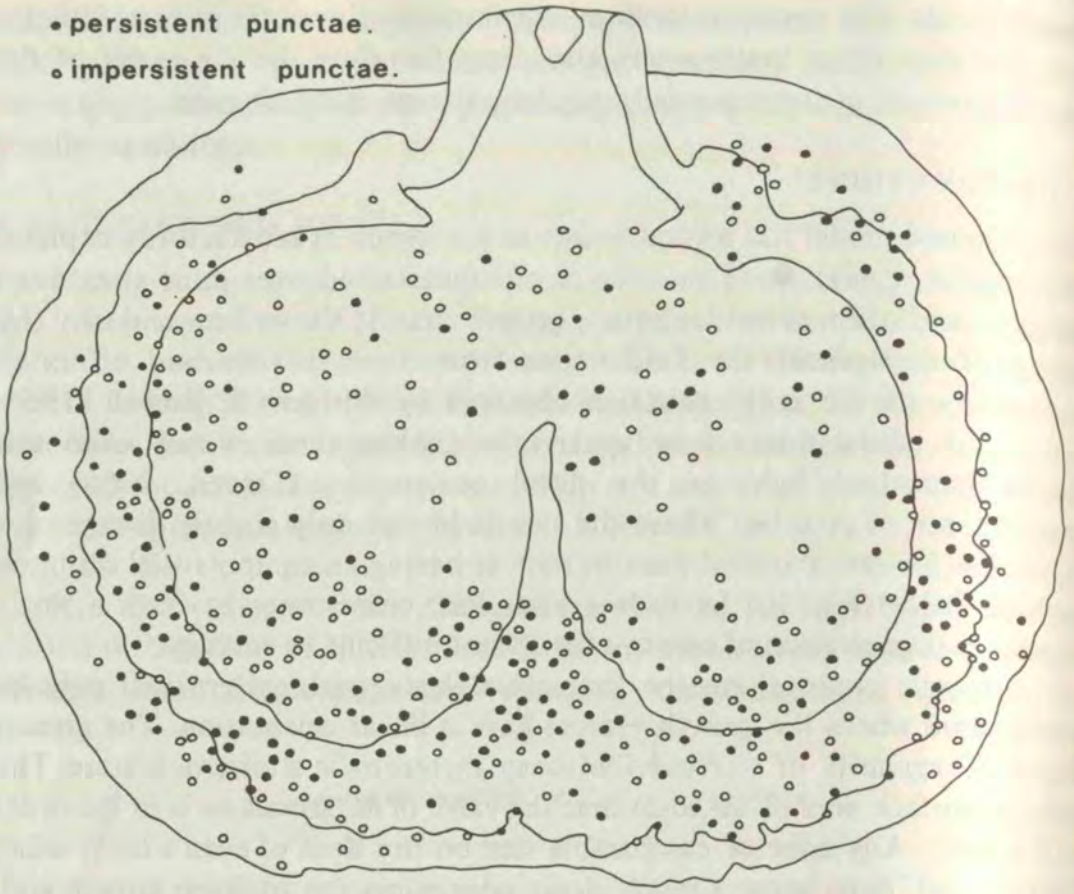


Fig. 3. Plot of persistent and impersistent punctae encountered during horizontal serial sectioning of a brachial valve of *M. granulosa.*

ACKNOWLEDGEMENTS

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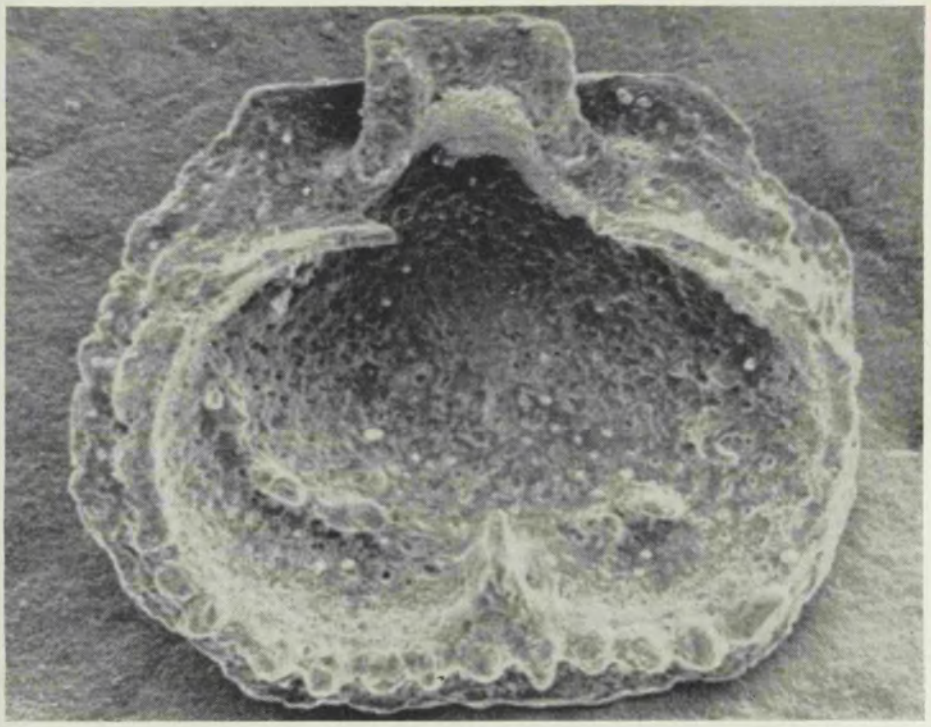
PLANATION OF PLATES

Stereoscan photomicrograph of the interior of a brachial valve of *Moorellina granulosa* ore) showing the appearance of endopunctae. x 50.
e. Scale represents 45μ.
Stereoscan photomicrograph showing the spacing of punctae in the floor of a brachial ity of *M. ornata.*
tereoscan photomicrograph of an aluminium shadowed cellulose acetate peel of a izontal section through a brachial valve of *M. granulosa* showing the occurrence of ctae in the primary layer (lower).
Stereoscan photomicrograph of an aluminium shadowed cellulose acetate peel of a izontal section through a brachial valve of *M. granulosa* showing the distribution of ctae close to the external surface.
Stereoscan photomicrograph of the sector of the interior of the brachial valve figured l, showing the decrease in the number of punctae at the inner surface of the shell.

Geol. Mag. Vol. **107**, 1970, P. G. Baker, plate 1, between pp. 112 and 113.



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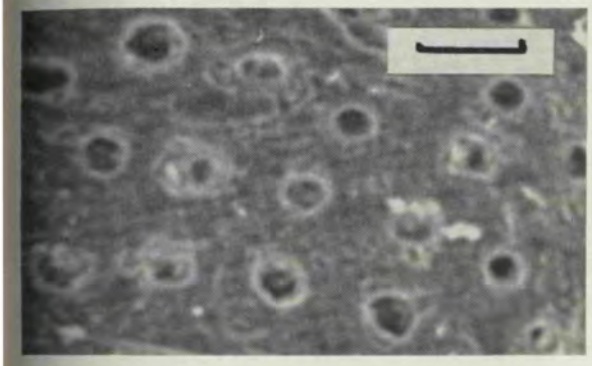

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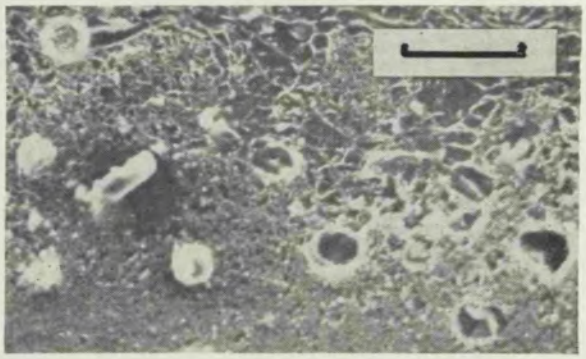

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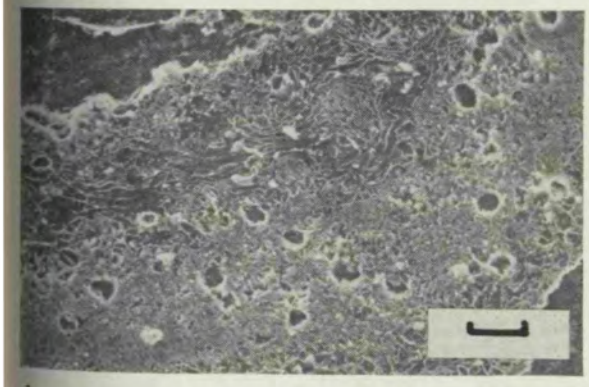

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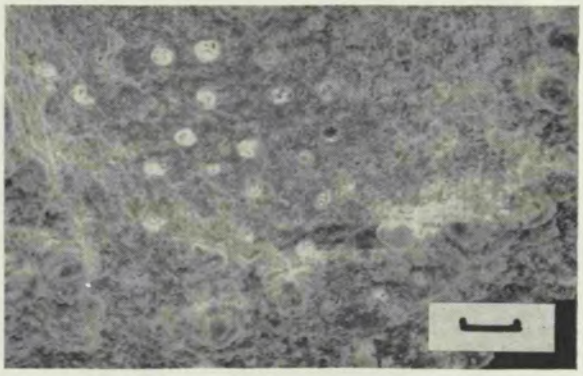

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The growth and shell microstructure of the thecideacean brachiopod *Moorellina granulosa* (Moore) from the Middle Jurassic of England

BY

P. G. BAKER

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THE GROWTH AND SHELL MICROSTRUCTURE OF THE THECIDEACEAN BRACHIOPOD *MOORELLINA GRANULOSA* (MOORE) FROM THE MIDDLE JURASSIC OF ENGLAND

by P. G. BAKER

ABSTRACT. Analysis of the growth habit of *M. granulosa* from a functional point of view has proved to be of value in the interpretation of shell microstructure. Serial sectioning of shells at 20 μ intervals has revealed that fibre orientation may change suddenly at various levels within a shell. The paper notes the need for detailed information regarding the orientation and location of sections through shells, as study of *M. granulosa* indicates this may be of critical importance. The shell-structure differs markedly from that of *Lacazella mediterranea* (Risso), as the shells of some, if not all Inferior Oolite thecidellinids were differentiated into primary and secondary layers. Interpretation of the microstructure has taken into account the effects of shell resorption in the brachial valve and the development of crescentic tubercles in the pedicle valve. Some evidence has been obtained which indicates that the pedicle opening of *M. granulosa* occupied a supra-apical position. Despite the general spiriferoid appearance of the shell-structure, the detailed microstructure of various morphological features of the two valves, together with bulk morphological similarities, are thought to suggest strophomenoid affinity.

THE microstructure outlined in this paper is based on combined evidence from serial sections and polished blocks prepared from fifty-three specimens, comprised of brachial valves, pedicle valves, and complete shells of *Moorellina granulosa* (Moore), from the Oolite Marl of Westington Hill Quarry in the Cotswolds. The stratigraphy and location of the quarry and the exact horizon from which the material was obtained have been described in a previous paper (Baker 1969). A further horizon has been located in a yellow-orange clay at the base of the Oolite Marl on the west face of the quarry but the material recovered was not sufficiently well-preserved for the study of shell microstructure.

In the material studied, many of the shells are recrystallized but some are well preserved. Partially recrystallized material is useful for comparing and contrasting the unaltered shell with diagenetic effects.

A discussion of the thecideacean environment and a detailed account of the morphology of the brachial valve (Pl. 18, fig. 1) is given in an earlier paper (Baker 1969).

The most prominent feature of thecideidines is the elaboration of the brachial apparatus. The inevitable result of interest in this structure is that in much of the published work the pedicle valve is neglected.

The pedicle valve of thecideaceans is subject to much less variation than the brachial valve and the pedicle valve of *M. granulosa* (Pl. 18, fig. 2) is morphologically very similar to that of *Bifolium faringdonense* (Dav.), described by Elliott (1948). Attachment to the substratum is by cementation and the shape of the pedicle valve is greatly influenced by the size of the scar of the area of attachment. Ontogenetic development of the valve concerns the appearance and development of crescentic tubercles, the change in position of the hinge teeth and the change in the relative proportion of the hemispondylium.

[Palaeontology, Vol. 13, Part 1, 1970, pp. 76–99, pls. 18–21.]

The shell of *M. granulosa* is endopunctate and shows the apparently random distribution noted by Elliott (1955). However, neither the models proposed by Kemežys (1965) nor Cowen (1966), satisfactorily explain the punctation mosaic observed in thecidellinids. An account of the punctation mosaic and the proposal of a new model is to be published separately.

During analysis of the microstructure, particular care has been taken to attach significance only to structures seen in at least six different specimens. Occasional peculiar features are noted which may be important but occur so infrequently in the material studied that firm conclusions must not be drawn from them.

Acknowledgements. The author is indebted to Dr. J. D. Hudson, Geology Department, University of Leicester, for supervision of the preparation of this paper. Thanks are due to Dr. M. Talbot, Geology Department, University of Dundee, for the loan of Upper Oxfordian material for comparison purposes and to Mr. G. McTurk for preparing the stereoscan negatives. Finally I wish to thank Professor P. C. Sylvester-Bradley for use of the research facilities of the University of Leicester.

Registration of material. The material figured in this paper, in the form of etched blocks and complete specimens, together with original peels and, where available, duplicates, is to be housed in the museum collection of the Department of Geology, University of Leicester, under the catalogue numbers quoted.

PREPARATION OF MATERIAL

A comprehensive account of the preparation of Oolite Marl material is given in Baker (1969) and the material studied in the present paper was obtained by the same method. For microstructure investigation however, it has been discovered that reduction of the etching time from ten seconds in 5 % HCl, to eight seconds in 3 % HCl yields better results. In addition it was found that fresh resin does not make a good bond with plain glass slides and blocks may become detached during sectioning. A more effective bond is obtained by the use of ground glass slides.

GROWTH AND DEVELOPMENT OF THE SHELL

General. The nature of shell growth is mixoperipheral, leading to a strophic condition (Rudwick 1959, p. 18), as, contrary to the belief of Elliott (1965), a small hypercline dorsal interarea (by definition, Williams 1965, H59) is present (Pl. 18, fig. 5). The lateral profile is obscured by the area of attachment but in forms with a small area of attachment, may be described as modified plano- to concavo-convex with a rectimarginate commisure. Certain differences in the development of structures in the brachial and pedicle valves have taxonomic significance and they will be discussed separately, following an account of the general shell growth.

A comprehensive account of shell deposition in living brachiopods is given by Williams (1956, 1966, 1968*a*, *b*), Williams *et al.* (1965) and it is reasonable to suppose the shell of *Moorellina granulosa* (Moore) was deposited in the same manner. Evidence presented in this paper shows that Williams (1968*a*) is in error in regarding the single layered shell of *Lacazella mediterranea* (Risso) as typical of the thecideidine shell structure. *M. granulosa* clearly shows the development of primary and secondary shell layers.

As described in an earlier paper (Baker 1969) the brachial valve of *M. granulosa* is initially almost circular, later becoming broader than long. However, study of a number

of specimens shows that the shape of the brachial valve is really controlled by the shape of the pedicle valve, which is itself strongly influenced by the size of the scar of the area of attachment. Williams (1956) has shown that although cell division occurs throughout the epithelium the enlargement of the brachiopod shell is controlled mainly by peripheral zones of growth.

Various aspects of the mode of shell growth have been defined by Rudwick (1959, p. 2). It is convenient for the purpose of demonstrating the mode of growth in *M. granulosa* to use his second interpretation, i.e. that the shell surface represents a series of sectors which were formed continuously by different arcs of the valve edge.

At a magnification of 250× linear, the external surface of the shell of well-preserved specimens of *M. granulosa* is seen to be covered with small fibres. These fibres are inclined radially outwards from the umbo at a low angle from the shell surface and show an orientation normal to the growth-lines and commissure (Pl. 18, fig. 3). If one assumes that the fibres are associated with the deposition of primary shell, either mechanically or crystallographically, their orientation directions may be used as growth vectors for the determination of points of relatively rapid increase in various arcs of the commissure.

Rudwick has shown how growth at any point on the valve edge may be resolved into component growth rates. By assigning a value of one growth unit to an arbitrary surface area corresponding to Rudwick's growth points (1959, text-fig. 1*a*), provided that the growth vectors are known, different rates of growth in different sectors of a shell can be fairly accurately determined. To demonstrate this adequately in *M. granulosa* necessitates the introduction of additional 'momentary' and 'cumulative' terms. The growth vector may be regarded as the cumulative product of the arrangement of growth units normal to the mantle edge. The total number of growth units per growth vector may be represented as $d/\sqrt{x}$, where d represents the length of the vector and x represents the surface area of the growth unit. *Proliferation points* occur where the distance between two growth vectors has doubled and *proliferation arcs* are represented by lines joining series of new proliferation points. The growth rate in any sectors may be determined by the *growth acceleration*, v, which is represented by the number of proliferation arcs in any sector. The *relative growth index* may therefore be expressed as $v(d/\sqrt{x})$ for any sector

EXPLANATION OF PLATE 18

Stereoscan photomicrographs of specimens of *Moorellina granulosa* (Moore) from the Oolite Marl, Westington Hill Quarry near Chipping Camden. All figures are of specimens coated with evaporated aluminium before photography.

Fig. 1. Interior view of a brachial valve (37512) showing the median septum and tuberculate sub-peripheral rim. Bridge and brachial apparatus broken. ×40.

Fig. 2. Interior view of a pedicle valve (37513) showing the teeth, supported hemispondylium and the sub-peripheral crescentic tubercles. Umbonal cavity filled by the broken cardinal process. ×40.

Fig. 3. External surface of a portion of the left postero-lateral region of a brachial valve (37512) showing the oriented fibres on the surface of the primary layer. Scale represents 30 μ.

Fig. 4. Lateral view of a complete specimen (37511) showing the growth habit and large free ventral anterior surface. ×50.

Fig. 5. Posterior view of specimen (37511) showing the large, ventral and small, dorsal interareas. Angle of incidence 40°. ×40.

Fig. 6. Profile view of an enlarged portion of specimen (37513) showing the supporting septum of the hemispondylium, with the dental ridges continuous with the outer edges of the hemispondylial plates. Angle of incidence 60°. ×65.

