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SHELL MORPHOLOGY IN A CARBONIFEROUS

SPECIES OF SPIRIFER.

GRACE MARGARET DUNLOP.

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I. INTRODUCTION

The study of spiriferid morphology has been approached in different ways by the various authors of the last century and a half. Some were systematists interested in the description and classification of the shells, others were stratigraphers concerned with the recognition of index fossils. While the outer form of numerous spiriferid shells became known to a greater or lesser extent, and to some degree the shape of the internal plates, very little was known of the intimate structure and development of the shell. It is this aspect of brachiopod morphology which is here considered.

The object of the study is to describe the development of a spiriferid shell, both external and internal, and to attempt to relate that development to the morphology of the soft parts and the mode of shell formation.

The species studied is one of the most common of the Scottish Carboniferous spiriferoid brachiopods. With many others, it was referred to Spirifer trigonalis (Martin) by Davidson (1858-63, p. 29) and subsequent authors. It is now referred to a new species, Spirifer brockleyensis.

II. REVIEW OF RESEARCH ON THE MORPHOLOGY
OF THE SPIRIFERIDAE

In the earliest studies of spiriferid morphology the feature considered of greatest importance was the external appearance of the shell. Though his monographs represented a great advance in knowledge for their time, and remain of value today as the only comprehensive survey of British spiriferids, Davidson (1858-63, pp. 43-66, 1860, p.25, 1874-82, pp. 274-276) merely described the shape of the shell and the external ornament and made scarcely any mention of other features.

The presence of the spiralia was of course essential to the diagnosis of the spiriferid (Sowerby 1812-45, p.41) and some fine dissections of these delicate structures were made by Glass (in Davidson 1874-82, pl. XXXI & XXXII), but the other characteristics of the interior of the shell, the apical plates, the cardinalia and the muscle scars were neglected for many years. Waagen (1883) and Hall & Clarke (1894) were the first to take note of these structures and described them most carefully. They determined the form of the interior of the shell as well as that of the exterior.

Later authors (Cooper 1945, pp. 486-8, Ivanow, 1943, Stainbrook/

Stainbrook 1943, 1945, pp. 52-59, 1947, pp. 318-322) dealt in greater detail with small groups of spiriferids; some described the micro-sculpture of the shell more minutely (Fenton 1931, George 1931, p. 37, Allan 1947, 444), while others, encouraged by Fredericks's (1926) classification, used a variety of methods, including the making of artificial moulds (Buckman 1917) and thin sections and serial sections (Fredericks 1924, text-figs., 1926, 1929, pp. 135-6, 1931, pp. 201-3, Graban 1931, George 1932, pp. 516-575, Paeckelman 1942) to learn more about the apical plates, but their aim remained the same, the accurate description of the shape of the shell.

Shell-form is one aspect of morphology. Another aspect is the structure of the substance of the shell. The initial work on this subject was undertaken by Carpenter (in Davidson 1851-55, pp. 23-32). He observed the fibrous nature of the spiriferid shell and showed that it might be either punctate or impunctate. No-one enlarged on Carpenter's work for many years and the only observations which were made on shell structure concerned punctation. This would appear to be due to the fact that, punctation apart, the micro-structure of the shell was not considered to be of systematic importance.

It/

It was the systematists who brought the structure of the shell to notice again. Thin sections of the apex of the pedicle valve were made to show the apical plates and in these thin sections the structure of the shell was clearly visible. A considerable knowledge of shell structure was gained, (Chao, 1928, text-figs., Semichatova 1936, p. 223, 1941, 1, p. 152, 1941, 2, 128).

This knowledge of the micro-structure of the apical plates induced speculation about their mode of formation. Chu (1933) remarked on a median line to be seen on sections of the dental plates. Semichatov (1934, p. 27) observed that this line marked a discontinuity of structure within the plate. Neither offered an explanation, but Miloradovitsch (1936, p. 69) came to the conclusion that the compound nature of the plate was due to its formation within a fold of the mantle. The conception of secretion by the mantle had long been assumed, but the attempt to explain the formation of distinct parts of the shell was novel. Yanishevsky (1935, pp. 27-29) also showed an awareness of the problems of growth in his study of the relation between the dental plates and the cardinal area. The study of shell structure had aroused interest in shell growth/

growth. The two fields of inquiry concerning shell form and shell substance became linked in the study of shell development.

As a step towards the understanding of the development of the shell it was found possible to recognise successive stages in growth. The development of external form was readily established from the growth lines (Grabau 1931). The development of the form of the interior also could be discovered in the successive layers of the shell. Ivanov and Ivanova (1937, p. 186) remarked on the possibility of such a study while Miloradovitsch (1937) actually undertook it. He confined himself to a consideration of the development of the apical plates in a number of spiriferids and was able to produce a general picture of the pattern of growth in the posterior part of the pedicle valve.

The present study of Spirifer brockleyensis carries the investigation further. The whole shell is considered, both exterior and interior, and some attempt is made to explain the mode of development as well as to show the successive forms taken on by the shell during its growth.

III. SYSTEMATIC DESCRIPTION OF SPIRIFER BROCKLEYENSIS

Genus Spirifer J. Sowerby.

Type species Spirifer striatus (Martin).

Since the type specimen of this species is lost the precise characters of the genus are unknown. The illustration by Sowerby (1821, fig. 270) is quite inadequate and gives only a general impression of the external characters of the genus.

The name "Spirifer" continues to be used for many costate spire-bearers, with transverse form, which have not been assigned to any other genus. It is in this wide sense that the name is retained here.

There are many differences in form between Spirifer s.s. and Spirifer brockleyensis. Spirifer s.s. is larger and more transverse, Spirifer brockleyensis has more convex valves and a more prominent fold. The ribs are the most distinctive characters, in their number, shape and micro-sculpture. At corresponding distances from the umbo, Spirifer s.s. has twice as many ribs as Spirifer brockleyensis. In Spirifer s.s. the ribs are broad and flat with narrow dividing furrows while in Spirifer brockleyensis they are broader and rounded, separated by broad, rounded furrows. The micro-sculpture of Spirifer s./

s.s. consists of fine costellae, but the longitudinal element in the micro-sculpture of Spirifer brockleyensis is represented only in a fine twilling of the growth lines.

Spirifer brockleyensis n. sp.

Holotype: A specimen (designated C1 meantime)
to be deposited in the University of Glasgow Hunt. Mus.
Coll.

Locality: Poneil Water at Brockley, 1½ miles south of Coalburn, Lanarkshire. Douglas Main Limestone of Lower Limestone Group.

Diagnosis: A transverse, costate spiriferid, with well developed costate fold and sulcus; ribs rounded separated by rounded furrows; fine twilling of growth lines. Dental plates short, dental flanges, ventral septum low and short, convex delthyrial plate in apex of delthyrium. Plates I-VI.

i) DESCRIPTION OF HOLOTYPE.

Plate I.

Dimensions	Length	27.1 mm.
	Width	35.4 mm.
	Thickness	17.6 mm.

The holotype is one of the largest specimens in the collection.

The/

The shell is subtriangular, biconvex, with the pedicle valve slightly more curved than the brachial. Width/length ratio is 1.3; the maximum width being close to the hinge line. The greatest thickness is at about mid-length. The right cardinal extremity is almost perfectly preserved, the cardinal angle being slightly obtuse. The left cardinal extremity is damaged. The ventral umbo is incurved, overhanging the low interarea. The dorsal umbo is small. The ventral interarea is distinctly delimited by beak ridges and its lateral extremities are rectangular rather than pointed. It is 3.5 mm. in height at the delthyrium. The tracks of the denticles are visible on the surface of the interarea as fine lines normal to the hinge line. The dorsal interarea is very low.

The sulcus of the pedicle valve extends from about 1 mm. from the umbo. It is wide with gently sloping sides, and has a small labial extension. At the anterior it is 10.8 mm. wide and about 5 mm. deep. The fold of the brachial valve is visible about 1 mm. from the umbo. At the anterior commissure the sulcus has the same width and height as the dorsal fold. The sulcus is distinctly defined from the flanks, though the bounding furrows are not deep. The anterior commissure is strongly uniplicate.

The/

The ribs on the flanks are strong, broad and rounded, separated by rounded furrows. On the brachial valve there are 10 ribs on the left and 11 ribs on the right flank; on the pedicle valve there are 13 ribs on the left and 12 ribs on the right flank. In each case the ribs close to the cardinal extremities are weak. The pair of ribs on each side of both fold and sulcus are formed by dichotomy of the first rib at about 5 mm. from the umbones. One rib on the left flank of the pedicle valve, and a corresponding rib on the right flank of the brachial valve, divide a short distance from the anterior margin. Along the commissure the ribs and furrows alternate regularly.

In the ventral sulcus a pair of lateral ribs divide from the bounding ribs 6 mm. from the umbo. A second pair of laterals divide from the bounding ribs 14 mm. from the umbo. In the centre of the sulcus a rib extends from a point 8 mm. from the umbo to the margin and becomes much more prominent, as it grows, than the lateral ribs. Within 1 mm. of the margin each of the first pair of lateral ribs divides. The ribs on the fold correspond in pattern, with one central rib and two pairs of laterals. The central rib is broad with a median furrow which develops 13 mm. from the umbo but becomes much less distinct 2-3 mm. from the anterior margin. The central rib of the fold is opposed by the central rib of the sulcus which forms a short linguiform/

form extension of the sulcus. Due to the prolongation of the sulcus and the corresponding elevation of the fold the two valves meet there at a higher angle than on the flanks and the alternation of ribs and furrows is less regular and well defined.

A large number of growth lines are to be seen of which two are notably prominent and a number are well marked towards the anterior margin. Where the less prominent growth lines are well preserved in the furrows of the anterior parts of the valves they are seen to be twilled, though the minute striations which produce the twilling are poorly preserved in this specimen.

The internal characters are unknown.

ii) VARIATION IN EXTERNAL FORM OF THIS SPECIES.

At the type locality 117 specimens were collected from the one exposure of the Main Limestone. Of these, 96 were sufficiently well preserved to be studied biometrically. Since they were distributed through about 20 feet of limestone they can in no sense be regarded as contemporaneous members of a single "population." Moreover, many specimens in this rock are separate valves, and it must be supposed that some degree of transport and sorting before burial took place; and the collection is therefore not a true random sample of a succession of populations.

They/

Fig. 1 The variation in shell shape in Spirifer
brockleyensis.

C1 the holotype

A1, A2 trigonal shells

F1 transverse shell.

