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

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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.

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*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.

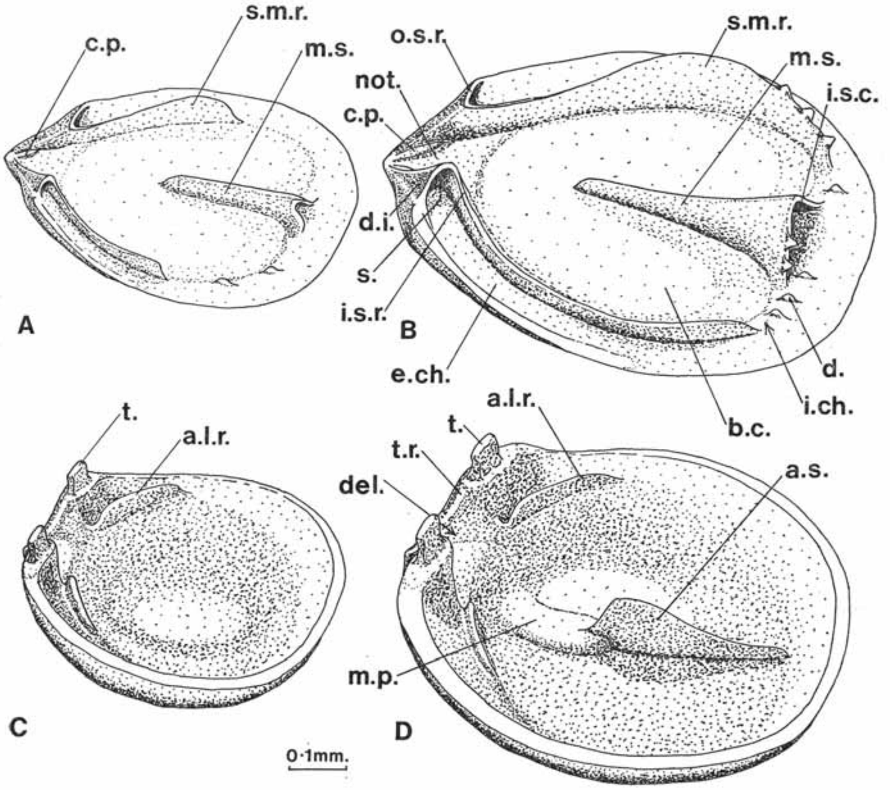
Fig. 8. Interior view of an adolescent brachial valve (37534) showing the short sub-marginal ridge and short median septum with no intra-septal cavity. ×60.

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

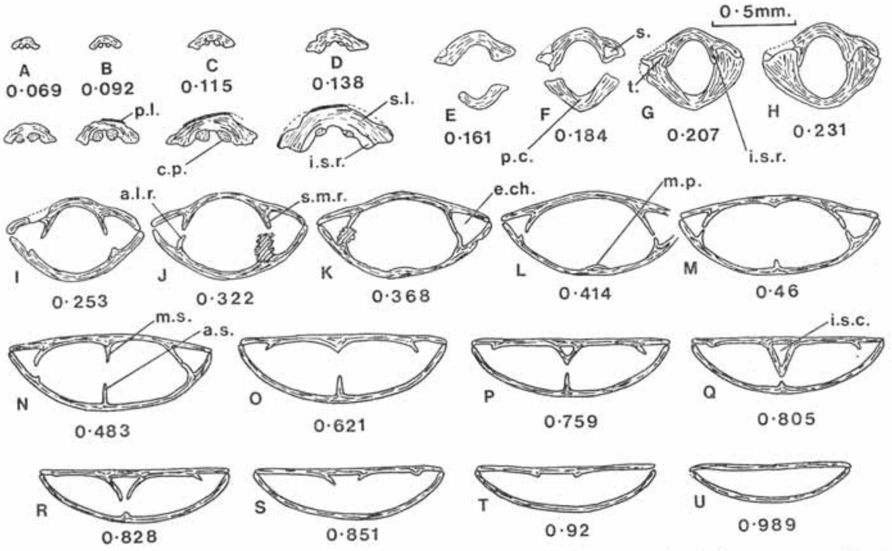


TEXT-FIG. 1. Three-quarter profile reconstructions from photomicrographs and serial sections to illustrate the internal morphology of the determinable growth stages of *Z. davidsoni*. A, B adolescent and adult brachial valves. C, D adolescent and adult pedicle valves. a.l.r. ancillary lateral ridge, 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.