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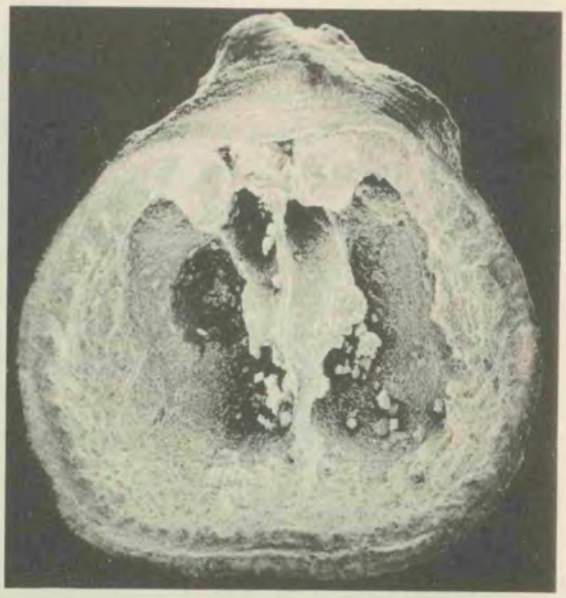

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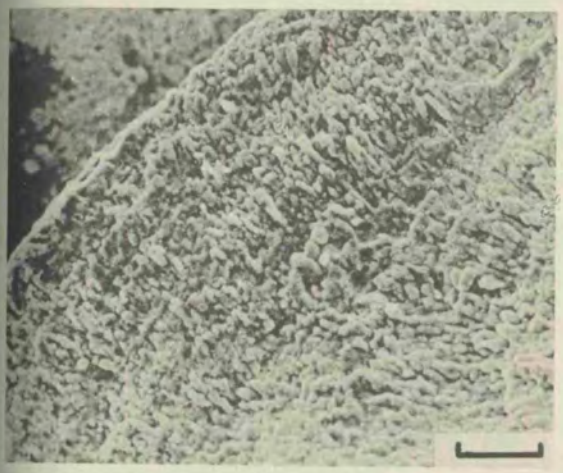

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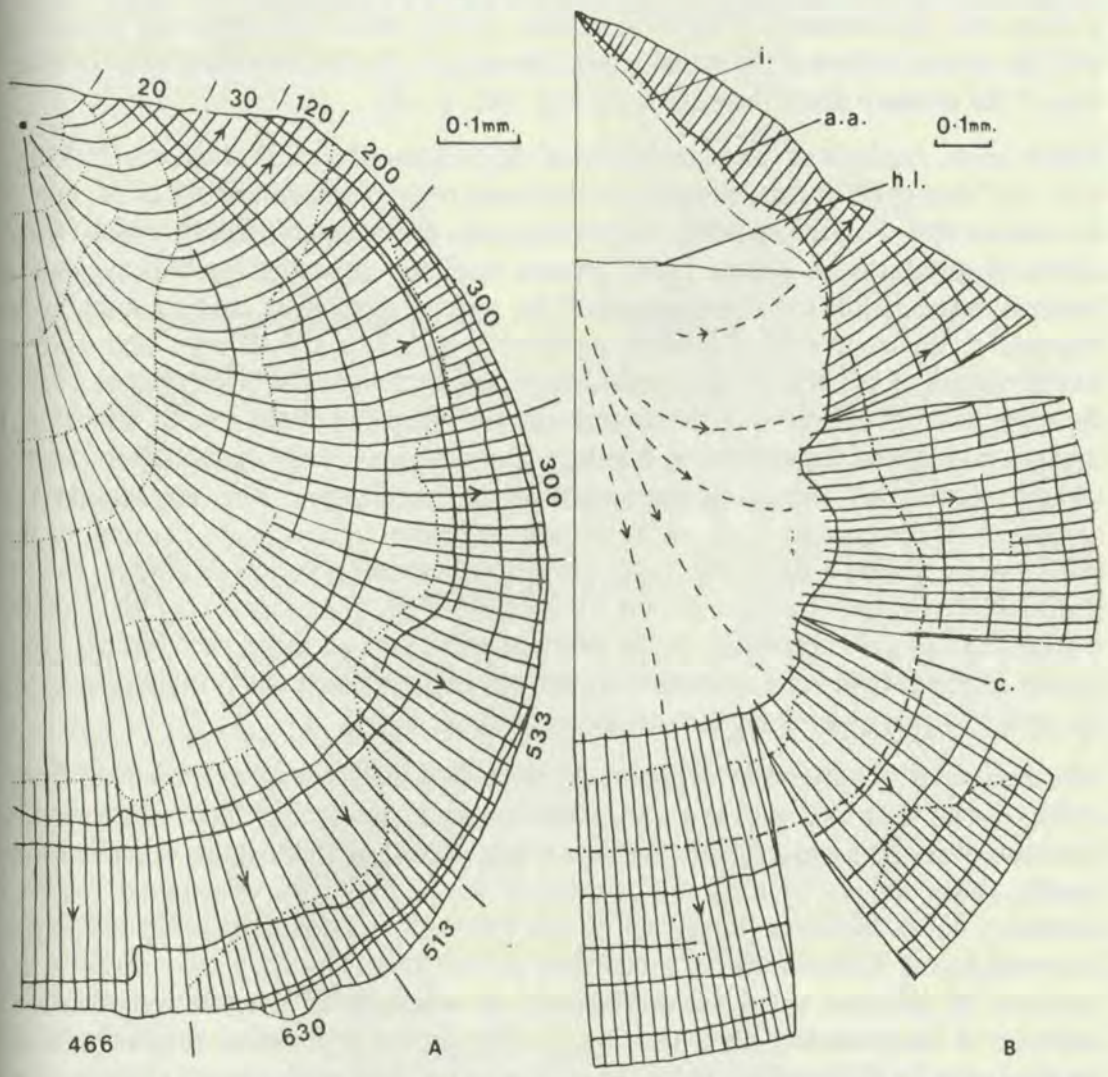
BAKER, *Moorellina granulosa*

of the valve. In Rudwick's terms, proliferation points and proliferation arcs are momentary and growth acceleration and relative growth index are cumulative.



TEXT-FIG. 1. Reconstruction of the primary growth vectors of *M. granulosa*, plotted from oriented fibres. Proliferation arcs dotted. Concentric lines represent visible growth-lines. A. Right half of a brachial valve. Numbers indicate relative growth indices in different sectors. B. Right half of a pedicle valve. Broken lines within the area of attachment represent the vector mosaic inferred by the brachial valve. Commissure projected stereographically to allow plotting of the primary growth vectors. The relative position of a.a. edge of the area of attachment, c. commissure and i. edge of interarea, plotted from cellulose acetate peels. h.l. hinge-line.

Brachial valve. The growth of the brachial valve of *M. granulosa*, when expressed in the manner outlined, shows a marked radial pattern with a high relative growth-rate anterolaterally (text-fig. 1A). For the reasons outlined in Williams and Wright (1963) it is considered that it is only necessary to plot the data for one-half of the valve.

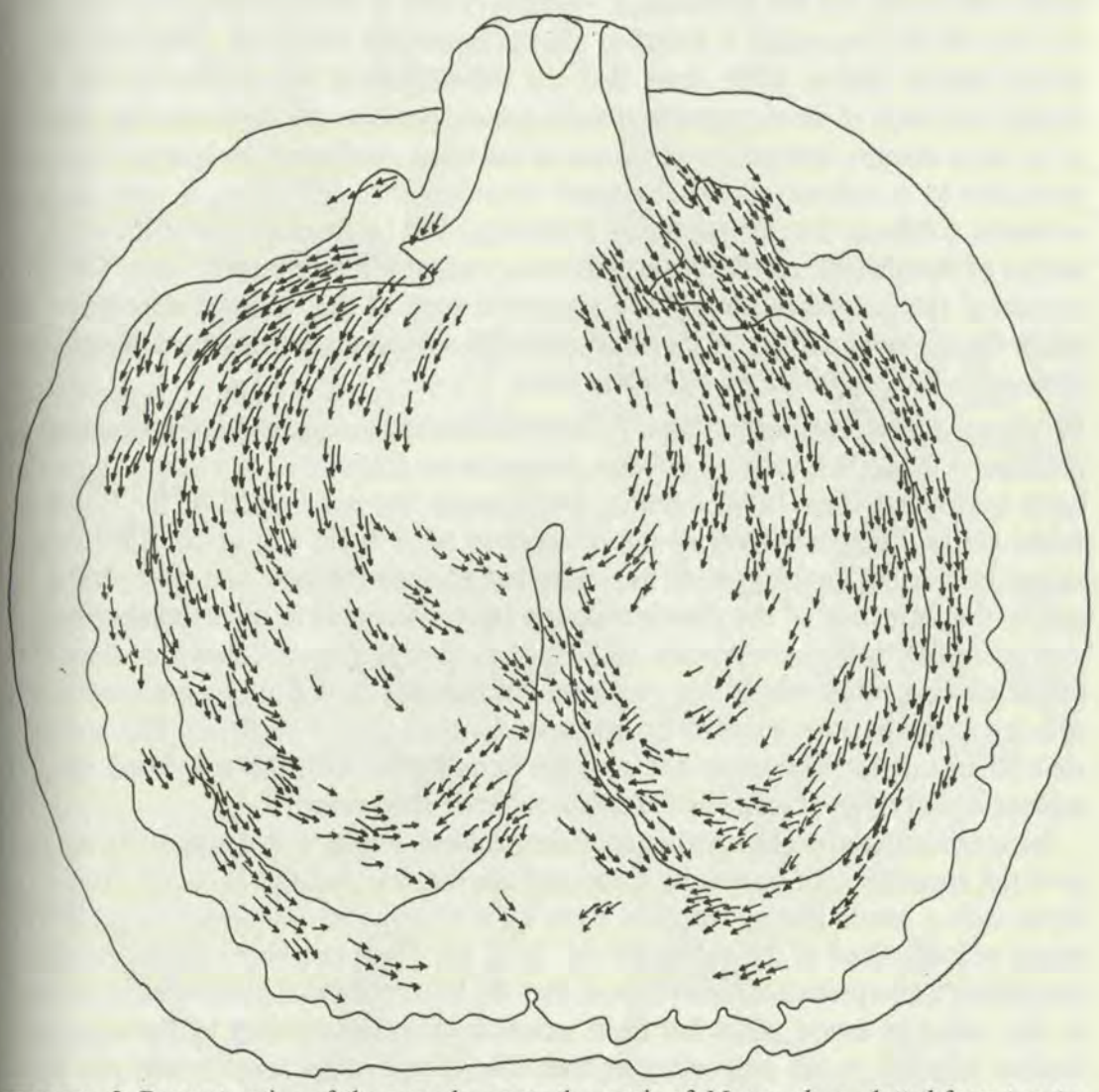
The validity of the above interpretation obviously rests on the assumption that the proposed association of fibre orientation with deposition of the primary layer is correct. The author is alive to the possibility that in the material investigated, the growth vectors

are not recorded from the exposed ends of primary fibres but from crystallites growing on their outer ends. However, the fibre orientation pattern shows a remarkable constancy in the thirty external brachial surfaces examined. Even if the development of the fibres is diagenetic, the constancy of their orientation pattern must be in some way connected with the microstructure of the primary layer, most probably the crystallographic orientation of the primary fibres themselves (Cloud 1942, p. 24).

Pedicle valve. Analysis of the growth-lines of the pedicle valve of *Thecidiopsis* (Nekvasilová 1967) has enabled determination of the mode of development. Study of *M. granulosa* shows that the pedicle valve exhibits the same development régime, which, when advanced, produces an almost linear pattern masking the radial growth typical of brachial valves. After the development of the area of attachment and presumably in response to environmental influence, material is added to the anterior and antero-lateral regions of the pedicle valve much more rapidly than in the other regions so that the angle between the plane of the commissure and the plane of the area of attachment changes rapidly and the anterior and antero-lateral regions of the shell develop rapidly without appreciably increasing the length of the commissure. This means that the deposition of the primary layer of the pedicle valve although remaining normal to the valve margin shows a distinctly linear growth orientation anteriorly (text-fig. 1B). In Rudwick's terms therefore, the growth of the shell of *M. granulosa* is characterized by a declining vertical component in the brachial valve and an increasing vertical component in the pedicle valve, a cumulative growth pattern which obviously serves to lift the anterior gape away from the substratum (Pl. 18, fig. 4).

Secondary layer. As shown by Williams the secondary shell consists essentially of fibres arranged with their long axes at a low inclination to the internal surface of the primary layer and overlapping to a greater or lesser extent according to the angle of inclination, usually about 10°. By plotting the orientation of the long axes of exposed parts of secondary fibres, Williams (1968*a*, pp. 10–15) has demonstrated a discernible lineation in several genera. Construction of a secondary growth mosaic for *M. granulosa* shows the existence of the same spiral arc arrangement in which there is a relatively constant deflexion of the secondary fibres (text-fig. 2). The pattern is modified anteriorly in the brachial valve by the development of the relatively very thickened anterior of the median septum. There is no sign of peripheral reorientation normal to the shell edge but this may simply be the result of the disruptive influence of the tubercle cores. Williams (1966, p. 1148) notes the blurring of the pattern in areas of excessive calcite deposition in terebratuloids. In the pedicle valve also, the spiral arc pattern is modified anteriorly by the development of the crescentic tubercles. However, although Williams is able to demonstrate the bulk migration of the mantle in the direction of growth (1968*a*, p. 8) in order to account for the inclination of secondary fibres, the reason for the migration has not been explained. Study of his text-figure makes it apparent that it is impossible to extend the fibre series anteriorly or posteriorly without changing their inclination. The situation is further complicated by trying to impose the model on a convex shell. There is ample figured evidence, however, to show that his account of fibre shape must be correct. The solution to the problem must, therefore, lie in the orientation of the fibres themselves. The length of the fibres in any zone of the shell seems to remain fairly constant, suggesting that the cells of the epithelium secreting them have a standard life and

secretory activity. Obviously the rate of cell division in the mantle groove must vary to account for the growth characteristics of the shell. If the organization of the cells is such that the calcite of the secondary fibres is secreted at a fairly constant rate, areas showing



TEXT-FIG. 2. Reconstruction of the secondary growth mosaic of *M. granulosa*, plotted from twenty-five superimposed peels. Solid outline represents the position of the sub-peripheral rim, median septum, and cardinal process.

a relatively slow vectoral primary growth rate, i.e. postero-lateral sectors, must suffer from a build-up of secondary shell, unless the fibres are deflected away from the primary growth vectors in order to prevent the shell from becoming excessively thickened. Conversely the fibres may be deflected towards areas where thickening of the shell is taking place, such as the development of the median septum (text-fig. 2). This orientation deflexion of the secondary fibres away from sectors of relatively decelerated deposition of primary shell material would readily explain the forward migration of the secreting cells and the difference in orientation between the vectors of the primary and secondary layers (text-figs. 1A, 2).

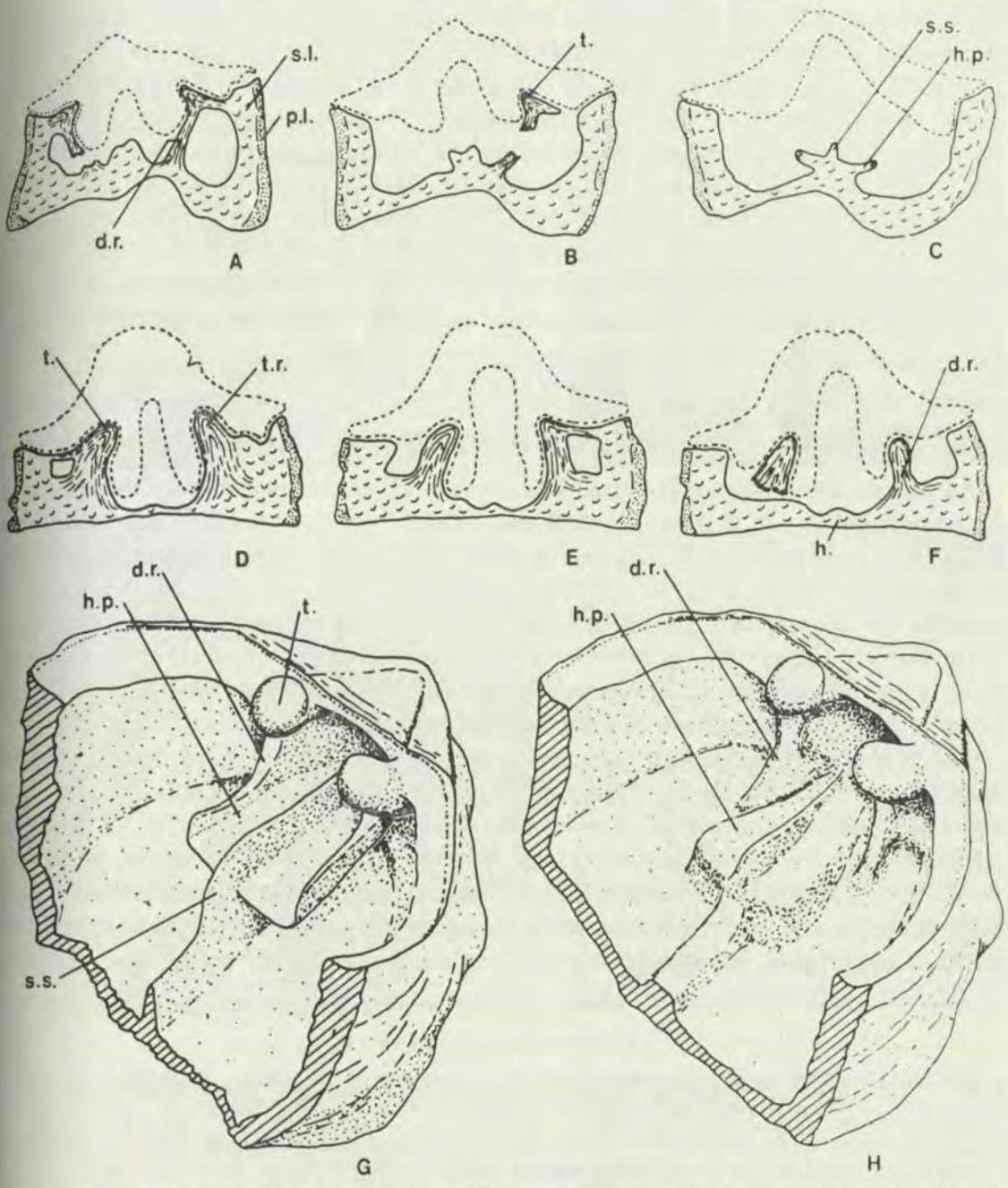
DEVELOPMENT OF SPECIFIC STRUCTURES

Development of the sub-peripheral rim. Very little progress regarding the determination of the microstructure of the brachial valve was made until the mode of development of the sub-peripheral rim was appreciated. Williams (1968*a*, p. 50) described local resorption in *Lacazella* and resorption is found to play an important role in *M. granulosa*. Ontogenetic studies (Baker 1969) show that the sub-peripheral rim appears at the pre-forbesiform stage of development and subsequently occupies the same position relative to the valve margin, irrespective of the size of the valve. As the sub-peripheral rim is too prominent to be submerged by subsequent secondary shell deposition, it must migrate outwards. Evidence that the migration is accomplished by development at the external margin of the rim and resorption along its inner margin will be presented later. The sub-peripheral rim is tuberculate and the generative zone of the tubercles appears to be where the secretory activity of the outer epithelial cells changes from the deposition of primary to the deposition of secondary fibres.

Development of the hemispondylium. Elliott (1948) noted the presence of a structure in the floor of the pedicle valve of *Bifolium faringdonense* (Davidson) to which he gave the name hemispondylium. In his opinion, the structure was not formed by the fusion of dental plates. Elliott also noticed the presence of what might almost be called dental ridges, buttressing the hinge teeth internally but adopted the view that they played no part in the formation of the muscle supports (spondylium) as in other brachiopods, a view confirmed by the present work. Some specimens of *M. granulosa* however, show that the buttressing ridges which may represent rudimentary dental plates, are continuous with the upturned outer edges of the hemispondylial plates (Pl. 18, fig. 6). This arrangement is an interesting feature and may be homologous with the ankylosed median septum–dental ridge structure of the davidsoniacean *Orthotetes*.

Sectioned material enables resolution of the problem. Forms with a supporting septum have the appearance of possessing a spondylium simplex (text-fig. 3A–C, G). However, forms with a sessile hemispondylium show quite clearly that the dental ridges simply merge with the floor of the valve (text-fig. 3D–F, H). There can be no doubt therefore, that Elliott's interpretation is correct and that the hemispondylial plates are not formed by the fusion of dental plates but from secretion of secondary shell by the outer epithelium adjacent to the supporting septum. The dental ridges may or may not unite with them depending on the growth habit of the valve. In forms with well-developed dental ridges it is possible to obtain sections which are strikingly similar to sections through the umbonal region of pedicle valves of *Derbyia* (Williams *et al.* 1965, H404, fig. 261 D). As Nekvasilová (1964) has recorded in *Lacazella* (*B*) *lacazelliformis* (Elliott) and as Elliott has recorded in *B. faringdonense*, the hemispondylium is present in the smallest valves studied and may be sessile or supported by a median septum. Rare specimens may show the hemispondylial plates supported by a double septum anteriorly. A single specimen of *M. granulosa* shows the hemispondylial plates supported by three septa whilst another (Pl. 19, fig. 1) shows a reticulate support. The form of the hemispondylium may be correlated with the form of the area of attachment and is apparently related to muscle efficiency (Elliott 1948, p. 20).