Fig. 1

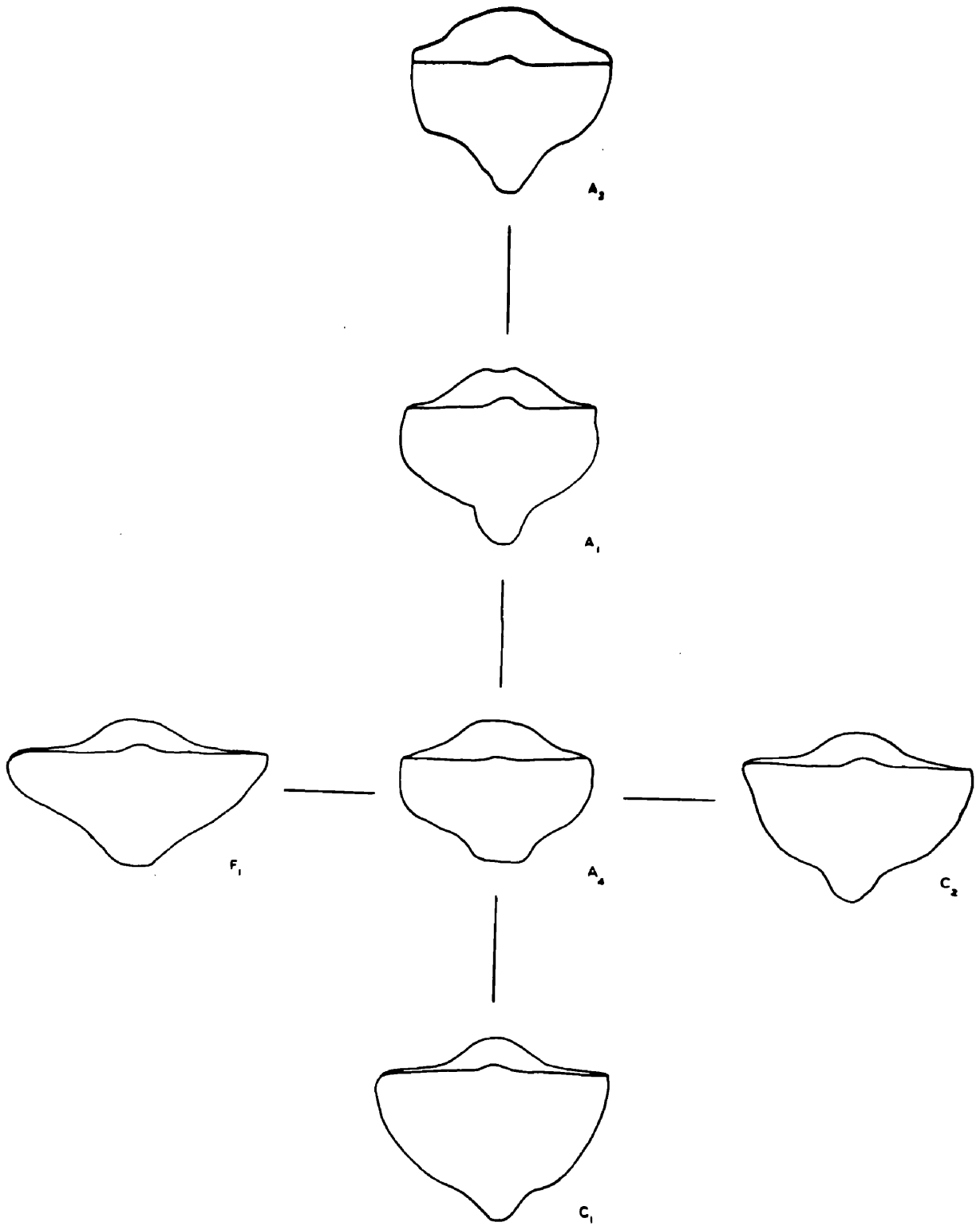
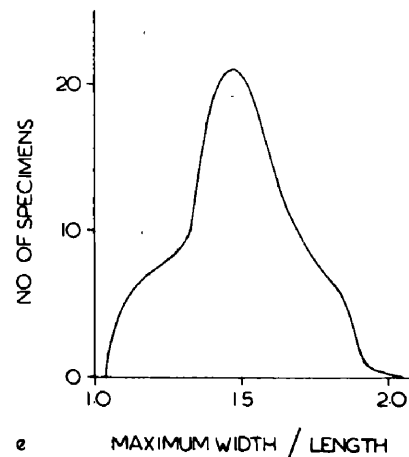
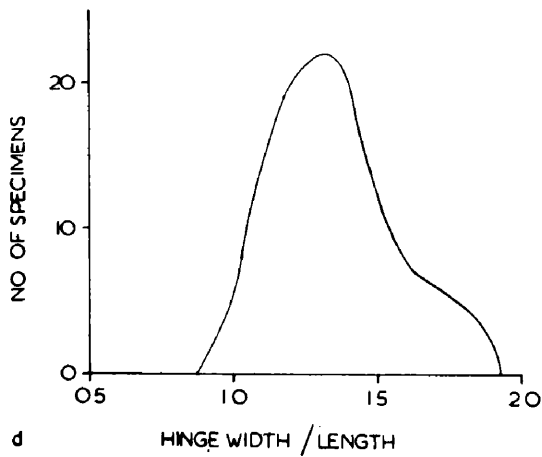
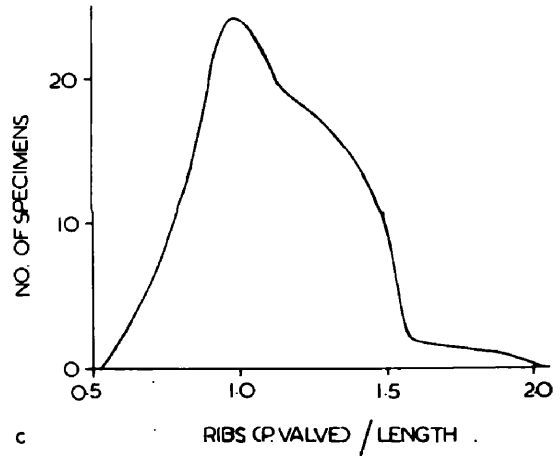
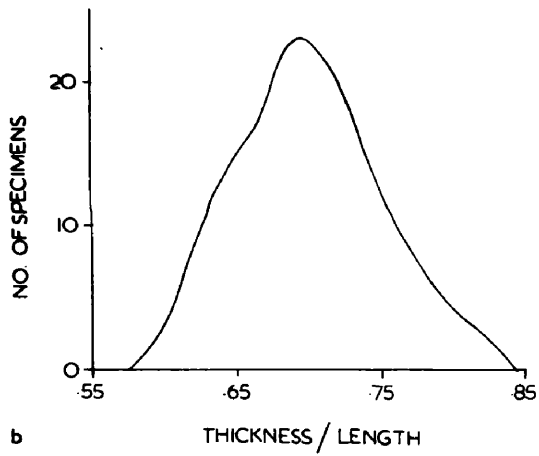
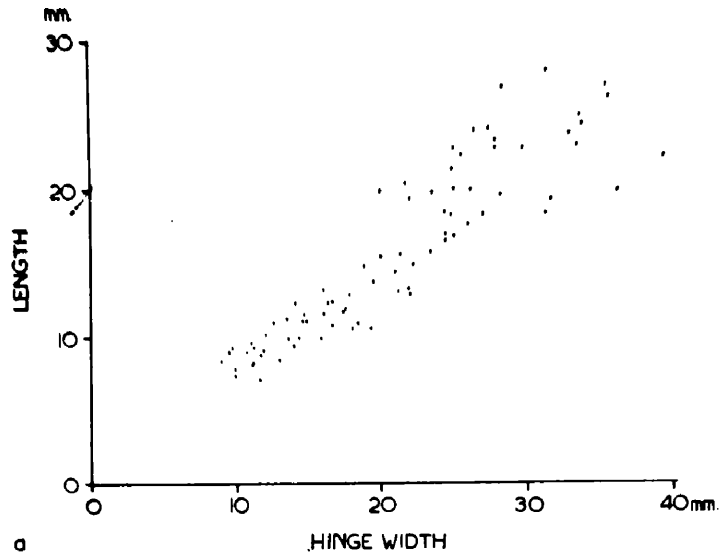


Fig. 2 The scatter plot and frequency curves of the specimens in the collection.

Fig. 2



They present considerable variation in shell shape, but the variation is continuous with intermediate forms linking the extremes. This is shown diagrammatically in fig. 1.

The distribution of points on the scatter diagram (fig. 2a) indicates that it is improbable that more than one species is present. Further evidence of this is found in the unimodal character of the frequency curves (fig. 2 b,c,d,e) for the ratios thickness/length, number of ribs on pedicle valve/length, hinge width/length, maximum width/length.

Table 1 shows the statistical measures of the principal external characters of the specimens. The standard deviations of the ratios maximum width/length, thickness/length are lower than those recorded by Parkinson (1954, p. 370) for a single species Schizophoria resupinata and it is therefore improbable that more than one species is represented in the collection. The coefficients of correlation of the same characters are also higher than would be expected if more than one species were present. The coefficient of correlation of thickness/length is so high as to indicate a close allometric relation between the two characters. The hinge width/length correlation is not so complete since there is a change in shell ratio with growth (see p.16)

Other characters show variation independent of the general/

Fig. 3 a The variation in the height of the dorsal fold and the depth of the ventral sulcus in relatively narrow specimens (A7, A4) and transverse specimens (B1, D2).

b The variable development of the median rib in the ventral sulcus

A7 wide, shallow sulcus, with prominent median rib

A3 wide, shallow sulcus, median rib not prominent

A9 narrow, deep sulcus, median rib not prominent

A12 narrow, deep sulcus, with prominent median rib.

c The variation in the cardinal angle

D1 acute

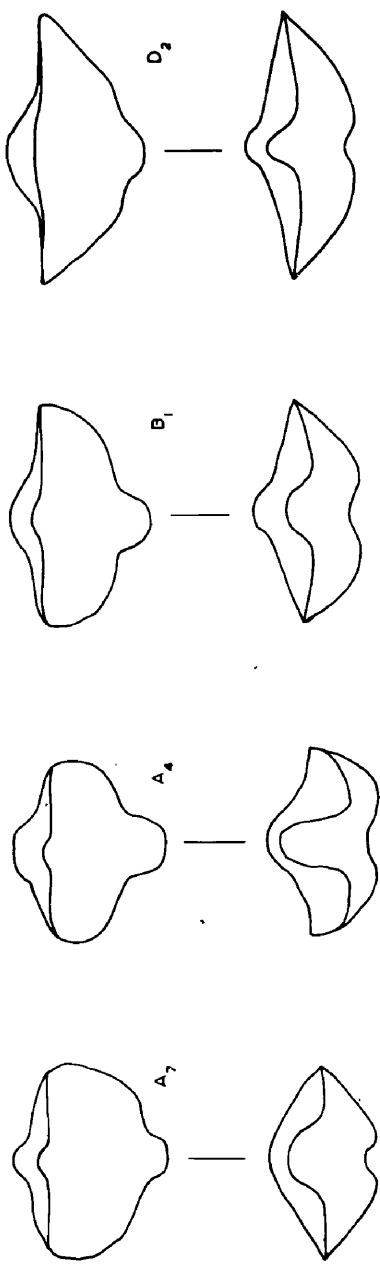
C2 sub-rectangular

A2 rectangular

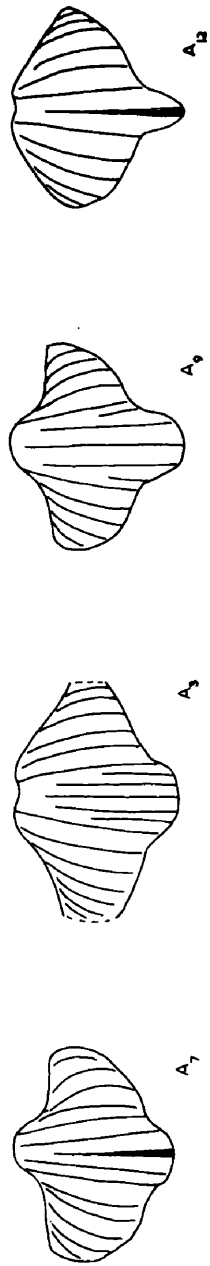
A12, well-formed ears

C1 obtuse.