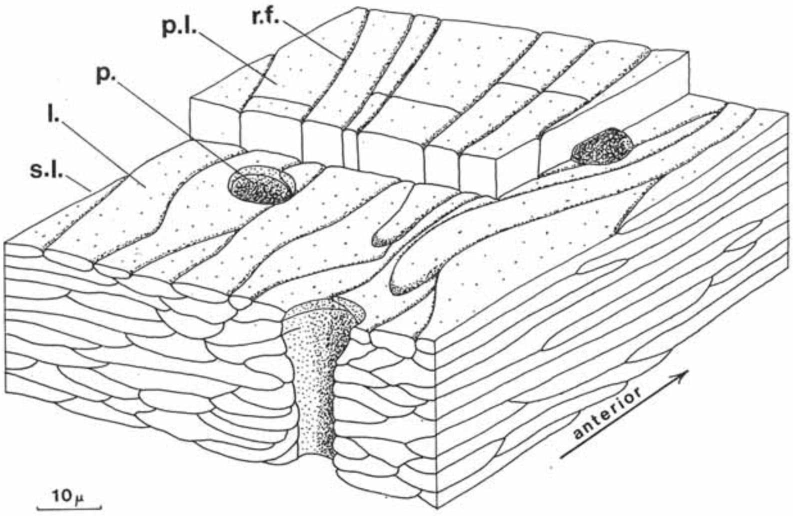
Fig. 5. Posterior view of specimen (37536) showing the delthyrium bounded by tooth ridges. Angle of tilt 57°. ×70.

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.

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 $\mu$m. 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.

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 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 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.

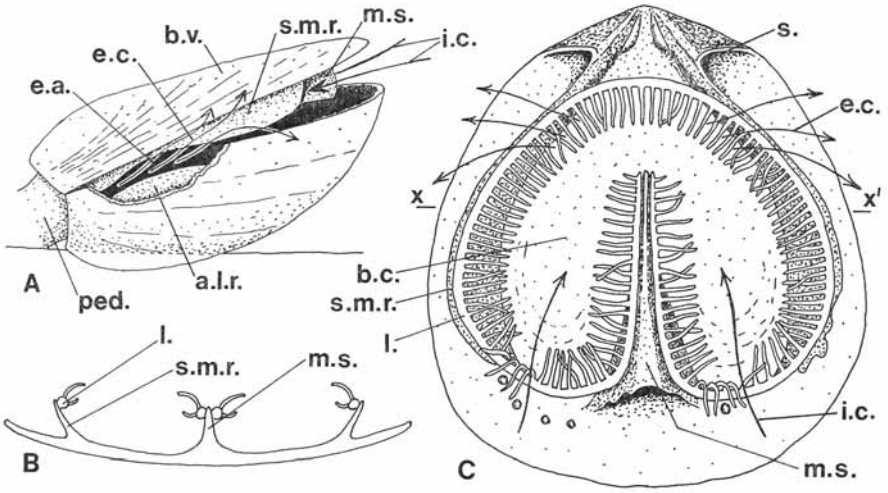
The association of micromorphic brachiopods with shell debris is noted by Swedmark (1967) who records the occurrence of *Gwynia capsula* (Jeffreys) in a sub-tidal mineral sand containing a high proportion of fine broken shell. In this environment the animal apparently seeks the shelter of serpulid tube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



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.

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.

## REFERENCES

AGER, D. V. 1965. The adaptation of Mesozoic brachiopods to different environments. *Palaeogeography, Palaeoclimatol, Palaeoecol*, **1**, 143–72.