Development of the crescentic tubercles. Post-forbesiform and adult pedicle valves are characterized by the development of structures along the internal edge of the valve



TEXT-FIG. 3. A–C. Three serial sections through *M. granulosa* to show the form of the supported hemispondylium. D–F. Three serial sections, showing the form of the sessile hemispondylium. G. Three-quarters profile reconstruction of a supported hemispondylium, showing the dental ridges continuous with the hemispondylial plates. H. Three-quarters profile reconstruction of a sessile hemispondylium, showing the dental ridges merging with the floor of the valve. Outline of brachial valve dotted. d.r. dental ridge, h. root of sessile hemispondylium, h.p. hemispondylial plate, p.1. primary layer, s.l. secondary layer, s.s. supporting septum, t. tooth, t.r. tooth ridge.

margin (Pl. 18, fig. 2; Pl. 19, fig 2). which Elliott in *B. faringdonense* has called sub-pustulose marginal ornament. In *M. granulosa* these structures can be shown to be modified tubercles and are thought to be of considerable importance. As their shape is quite characteristic it is proposed to designate them crescentic tubercles. They appear

to be most strongly developed in the anterior and antero-lateral sectors of the valve and show a development pattern entirely different from that of the tubercles of the sub-peripheral rim. Crescentic tubercles do not appear until the anterior of the pedicle valve begins to grow away from the attachment surface. They apparently grow simply by the incremental addition of material at their distal ends and the secreting cells must occupy an invagination of the outer epithelium so that the tubercle cores stay slightly in advance of adjacent outer epithelial secretory cells. Their relationship with adjacent secondary fibres would indicate that their long axes are not quite parallel with the internal shell surface but inclined dorsally inwards at an angle of about 2°. This development pattern of the crescentic tubercles is obviously related to the maintenance of a constant orientation relative to the tubercles of the sub-peripheral rim (text-fig. 6A, C).

DETAILED MICROSTRUCTURE

As already noted, *Moorellina granulosa* (Moore) offers conclusive proof that in some Jurassic thecidellinids at least, the shell was differentiated into primary and secondary layers. The primary layer is best seen in the pedicle valve where it is relatively much thicker than in the brachial valve. It is possible that in some specimens the thin primary layer may occur only sporadically as in orthoids and strophomenoids where its absence is attributable to wear of a very thin layer. The possibility of the removal of the primary layer is important in the interpretation of occasional pitted structures, described later, occurring in the outer surface of some brachial valves.

The primary crystallite mat gives the typical fibrous, transverse (Pl. 19, fig. 3) and pitted, horizontal (Pl. 19, fig. 4) sections described by Williams. Transverse sections through secondary fibres show typical cross-sections (Williams 1968*a*, p. 9) with the exception that the lateral areas are much reduced so that a sub-hexagonal pattern is produced (Pl. 19, fig. 5). This standard shape appears to persist throughout the secondary layer of the pedicle valve but shows some modification in the brachial valve. Patches of fibres in the brachial valve show dorso-ventral flattening distally so that they develop

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EXPLANATION OF PLATE 19

Stereoscan photomicrographs of specimens of *Moorellina granulosa* (Moore). Material of all figures coated with evaporated aluminium before photography.

Fig. 1. Interior view of a broken pedicle valve (37514) showing the hemispondylial plates supported by a reticulate structure. Umbonal region missing. × 40.

Fig. 2. Enlarged portion of the margin of pedicle valve (37515), showing the position and characteristic shape of the crescentic tubercles. × 170.

Fig. 3. Etched surface prepared from polished block (37516) showing the primary layer in transverse section, lower right, and detail of the junction with the secondary layer. Section orientation: vertical, longitudinal. Section location: pedicle valve, free anterior surface, close to the area of attachment. Scale represents 4 μ.

Fig. 4. Stereoscanned cellulose acetate peel (37518), showing the primary layer in horizontal section, lower right. Section orientation: perpendicular to the plane of the commissure at 75° to the long axis. Section location: pedicle valve, left postero-lateral sector. Scale represents 8 μ.

Fig. 5. Stereoscanned cellulose acetate peel (37518) showing transverse section through secondary fibres. Section orientation and location as fig. 4. Scale represents 5 μ.

Fig. 6. Interior of the brachial valve of a pre-forbesiform individual (37503) showing endopuncta and the exposed inner ends of secondary fibres on the floor of the left brachial cavity. Scale represents 5 μ.

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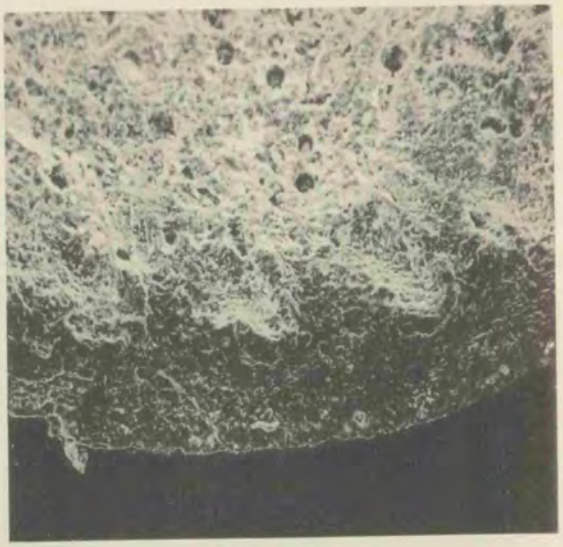

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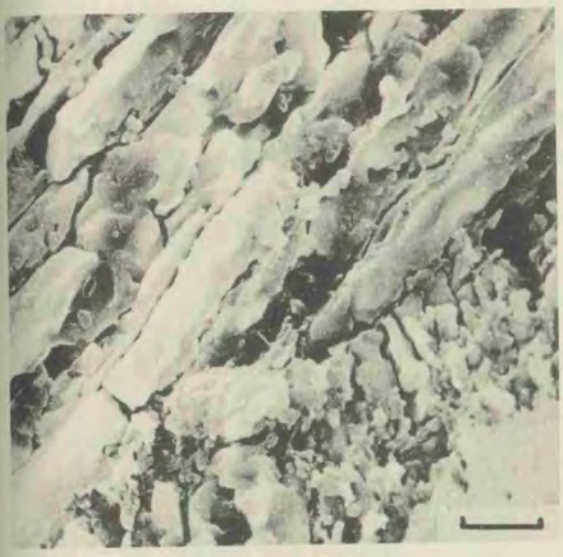

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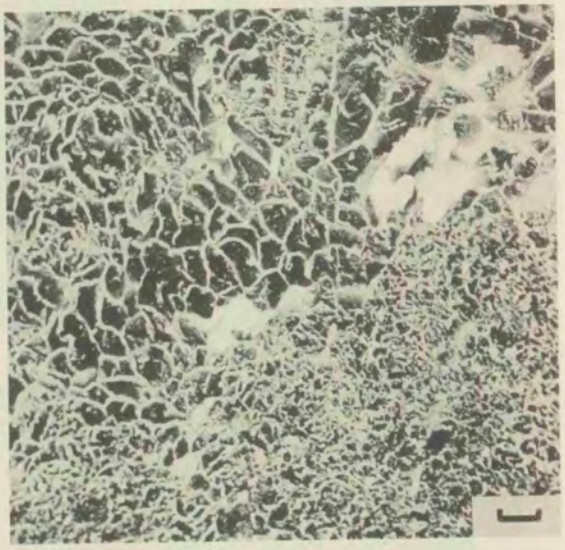

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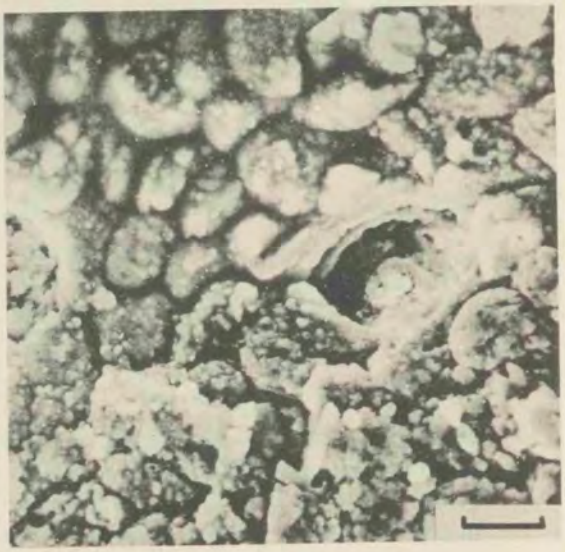

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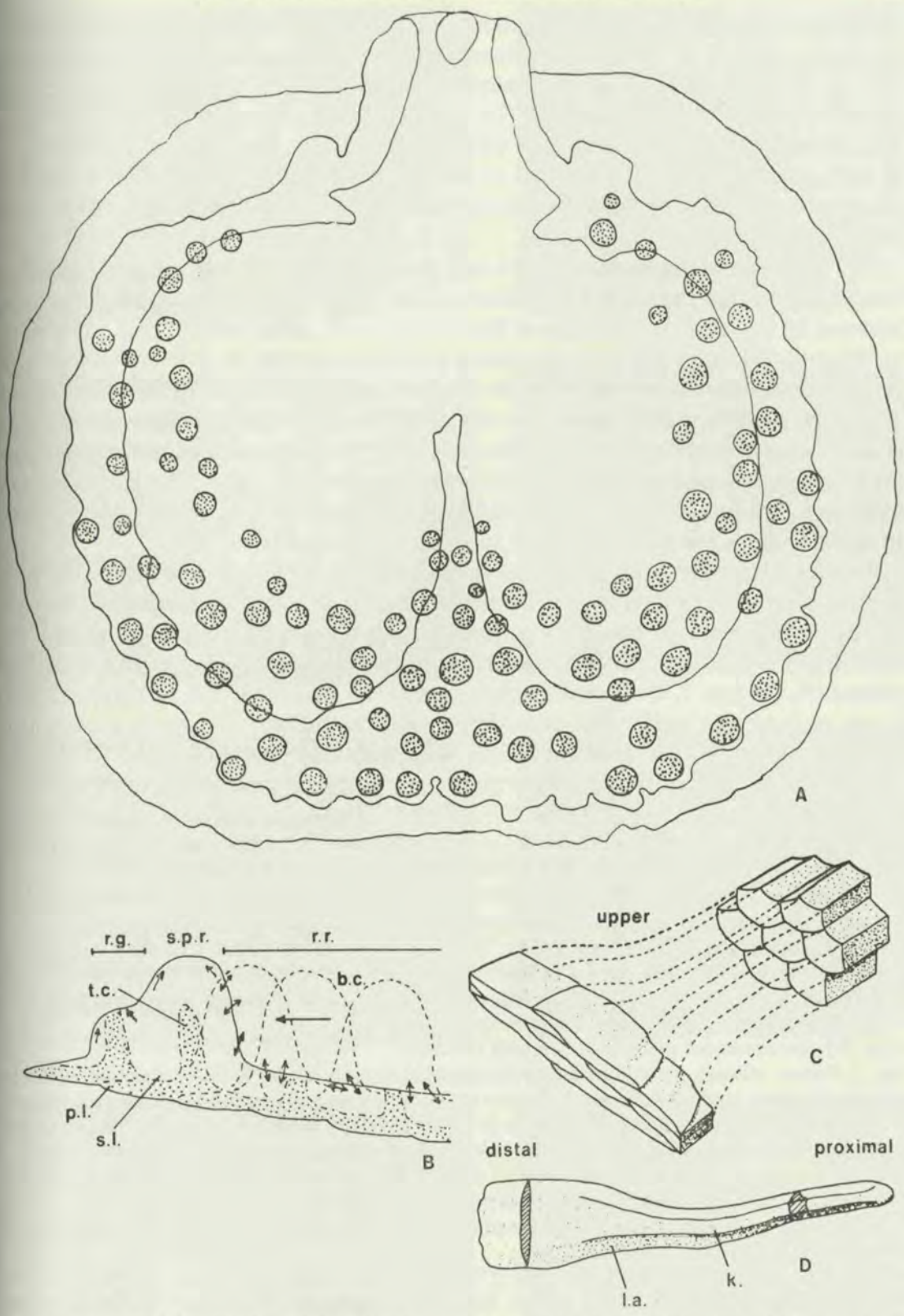
BAKER, *Moorellina granulosa*



TEXT-FIG. 4. A. The distribution of the tubercle cores (dotted) in the brachial valve of *M. granulosa*, plotted from twenty-five superimposed peels. The core distribution inside the sub-peripheral rim, outlined, indicates the areas of the brachial cavities where resorption has occurred. B. Diagrammatic representation of the probable mode of migration of the sub-peripheral rim during growth. C. Normal and flared transverse mosaics. D. Diagram to show the shape of an individual fibre. b.c. brachial cavity, k. keel, l.a. lateral area, p.l. primary layer, r.g. rim generation zone, r.r. rim resorption zone, s.l. secondary layer, s.p.r. sub-peripheral rim, t.c. tubercle core.

flared ends (text-fig. 4C, D). The possibility that these were merely apparent transverse sections, produced by fibre reorientation was checked against horizontal longitudinal sections through fibres. The flared secondary fibres have a characteristic strap-like appearance and are up to three times (10–12 μ) the width of normal fibres. It is possible that the modified fibres are associated with muscle scars but this could not be confirmed in the material studied. The location of the sections however, would suggest that the fibres occur in zones of the valve which were not areas likely to be associated with muscle attachment.

The variability of the fibres in section and the consequent possibility of misinterpretation of sections has been noted by Williams (1966, p. 1148). The present work has been hindered by the same rapid changes of fibre orientation. Studies indicate that orientation variation in the secondary layer may occur at different depths, in different sectors of a valve, and that the microstructure of the brachial and pedicle valves of the same animal may show significant differences. For this reason it is felt that all future plate figures must be accompanied by accurate data concerning the orientation of sections through the specimen and the exact location of the section on the shell. The author has attempted to present such data in a concise form in the plate explanations, to enable other workers to avoid or duplicate these sections in subsequent investigations.

Relatively large areas of the brachial cavities of *M. granulosa* are formed by the progressive resorption of the sub-peripheral rim (text-fig. 4A, B). As a result of resorption in these areas, the fibre orientation persisting at the bases of former sub-peripheral rim tubercles is exposed on the internal surface of the valve, producing a very disturbed pattern (Pl. 20, figs. 1, 2). Once the significance of rim resorption had been appreciated, it was realized that undisturbed secondary mosaic would only be seen in areas which were not affected by shell resorption. This suggested three possible sites, (*a*) the border

EXPLANATION OF PLATE 20

Stereoscan photomicrographs of *Moorellina granulosa* (Moore) except figs. 7 and 8. Material of all figures coated with evaporated aluminium before photography.

Fig. 1. Interior view of a brachial valve (37519), showing an endopuncta and disturbed secondary mosaic, right, in the area affected by resorption of the sub-peripheral rim. Scale represents 5 μ.

Fig. 2. Stereoscanned cellulose acetate peel (37520), showing the disturbed secondary layer of the brachial valve and the development of flared fibres, lower centre. Section orientation: parallel with the plane of the antero-lateral surface. Section location: right antero-lateral sector 0·12 mm. from the external surface of the valve. Scale represents 25 μ.

Figs. 3–5. Stereoscanned cellulose acetate peel (37522).

Fig. 3. Section through the sub-peripheral rim showing the tubercle cores in cross section, offset by one half-phase. Two partially resorbed cores are visible along the inner margin of the rim, top left. Section orientation: parallel with the plane of the commissure. Section location: brachial valve, left antero-lateral sector 0·048 mm. from the distal ends of tubercles. Scale represents 20 μ.

Figs. 4, 5. Isolated tubercle cores in areas of the brachial cavity affected by resorption of the sub-peripheral rim (fig. 4) and tubercle cores continuous with the primary layer (fig. 5, centre and lower right). Section orientation and location as in fig. 3, but 0·144 mm. from the distal ends of tubercles. Scale represents 20 μ.

Fig. 6. Stereoscanned cellulose acetate peel (37523). Vertical section through the sub-peripheral rim showing tubercle cores in oblique section. Section orientation: perpendicular to the external shell surface at 85° from the long axis. Section location: brachial valve, right antero-lateral sector. Scale represents 30 μ.

Figs. 7, 8. Stereoscan photomicrograph of the external surface of a brachial valve of *Moorellina ornata* (Davidson) (37524), showing detail of the structures interpreted as weathered tubercle cores. × 1000.

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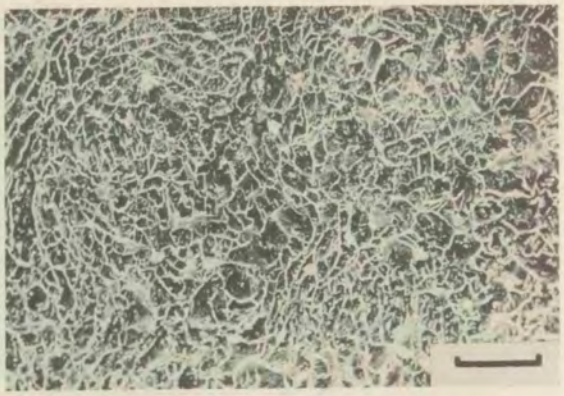

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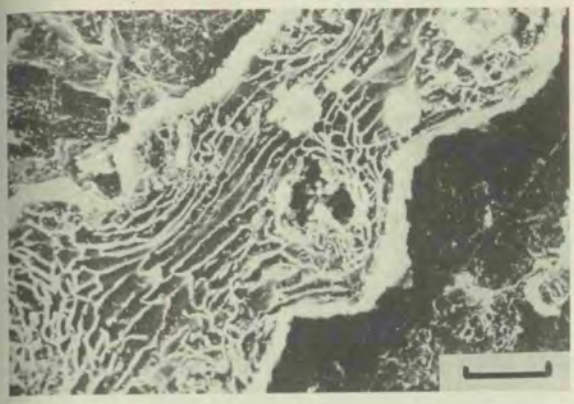

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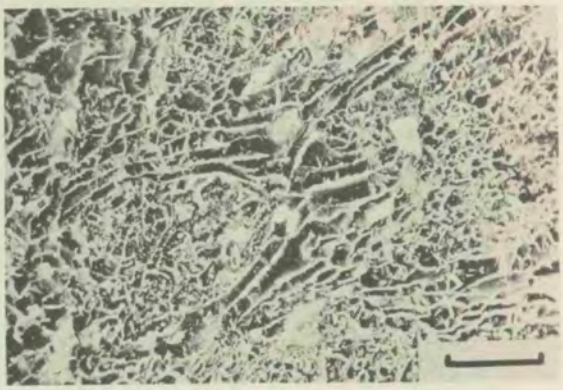

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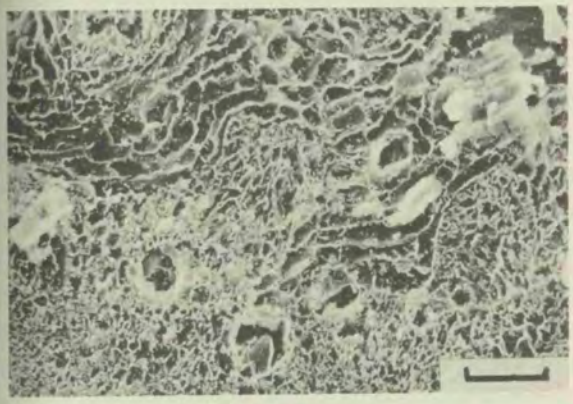

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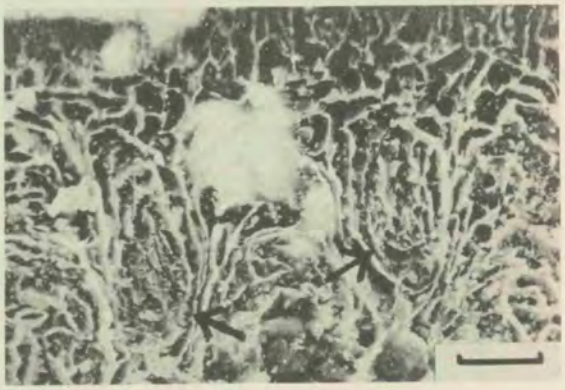

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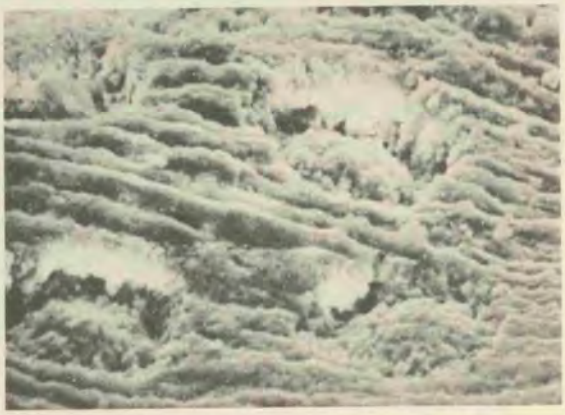

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BAKER, *Moorellina granulosa*

region outside the sub-peripheral rim, (*b*) the pedicle valve, and (*c*) the brachial cavities of pre-forbesiform (Baker 1969) individuals, where rim resorption had not yet begun. A detailed examination of brachial and pedicle valves was then undertaken with these considerations in mind. The border region has proved to consist entirely of primary shell and the mosaic on the inner surface of the pedicle valve is obscured by the development of crescentic tubercles. A pre-forbesiform brachial valve (37503) however, clearly shows traces of the internal mosaic of the secondary layer (Pl. 19, fig. 6).