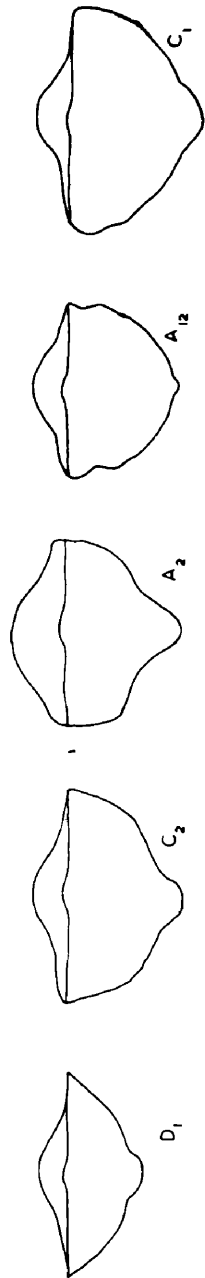
Fig. 3



d



b

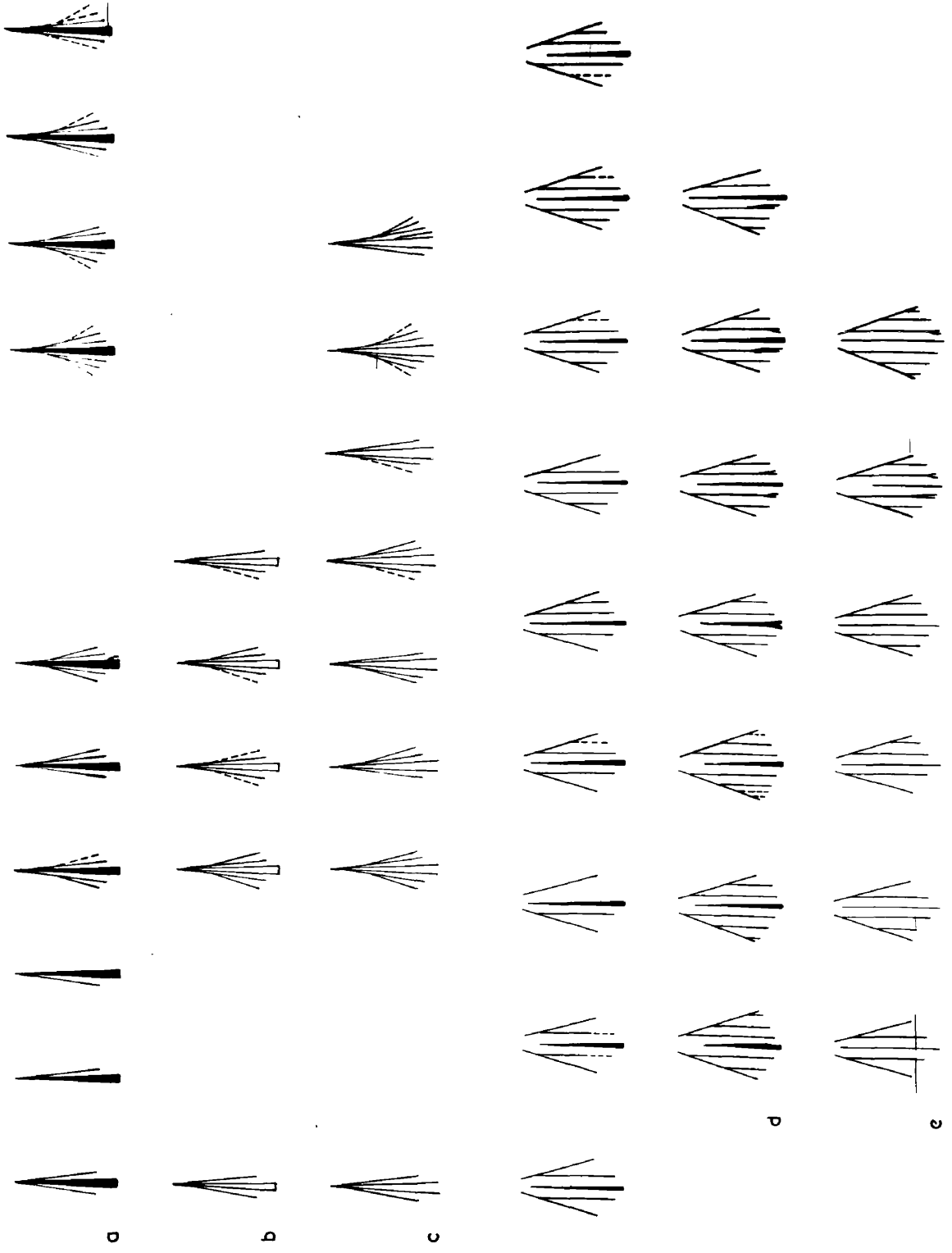


c

Fig. 4 Diagrammatic representation of the ribs on the fold and in the sulcus.

- | | |
|---------|-------------------------------------|
| a, b, c | Ribs on fold |
| a | median rib undivided |
| b | median rib with longitudinal furrow |
| c | median rib divided |
| d, e | Ribs in sulcus |
| d | median rib prominent |
| e | median rib not prominent |

Fig.4



general shape of the shell. Fig. 3a, b show the variation in the height of the dorsal fold and the width, depth and prolongation of the ventral sulcus, quite independent of the shell index.

The variation in the cardinal angles (fig. 3c) is dependent on the shape and size of the shell, the obtuse angles being found in the smaller shells and the most acute angles being found in the transverse specimens. Ears may or may not be developed in the shorter-hinged specimens. The cardinal angles change with the changing proportions of the shell during growth being obtuse at an early stage and either acute or rectangular later.

The ribs are one of the most variable characters. The ratio between the number of ribs and the width of the shell varies in different specimens (fig. 6c). The variation in dichotomy of ribs is small. The maximum number of divided ribs is two on each flank and 62% of the specimens show no dichotomy at all.

The numerous patterns of the ribs of the fold and sulcus are shown in fig. 4. These are all based on the basic pattern present in the holotype. In the sulcus the central rib may or may not be more prominent than the others. On the fold the central rib may be entire, may have a median furrow/

furrow or may be divided in two. In one case a rib develops in the median furrow. The lateral ribs vary in number and also show occasional dichotomy.

iii) COMPARISON WITH SIMILAR SPECIES.

Spirifer trigonalis (Martin), recently validated by the International Commission on Zoological Nomenclature (1956) is known only from Martin's illustration of the dorsal aspect of the shell (Martin 1809, tab. XXXVI, fig. 1). There is a resemblance between this illustration and Spirifer brockleyensis, a resemblance in size, shape and number of ribs. The ribs are broad and rounded in each. But there are differences. The prominent ribs shown on the cardinal extremities in the illustration and the longitudinal striations on the surface are quite lacking in Spirifer brockleyensis. No specimen of S. brockleyensis is quite comparable with Martin's illustration.

The field of S. trigonalis became widely comprehensive during the 19th century with the result that, though there is a resemblance between Martin's illustration of S. trigonalis and S. brockleyensis, many of the specimens assigned to S. trigonalis by Sowerby (1821, p. 117), de Koninck (1887)/

(1887) and Davidson (1858-63, p. 29) are quite unlike S. brockleyensis both in shape of shell and shape and number of ribs. Two specimens illustrated by Davidson (1858-63, pl. V, figs. 29-33), one from Cousland, Dalkeith and the other from Northumberland appear to be closer to S. brockleyensis, though the latter may have more angular ribs.

The specimens recognised as S. trigonalis var. lata by Schellwein (1892), Scupin (1900) and Rakusz (1930), are outside the range of variation of S. brockleyensis.

Some Russian specimens seem to be more closely allied. Those referred to S. trigonalis by Trantschold (1876), Lebedew (1929) and Rotai (1931, p. 32) are not described in sufficient detail for comparison but the specimens from the Moscow basin studied by Schwezow (1925, p. 177) and Semichatova (1941, 1, p. 152) seem to have many points in common with S. brockleyensis.

None of the species recognised by Schwezow from the Viséan is quite the same as S. brockleyensis though S. trigonalis var typica resembles it. The illustrations are not adequate for close comparison.

Semichatova remarks on the similarity between some of the specimens from the Upper Viséan Serpukhov Beds and S. trigonalis (Martin) but, disregarding precedence, erects the/
the/

the new species S. pseudotrigonalis giving as a reason the lack of type material for comparison. S. pseudotrigonalis is probably a synonym of S. trigonalis.

A comparison of S. pseudotrigonalis and S. brockleyensis shows that they are very much alike both externally and internally, but there are distinctions externally. S. pseudotrigonalis is never transverse, the fold is less prominent, there are fewer ribs on the flanks and there is no dichotomy of the ribs in the sulcus. While some specimens of S. brockleyensis agree with S. pseudotrigonalis in some characters, no specimen agrees in every aspect and many have features not found in S. pseudotrigonalis. The variation in S. brockleyensis is much wider. Semichatova distinguishes several other species, S. parabisulcatus, S. serpuchoviensis, S. tarussaensis, and S. sarytchevae which are related to S. pseudotrigonalis and which are distinguished by size, shape, shape of fold and sulcus and details of rib patterns. They present a range of variation in form similar to that found within S. brockleyensis and their validity is therefore doubtful: they may be no more than named variants of a single species.

IV. THE DEVELOPMENT OF EXTERNAL FORM
IN SPIRIFER BROCKLEYENSIS

Many of the smaller individuals differ in proportion from the larger showing that during growth the shell does not merely increase in size but changes in shape. The fully grown shell is not the enlarged replica of the young shell. That this is in fact an ontogenetic change can be seen from an examination of the growth lines on individual specimens.

The varying proportions of the shell at successive growth stages may be expressed as shell ratios (hinge width/length). At the earliest stages which can be measured the shell ratio is 1.1, the width ranging from 3.0 to 6.0 mm. The ratio increases as the shell becomes relatively wider. In one specimen the ratio is 2.1 at a width of 23.2 mm., but more often it does not exceed 1.8. With subsequent growth the shell becomes relatively longer and the ratio decreases to a minimum of 1.1 at widths varying from 26.3 to 31.3 mm. In none of the specimens does the length equal the width. The changes in shell index in 36 specimens are shown in Table 1, the general pattern of the change being given by the average values for 35 specimens.