BAKER, P. G. 1969. The ontogeny of the thecideacean brachiopod *Moorellina granulosa* (Moore) from the Middle Jurassic of England. *Palaeontology*, **12**, 388–99.

—— 1970. The growth and shell microstructure of the thecideacean brachiopod *Moorellina granulosa* (Moore) from the Middle Jurassic of England. Ibid., **13**, 76–99.

DAVIDSON, T. 1874. Supplement to the British Jurassic and Triassic Brachiopoda, 4, 113, Suppl. Pl. 11. *Palaeont. Soc.* (*Monogr.*), *London*.

ELLIOTT, G. F. 1965. *Zellania*. *In* MOORE, R. C., ed., *Treatise on invertebrate paleontology*, Part H, *Brachiopoda*, H857. Geol. Soc. Am. and Univ. Kansas Press.

MOORE, C. 1855. On new Brachiopoda from the Inferior Oolite of Dundry. *Proc. Somerset Arch. Nat. Hist. Soc.* **5** (for 1854), 107–28, pl. 1.

RUDWICK, M. J. S. 1959. The growth and form of brachiopod shells. *Geol. Mag.* **96**, 1–24.

—— 1965. Ecology and Palaeocology. In MOORE, R. C. ed., *Treatise on invertebrate paleontology*, Part H, *Brachiopoda*, H199–213. Geol. Soc. Am. and Univ. Kansas Press.

—— 1968. The feeding mechanisms and affinities of the Triassic brachiopods *Thecospira* Zugmayer and *Bactrynium* Emmrich. *Palaeontology*, **11**, 329–60.

STEHLI, F. G. 1965. Palaeozoic Terebratulida. In MOORE, R. C., ed., *Treatise on invertebrate paleontology*, Part H, *Brachiopoda*, H730–40. Geol. Soc. Am and Univ. Kansas Press.

SWEDMARK, B. 1967. *Gwynia capsula* (Jeffreys) an articulate brachiopod with brood protection. *Nature*, 213, 1151–52.

WESTBROEK, P. 1969. The interpretation of growth and form in serial sections through brachiopods, exemplified by the trigonorhynchiid septalium. *Palaeontology*, **12**, 321–32.

WILLIAMS, A. 1956. The calcareous shell of the Brachiopoda and its importance to their classification. *Biol. Rev.* **31**, 243–87.

—— 1966. Growth and structure of the shell of living articulate brachiopods. *Nature, Lond.* **211**, 1146–8.

—— 1968*a*. Evolution of the shell structure of articulate brachiopods. *Spec. Pap. Palaeont.* **2**, 55 pp.

—— 1968*b*. Shell-structure of the billingsellacean brachiopods. *Palaeontology*, **11**, 486–90.

—— *et al.*, 1965. Glossary of morphological terms. *In* MOORE, R. C., ed., *Treatise on invertebrate paleontology*, Part H, *Brachiopoda*, H139–55. Geol. Soc. Am. and Univ. Kansas Press.

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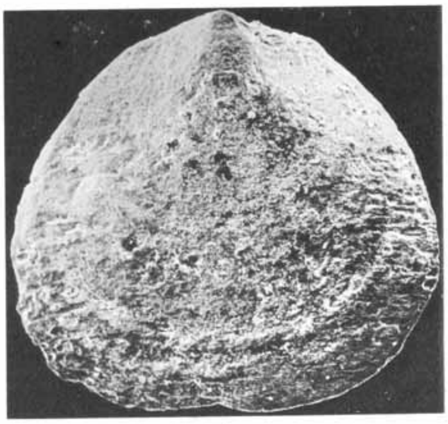

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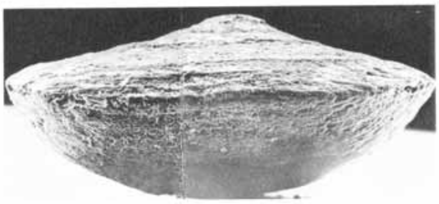