The observed differences in the brachial and pedicle valves of *M. granulosa* have produced significant differences in microstructure and render it necessary that the microstructure of the two valves be described separately.

Brachial valve. A thin primary and a disturbed secondary layer associated with the development and migration of the sub-peripheral rim are present.

A detailed investigation of the tubercles of the sub-peripheral rim was undertaken. If the concept of resorption is correct, it should be possible to distinguish the remains of tubercle cores in areas of the brachial cavity formerly occupied by the sub-peripheral rim. Horizontal, transverse, oblique, and longitudinal sections were prepared in order to establish their presence. Horizontal serial sections (Pl. 20, figs. 3–5) show that the tubercles are cored structures and that the tubercle cores are, in fact, continuous with the material of the primary layer (Pl. 20, fig. 5). The tubercle cores may be regarded therefore, as being composed of primary shell type material. The question of whether the primary layer has suffered diagenesis has little significance as the material of this layer and of the tubercle cores has the same characteristics and may logically be considered to have the same origin. The author envisages localized patches of outer epithelium continuing to secrete primary shell. It seems probable that the mechanism of development is similar to that which controls the initiation of punctae, as tubercles also are normally, but not universally, offset by one half-phase (Pl. 20, figs. 3, 5). A plot of the tubercle cores in superimposed serial sections through a brachial valve of *M. granulosa* shows that they persist through several sections and are intimately connected with the development of the sub-peripheral rim. They do not appear in zones of the shell which may be logically considered to have been deposited prior to the appearance of that structure (text-fig. 4A). Horizontal sections through the sub-peripheral rim (Pl. 20, fig. 3) confirm that the tubercle cores originate near the mantle edge, in fact at the outer boundary of the sub-peripheral rim itself, and close to the point where the secretion of secondary shell begins. Subsequent isolation of eroded tubercle cores in the brachial cavities is brought about by the mode of development of the sub-peripheral rim during ontogeny (Pl. 20, fig. 4). Vertical sections (Pl. 20, fig. 6) show that the tubercle cores are inclined at a high angle, almost normal to the external shell surface, with a slight outward deflection.

That the tubercle cores of the brachial valve are composed of primary shell material would appear to be confirmed by occasional curious pitted structures occurring on the external surface of valves. Although these occur in *M. granulosa* they are better preserved in the Upper Oxfordian, *Moorellina ornata* (Moore) (Pl. 20, figs. 7, 8). Each pit has a central granular mound and may possibly be interpreted as some form of exopuncta. However, in the light of observations regarding the thickness of the primary layer and the fact that the tubercle cores are shown to be continuous with it, it would appear that what is actually seen is the outer boundary of the secondary layer, exposed by the

removal of primary shell. In which case, the apparent bands are the long axes of fibres and the central mounds of the pits are really weathered tubercle cores. This is supported by: (*a*) the orientation of the fibres is correct if they constitute part of a normal spiral arc, (*b*) they are the right thickness, about 4 μ, (*c*) the granular nature of the central mound is the same as that of sectioned tubercle cores, (*d*) the diameter of the pits is the same as the diameter of tubercle cores in section, i.e. 25–30 μ, and (*e*) they are too large to be normal punctae which have a diameter of only 8–10 μ.

Pedicle valve. A well-developed primary and secondary layer are present. The primary layer thins posteriorly and the secondary layer shows modification anteriorly as a result of the growth habit of the valve.

Attempts to reconstruct a secondary mosaic in the manner described above, failed to produce a decipherable pattern because the secondary layer of the pedicle valve of *M. granulosa* is itself composed of two regions with regard to fibre orientation. There is an outer, essentially normal, spiral arc orientation and an inner layer in which the fibre orientation is intimately bound up with the development of the crescentic tubercles (Pl. 21, figs. 1, 2). In the lateral and postero-lateral sectors of the valve, the secondary fibres show a normal spiral arc arrangement. In the zones of the anterior surface adjacent to the area of attachment, the orientation of the fibres of both regions of the secondary layer appear to follow the primary growth vectors and longitudinal sections produce typical longitudinal sections through fibres (Pl. 21, fig. 3). However, as growth of the pedicle valve proceeds away from the substratum, the secondary layer is differentiated into outer and inner regions. The orientation of the fibres in the outer region changes in such a way that they come to lie almost parallel with the commissure. Longitudinal

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EXPLANATION OF PLATE 21

Stereoscan photomicrographs of specimens of *Moorellina granulosa* (Moore). Material of all figures coated with evaporated aluminium before photography.

Fig. 1. Stereoscanned cellulose acetate peel (37520). Transverse section through a pedicle valve showing the orientation of the outer fibres of the secondary layer and the reniform tubercle cores. Section orientation: parallel with the plane of the commissure. Section location: left antero-lateral sector, 0·4 mm. from the distal ends of the tubercles. Scale represents 50 μ.

Fig. 2. Stereoscanned cellulose acetate peel (37521). Section through the secondary layer showing fibres deflected by the crescentic tubercles. Section orientation: parallel with the anterior surface. Section location: pedicle valve, anterior surface, 0·168 mm. from the external surface. Scale represents 20 μ.

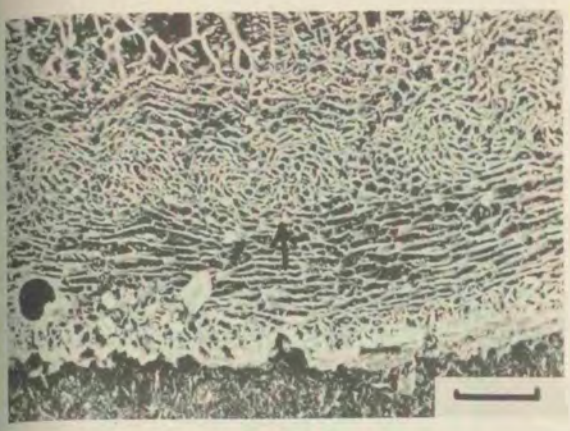
Figs. 3, 4. Etched surface prepared from polished block (37516). Section orientation and location as in fig. 3 (Pl. 19). Fig. 3 shows the primary layer, bottom and detail of the secondary fibres in longitudinal section. Fig. 4 shows reorientation of the fibres of the outer region of the secondary layer to give almost transverse section. The elongate fibres (oblique section), upper left, represent a tubercle core sectioned near the axis. Scale represents 10 μ.

Fig. 5. Stereoscanned cellulose acetate peel (37521). Section through the secondary layer showing the fibrous cores of the crescentic tubercles. Section orientation and location as in fig. 2, but 0·096 mm. from the external surface. Scale represents 50 μ.

Fig. 6. Interior view of the anterior surface of a pedicle valve (37515) showing the arrangement of the punctae in rows relative to the crescentic tubercles. × 50.

Fig. 7. Stereoscanned cellulose acetate peel (37523). Transverse section through the ventral umbonal region showing the plugged pedicle opening and dorsally exposed pedicle sheath. Section location: 0·08 mm. from the umbo. Scale represents 50 μ.

Fig. 8. Retouched photomicrograph of fig. 7.



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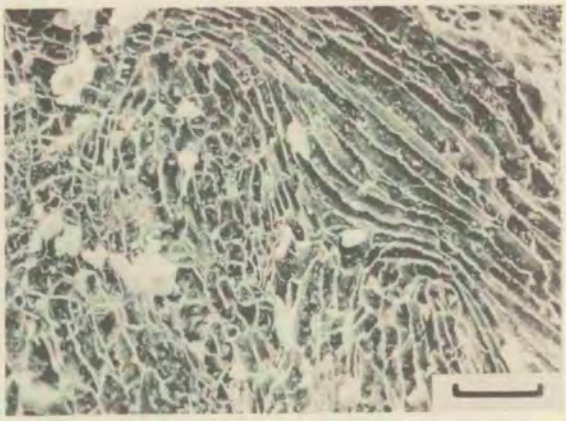

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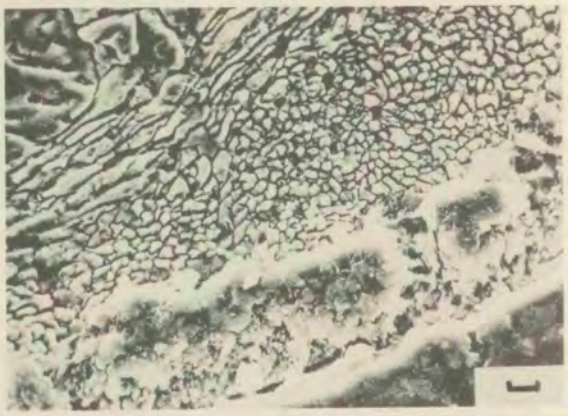

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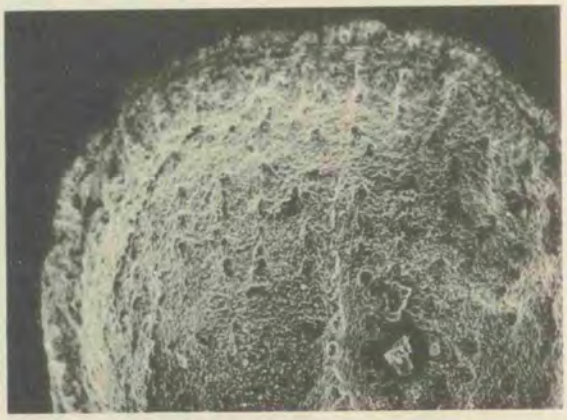

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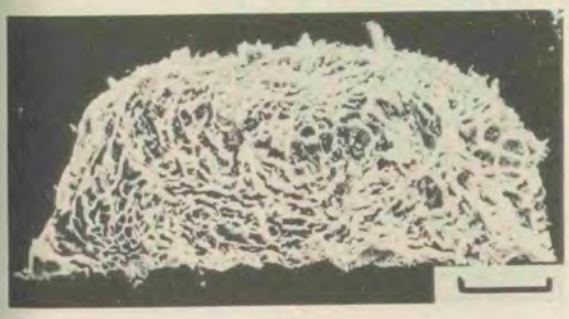

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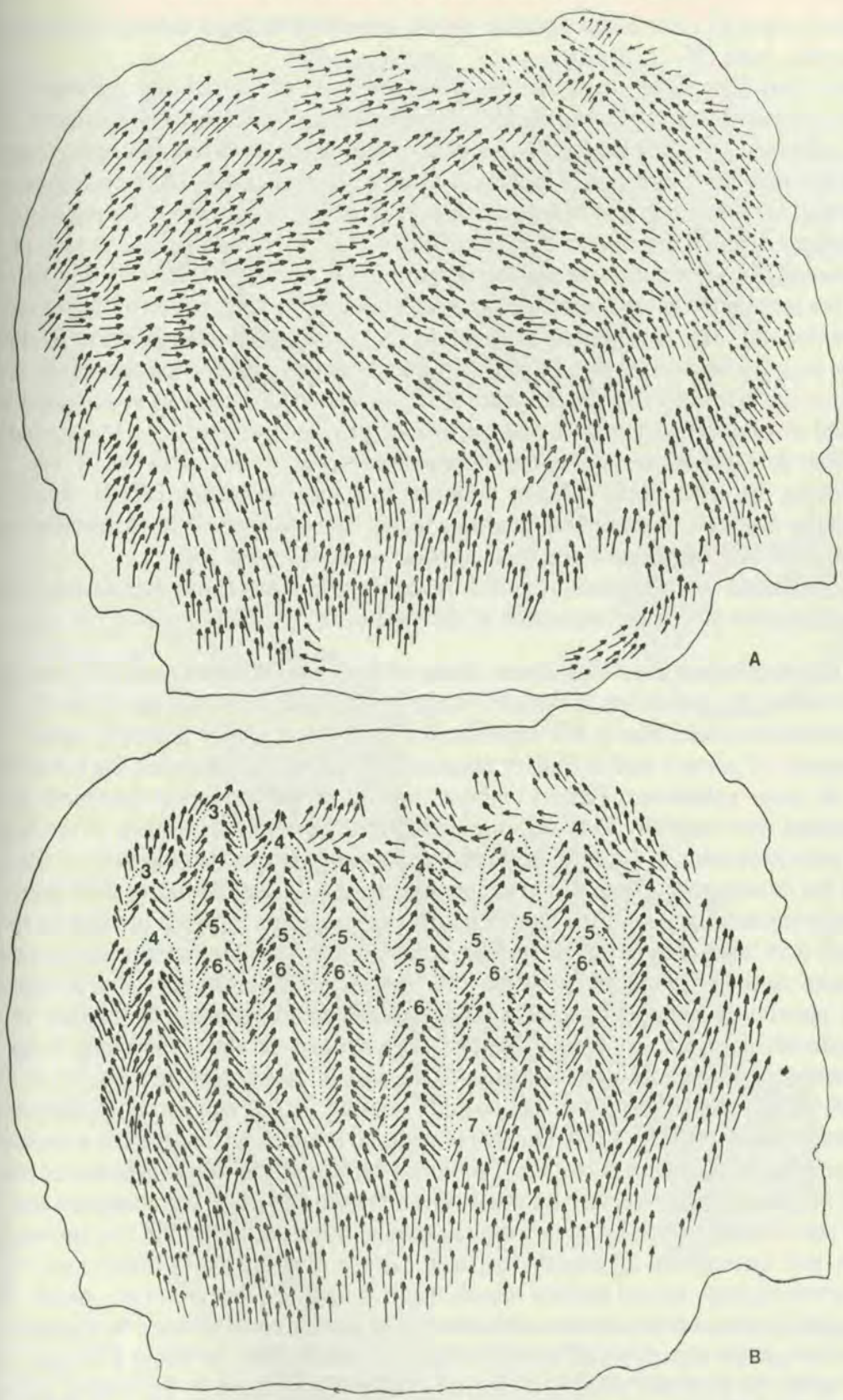
8

BAKER, *Moorellina granulosa*



TEXT-FIG. 5. Reconstruction of the fibre orientation of the outer and inner regions of the secondary layer of the free anterior of the pedicle valve of *M. granulosa*, from eight superimposed peels. A. Fibre orientation of the outer region. B. Fibre orientation and tubercle cores of the inner region. Numbers indicate the position of the tubercles in successive peels, from the internal surface of the valve.

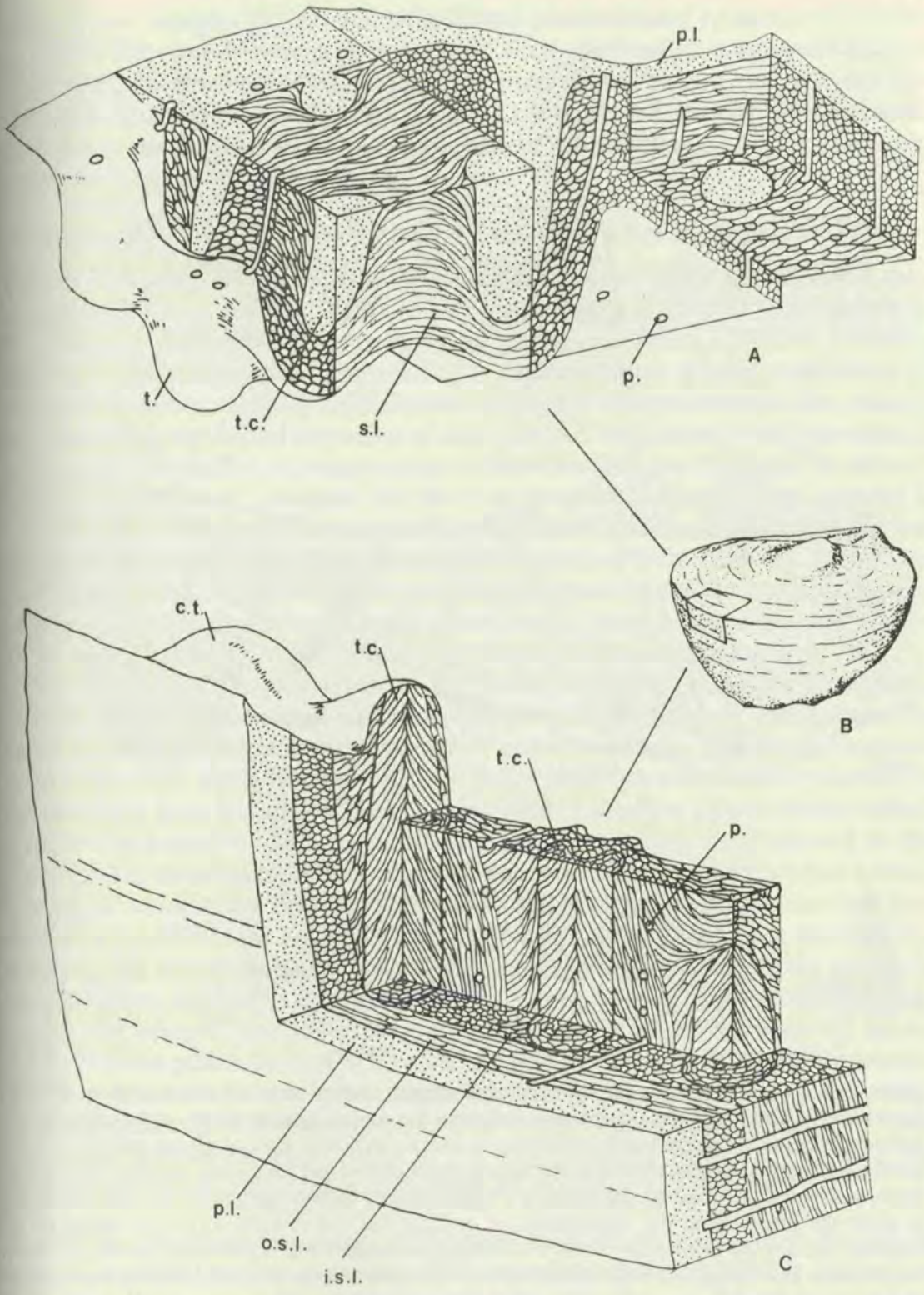
sections through these zones produce almost transverse sections through the fibres of this outer layer (Pl. 21, fig. 4).