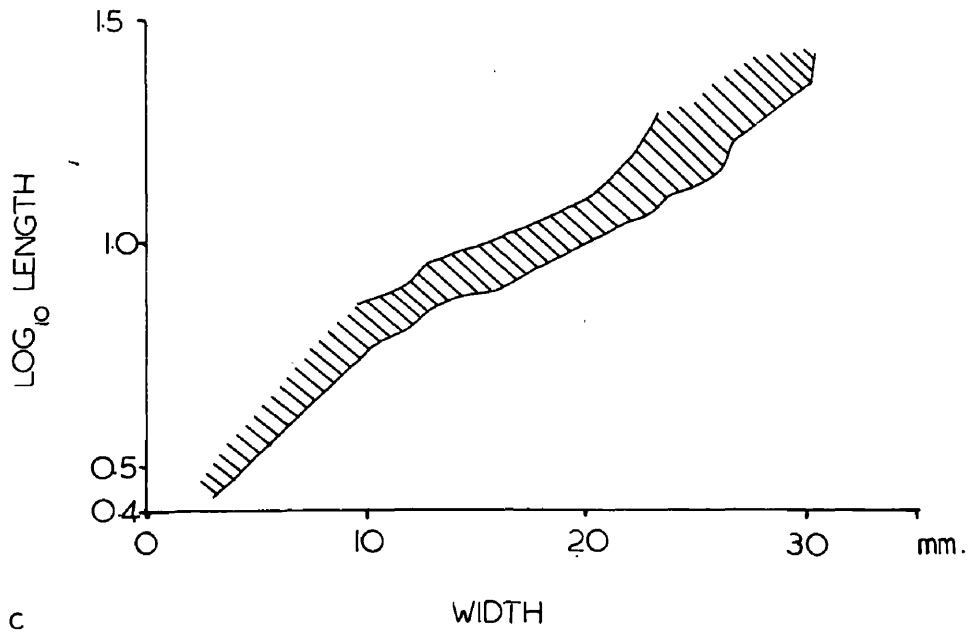
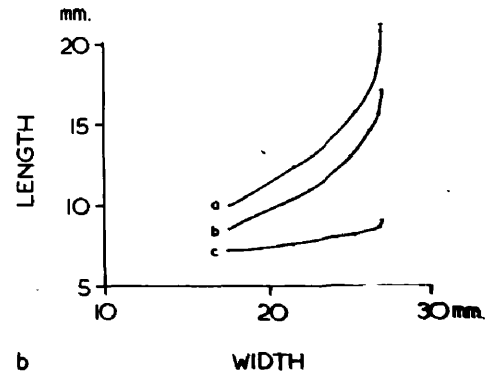
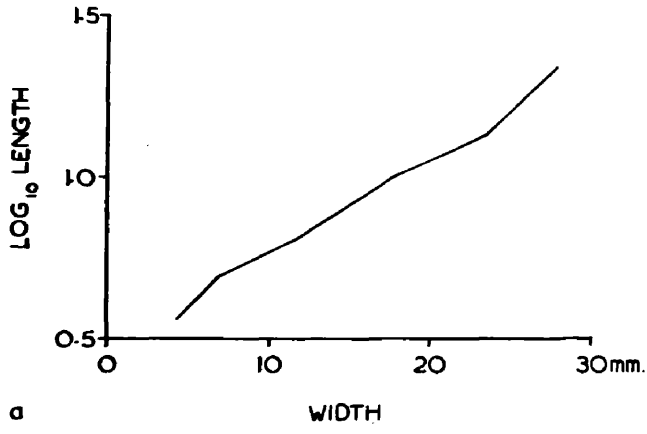
The same data may be recorded graphically (fig. 5c).
This/

Fig. 5

The change in growth ratio in the shell

- a Graph of the growth of the shell (log length/
width) in one individual, C5, showing a change
of gradient at 24 mm. width.
- b Graphs of the growth of the shell (length/
width) in one individual, JI, showing a change
in growth ratio at 27 mm. width.
 - a pedicle valve
 - b brachial valve
 - c ventral inter-area
- c Zone diagram of the growth of the shell in 35
individuals showing the variation in the size
of the shell when the change of growth ratio
occurs.

Fig. 5



This zone diagram shows the changes in shell index with growth in a number of specimens. Fig. 5a shows the changes in shell proportions in one specimen.. C5. The graph is linear, the change in gradient corresponding with the reversal of the shell ratio and indicating a change in growth ratio.

In most of the specimens the growth of the pedicle valve only has been measured, but when the growth stages of the brachial valve are plotted similar graphs are obtained (fig. 5b), showing the same change in growth ratio. The spiral angle of the brachial valve is less than that of the pedicle valve, and in the early stages is so low that the valve is sensibly flat.

The ventral and dorsal interareas also grow in spiral fashion, forming the inner curve of the coiled cone which constitutes each valve. The curvature of the dorsal interarea is not appreciable, but the ventral one forms a distinctly curved surface. On one specimen, J1, the growth lines on the ventral interarea are sufficiently well marked to allow measurements to be made on them. These are plotted on the graph, fig. 5b. There is a marked change in the gradient of the graph showing that here too there is a change in growth ratio.

There/

Table 1. Statistical measures of the specimens in
the collection.

TABLE I

Specimen Number	Shell Ratio with Increasing Width/mms.												
	1-3	4-6	7-9	10-12	13-15	16-18	19-21	22-24	25-27	28-30	31-33	34-36	
G.21			1.7	1.4									
H.2			1.8		1.6		1.6						
G.11	1.3		1.8	1.7		1.6							
G.13				1.8		1.6							
H.14		1.2	1.5		1.4								
K.7		1.3	1.5	1.4									
C.5		1.3		1.8		1.7		1.7	1.4				
I.2				1.6		1.3							
I.4				1.7		1.6							
H.12				1.6		1.6							
I.3						1.8		1.5					
G.19	1.1	1.4	1.4	1.5									
G.14	1.1		1.4		1.6								
G.17		1.2	1.5		1.6								
D.5					1.8				1.7	1.5			
C.4				1.5	1.7				1.5	1.3			
J.2				1.7		2.2		1.6		1.2			
F.7					1.6			1.3					

TABLE I (Continued)

Specimen Number	Shell Ratio with Increasing Width/mms.												
	1-3	4-6	7-9	10-12	13-15	16-18	19-21	22-24	25-27	28-30	31-33	34-36	
D. 4			1.3	1.6		1.8		1.6	1.4				
H. 6			1.6	1.6		1.7							
J. 1						1.8	1.7		1.4				
F. 2						1.8			1.5				
A. 12						1.7		1.4	1.1				
F. 9		1.5					2.0						
I. 1			1.3	1.6				2.1	1.9				
F. 8				1.7									
K. 4			1.3				1.6						
B. 3							1.8	1.8					
A. 1								1.9	1.6	1.2			
G. 23			1.3									1.1	
E. 3			1.3				1.6						
A. 9								1.6					
G. 2				1.7					1.2				
A. 5									1.6				
D. 6								1.5	1.1				
D. 1				1.6				1.4	1.2			1.7	
Mean Ratio	1.17	1.31	1.49	1.63	1.63	1.69	1.66	1.62	1.44	1.28	--	--	

TABLE I (Continued)

Specimen	Shell Ratio with Increasing Width/mms.												
	1-3	4-6	7-9	10-12	13-15	16-18	19-21	22-24	25-27	28-30	31-33	34-36	
D. 4			1.3	1.6		1.8		1.6	1.4				
H. 6			1.6	1.6		1.7							
J. 1						1.8	1.7		1.4				
F. 2						1.8			1.5				
A. 12						1.7		1.4	1.1				
F. 9		1.5					2.0						
I. 1			1.3	1.6				2.1	1.9				
F. 8				1.7			1.6						
K. 4			1.3		1.7		1.8	1.8					
B. 3								1.9	1.6	1.2			
A. 1			1.3				1.6			1.1			
G. 23			1.3				1.6						
E. 3							1.8	1.6					
A. 9							1.6		1.2				
G. 2				1.7	1.6				1.6				
A. 5								1.5	1.1				
D. 6								1.4	1.2				
D. 1				1.6	1.6							1.7	
Mean Ratio	1.17	1.31	1.49	1.63	1.63	1.69	1.66	1.62	1.44	1.28	--	--	

Table 2 The shell ratio (hinge width/length) at successive growth stages in 35 specimens.

The shell ratio changes with the growth of the shell. A reversal of the shell ratio corresponds with a change in the growth ratio. This change takes place in different specimens at different sizes (as measured by the width of the hinge).

TABLE 2

Character	Number of Specimens	Range	Mean	Standard Deviation
Hinge-Width mms.	72	9.5-39.3	20.4	7.46
Maximum Width mms.	53	11.0-39.3	21.3	6.98
Length mms.	72	7.2-28.1	15.6	5.79
Thickness mms.	87	5.2-18.2	10.8	3.59
Maximum Width Length	51	1.11-1.98	1.46	0.179
Thickness Length	87	0.59-0.82	0.69	0.0477
Number of Ribs Length/mms.	71	0.64-1.89	1.11	0.232

$$\frac{\text{hinge-width}}{\text{length}}$$

Coefficient of correlation

.77

$$\frac{\text{thickness}}{\text{length}}$$

Coefficient of correlation

.90

There is a wide range in size at which the change in growth ratio may occur (Table 1). The smallest size is 5.5 mm. length, 9.8 mm. width and the largest size is 14.3 mm. length, 25.2 mm. width. Nor does the change occur when the shell reaches certain proportions, the two extremes being represented by the shell ratios 1.5 and 2.1.

One specimen, D1, reaches 19.9 mm. in length and 35.3 mm. in width without the growth ratio changing, while another specimen, F1, seems to be an extreme example of this, having attained 22.3 mm. in length and 39.3 mm. in width apparently without a change in the ratio. These elongate specimens produce the skewness in the frequency curves (figs. 2c, d).

In those specimens in which the growth ratio changes at a small size, the anterior elongation never proceeds so far as to produce a large shell which is longer than wide. The shell remains a small individual of the same proportions as the larger specimens. The reason for this is unknown.

In contrast to the variable width/length ratio is the constant thickness/length ratio (fig. 2b, table 2) indicating an allometric relation.