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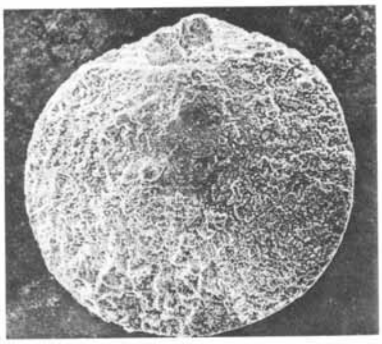

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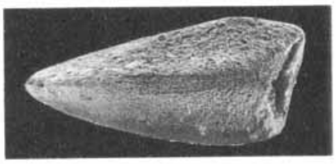

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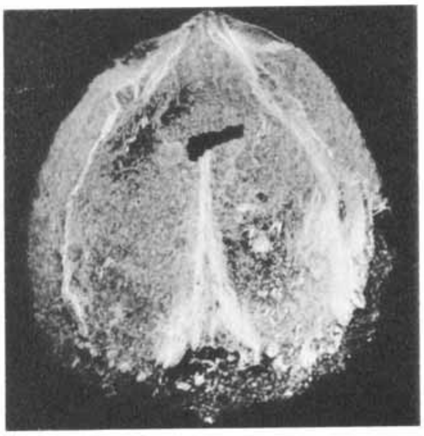

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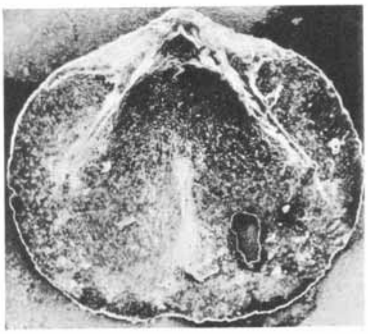

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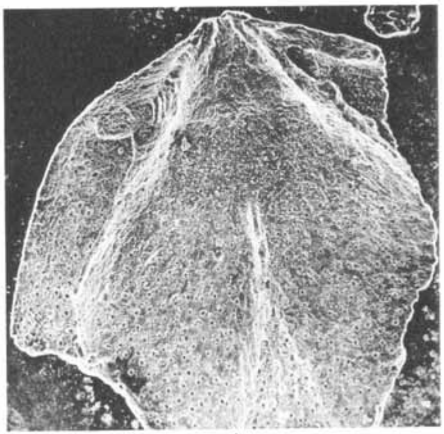

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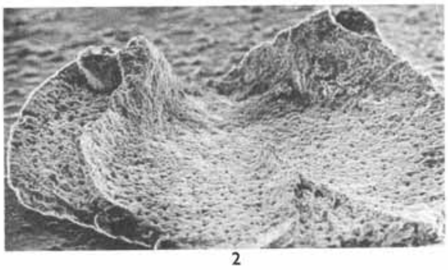

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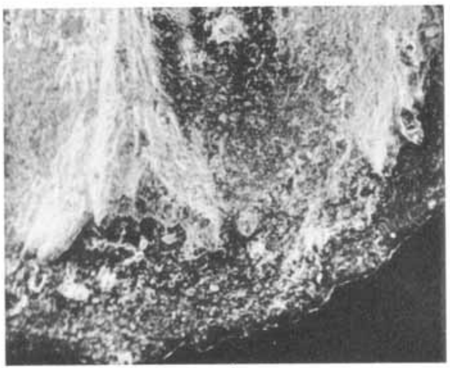

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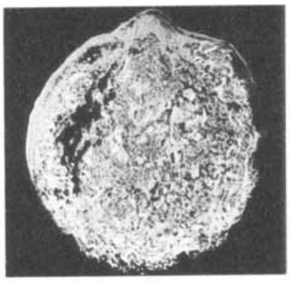

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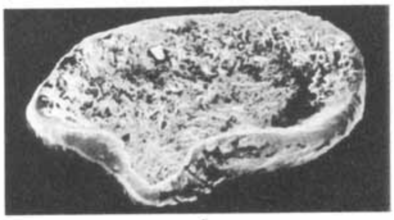