With this information available the growth mosaics of the two regions were fairly easily reconstructed by plotting the fibres of the outer and inner regions separately. This was achieved by plotting the primary/secondary layer junctions of serial sections, together with the orientation direction of the fibres adjacent to the junctions. The mosaic produced (text-fig. 5A) was interpreted as representing the growth mosaic of the outer region of the secondary layer of the anterior surface of the pedicle valve. Similarly, a re-plot of the remaining fibre orientation on each serial section, i.e. omitting those plotted in text-fig. 5A, was interpreted as representing the growth mosaic of the inner region of the secondary layer (text-fig. 5B). A suggested explanation for this anterior differentiation is offered later, as it can be shown not to be present throughout the whole of the secondary layer.

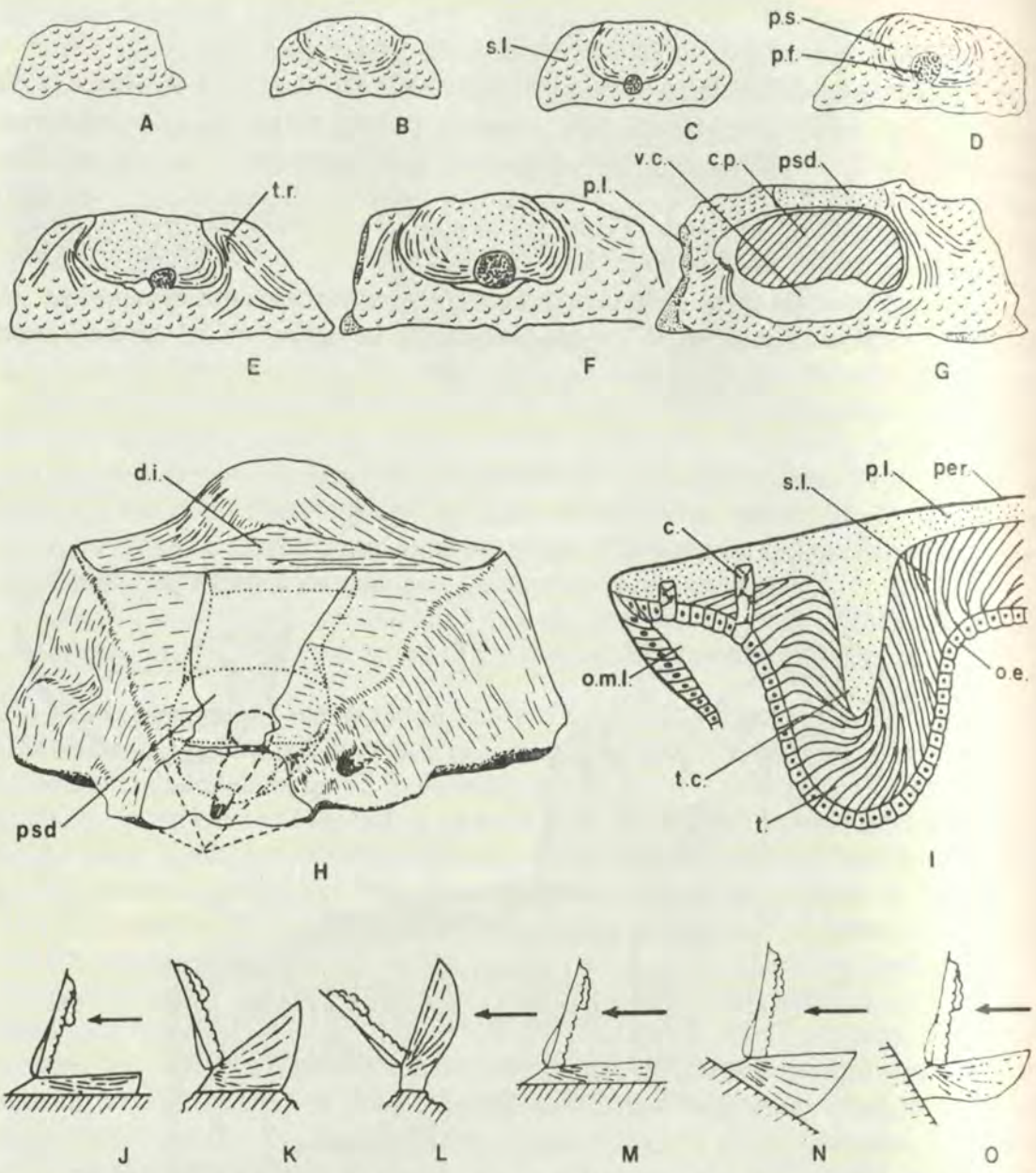
As in the brachial valve, the structure of the crescentic tubercles was investigated with the aid of transverse, horizontal, oblique, and longitudinal serial sections. In longitudinal sections the tubercles are seen to be composed entirely of fibrous cones (Pl. 21, figs. 2, 5) deflecting the other fibres adjacent to them. In transverse section (Pl. 21, fig. 1) the tubercles exhibit a characteristic reniform shape. The presence of these structures may be of profound significance and their implication is discussed later.

Compilation of the features exhibited by serial sections at various orientations allows reconstruction of the microstructure of the shell of *M. granulosa* (text-fig. 6A–C).

The pseudodeltidium and pedicle sheath. Study of *Lacazella* (Williams *et al.* 1965) indicates that neither the pedicle nor its muscle system is developed. The structure of the strophomenoid pseudodeltidium is still imperfectly known but it is now generally agreed that it consists of primary and secondary material and was secreted between the teeth ridges by the outer epithelium. Ventral umbonal regions of well-preserved specimens of *M. granulosa* were carefully sectioned in an attempt to resolve the problem of the fate of the pedicle opening in Jurassic thecidellinids. Owing to the mode of growth of the area and the minute proportions of the structures involved, it was difficult to distinguish the pseudodeltidium at all. Of the limited number of specimens in which it could be recognized, only three showed any discernible microstructure. In these specimens, transverse sections close to the ventral umbo show the presence of a minute pore 50 μ in diameter and apparently plugged by calcite having a different orientation from that of the pseudodeltidium (Pl. 21, figs. 7, 8). The pore appears at about 0·06 mm. from the posterior of the pedicle valve and close to the area of attachment (text-fig. 7C) in what must be regarded as a supra-apical position (text-fig. 7H). It appears to be surrounded laterally and dorsally by a collar or ring of material in which the fibres show a concentric orientation in the plane of section. The dorsal surface of the ring is exposed externally and is obviously the structure interpreted as a pseudodeltidium. In subsequent sections the pore migrates dorsally away from the area of attachment and the ring increases in size, still maintaining its dorsally exposed surface (text-fig. 7C–F). Continuity of the structure through several sections reveals that it is really a calcareous tube, which, if the plugged pore represents the site of the atrophied pedicle opening, may be regarded as a form of pedicle sheath which initially closed the delthyrium. At about 0·14 mm. from the umbo the structure terminates (text-fig. 7G) and is replaced by the ventral umbonal cavity, housing the posterior tip of the cardinal process. The space between the tooth



TEXT-FIG. 6. Diagrammatic reconstruction of the shell microstructure of *Moorellina granulosa* (Moore). A. Block diagram showing the microstructure of the brachial valve. B. Complete specimen showing relative position of the reconstructed segments. C. Block diagram showing the microstructure of the pedicle valve. c.t. crescentic tubercle, i.s.l. inner secondary layer, o.s.l. outer secondary layer, p. puncta, p.l. primary layer, s.l. secondary layer, t. tubercle, t.c. tubercle core.



TEXT-FIG. 7. A–G. Drawings prepared from cellulose acetate peels of serial transverse sections through the ventral umbonal region of *M. granulosa* showing the continuity and anterior termination of the pedicle sheath and the plugged pedicle foramen. H. Reconstruction of the ventral umbonal region from thirteen superimposed peels. Outline of the pedicle sheath dotted and the pedicle opening, broken line. Position of umbo projected by dotted lines. I. Diagrammatic section through the sub-peripheral rim to show the difference in the development of endopunctae and tubercle cores. J–O. Series of six diagrams to show the orientation of the brachial apparatus relative to a prevailing current, arrowed. J–L, constant growth position with variable size of the attachment surface. M–O, constant orientation at various growth positions. c. caecum, c.p. cardinal process, d.i. dorsal interarea, o.e. outer epithelium, o.m.l. outer mantle lobe, per. periostracum, psd. pseudodeltidium, p.f. pedicle foramen, p.l. primary layer, p.s. pedicle sheath, s.l. secondary layer, t. tooth, t.c. tubercle core, t.r. tooth ridge, v.c. ventral umbonal cavity.

ridges is now occupied by a plate of more normal pseudodeltidial appearance. Unfortunately, at the moment there is no evidence to show whether this is a discrete plate or whether it is the product of overgrowth by the outer epithelium at the anterior termination of the calcareous tube. Atrophy of the pedicle would explain why the tube ceased to develop and only closes the posterior part of the delthyrium, an operation subsequently taken over by the outer epithelium.

SIGNIFICANCE OF THE OBSERVED GROWTH AND MICROSTRUCTURE

Growth orientation. Obviously there must be some genetic control of the proliferation of epithelial cells in the mantle fold and it is not possible to show absolute growth in *M. granulosa*. However, the use of a system of growth units makes it possible, providing one knows the primary growth orientation, to determine areas of rapid proliferation of cells and, therefore, relatively rapid increase in size. The observed external fibre orientation is clearly a topological expression of shell growth. There is a very close resemblance between the distribution of primary costae in *Rhipidomella oblata* (Hall) and the external fibre orientation of *M. granulosa* but this is to be expected if addition of material is normal to the commissure with mixoperipheral growth. This would clearly suggest that the radial ornament of the dalmanellaceids (Williams and Wright 1963, p. 22) is topological also. Work on the orientation pattern of *M. granulosa* would therefore appear to confirm their view that dalmanellaceid ornamentation patterns of 'progressive' species of *Watsella* (Bancroft 1945, p. 190) have no supra-specific taxonomic status.

The anteriorly modified spiral arc of the pedicle valve of *M. granulosa*, producing a secondary layer differentiated into two regions can only be clearly demonstrated in valves having a large free anterior surface. If one considers the thecideacean environment (Ager 1965, 1967; Nekvasilová 1967; Baker 1969) this anterior differentiation of the secondary layer is readily explained. Forms with a large free anterior surface (small area of attachment) would have relatively more of the pedicle valve exposed to the rigours of the environment. Development of crescentic tubercles would produce a structure which would secure the commissure (interlocking effect) but at the same time produce an exposed anterior surface which could be more easily breached at the relatively weak juctions between adjacent tubercles (Pl. 21, fig. 5). Differentiation of the secondary layer anteriorly into what might be described as a cross-laminate structure would greatly increase its strength. The above seems a logical explanation for the observed microstructure of the pedicle valve of *M. granulosa* and the relationship between fibre orientation and microstructure of other attached brachiopods is well worth investigating. Strophomenides, for example, may have solved the problem by the modification of fibres to produce laminae (Williams 1968*a*, p. 37). The fibres with flared ends noted in the brachial valve of *M. granulosa* may represent an attempt in this direction.

Ecology and functional morphology. Consideration of the growth habit of the pedicle valve in ecological terms is interesting. If the cumulative growth pattern is designed to lift the anterior gape away from the substratum, it is difficult to see why the characteristic is suppressed in forms with a large area of attachment. It seems probable that it is the degree of inclination, rather than the size of the surface to which the animal attaches itself, which is the major control. Elliott's (1948) paper would suggest that the relatively enormous gape (Rudwick 1968) of the thecideidines is associated with orientation of the

brachial apparatus relative to the 'prevailing' environment, probably represented by a persistent current direction.

The above relationship seems entirely probable and supports the author's argument. Individuals attaching themselves to surfaces of suitable inclination already have their commissures in the 'ideal' orientation position from an ecological standpoint. Such individuals would have no need to develop elaborate anterior surfaces, although development of even the relatively small anterior surface encountered in these specimens must inevitably require the cumulative growth pattern postulated.

There seems to be a correlation between size of animal and degree of elaboration of the brachial apparatus (Elliott 1948), interpreted as being related to the animal's food-gathering ability in a competitive sense. This may partially explain the onset of the development changes which lead to the freeing of the anterior of the pedicle valve from attachment to the substratum. Size of the animal is obviously critical where small size of the attachment surface is concerned but observations indicate that size may be critical independently. Attainment of a certain size might render necessary a change in organization, to effectively meet the increasing nutritional demands.

There are obviously other factors to be considered such as accommodation of the brachial apparatus and the developing sub-peripheral rim, the relative efficiency of the lophophore and the ecological niche (Rudwick 1962) occupied by any particular individual. However, if, as there would appear to be, there is any order associated with the growth habit of thecideidines, it is easier to reconcile this, in ecological terms, with the attainment of a certain orientation position of the gape (text-fig. 7J–O) rather than the size of the surface to which the animal was attached. One feels that the orientation of the gape, in terms of functional efficiency of the brachial apparatus, is the more satisfactory explanation for the variable growth habit observed in the pedicle valves of thecidellinids.

As *M. granulosa* is a member of the surf-zone fauna, the interlocking tubercles of the two valves on such cemented forms may have acted as accessory teeth and sockets to help secure the brachial valve in position during adverse conditions. The preponderance of brachial valves in any collection may be a measure of the relative vulnerability that the abnormally wide gape exposed in the existing hinge.

Microstructure. Williams, in his work on *Lacazella* (1968*a*, *b*) apparently abandons his earlier interpretation (1955, 1956, 1965) that a secondary layer is present, in favour of a shell composed only of primary material. The three earlier accounts are essentially similar. The 1955 paper records the presence of fibre bundles almost perpendicular to the 'lamellar' layer, producing the appearance of pseudopunctae but, in the absence of a non-fibrous core, unrelated to the strophomenid spicules. These core bundles are figured in the rather vague reconstruction of the shell of *Lacazella mediterranea* (Risso) in (1965, H67), but their orientation is apparently in the wrong direction. Attention is, however, drawn to the similarity of this type of shell structure and that of the terebratellaceid *Megerlina lamarkiana* (Dav.). The 1956 paper records the same fibrous cores in thecidaceids but offers no information as to which were studied. It is felt that the structures described must be referred to the microstructure of the crescentic tubercles of *M. granulosa* (Pl. 21, figs. 2, 5, text-fig. 6C).

The absence of a secondary layer in *Lacazella* is interpreted as being the result of

neotenous suppression (Williams 1968*a*). Although changes in the secretory habit of the epithelial cells in *M. granulosa* appear to follow a normal pattern, the stability of the thickness of the primary layer does not appear to be quite as constant as Williams has suggested and it is possible to see groups of secondary fibres apparently embedded in primary shell. This irregularity of deposition of the secondary layer in *M. granulosa* may be the first expression of its ultimate suppression.

Although *M. granulosa* is not costellate, it is worth noting that the external expression of the crescentic tubercles on the inner edge of the margin of the pedicle valve, bears a strong resemblance to the follicular eminences and embayments of the Recent *Terebratulina* and also fossil enteletacean (Williams and Wright 1963, p. 19; Williams and Rowell 1965, H81) brachiopods and may have served a similar purpose. Similar structures are seen in the cemented inarticulate *Crania anomala* (Müller) where they are not associated with setae but control the distribution of punctae. In *M. granulosa*, the crescentic tubercles appear to exercise a similar control over the distribution of punctate (Pl. 21, fig. 6).

Elliott (1953, 1955) has arrived at the conclusion that all thecideidines are enodpunctate with the possible exception of *Davidsonella*. Study of *M. granulosa* and *M. ornata* shows that although the endopunctae are formed in a terebratuloid manner, the cup-shaped distal enlargements and the deflexion of secondary fibres have not been seen.

Deeper issues are at stake with regard to the implication of the described tubercle structure. They occur together with endopunctae and the initiation of punctae and tubercle cores seems to follow the same pattern. Upon consideration of their structure, the question arises whether the tubercles are homologous with pseudopunctae. Tubercle cores must arise in a very different manner from endopunctae (text-fig. 7I), and therefore if homologous with pseudopunctae, pseudopunctae and endopunctae must be totally unrelated.

Williams (1965, H72) has stated that taleolae are comparable in texture with the terebratuloid primary layer. Sections parallel with the plane of the commissure through *M. granulosa* have shown that the tubercle cores of the brachial valve are in fact continuous with the primary layer and as far as can be ascertained, represent imperfectly developed primary shell, secreted by persistent patches of columnar epithelium, surviving from the tip of the outer mantle lobe.

Williams (1965) has shown that pseudopunctae are markedly asymmetrical in longitudinal section, with their apices directed inwardly and anteriorly to protrude from the internal surfaces of both valves as tubercles. The orientation of the tubercles in the brachial valve of *M. granulosa* shows this approximate pattern. In the pedicle valve, it only requires a slight exaggeration of this trend to produce, in *M. granulosa*, tubercle cores running almost parallel with the plane of the valve in such a way that they emerge as tubercles along the inner edge of the anterior margin. In which case, they may be regarded as homologous with the pseudopunctae of davidsoniaceans such as *Derbyia*, which consist of fibrous cones of the type shown to exist in the pedicle valve of *M. granulosa* (text-figs. 5B, 6C, Pl. 21, fig. 5).

The suspected close relationship between pseudopunctae with and without taleolae is confirmed by the presence of both types in a single animal. A careful sectioning technique, supported by the fact that the structures are located in different valves, enables one to show that the tubercles of the brachial valve have cores, whilst those of the pedicle

valve are without cores. If one considers the pure mechanics of this arrangement it would appear to be quite logical. In the brachial valve where orientation of the tubercle axis is near perpendicular to the surface of the valve, the development of the primary core in the manner suggested is the simplest way of bringing about an invagination of the outer epithelium. On the other hand, in the pedicle valve, where by virtue of the growth habit, the orientation of the tubercles must necessarily be nearly parallel with the valve inner surface, a primary core would become very attenuated. In this situation it would be far easier to produce a tubercle core by a slight change in the orientation of secondary fibres.

If one considers the tubercles in terms of this functional requirement, they may be regarded as the modified counterpart of strophomenoid pseudopunctae. They deflect secondary fibres in the same way and the similarity of the disposition of the fibres presumably indicates a similar pattern of development.