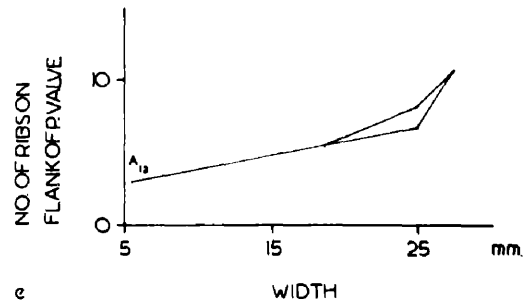
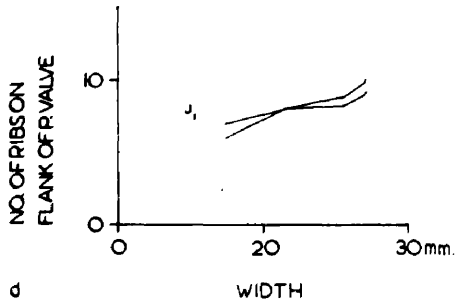
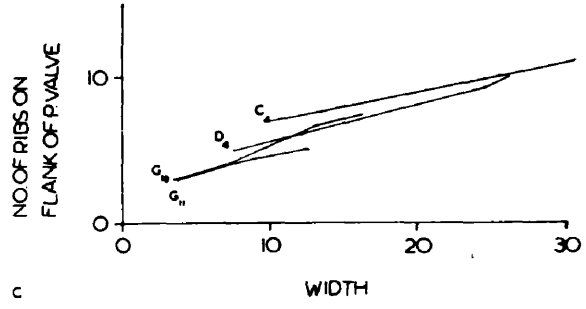
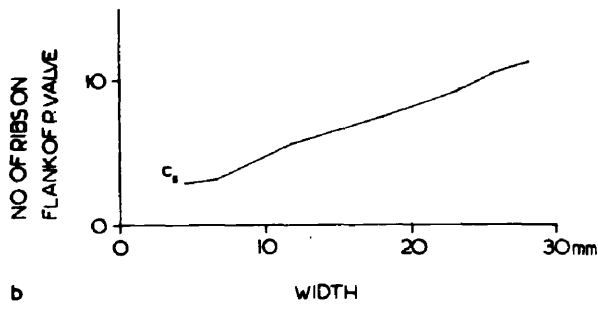
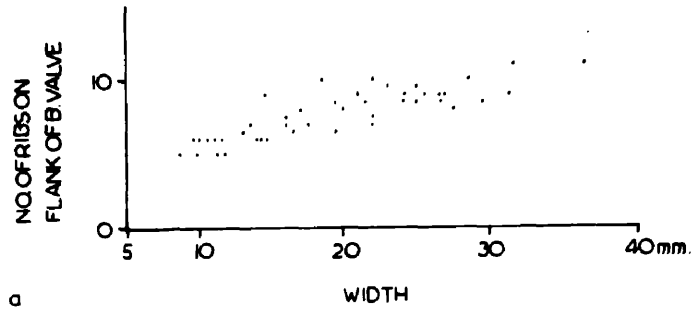
The ribs on the flanks of the shell increase in number with growth, new ribs appearing at the cardinal extremities. The number of ribs is proportional to the width of the hinge, both/

Fig. 6

The relation between the number of ribs on the flanks of the shell and the width of the shell measured at the hinge-line.

- a Scatter plot (no. of ribs/hinge width) of those specimens with no dichotomy of ribs showing the direct relation between the number of ribs and the width of the hinge.
- b Graph showing the increase in the number of ribs with the increase in the width of the hinge in one specimen, C5.
- c Graphs showing the variation in the rate of increase of ribs in four specimens.
- d&e Graphs showing the change in the ratio, no. of ribs/hinge width, which occurs when the number of ribs is increased by dichotomy. The data for each flank of the shell is plotted.

Fig. 6



both in individual cases (fig. 6 b,c) and in the collection as a whole (fig. 6a).

However, in several specimens there is dichotomy of ribs, one or two ribs on either or both flanks may divide, and then the proportional relation between the number of ribs and the width of the shell changes (fig 6d, e). The data for each flank of the shell is plotted separately.

The number of ribs on the fold and sulcus is not related to the height of the fold. The greatest number is found on the widest specimens so that, as on the flanks, the number of ribs is apparently dependent on the width of the shell.

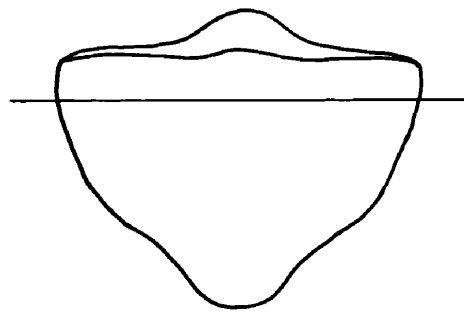
Fig. 7

The orientation of the serial sections

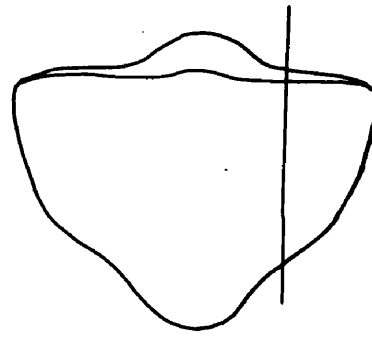
a Transverse

b Longitudinal

Fig.7



a



b

V. TECHNIQUE FOR THE STUDY OF INTERNAL STRUCTURES

The detailed morphology of the shells has been reconstructed from serial sections. Crofts' (1950) parallel grinder was used so that the desired orientation of the sections was maintained. The micrometer on this instrument is accurate enough to record an interval between sections as small as 0.05 mm. The specimens were embedded in marco resin to protect the outer shell layer, which is liable to flake off during grinding.

The sections were recorded on cellulose peels, taken from an etched surface. Greater detail can be seen on peels than on the surface itself due to their translucency. Indeed the reproduction is so accurate that magnifications of fifty or even one hundred times bring out the fine detail of shell structure (pl. VIII).

Thin sections were necessary for the observation of the crystallographic properties of the shell material but serial sectioning is impracticable in most cases since too much of the shell is destroyed.

The serial sections are, for the most part, transverse sections made normal to the length of the shell (fig. 7a). In a few cases longitudinal sections, normal to the width of the shell (fig. 7b), were also made. No attempt was made to follow the actual stages round the spiral as Semichatova/

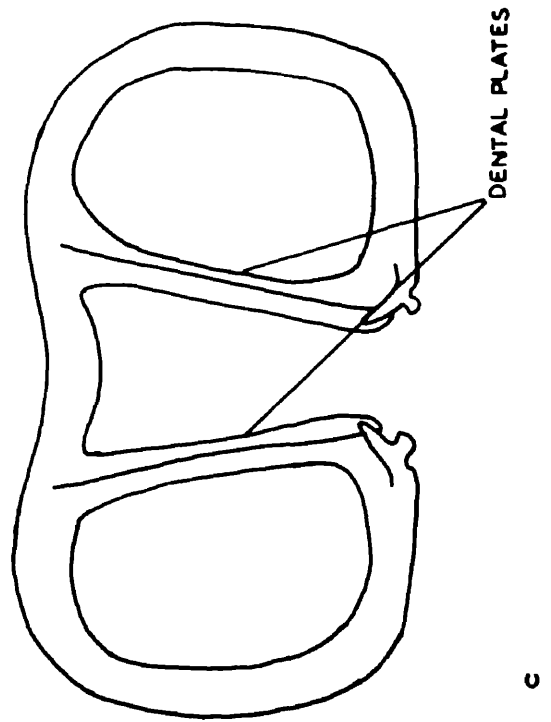
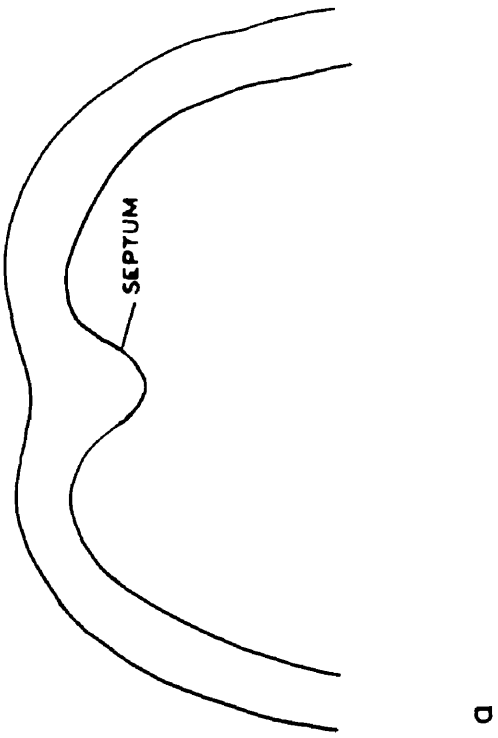
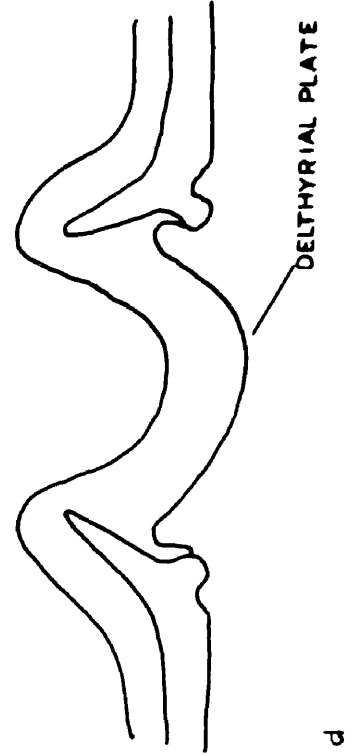
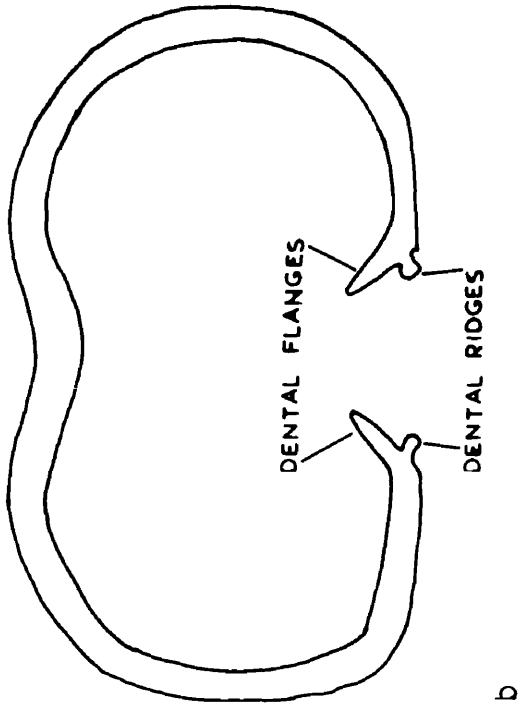
Semichatova (1941, 1, p. 152) did since it is then difficult to determine the orientation of one section relative to another, and it is in any case impossible to section the incurved part of the ventral umbo without sectioning some other part of the shell at the same time.

Fig. 8

The internal plates of the pedicle valve in transverse section.