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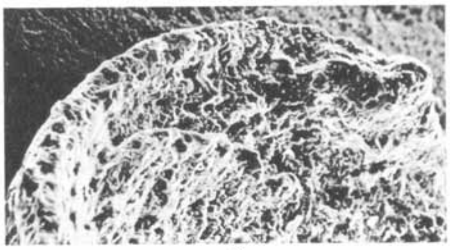

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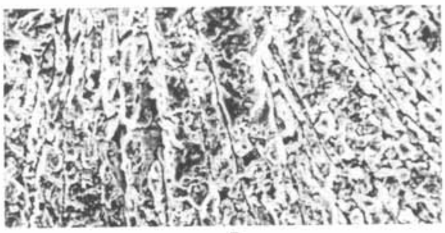

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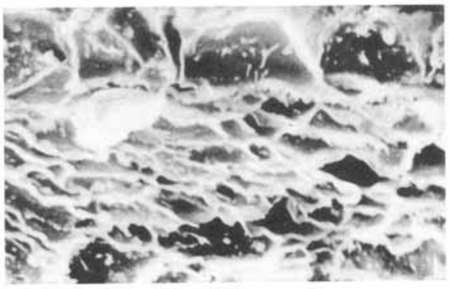

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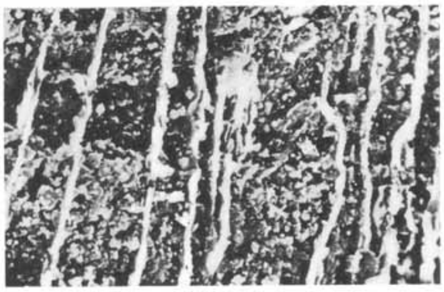
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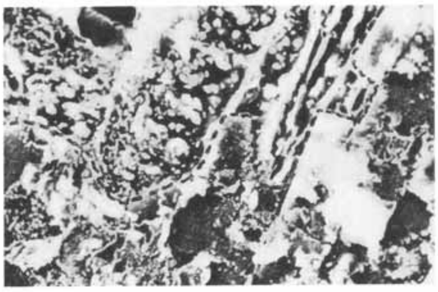
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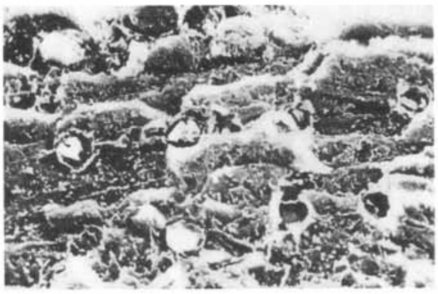
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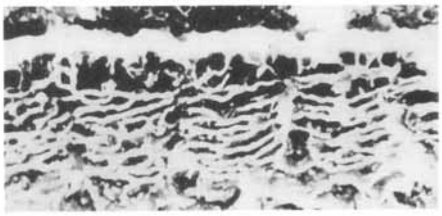
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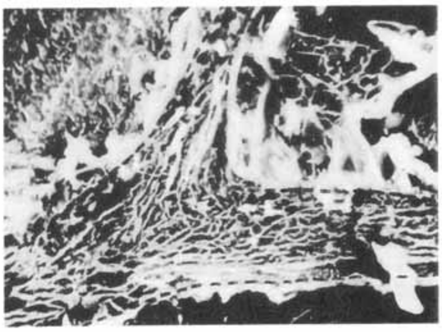
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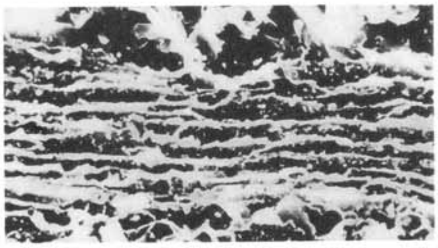
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