AFFINITIES

The affinities of the Thecideidina have been a subject of interest and speculation for a number of years, Elliott (1948, 1953, 1958), Rudwick (1968), and Williams (1965, 1968*a*, *b*) being notable among the later works. Demonstration of a primary and secondary shell layer in *M. granulosa* invalidates only Williams's (1968*a*, *b*) conclusion that *Lacazella* is a typical model of the thecideidine shell and in no way impairs his line of descent. If, as Williams's work suggests, the secondary layer of *Lacazella* has been neotenously suppressed to the point of exclusion, *M. granulosa* occupies an attractive position, as Jurassic forms in which this process might just be beginning, represent an important contribution to our knowledge. One feels that the diversity of shell microstructure encountered in a single specimen of *M. granulosa*, must represent a genetic disturbance which could quite easily result in the ultimate suppression of the secondary layer. The banded shell of *Lacazella* might in environmental terms, more easily satisfy the requirements for a reinforced shell and render the structurally reinforced secondary layer of *M. granulosa* obsolete, thus accounting for its disappearance. The secondary shell mosaic seems closer to terebratulide or spiriferide than any other. However, the shape of the fibres is different and also variable within an individual, so that one may see fibres with flared outer ends reminiscent of the laminae of plectambonitaceans. Still other features of the microstructure may be reconciled with davidsoniaceans.

The value of functional analysis of morphology, demonstrated by Rudwick (1968) and the significant correlation between the modification of the microstructure of *M. granulosa* and environmental influence, underlines an advance in our knowledge of taxonomic technique. Obviously, not only structures but also their significance in environmental terms must be critically examined before assigning a species to a particular systematic position, as convergence may be encountered at the microstructure level. It is felt therefore, that the taxonomic importance of some aspects of shell microstructure should not, as has happened frequently in the past on discovery of a character, be overestimated.

The value of shell microstructure from a taxonomic point of view has been discussed by Williams (1956, 1968*a*, *b*), Rudwick (1968), and Gauri and Boucot (1968). As the present investigations have shown, there are important differences between the microstructure of the brachial and pedicle valves of *M. granulosa*. That this is not a feature

peculiar to thecidellinids has been demonstrated by Gauri and Boucot (1968) who record that in the pentamerids *Antirhynchonella*, *Clorinda*, and *Zdimir*, the prismatic layer is absent from the brachial valve. Their study of pentameraceans and the gulf which exists between Williams's (1968*a*) thecideidine model and the observed microstructure of *M. granulosa* indicates that the state of our knowledge of shell microstructure in brachiopods is not yet sufficiently advanced to allow anything other than a tentative taxonomic significance to be ascribed to it.

With regard to the fate of the pedicle, it appears unlikely that *M. granulosa* will yield the quality of evidence to enable one to make categoric statements concerning the microstructure of the pedicle opening. Evidence yielded by *Lacazella mediterranea* (Risso) must remain suspect in view of the neotenous modification of this species. The main hope seems to lie in the discovery of well-preserved, larger thecideidines from other horizons. Only limited significance should therefore be attached to the pseudodeltidium of *M. granulosa* until the evidence has been strengthened. If a pedicle sheath does arise supra-apically, then it is possible to equate this with the strophomenoid pseudodeltidium. Arber (1942) has recorded a very similar solid pseudodeltidium, fused with the floor of the pedicle valve in the Orthotetinae and Rafinesquinae. However, Williams (1956) has noted an imperforate delthyrial cover in *Eospirifer*. The indication that the pseudodeltidium of *M. granulosa* was deposited by the ventral edge of the capsule of a pedicle undergoing atrophy, appears to confirm the views of Arber (1942) and Williams (1956) regarding the form of the pseudodeltidium of *Lacazella*.

Although it appears that the thecideacean pseudodeltidium is homologous with the pseudodeltidium of strophomenoids, Williams and Rowell (1965, H188) regard the similarity between strophomenoids and thecideaceans as an expression of convergence and derive the thecideidines from possible suessiacean ancestors. One must agree that the secondary mosaic is very similar to *Cyrtina* but encounters the same time-gap objection raised by Williams (1956) to the affinity proposed by Kozlowski (1929) for the lophophore platforms of some plectambonitaceids and thecidaceids.

Structurally there appears to be no significant difference between strophomenoid pseudopunctae and the tubercles of *M. granulosa*. The similarity between them and pseudopunctae of the davidsoniacean *Derbyia* is even closer. On this basis, it would not be unreasonable to conclude that the tubercles of thecidellinids are homologous with strophomenoid pseudopunctae, functionally modified.

Elimination of obscure similarities, plectambonitaceid, enteletacean, terebratellacean, etc., leaves one with the basic problem of whether the thecideidines show strophomenide or spiriferide affinity. An analysis of the literature shows that the systematic position of *Thecospira* is of critical importance as far as the thecideidines are concerned. It seems strange that Williams (1968*a*), after lengthy discussion of the low taxonomic value of a limited number of characters, should re-assign the genus to the Spiriferida solely on the basis of its shell structure and admitted non-spiriferoid calcareous spires. If one considers the points of similarity between *M. granulosa* and *Thecospira* they are most striking. Both are strophic and show the same lateral profile. *Thecospira* shows punctate and obscurely pseudopunctate representatives. *M. granulosa* is endopunctate but probably independently from terebratuloid endopunctation (Williams 1968*c*, p. 489). The similarity in *Thecospira* and *M. granulosa*, of the cardinal process, the hinge articulation, the sub-marginal structures, the coalesced punctae and lateral shift of the main adductor

muscles is thought to be more than coincidental. Differences such as the lack of costellate ornament may not be profound, as radially arranged fibres have been recognized in *M. granulosa*. As spiral brachidia apparently evolved twice among the Spiriferida, there is no reason why similar brachidia should not evolve in non-spiriferide forms, e.g. *Thecospira* and *Cadomella* (Cowen and Rudwick 1966) whose epithelia had the ability to resorb material. If one bears in mind the neotenous origin of the thecideidines and extends the posterior horns of the brachial lobes of *M. granulosa* (Baker 1969, text-fig. 3F) back to unite with the bridge extensions, one may derive or 'lose' a simple spiral brachidium as a result of the demonstrated resorptive activity taking place in the brachial cavities.

Rudwick (1968) has put forward a reasoned argument for the assignment of the Thecideacea to the Strophomenida, close to, but distinct from the Davidsoniacea. As outlined in the discussion of possible environmental influence, the possibility of a convergent origin of the davidsoniacean characters of *M. granulosa* must not be overlooked but the similarity between *Moorellina granulosa* (Moore), the spire-bearing *Thecospira*, and known davidsoniaceans such as *Derbyia* and *Orthotetes* is thought to be much too close to be merely convergent. The weight of evidence now accumulated would suggest that the thecideidines show affinity closer to the davidsoniaceans than any other group. The author must agree with Rudwick, that on the basis of our present knowledge the Thecideacea should be assigned to the Strophomenida.

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The morphology and microstructure of *Zellania davidsoni* Moore (Brachiopoda), from the Middle Jurassic of England

BY

P. G. BAKER

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THE MORPHOLOGY AND MICROSTRUCTURE OF *ZELLANIA DAVIDSONI* MOORE (BRACHIOPODA), FROM THE MIDDLE JURASSIC OF ENGLAND

by P. G. BAKER

ABSTRACT. Investigation of Oolite Marl samples from the mid Cotswolds has yielded occasional minute brachiopods which are undoubtedly specimens of the little-known species *Zellania davidsoni* Moore 1855. The material studied has enabled determination of the correct orientation, growth, development, and microstructure of the shell and provides the first record of the internal morphology of the pedicle valve. Adolescent and adult shells may be recognized, which enables the mode of development of certain internal structures to be determined. Sectioned material shows that the shell of *Z. davidsoni* is differentiated into primary and secondary layers of a type which, although unusual, may be reconciled with the shell of primitive terebratulides. Although *Z. davidsoni* occurs together with thecidellinids the form of the shell is thought to be indicative of a sheltered environment. Microstructural features exhibited by shells support the view that *Zellania* is of terebratellacean affinity. The paper records the probable location of Moore's type specimens, missing since before 1927.

Zellania is a rare, little-known micromorphic brachiopod genus of uncertain affinities, which occurs in the Jurassic of England. Material of the species *Z. davidsoni* (Moore 1855) has been obtained during a study of the brachiopod fauna of the Oolite Marl (Upper Aalenian, *murchisonae* zone) of the Cotswolds, South England.

Information on *Z. davidsoni* is singularly lacking. The account in the *Treatise on Brachiopoda* has perpetuated a misinterpretation of the type material by Moore in his original description.

Of the specimens of *Z. davidsoni* figured in the *Treatise* (fig. 741, 1*a–c*, H857) and presumably, in the absence of the types, taken from Moore (1855), 1*a* is in fact a pedicle valve and 1*b* figures the exterior of a brachial valve.

The type specimens of *Z. davidsoni* were found to be missing from the Moore collection, held in Bath City Reference Library, when it was catalogued by Dr. Wallis in 1927. The only zellanid material in the collection was a tube containing three specimens identified as types of *Zellania oolitica* Moore, ref. no. M3036. Study of these specimens reveals that they bear little resemblance to any of the published figures (Moore 1860, Davidson 1874) of *Z. oolitica* but are certainly specimens of *Z. davidsoni* bearing a very close resemblance to Moore's figured types. The author is of the opinion therefore, that it is the type material of *Z. oolitica* which is missing and inadvertently represented by the specimens of *Z. davidsoni* (M3036) which should be reinstated as the types of *Z. davidsoni.*

The rarity of *Z. davidsoni* in the Oolite Marl is indicated by the fact that the collection of specimens over a period of more than four years has yielded only two complete pedicle valves, four complete brachial valves and twenty-eight complete specimens, together with numerous brachial and a few pedicle valve fragments. It is possible that the rarity of the species may be, in part, an artefact of the fragility of the shell. The rarity of the pedicle valve is undoubtedly due to its form and lack of the strengthening effect

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of structures such as the ridge and septum which occur in the brachial valve. The weakness of the pedicle valve may be gauged by the fact that it is often crushed into the brachial valve during compaction of the sediment. The observations contained in this paper are therefore based on a very small collection. However, the uniformity of character exhibited by the material studied indicates that the observations are nevertheless valid.

Acknowledgements. The author is indebted to Dr. J. D. Hudson, Department of Geology, the University of Leicester, for supervision of the preparation of this paper. Thanks are due to Mr. G. McTurk for preparing the stereoscan negatives and to Mr. P. Pagan, City of Bath Reference Library for access to zellanid material from the Moore collection. I wish to thank Professor P. C. Sylvester-Bradley for use of the research facilities of the Department of Geology, the University of Leicester.

Registration of material. The material figured in this paper, together with original and duplicate peels is to be housed in the museum collection of the Department of Geology, the University of Leicester, under the catalogue numbers quoted.

PREPARATION OF MATERIAL

The material studied was obtained during the collection of thecidellinids from the Oolite Marl. A detailed account of the preparation of Oolite Marl residues and the investigation techniques employed, is given in Baker (1969) with minor amendments in Baker (1970).

Early attempts to section *Z. davidsoni* by the methods employed for *M. granulosa* were unsuccessful because peculiarities of the microstructure of the shell allowed blocks of shell to be lifted away during the production of cellulose acetate peels. This, combined with the relatively very thin zellanid shell and poorly consolidated matrix led to rapid disaggregation of the shell layers. Vacuum embedding was tried with considerable success but some difficulty with peel bubbling was still encountered owing to the porous matrix. This can be eliminated by running hot paraffin wax on to the specimen prior to each successive stage of sectioning. The wax soaks into the matrix and solidifies. The wax overlying the shell material is, of course, removed as the block is ground preparatory to re-etching but sufficient wax remains in the matrix to act as an effective sealant.

MORPHOLOGY

Information concerning the morphology of *Zellania davidsoni* is limited. The accounts in Moore (1855) and in the *Treatise on Brachiopoda* (1965) concern only the brachial valve and need some amplification. Detailed examination of the internal ridges (Moore 1855) (inner ridges, Treatise) of the brachial valve in serial transverse section (Pl. 120, fig. 7) shows that they are structurally ridges (by definition, Williams 1965 H152), though appearing more in the manner of outwardly inclined flanges (Pl. 118, fig. 7; text-figs. 1B, 2K–P). They occupy a position similar to that of the sub-peripheral rim of thecidellinids (Baker 1969) but arise in a different manner (Baker 1970) and apparently performed a function similar to the lophophore platform of the plectambonitacean *Leptellina*. There is no evidence that the structure seen in the brachial valve of *Z. davidsoni* is any way related to the lophophore platform of *Leptellina*. It is by definition not a flange. It performed a function different from that of the thecidellinid

sub-peripheral rim. In order to avoid confusion therefore, it is proposed to refer to the structure as a *sub-marginal ridge*.

Figures of the interior of the brachial valve in Moore, C. (1855) and Elliott (in Moore, R. C. 1965) indicate a depression at the end of the median septum (clearly visible in specimen M3036). Studies show that the septum is a hollow structure for much of its length (Pl. 119, figs. 1–3, text-figs. 1B, 2P–R) and that the floor of the cavity is endopunctate in the normal manner (Pl. 119, fig. 1). It is proposed to refer to this cavity as an *intra-septal cavity*. Counterparts of the sub-marginal ridge and median septum are found in the pedicle valve and it is proposed to term them *lateral ancillary ridges* and *ancillary septum* respectively.

Growth and external morphology. Z. davidsoni (Pl. 118, figs. 1–4) is a very small form. The growth is mixoperipheral, leading to a strophic condition, with a rectimarginate commissure. The width : length ratio of the shell is in the order of 1·2 : 1 and specimens rarely exceed 1·3 mm. in length. Specimens in which the protegulum (Pl. 118, fig. 4) and growth-lines are visible, show that the width:length ratio does not change appreciably throughout the life of the animal. Small forms, here correlated with adolescents (Pl. 118, fig. 6), are almost biconvex. During growth the pedicle valve retains its convexity but the brachial valve shows a declining vertical growth component (Rudwick 1959) so that adults have a characteristic plano-convex lateral profile (Pl. 118, fig. 2). The adult shell outline is typically shield-shaped (Pl. 118, fig. 1) but subject to some variation, adolescents particularly having a more rounded outline (Pl. 118, fig. 5). The interareas are anacline and relatively well developed, the dorsal interarea being only slightly smaller than that of the pedicle valve. The pedicle opening (Pl. 118, fig. 4), as stated in the *Treatise on Brachiopoda*, is amphithyridid and it is relatively very large. Stereoscan photomicrographs reveal that the feeble striate ornamentation of shells is in fact a series of radially arranged fissures (Pl. 119, figs. 7, 8) penetrating the primary shell but not extending down into the secondary shell layer. At ×250 magnification incipient striae are found to be present on smooth shells also.

Z. davidsoni is unusual in that the umbo of the brachial valve projects posteriorly to a greater degree than the umbo of the pedicle valve and gives the appearance of being

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EXPLANATION OF PLATE 118

Stereoscan photomicrographs of *Zellania davidsoni* Moore, from the Oolite Marl, Westington Hill Quarry near Chipping Campden. All specimens coated with evaporated aluminium before photography.

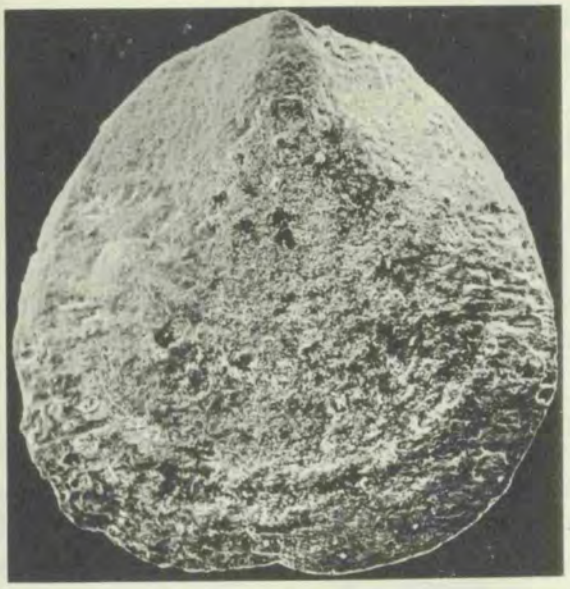
Figs. 1–4. Brachial, lateral, anterior and posterior views of an adult specimen (37530), showing the shield-shaped outline, fig. 1; the posterior extension of the brachial umbo and plano-convex lateral profile, fig. 2 (tilt angle 88°); the rectimarginate commissure, fig. 3; the interareas, protegula and large amphithyridid pedicle opening, fig. 4. ×60.

Fig. 5. Pedicle view of an adolescent shell (37531) showing the rounded profile. Shell surface coated with crystallites. ×66.

Fig. 6. Near lateral view of an adolescent shell (37532) showing the relatively more biconvex lateral profile. ×60.

Fig. 7. Interior view of an adult brachial valve (37533) showing the cardinal process, sockets, and the sub-marginal ridge and hollow median septum with denticulate anteriors. ×55.

Fig. 8. Interior view of an adolescent brachial valve (37534) showing the short sub-marginal ridge and short median septum with no intra-septal cavity. ×60.



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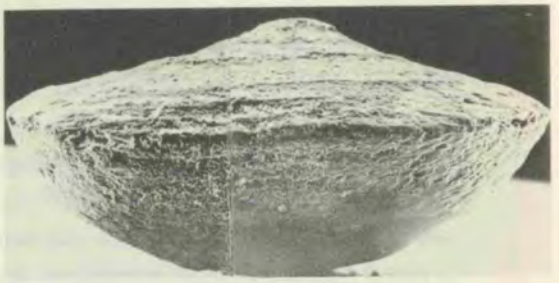

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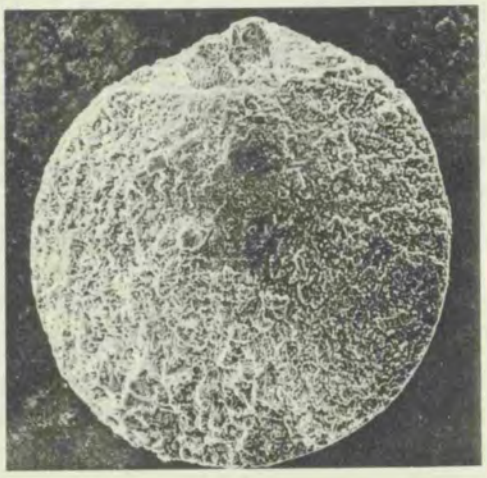

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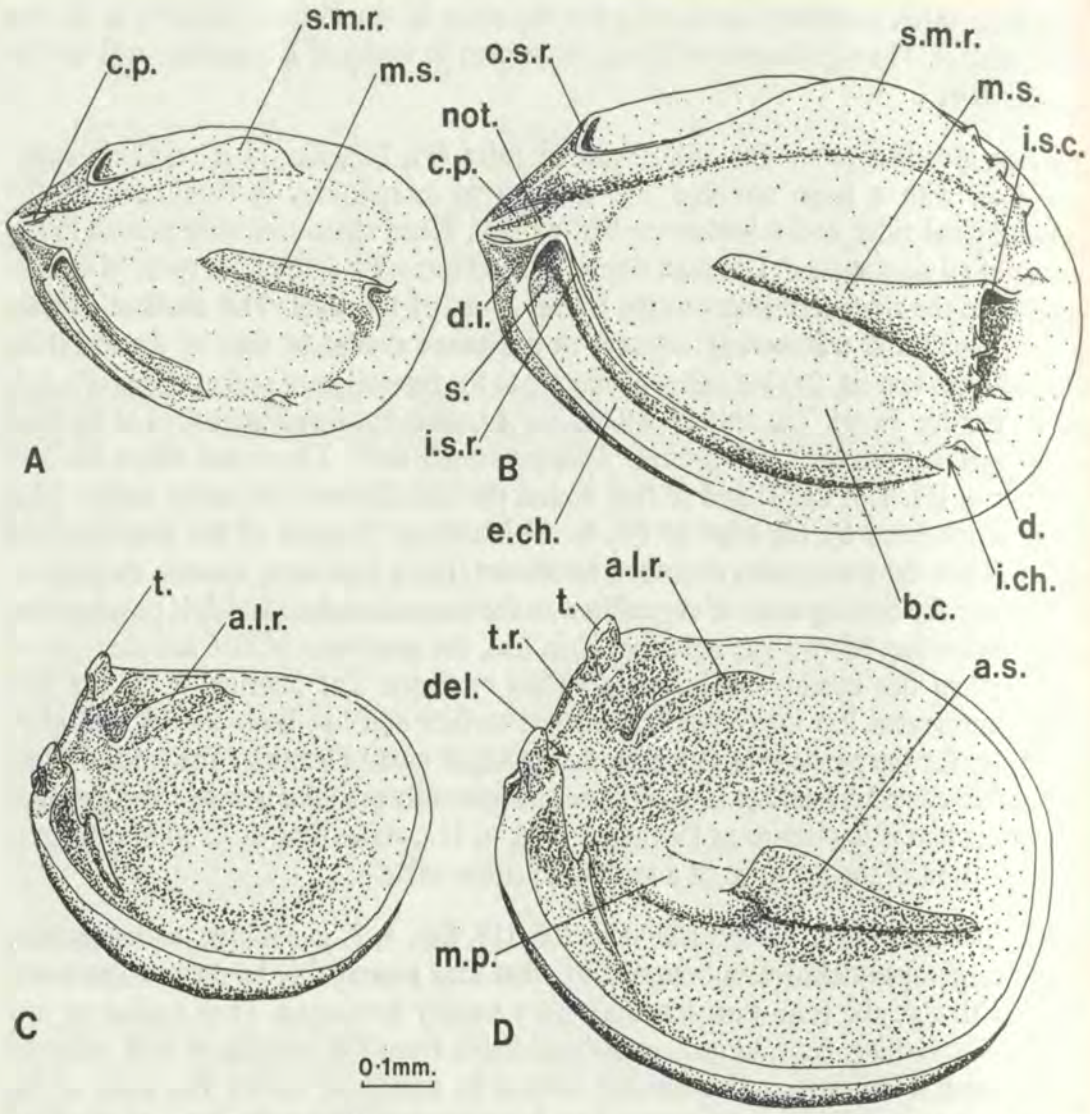
BAKER, *Zellania davidsoni*

a pedicle valve, probably accounting for the error in the *Treatise* (Elliott, in Moore 1965, H857). The significance of this arrangement in terms of life-attitude will be discussed later.