- a The ventral septum
- b The dental ridges and dental flanges
- c The dental plates, dental ridges and dental flanges
- d The delthyrial plate, dental ridges and dental flanges

Fig. 8



VI. TERMINOLOGY

i) INTERNAL PLATES

Apical Plates

This is a general term for the vertical plates in the apex of the pedicle valve, including the dental plates and median septum. It is a convenient term free from functional interpretation, but it is of limited value on account of its wide meaning. Fredericks (1927, p. 2) also used the term as the equivalent of dental lamellae and delthyrial supporting plates. The following defines the present usage of certain terms:-

Median Septum (fig. 8a).

Any ridge or partition developed in the longitudinal median plane of either valve, extending anteriorly from the apex, is referred to as a median septum.

Fredericks (1927, p. 2) recognised three types of septum in the pedicle valve, the euseptoid, the euseptum and the pseudoseptum. The euseptoid is a low ridge while the euseptum is a more fully developed partition, a distinction which at best is arbitrary, and seems unnecessary. Both are formed by an infolding of the shell wall on the floor of the valve.

The pseudoseptum extends from the inner surface of the delthyrial/

delthyrial plate to the floor of the valve. It forms as an infolding of the delthyrial plate and is only attached to the shell wall, for there is an infolded shell layer beneath the junction of the pseudoseptum and the floor of the valve. It is useful to make a distinction between the septum which arises on the floor of the valve and the septum which arises from the delthyrial plate and in this sense the pseudoseptum is clearly different from the euseptum. The further distinction based on the primary or secondary relation of the septum to the shell wall is less definite for the euseptum as well as the pseudoseptum can be of the secondary formation. absent from the area between the Dental Plates (fig. 8c). no evidence that any functional

The term was first used by King (1850, p. 68) to convey the same meaning as Van Buch's term "les lamelles de soutien des dents." It refers to the two vertical plates which project from the delthyrial margin, across the apical cavity, to the floor of the valve, extending anteriorly to a greater or lesser degree.

Objections have been raised to the term on the grounds that it implies a functional relation between the plates and the teeth. This term was used by Fredericks (1927, p. 2) to describe dental plates which do not extend to the floor of the valve but merely form ridges on either side of the delthyrium. Thomas (1910, p. 101) proposed the alternative term "delthyrial supporting plates" which is open to similar/

This term was used by Alexander (1948, Figs. 1f and 5a)

to/

similar criticism. Though it would seem that dental plates strengthen the delthyrial margin, and when well developed buttress the teeth, they may also fulfil some other purpose. It is possible that the plates served for the attachment of some of the viscera, or at least formed three chambers for the separation of various organs. In recent brachiopods the viscera are arranged in a three-fold fashion, with the digestive tract medial in position and the nephridia, genital glands and liver lobes in pairs on either side of it. Though it is probable that a similar arrangement was present in the spiriferids, for ovarian impressions on the floor of the valve are absent from the area between the dental plates, there is no evidence that any functional relation exists between the viscera and the dental plates. Until some more definite information is forthcoming it is convenient to continue to refer to them as dental plates, for this is the term which is most widely used in the literature.

Delthyrial Ridges.

This term was used by Fredericks (1927, p. 2) to describe dental plates which do not extend to the floor of the valve but merely form ridges on either side of the delthyrium.

Dental Ridge (fig. 8b).

This term was used by Alexander (1948, figs. 3f and 6a)
to/

to describe a ridge along the delthyrial margin in pentamerids. The ridge represents the successive growth stages of the hinge tooth. No corresponding term appears to be in use in descriptions of spiriferids. Cooper (1954, p. 328) referred to "the growth track of the tooth."

Alexander's term is adopted here.

Dental Flange (fig. 8b).

This is a new term proposed for a subsidiary dental structure. The dental flange is a projecting plate on the inner side of the dental ridge. It extends along the length of the dental ridge and is directed into the delthyrial cavity making an obtuse angle with the interarea. The two flanges, one on each side of the delthyrium, are thus convergent. For part of its length the dental flange is buried within the dental plate,

Delthyrial Plate (fig. 8d).

Transverse delthyrial plate was the term used by Hall and Clarke (1894) to describe a plate which extends across the delthyrium, between the dental plates. It closes the delthyrium at the apex and extends anteriorly to a greater or lesser extent. The term is used in the same sense by Cooper (1954, p. 328) and Stainbrook (1943, p. 421; 1945, p. 53; 1947, p. 321).

Fredericks (1927, p. 3) used the term delthyrial plate in two senses. One sense corresponded with Hall and Clarke's/

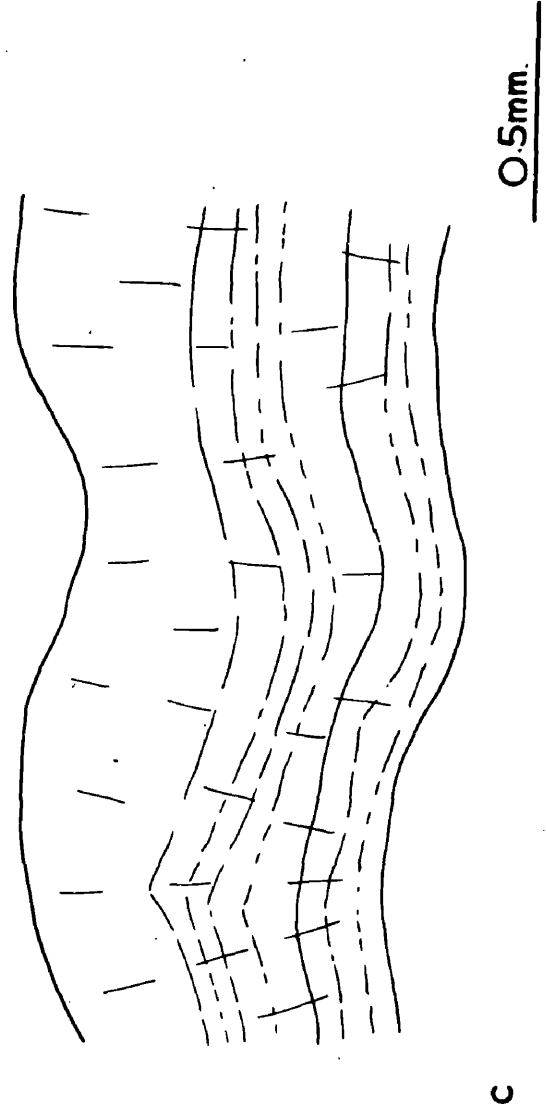
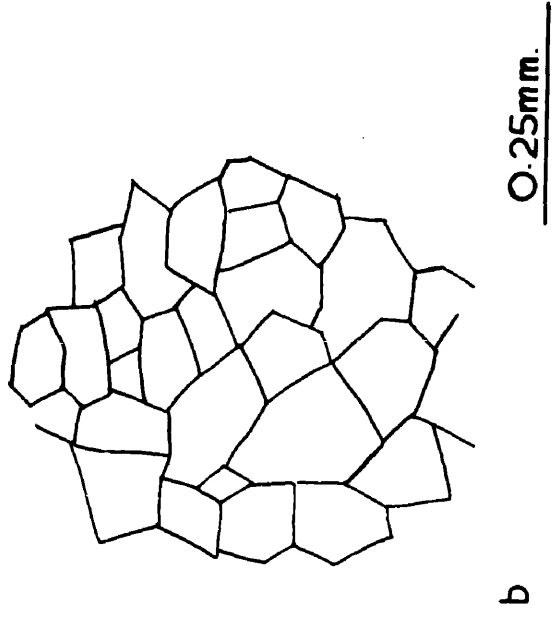
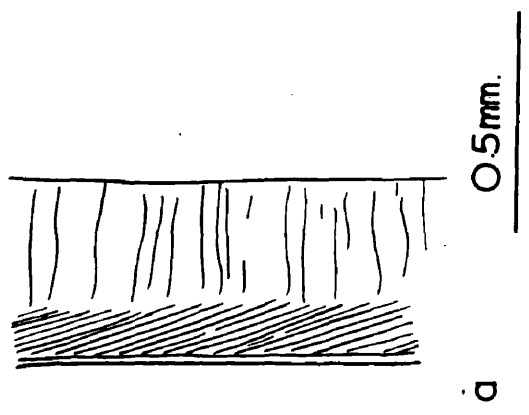
Fig. 9

The micro-structure of the shell.

a The lamellar layer, oblique layer, and normal layer
in longitudinal section.

b The normal layer in tangential section.

c The normal layer in transverse section, showing growth lines.



Clarke's "transverse delthyrial plate" but in the other usage the term applied to a plate which lies on the surface of the spondylium and also extends between the two plates of the spondylium to the floor of the valve. The latter structure is not present in Spirifer brockleyensis. The term delthyrial plate is here used in the first sense.

ii) SHELL LAYERS.

The shell is composed of three layers, all of which are impunctate. The outermost layer is the lamellar layer (fig. 9a). It is non-fibrous, of uniform thickness, about 0.02 mm. and extends over the whole surface of the shell. Frequently it is not preserved on specimens for it tends to remain adhering to the rock matrix when the specimen is extracted.

The two inner shell layers (fig. 9a) are of variable thickness and are not both present in all parts of the shell. They are distinguished from the lamellar layer by their inconstant thickness and irregular distribution as well as by their structure. Both layers are composed of elongate crystals, which in one case are long, slender and fibrous, and in the other are relatively short and prismatic. The two layers might well be called fibrous and prismatic if it were/

were not that both these terms have already been used synonymously in descriptions of brachiopod shell structure (prismatic layer in Cooper in Shimer & Shrock, 1944, p. 281; fibrous layer, Williams 1953, p. 280). The layers are also distinct in the orientation of the crystals within the layers, the outer one having them oblique and the inner normal to the shell surface. The two layers are accordingly designated the oblique layer and the normal layer.

The oblique layer consists of very fine fibres about 0.007 mm. in width. The fibres lie longitudinally, inclined inwards, in an anterior direction, at a low angle (pl. IX).

The normal layer is composed of crystals larger than those of the oblique layer. They vary in length up to 1 mm., according to the thickness of the layer, and in width are 0.05 to 0.06 mm. Tangential sections show the general prismatic nature of the layer (fig. 9b) while longitudinal and transverse sections show the elongate crystals. The crystals are elongate parallel to the c-axis. The crystals of the normal layer conform to the ribbing of the shell as is shown in transverse section (pl. Xa). Because of this variation in optical orientation of the crystals from furrows to ribs, thin sections normal to the shell surface have a banded appearance in crossed nicols (pl. X, b).

Transverse/

Transverse and longitudinal sections show lines cutting across the crystals of the normal layer, normal to their length (pl. XI & fig. 9c). The lines are marked by inclusions or cavities in the crystal, and indicate slight discontinuity within the crystal which is considered to represent a pause during growth. The lines are growth lines, and are the traces of surfaces of discontinuity which pass through the layer, representing the inner surface of the shell at various stages of growth. The optical orientation of the crystals is constant across the growth lines (pl. XI).

In thin sections, inclusions along growth lines form a dark band. When no inclusions are present the growth lines can be revealed by etching the surface. The growth lines on such a surface are distinctly recorded on cellulose peels. Growth lines were recorded by Miloradovitsch (1937, p. 526) from Russian spiriferoid brachiopods.

Since the normal layer is considerably more coarse grained than the oblique layer it might be considered that the normal layer is a recrystallisation product of the oblique layer. The presence of the growth lines in the normal layer makes this improbable.

Cooper, (in Shimer and Shrock 1944, p. 281) discussing the/

the formation of the various shell layers, stated that the "thin outer lamellar layer, growing only at the shell edges, determines the outline, plications and other radial ornament; and a thicker inner layer (prismatic layer) deposited by the mantle proper, thickens the shells, obliterating plications and other internal inequalities and often burying apical and cardinal structures." In the present study there is the further complication of two inner layers. The relation between the two inner layers, both in the internal plates and on the flanks of the shell, is studied and their significance discussed in later sections.

Fig. 10

A reconstruction of the apex of the pedicle valve.

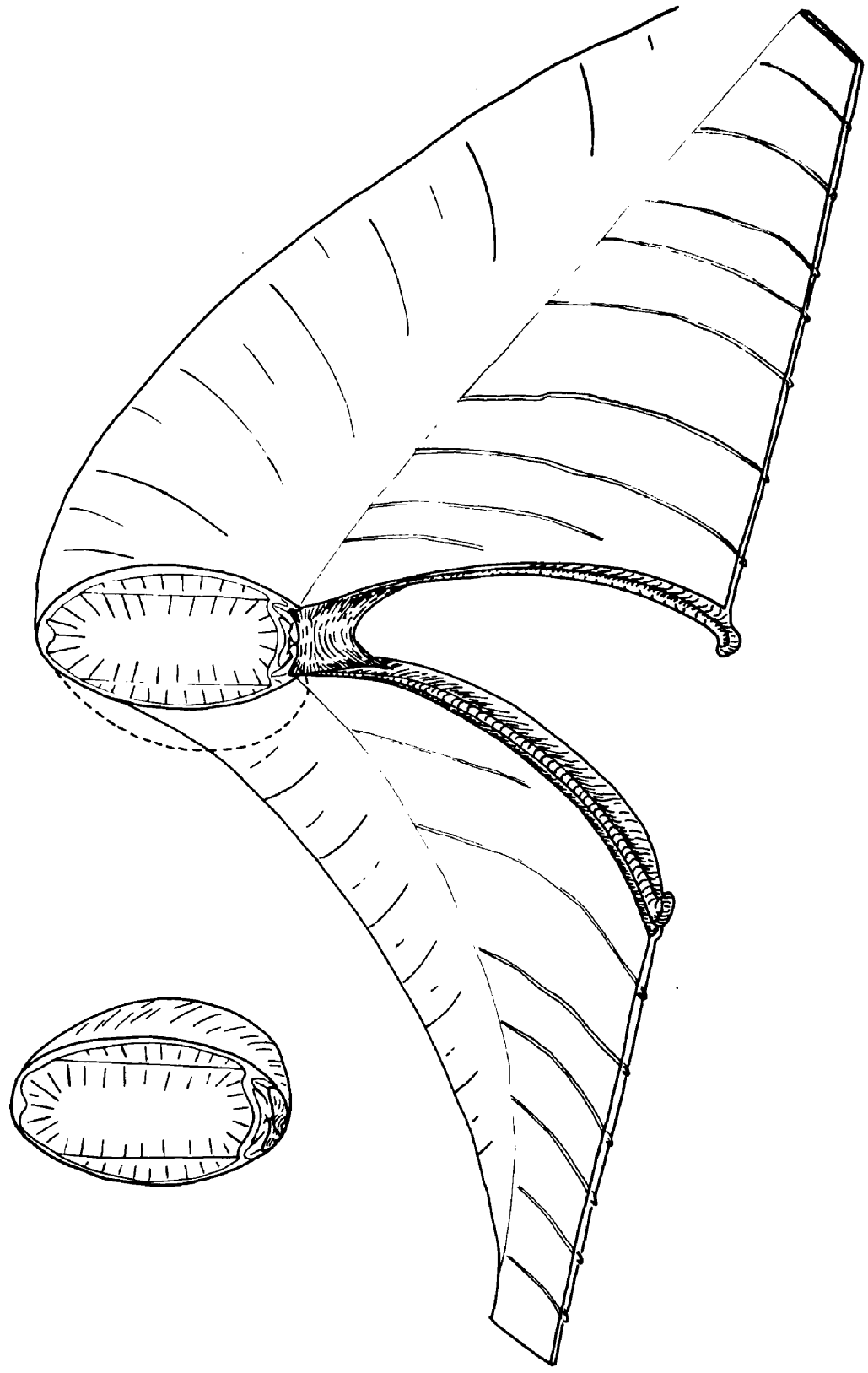
The umbo is removed and shown in the inset.

The structures illustrated are as follows:-

denticles and denticle tracks on interarea,
dental ridges and dental flanges bordering the delthyrium,
delthyrial plate at apex of delthyrium,
dental plates, dental flanges and delthyrial plate in

T.S. of umbo.

Fig. 10



VII. INTERNAL MORPHOLOGY OF SPIRIFER BROCKLEYENSIS

i) THE PEDICLE VALVE.

The pedicle valve is of typical spiriferoid form, moderately convex with an incurved beak, the hinge-line long and straight, the interarea well developed (fig. 10). The interarea is divided by the delthyrium which is bounded by dental ridges, dental flanges and dental plates (fig. 8c).

a) The Delthyrium

At its apex the delthyrium is open and its margins are not bounded by any ridges or septa (figs. 11a, 13a). At widths in excess of 0.25 mm. the delthyrium is closed by the delthyrial plate (figs. 11a, 13 b-g) which extends across the delthyrium and continues anteriorly about a quarter of the length of the delthyrium. The anterior part of the delthyrium is open (figs. 10, 13 h, i).

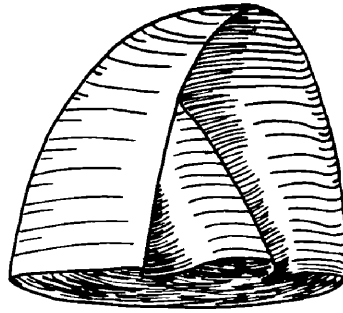
b) The Dental Ridges

The dental ridges do not extend to the apex of the delthyrium (figs. 12 a,b,c), but appear about 0.5 mm. from the umbo. Each ridge is separated from the interarea by a groove which is parallel to the margin of the delthyrium (fig. 11 d). This may be the groove which in some spirifers accommodates the deltidial plates, but no deltidial plates have been seen in any specimen of *S. brockleyensis*. In-
side/

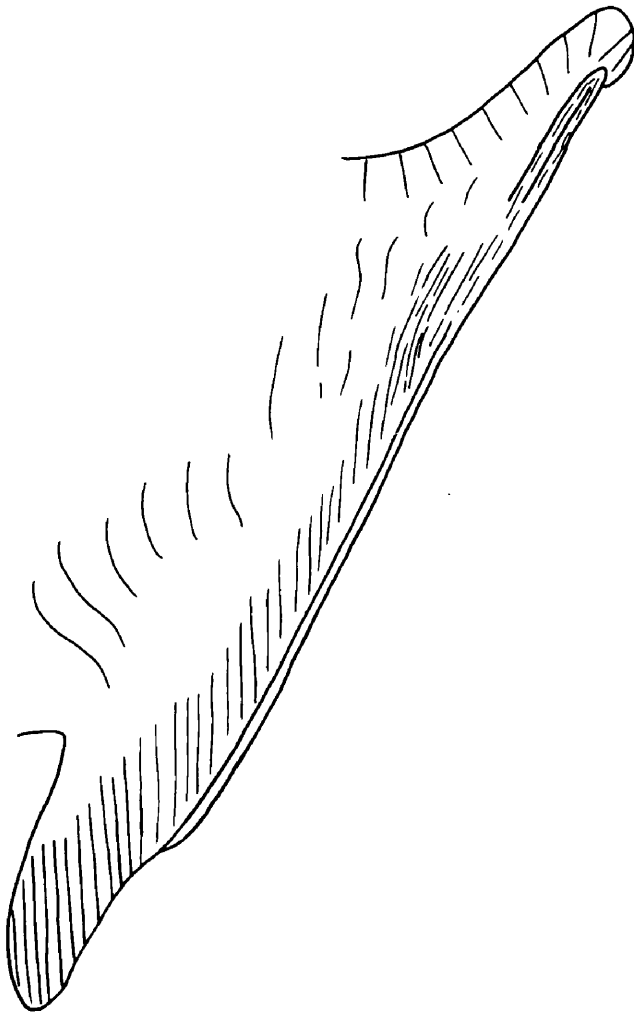
Fig. 11

- a Reconstruction of the umbo of the pedicle valve showing the delthyrial plate arising from the floor of the valve a short distance from the umbo.
- b L.S. of dental ridge and tooth.
The dental flange is at the inner end of the dental ridge, distinguished by the different orientation of its fibres. The dental flange is partially covered by normal layer.
- c T.S. of dental ridge and dental flange with the adjacent part of the inter-area.
- d Reconstruction of dental ridge and dental flange showing the grooves which define these structures laterally, and dissected to show the orientation of the fibres within.

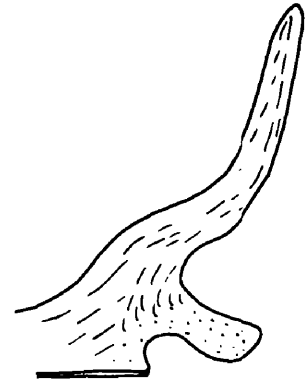
Fig. II



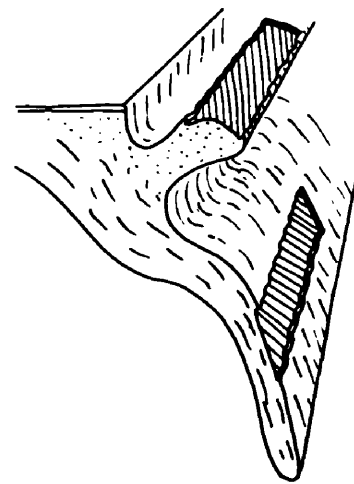
a



b



c



d

0.5mm.

side the delthyrium the dental ridge is also defined by a groove which separates it from the dental flange (figs. 8b, 11d). The ridge is sub-circular in transverse section, gradually increasing in diameter anteriorly to a maximum of about 0.25 mm.

The dental ridge is fibrous (fig. 11d), formed by the oblique layer. The fibres lie along the length of the ridge so that in cross-section the ends of the fibres are seen (fig. 11c). The dental ridge, edging the delthyrium, crosses the interarea obliquely but the fibres of the dental ridge are normal to the hinge-line and intersect the edge of the dental ridge (fig. 11b). From apex to tooth the fibres succeed each other laterally, each slightly in advance of its neighbour.