Interior. Brachial valve. The adult brachial valve (Pl. 118, fig. 7) is regularly endopunctate, with a large notothyrium. Its internal morphology is dominated by the sub-marginal ridge and a hollow median septum. These structures were present in the valves of all sizes studied, although degree of development was found to vary. In smaller specimens the ridge terminates in the lateral zones of the shell. The cardinal process is very small and transversely concave in a manner similar to that of thecidellinids (Baker 1969, text-fig. 2B) but not contributing to the formation of socket ridges (Pl. 119, fig. 1; text-fig. 2A–D). The muscle pattern is not known but two depressions at the base of the cardinal process may represent diductor muscle scars. The socket ridges are very prominent (Pl. 119, fig. 2) and in fact bound the notothyrium, the outer socket ridge being represented by the edge of the dorsal interarea. In none of the stereoscanned material has the granulation described by Moore (1855) been seen. Certain shells however, show the development of crystallites on the internal surface and it is possible that it is to these that Moore was referring. If, in fact, the specimens M3036 are the types of *Z. davidsoni* this speculation becomes virtual certainty. The interior of the brachial valve represented has this crystallite covered surface and has been coated with glue, obviously for the purpose of repairing the damaged median septum. The optical effect of the glue-coated crystallites is to produce an apparently granular interior. The presence of this septum is important as Davidson 1874, p. 113, states that in *Z. oolitica* there is no indication of the presence of a septum in either valve.

Interior. Pedicle valve. The pedicle valve (Pl. 119, figs. 4, 5) is concave, endopunctate, with a large open delthyrium bounded by what may presumably be regarded as tooth ridges although the teeth themselves are very weakly developed. They appear as two posteriorly arching flaps, almost indistinguishable from the secondary shell material of the ventral interarea and invariably broken in separated valves. The apex of the delthyrium is occupied by a concave plate, lying between the tooth ridges on the floor of the valve in the position of a pedicle collar. Serial sections show the development of a small ridge, the lateral ancillary ridge (text-fig. 2I–N) also sub-marginal in position and situated in the postero-lateral and lateral zones of the shell (Pl. 119, fig. 6). The orientation of these ridges is such that they abut against the edge of the sub-marginal ridge when the valves are closed. There are no visible muscle scars but transverse sections of shells show a callus on the floor of the valve which may have been the site of muscle scars. From the anterior of this thickened region, a thin blade-like septum extends almost to the anterior of the valve (text-fig. 1D) and is almost in contact with the median septum when the valves are closed.

Development of structures. On the basis of faunal analyses conducted for other studies, *Z. davidsoni* may be regarded as comprising approximately 0·04% of the brachiopod fauna of the Oolite Marl in Westington Hill Quarry (Baker 1969); and even if the number of specimens is drastically reduced by fragmentation it is indeed a rare species. Any attempt at detailed ontogenetic studies would therefore be fruitless. Owing to the delicate nature of the shell, valves are usually fragmented but sufficient material has

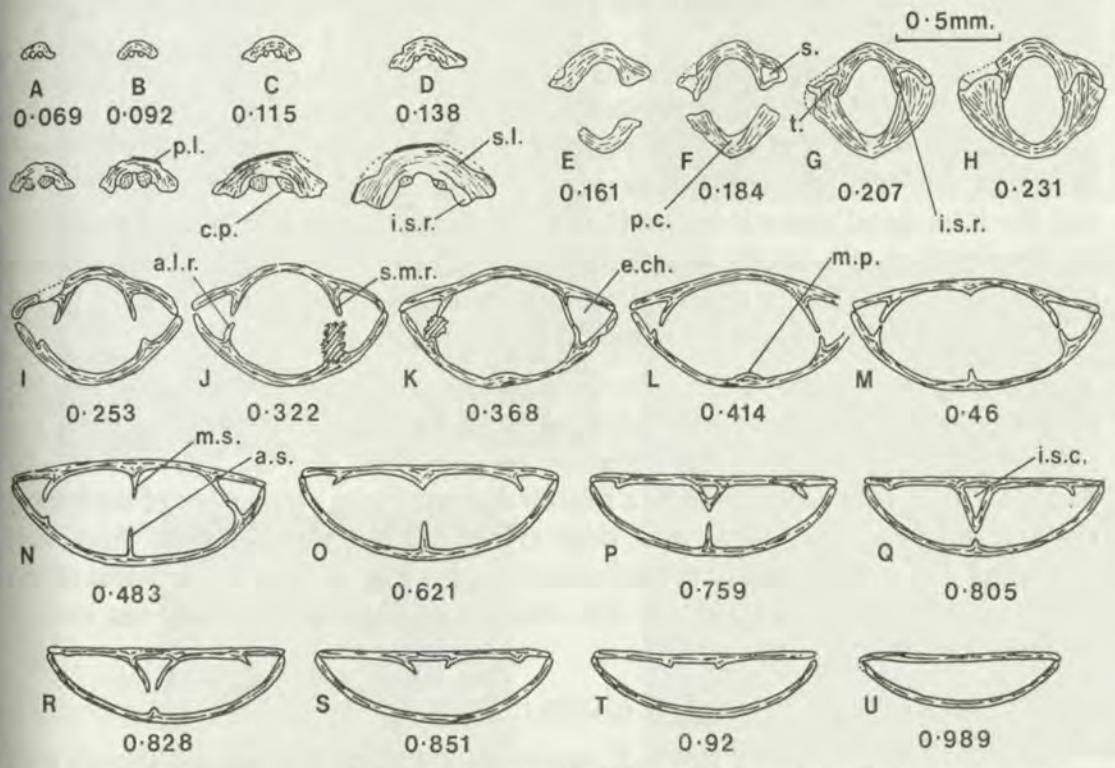


TEXT-FIG. 1. Three-quarter profile reconstructions from photomicrographs and serial sections to illustrate the internal morphology of the determinable growth stages of *Z. davidsoni*. A, B adolescent and adult brachial valves. C, D adolescent and adult pedicle valves. a.l.r. ancillary lateral ridge, a.s. ancillary septum, b.c. brachial cavity, c.p. cardinal process, d. denticle, del. delthyrium, d.i. dorsal interarea, e.ch. exhalent channel, i.ch. inhalent channel, i.s.c. intra-septal cavity, i.s.r. inner socket ridge, m.p. muscle platform, m.s. median septum, not. notothyrium, o.s.r. outer socket ridge, s. socket, s.m.r. sub-marginal ridge, t. tooth, t.r. tooth ridge.

been recovered to enable determination of the mode of development of various structures and the recognition of certain growth stages (text-fig. 1A–D).

It is possible to distinguish specimens which, by their invariably smaller size, although morphologically similar to the larger shells, may be regarded as adolescent forms. The largest shells do not exceed a length of 1·4 mm. and the argument that they represent adults is essentially that outlined in earlier studies (Baker 1969). The primitive aspect of the cardinalia and the small size, together with the form of the pedicle opening and probable form of the lophophore, suggests that, like the thecidellinids, *Zellania* is the product of neotenous modification.

Development of the sub-marginal ridge and median septum. Existing accounts state that the inner ridges (sub-marginal ridge) are reflexed anteriorly into a posteriorly directed septum. In fact, adolescent brachial valves show that the sub-marginal ridge and median septum arise separately (Pl. 118, fig. 8), and are extended anteriorly as growth proceeds.



TEXT-FIG. 2. Drawings prepared from microprojected cellulose acetate peels of serial transverse sections through *Z. davidsoni* showing the morphological features in section. Number indicates distance o section in mm. from the brachial umbo. A–D reproduced at ×2 scale to show microstructure. Apparently thick pedicle valve, F–H due to obliquity of valve posteriorly relative to the plane of section (see Westbroek 1969). Recrystallization shaded. a.l.r. ancillary lateral ridge, a.s. ancillary septum, c.p. cardinal process, e.ch. exhalent channel, i.s.c. intra-septal cavity, i.s.r. inner socket ridge, m.p. muscle platform, m.s. median septum, p.c. pedicle collar, p.l. primary layer, s. dental socket, s.l. secondary layer, s.m.r. sub-marginal ridge, t. tooth.

At this adolescent stage of development the sub-marginal ridge extends little more than half the length of the valve and the median septum is a low structure, extending from near the anterior margin, posteriorly, about half-way to the cardinal process. It is only hollow at the extreme anterior end.

In adult brachial valves the sub-marginal ridge extends almost to the anterior margin and may extend in the direction of the median septum as a row of denticles (Pl. 118, fig. 7). The posterior termination of the median septum however, maintains a constant position relative to the socket ridges and cardinal process (Pl. 118, figs. 7, 8). Increase in the size of the structure must therefore, be achieved by addition of material at the anterior end and, as the walls diverge, so the intra-septal cavity increases in size.

Serial sections (Pl. 120, fig. 7; text-fig. 2K–P) show that the ridge, on the evidence of the orientation of fibres, develops from the floor of the valve. Therefore, both the ridge and median septum, in terebratuloid terms, represent ascending elements, a point of

significance in consideration of affinities. The ridge increases in size by the simple incremental addition of secondary material. Exactly how this occurs is not clear, but the development of denticles may be an initial feature of the anterior extension of the sub-marginal ridge and also the median septum (Pl. 119, fig. 3). Posteriorly the sub-marginal ridge forms the inner socket ridges, and the dental sockets are obviously much deepened as the ridge develops.

The sub-marginal ridge is not vertical but directed outwards (Pl. 119, fig. 2; text-fig. 2 K–P). As material is added at the summit therefore, the size of the brachial cavities must be increased. A similar trend is exhibited by the median septum. As it increases in height, the walls become more divergent (Pl. 119, figs. 1–3; text-figs. 1B, 2P–R) so that the intra-septal cavity increases in size. The result of this development pattern is the development of a border morphologically similar to that of certain thecidellinids (Baker 1969) but differing structurally and with no migration as encountered in the sub-peripheral rim of *Moorellina granulosa* (Moore) (Baker 1970).

Development of the pedicle valve. The two complete pedicle valves discovered, judging from their small size, apparently belonged to adolescent individuals. The teeth are missing but the only discernable difference between these and the valves of serially sectioned larger forms appears to be a relative decrease in the prominence of the lateral ancillary ridges as the sub-marginal ridge of the brachial valve becomes more well developed. The development of the callus on the valve floor and the development of the thin ancillary septum are apparently late ontogenetic features as they are not seen in adolescent valves of the size studied.

MICROSTRUCTURE

The material studied shows that in *Z. davidsoni* the endopunctate shell, although very thin, was clearly differentiated into primary and secondary layers (Pl. 119, fig. 8; Pl. 120,

EXPLANATION OF PLATE 119

Stereoscan photomicrographs of specimens of *Zellania davidsoni* Moore. Material of all figures coated with evaporated aluminium before photography.

Fig. 1. Interior view of a brachial valve fragment (37535) showing the endopunctation and cardinal process. The left dental socket is damaged and the hollow anterior region of the median septum has been broken away to reveal the endopunctate floor of the intra-septal cavity. ×60.

Fig. 2. Profile view of specimen (37535) to show the relative prominence of the inner socket ridges bounding the notothyrium, the inclined sub-marginal ridge, left, and the divergent anterior of the median septum. Angle of tilt 70°. ×65.

Fig. 3. Enlarged view of specimen (37533) to show detail of the denticulate anterior of the hollow median septum and sub-marginal ridge. ×110.

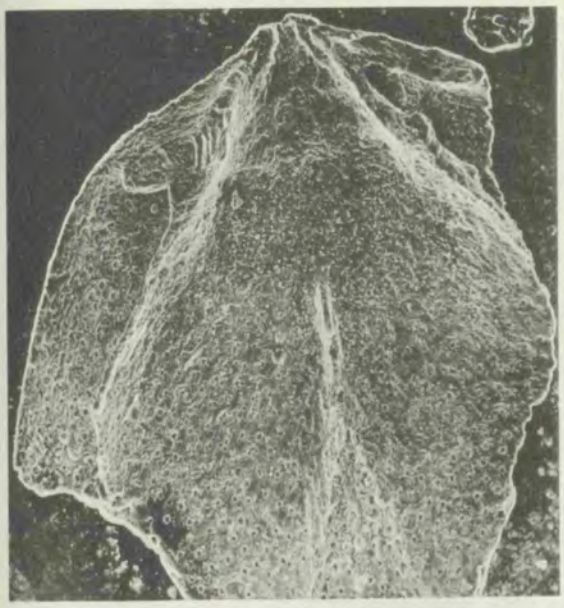
Fig. 4. Interior view of an adolescent pedicle valve (37536). Detail obscured by a heavy coating of crystallites but the left lateral ancillary ridge is just visible, upper left. Teeth missing. ×58.

Fig. 5. Posterior view of specimen (37536) showing the delthyrium bounded by tooth ridges. Angle of tilt 57°. ×70.

Fig. 6. Profile view of the interior of a fragment of an adolescent pedicle valve (37537) showing the lateral ancillary ridge, centre-left. Angle of tilt 70°. ×150.

Fig. 7. Enlarged portion of the exterior of the brachial valve of specimen (37538) showing the radial fissuring of the primary shell layer. ×400.

Fig. 8. Stereoscan photomicrograph of a cellulose acetate peel of a transverse section through the shell of specimen (37543) showing the fissures in the prismatic primary layer, upper, and the fibrous secondary layer. Section location: Pedicle valve, right antero-lateral sector. ×1080.



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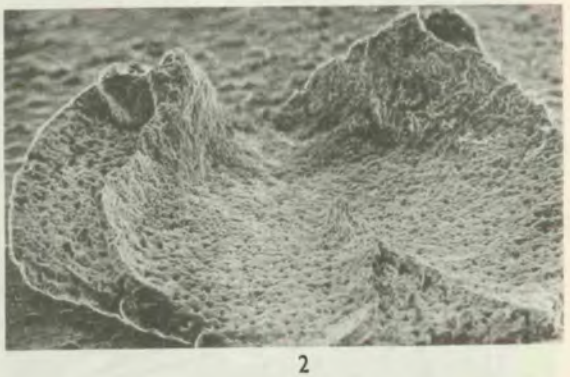

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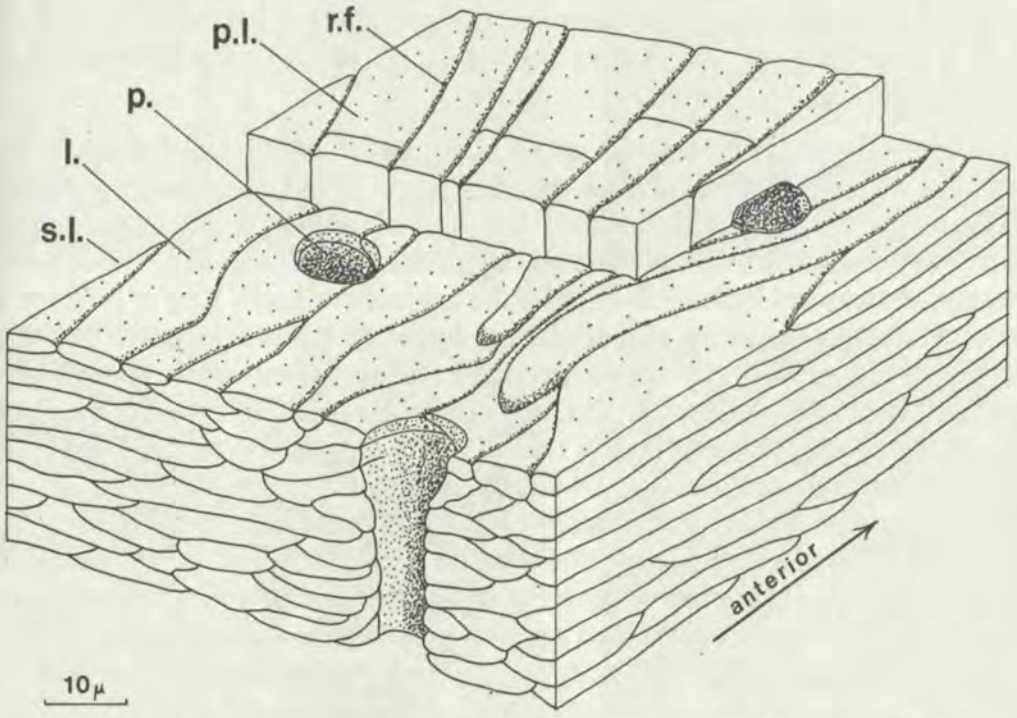
fig. 2). Although the punctae deflect the secondary fibres in a normal (Williams 1968*a*) terebratulide manner (Pl. 120, figs. 5, 6), the microstructure of the layers themselves differs from the normal terebratulide pattern.



TEXT-FIG. 3. Block reconstruction of the shell of *Z. davidsoni* from photomicrographs of cellulose acetate peels, to show the form of the primary layer and the orientation and variability of the fibres of the secondary layer. l. lamina, p. puncta, p.l. primary layer, r.f. radial fissure, s.l. secondary layer.

Primary layer. The zellaniid primary layer is thin and apparently of an unusual type. Reference has already been made to the radially arranged fissures in the primary shell (Pl. 119, figs. 7, 8; Pl. 120, fig. 1). In transverse sections (Pl. 119, fig. 8) the shell material is seen to be of crystalline type and without the normal pitted appearance described by Williams (1968*a*). The persistence of the radial arrangement of the fissures and their failure to penetrate the secondary layer must indicate a more than coincidental relationship with the primary shell material. The radial pattern is relieved at intervals by cross-joints so that the primary layer in effect, consists of a series of sub-rectangular blocks of prismatic calcite (text-fig. 3). The primary layer is usually poorly preserved because the physical characteristics described contribute to its easy removal mechanically, as evidenced by the difficulties encountered during the preparation of cellulose acetate peels.

Secondary layer. Stereoscan photomicrographs of etched secondary shell surfaces and investigation by horizontal, transverse, and longitudinal serial sections, shows that the secondary shell mosaic also is of rather unusual type. Even the most careful orientation of sectioned material has failed to produce anything approaching a typical (Williams 1968*a*) terebratulide or spiriferide transverse mosaic except at the base of the teeth

(horizontal sections). Horizontal (Pl. 120, fig. 4) and transverse (Pl. 120, fig. 5) sections show that the secondary shell material appears typically as a series of sheets or very broad (20–30 μm. wide) laminae which are, in longitudinal section, disposed with normal (Williams 1956, 1966, 1968*a*) secondary orientation relative to the primary layer (Pl. 120, fig. 8). Horizontal sections show that the orientation of laminae changes rapidly, so that, in places, a zigzag rather than a spiral arc (Williams 1968*a*) secondary growth mosaic is produced.

General observations. At present the origin and purpose of the radial fissuring is unknown, but it may represent the diagenetic expression of some peculiarity in the mode of deposition of the primary shell material. The uncertainty of whether the fissures are of primary or diagenetic origin is obviously a point of considerable importance because, if primary, the features indicate in *Zellania* the existence of a new type of primary shell material. Owing to the rarity of material resolution of the problem will be difficult. A certain amount of indirect evidence is available: (*a*) shells coated with crystallites, and in which some recrystallization has obviously occurred, show obliteration of the fissuring effect, (*b*) the fissures are most clearly seen in the best-preserved material, (*c*) they are a pronounced feature of all horizontal sections through the primary layer and (*d*) it is difficult to envisage a diagenetic process which would, universally, affect the primary layer to such an extent, with no apparent effect on the secondary layer. Williams (1968*b*) suggests that the finely crystalline covering of *Billingsella* represents the recrystallized primary layer. Similar recrystallization may have occurred in *Zellania*, but it is odd that the line of demarcation between recrystallized and unaltered material should be so

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EXPLANATION OF PLATE 120

Stereoscan photomicrographs of *Zellania davidsoni* Moore. Material of all figures coated with evaporated aluminium before photography and all, with the exception of fig. 3, taken from cellulose acetate peels.

Fig. 1. Horizontal section through the primary shell layer of specimen (37540) showing the radially arranged fissures and block-like nature of the primary shell. Section location: Brachial valve, anterior sector. ×1200.

Fig. 2. Horizontal section through the shell of specimen (37541) showing the primary/secondary layer junction, broken line. Shell partially recrystallized. Section location: Brachial valve, left antero-lateral sector. ×1200.

Fig. 3. External surface of specimen (37542) from which the primary layer has been removed, showing detail of the fibre mosaic at the external surface of the secondary shell layer. Normal proximal, centre right, and laminar distal, centre, regions of fibres are visible. Figure location: Brachial valve, left antero-lateral sector. ×900.

Fig. 4. Oblique section through the secondary shell layer showing endopunctae and the secondary fibres arranged as overlapping laminae. Section location. Brachial valve, right lateral sector. Section orientation: Parallel with the plane of the commissure. ×550.

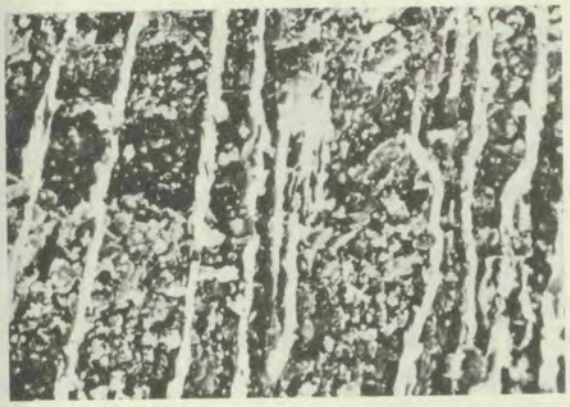
Fig. 5–7. Transverse sections through specimen (37543).

Fig. 5 shows the primary layer, upper and the fibres of the secondary layer deflected by punctae. Section location: Brachial valve, right antero-lateral sector. ×540.

Fig. 6. Enlarged section to show detail of an endopuncta and deflected secondary fibres. Section location as Fig. 5. ×2000.

Fig. 7. Transverse section through the sub-marginal ridge showing the orientation of the secondary fibres. Section location. Brachial valve, right lateral sector. ×400.

Fig. 8. Longitudinal section through specimen (37544) showing the orientation of the secondary fibres relative to the primary shell layer, lower. Section location: Pedicle valve, 0·086 mm. to the left of the mid-line. ×1000.



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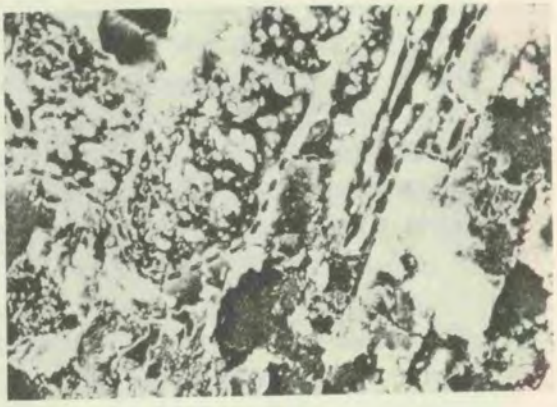

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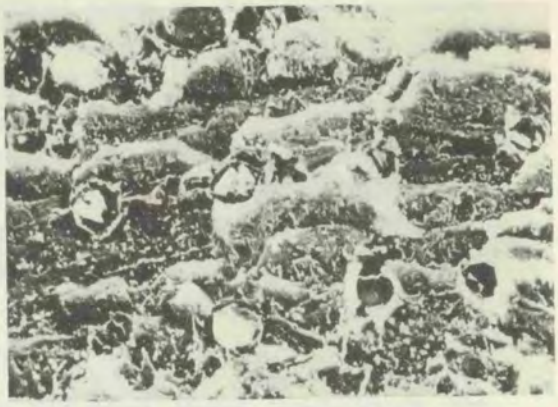

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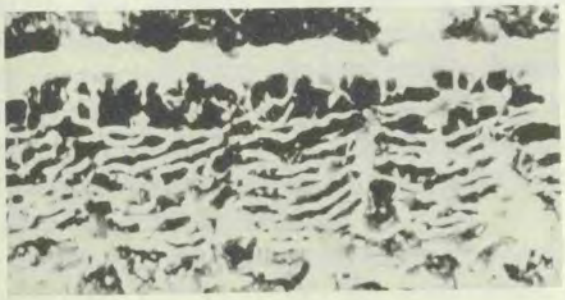

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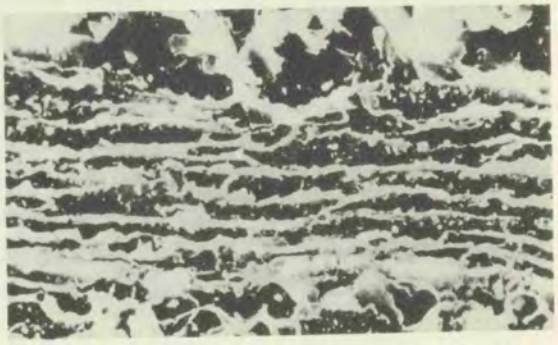

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abrupt, and also that the structure is present in all sections involving primary shell. Williams (1968*a*, p. 31) states that the primary layer of all specimens of *Spiriferina walcotti* (Sow.) examined is recrystallized but that the secondary shell is normally well preserved. He notes a strong lineation in the primary layer (Williams 1968*a*, pl. 11, fig. 5) normal to the shell surface and is of the opinion that this lineation may represent an original fabric. The evidence available, therefore, indicates that the microstructure of the zellanid primary layer is of secretory rather than diagenetic origin. Some transverse sections of secondary shell (Pl. 120, fig. 6) are very similar to the recrystallized secondary mosaic of *Nisusia ferganensis* (Williams 1968*b*, p. 487). However, if recrystallization in *Zellania* extended below the primary layer, so that some of the secondary fibres have been recrystallized whilst retaining their morphological characteristics, the observed features of the primary layer may also be regarded as original.

The zellaniid laminae are curiously like the flared fibres of *Moorellina granulosa* (Moore) described in Baker (1970, p. 84). In *M. granulosa*, only the distal ends of the fibres are affected but in *Z. davidsoni* this expansion has a tachygenetic expression and affects all but the extreme proximal end of the fibre. The unmodified proximal ends of some secondary fibres (Pl. 120, fig. 3) are similar to the secondary fibres (Williams 1968*a*, pl. 7, fig. 4) of *Terebratulina caput-serpentis* (Linné). However, the microstructure of the shell as a whole most closely resembles that of the stringocephalacean *Mutationella podolica* (Siemiradzki), illustrated in Williams (1968*a*, pl. 11, figs. 1–3).

PALAEOECOLOGY

Z. davidsoni occurs together with thecidellinids and other, larger, brachiopods; the probable environment of the thecidellinids is discussed in Baker (1969). It may be argued that *Zellania*, by association, occupied the same environment. The close morphological similarity between certain internal characters of *Zellania* and thecidellinids has been noted, but it has been clearly shown that the structures arise in different ways and probably performed different functions. Morphological similarity produced by convergent evolution is to be expected if the animals did occupy a similar environment. However, there are certain features of the organization of *Z. davidsoni* which render the above argument hazardous.

Analysis of the microstructure of the thecidellinid *Moorellina granulosa* in functional terms (Baker 1970) reveals the development of a reinforced shell which is entirely in agreement with the turbulent environment suggested by Ager, Baker, and Nekvasilová (in Baker 1969). The pedicle opening of *Z. davidsoni* is disproportionately large relative to the size of the animal. *Moorellina* is a cemented form and it is possible that *Zellania* required a large pedicle for anchorage. However, the shells of the two genera are in direct contrast. In *M. granulosa* the shell is thick and reinforced. In *Z. davidsoni* the shell is thin and very brittle; so brittle in fact that shells are often crushed by a degree of compaction of sediment which does not deform *Moorellina* at all. Such a shell could not survive in anything other than a sheltered environment. Dr. J. D. Hudson (personal communication) has suggested that *Zellania* may have occupied a sheltered microenvironment, e.g. protected cavities under large shells (*Ostrea*, etc.). This would afford protection whilst the animal was alive but when the pedicle decayed the shell would be liberated into the turbulent general environment. The cardinal process and teeth of

M. granulosa are strongly developed. The cardinal process of *Zellania* is small and the teeth are very fragile so that unless transportation of the shell occurred before the musculature of the animal decayed, the valves would almost certainly become disarticulated. It seems likely that the musculature would decay before the pedicle, thus allowing separation of the valves. Of the material collected however, complete specimens are the most common although the broken teeth of the pedicle valves and perforations in some brachial valves (Pl. 118, figs. 7, 8) do indicate a degree of abrasion consistent with some transportation.

There exists therefore, the apparent anomaly of a strong pedicle and a weak shell. Analysis of the shell characters of *Z. davidsoni* in environmental terms is indicative of a sublittoral mud-grade environment (Ager 1965) into which the thecidellinids, the organodetrital remains and the peri-reefal brachiopods (Baker 1969) were drifted. It is possible to reconcile a large (rather than strong) pedicle with this view, as it would afford anchorage in a soft substratum, although the anatomy of the pedicle itself is unlikely ever to be described.

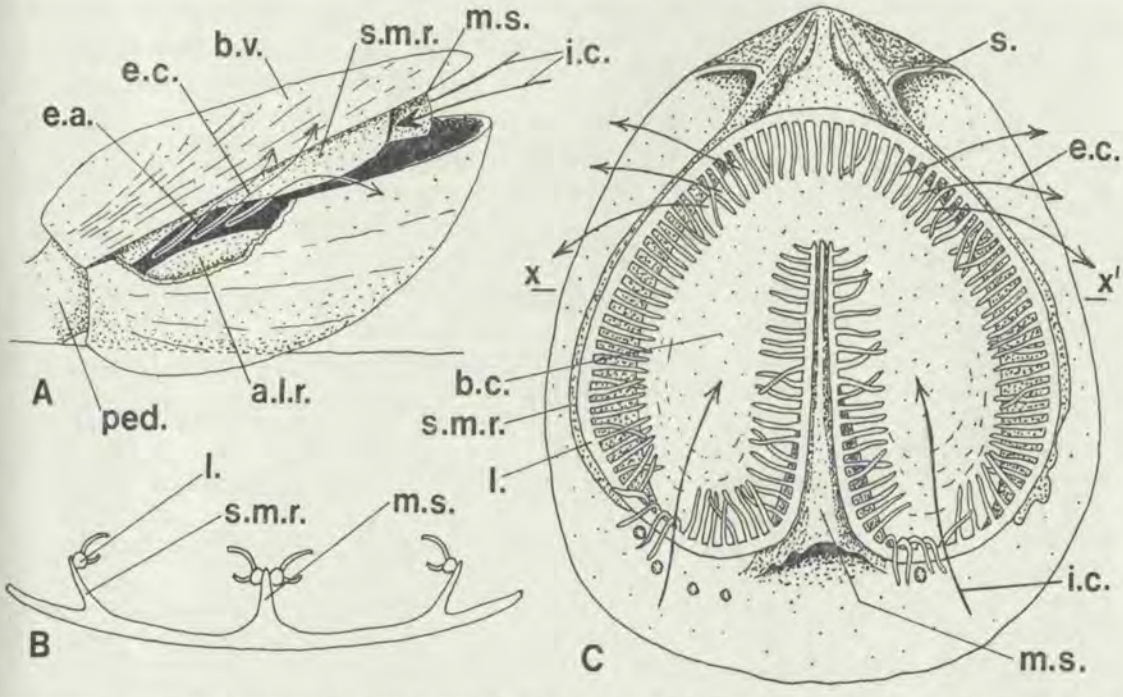
The association of micromorphic brachiopods with shell debris is noted by Swedmark (1967) who records the occurrence of *Gwynia capsula* (Jeffreys) in a sub-tidal mineral sand containing a high proportion of fine broken shell. In this environment the animal apparently seeks the shelter of serpulid tube fragments.

Circumstantial evidence is provided by speculation concerning the life-attitude and the functional significance of the internal structures of *Zellania*. Analysis of the growth habit of *M. granulosa* indicates a growth pattern designed to lift the brachial apparatus away from the attachment surface (Baker 1970). This growth habit requires that the brachial valve be uppermost in position. The posteriorly projecting brachial umbo of *Z. davidsoni* may indicate similar orientation. The convex pedicle valve, possibly partially buried in the sediment, would enable the dorsally oriented, relatively plate-like brachial valve to be lifted clear of the sub-stratum (text-fig. 4A). This hypothesis is supported by a consideration of the functional significance of the sub-marginal ridge and ancillary structures. From a consideration of the thecidellinid brachial apparatus it is probable that the inner surface of the sub-marginal ridge and the sides of the median septum (text-figs. 4B, C) supported a simple schizolophe (Rudwick 1968). Study of brachiopod feeding mechanisms (Rudwick 1965, H206) indicates that in schizolophous forms the valves gape fairly widely and the filaments form a bell-like inhalent chamber. If *Zellania* occupied a mud-grade environment it is possible that under certain conditions, e.g. high turbidity, the valves did not gape as widely as normal. The denticulate anterior of the brachial valve (text-fig. 1B) may, therefore, represent the point of entry of the inhalent current when the valves were almost closed (text-figs. 4A, C). In this case it is thought that the exhalent apertures were situated postero-laterally in the zones occupied by the lateral ancillary ridges. The current flow would now be influenced by the degree of gape of the valves, as the exhalent apertures would be closed as the sub-marginal ridge and lateral ancillary ridges came together (text-fig. 4A). The virtual compartmentation of the shell (text-fig. 2) must have some significance and may be an expression of the lack of turbulence in the water, thus assisting in the separation of the inhalent and exhalent currents produced by the filaments of the lophophore.

These arguments, of course, apply equally well to occupation of a sheltered microenvironment but it is considered that the sum of the morphological and microstructural features of *Z. davidsoni* favours the postulated mud-grade environment.

AFFINITIES

The close morphological similarity between the internal characters of *Zellania* and thecidellinids has been noted, but it has been clearly shown that the structures arise in different ways, and therefore contradict Moore's (1855) view that thecideaceans and *Zellania* are related. In the *Treatise*, *Zellania* is tentatively linked with the terebratellaceans. The material studied shows all degrees of preservation but there is little doubt that the secondary mosaic is of modified terebratulide or spiriferide type. The similarity



TEXT-FIG. 4. A. Diagrammatic reconstruction of the possible life-attitude of *Z. davidsoni* with the valves gaping slightly. A small portion of the pedicle valve is omitted to show the postulated exhalent aperture. B. Transverse section through X–X′, fig. C. to show the postulated position of the schizolophe relative to the sub-marginal ridge and median septum. C. Diagrammatic representation of the interior of a brachial valve of *Z. davidsoni* showing the probable form and position of the lophophore and inhalent and exhalent apertures. a.l.r. ancillary lateral ridge, b.c. brachial cavity, b.v. brachial valve, e.a. exhalent aperture, e.c. exhalent current, i.c. inhalent current, l. lophophore, m.s. median septum, ped. pedicle, s. socket, s.m.r. sub-marginal ridge.

between some secondary fibres of *Z. davidsoni* and secondary fibres of *Terebratulina caput-serpentis* (Linné), and the similarity between the primary shell of *Zellania* and *Spiriferina walcotti* (Sow.), has been noted. The sub-marginal ridge is very like the loop of stringocephalids such as *Rensselandia johanni* (Hall) in a sessile position. However, the shell microstructure of *Z. davidsoni* appears to most closely resemble that of the Lower Devonian stringocephalacean *Mutationella podolica* (Siemiradzki). Studies strongly indicate that the secondary shell mosaics of even distantly related brachipods may show a similar initial development pattern, although subsequently diverging. The evidence presented in the present paper, although not solving the problem of immediate affinity, indicates that the microstructure of *Zellania* may partially recapitulate the phylogeny of the genus. It is generally accepted that recapitulation in organisms can occur, although

its value as an evolutionary criterion is open to criticism. If it is possible for the secretory regime of the secondary fibres to recapitulate phylogeny, accompanied by tachygenesis, the process may be arrested and the evidence thus preserved in neotenous forms such as *Zellania*. The dorsal cardinalia are of billingsellacean type, i.e. primitive, and work in progress, on very young terebratulides, shows that the initial development of the cardinal process of *Moorellina*, *Zellania*, and terebratulides follows the same pattern and supports the hypothesis of recapitulation.

Stehli (in Moore 1965, H739) derives both the Terebratulidina and Terebratellidina from mutationellin ancestors. The shell of *Zellania* shows mutationellin affinities. Owing to the enormous time-gap it would be ambitious to suggest that *Zellania* is descended from a stringocephalacean ancestor. However, consideration of features such as the recapitulatory nature of secondary fibre secretion, the development of the submarginal ridge from ascending elements and the typical endopunctation certainly suggest that *Z. davidsoni* may be closely related to terebratellacean stock.

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