A film of oblique layer covers the dental ridge along the delthyrial margin (fig. 11b). The fibres in this film have a different orientation from those in the dental ridge. The covering layer is a continuation of the oblique layer on the outer surface of the dental flange, and its extension on to the dental ridge partly infills the groove on the inner surface of the dental ridge (fig. 12f). Anteriorly it does not reach the functional tooth (fig. 11b).

c) The Dental Flanges

The/

angular. Flanges convergent. Dental ridges present, no delthyrial plate.

f,g Transverse sections from one specimen.

Interval between sections 1.25mm.

f Dental flanges with many layers, delthyrial plate and dental ridges.

g Dental flanges with several layers, dental ridges and no delthyrial plate.

h Dental flanges and dental ridges enclosed in successive layers, delthyrial plate and, covering all these structures, the bases of the dental plates.

Fig. 12 The dental flanges and delthyrial plate.

a, b, c, d, e Series of transverse sections.

Interval between sections

a-b 0.05mm. b-c 0.05mm.

d-e 0.63mm.

a Dental flanges and delthyrial plate forming a single plate. Dental flanges are convergent.

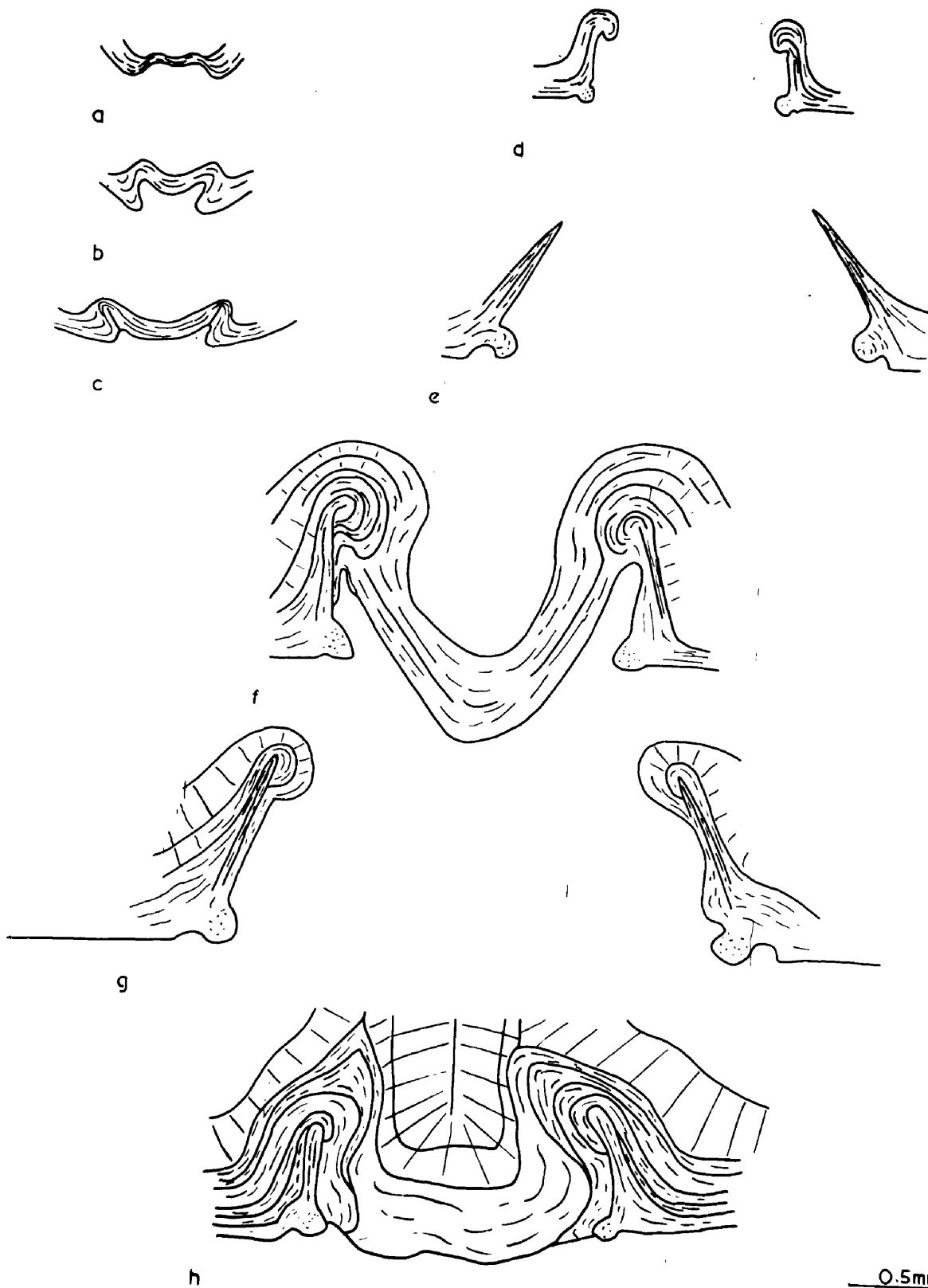
b Dental flanges slightly delimited from delthyrial plate. Dental flanges are divergent.

c Delthyrial plate closely adherent to dental flanges. Dental flanges are divergent.

d Dental flanges with dental ridges forming outer margin of delthyrium. Median plane in dental flanges distinct. Inner edge of dental flange curved. Flanges slightly convergent. No delthyrial plate.

e Dental flanges with median plane. Inner edge angular/

Fig. 12



0.5mm

The dental flanges, like the dental ridges, do not extend to the umbo, the extreme apical section of the delthyrium not being bounded by any ridge or plate (fig. 13a). However the dental flanges are present close to the apex at a part where the dental ridges are not clearly differentiated (figs. 12a, b, c). Where the dental ridges are developed the dental flanges extend along the inner surface of the ridges. The flanges increase in width anteriorly, reaching a maximum of about 1 mm. close to the cardinal margin. Thereafter they rapidly decrease in width and die out before reaching the teeth (fig. 10).

Throughout the greater part of their length the dental flanges are convergent (figs. 12d, e) but there is some variation in their orientation near the apex of the delthyrium. At their posterior extremities they are convergent (figs. 12a, 13b, c). Within a very short distance their inclination changes (fig. 12b) and they become divergent (figs. 12c, 13d, e). The return to the original inclination is gradual so that for a distance of about 0.5 mm. the dental flanges are nearly parallel (fig. 12d, 13f, g, h). Anteriorly the angle between dental flange and interarea increases to as much as 130° (fig. 12e).

Like the dental ridge the dental flange is composed of oblique/

oblique layer. The fibres lie along the width and almost normal to the length of the flange (figs. 11c, d). The orientation of the fibres in the flange is thus quite different from their orientation in the ridge (fig. 11c), but there is a merging junction between the two (fig. 11b).

In detail the dental flanges are complex in their internal structure and in their relation to other structures, especially the delthyrial plate and the dental plates.

The dental flanges vary in form along their length. They increase in thickness from the umbo to the anterior margin of the delthyrial plate and then decrease in thickness towards the cardinal margin. The thickness is also variable across the width of the flange, the inner edge being either thinner or much thicker than the adjacent part of the flange. This variation is directly related to their internal structure.

At the apex of the delthyrium the dental flange is a relatively thin plate, parallel-sided and uniform in structure (fig. 12a). Anteriorly the dental flanges become thicker though they retain their simple structure (figs. 12b, c).

About 0.5 mm. from the umbo the flange is still thicker and its inner edge is curved over and outwards, forming a low ridge on the outer surface (fig. 12d). The external form/

form of the flange reflects the internal structure.

In transverse section the core of the flange is marked by a prominent line, the trace of a plane which passes through the interior of the flange (fig. 12d). This plane is median in position, parallel to the surfaces of the flange and extends from the delthyrial ridge inwards but does not reach the inner edge of the flange. The median plane marks a discontinuity of structure within the flange, the fibres of the oblique layer lying parallel to the width of the flange, and never traversing the median plane. At the inner edge of the flange the fibres follow the curvature of the surface of the flange and wrap around the median plane. This more complex form of the dental flange is attained where the dental flanges are parallel or only slightly inclined (fig. 12d).

Anteriorly, where the dental flanges are convergent, the flange is thinner and it is not curved at the inner edge (fig. 12e). It retains the prominent median plane and the fibres conform with the surfaces.

The basic pattern of the dental flanges which has just been described is modified by further increase in thickness, by the addition of material on the external surfaces (figs. 12f, g, h).

Fig./

Fig. 12f shows an example in which the dental flange, originally curved, has the curvature emphasised by the development of two or three layers of shell substance around the earlier structure. With the addition of each layer the flange projects more prominently towards the delthyrium. Though not so clearly defined in terms of individual layers the thickening of the flange also extends to the inner and outer surfaces of the flange. The thickening is greater on the inner surface where some of the material is normal layer. On the outer surface the additional layer is very variable in thickness but it is particularly thick close to the dental ridge where it fills in the groove adjacent to the ridge.

Fig. 12g shows a section cut in a plane slightly anterior to that of fig. 12f. In this section the core of the dental flange is a straight plate, thinning towards the inner edge, the structure typical of the anterior part of the dental flange (fig. 12e). The additional layers, covering the central plate, produce a curvature of the inner edge of the flange, so that the flange has the same curved form externally as internally in the posterior part of the flange (fig. 12f). The thickening is greater on the inner than on the outer surface. The groove along the dental ridge is/
is/

is not completely filled in by the thickening on the outer surface.

Fig. 12h, a section from another specimen, also shows a straight central plate wrapped round by successive films of oblique layer. The innermost film is present on only one surface of each flange. The overlying film is more extensive and curves over at the inner edge of the flange, giving it the characteristic ridge along the outer surface as in figs. 12f & g. The third film extends right to the dental ridge, and is as thick on the outer surface as on the inner face. The form of this film is different from the inner one for it obscures the curved edge making the outer surface flat once more. The outermost film on the flange does not extend to the dental ridge but projects much further into the dethyrial cavity than any of the previous layers. The development of the dental flanges in this section increases the width of the flange and effectively decreases the width of the delthyrium.

Anteriorly the thickening of the dental flanges becomes progressively less. The later formed layers are thicker on the inner surface than on the outer surface and contain a high proportion of normal layer.

The variation in the structure of the dental flanges is due/

Fig. 13

Series of transverse sections showing the development of the delthyrial plate.

Interval between sections

a is 0.05mm. from umbo

a-b 0.1mm. b-c 0.05mm.

c-d 0.1mm. d-e 0.05mm.

e-f 0.25mm. f-g 0.2mm.

g-h 0.3mm. h-i 0.5mm.

a Delthyrium open.

b Delthyrial plate slightly convex.

c Inverted Y stage.

d, e, f, g. Points of Y coalesce and plate becomes distinctly delimited from the dental flanges - U stage.

h Anterior prolongation of lateral margins of plate.

i Delthyrium open.

Fig. 13

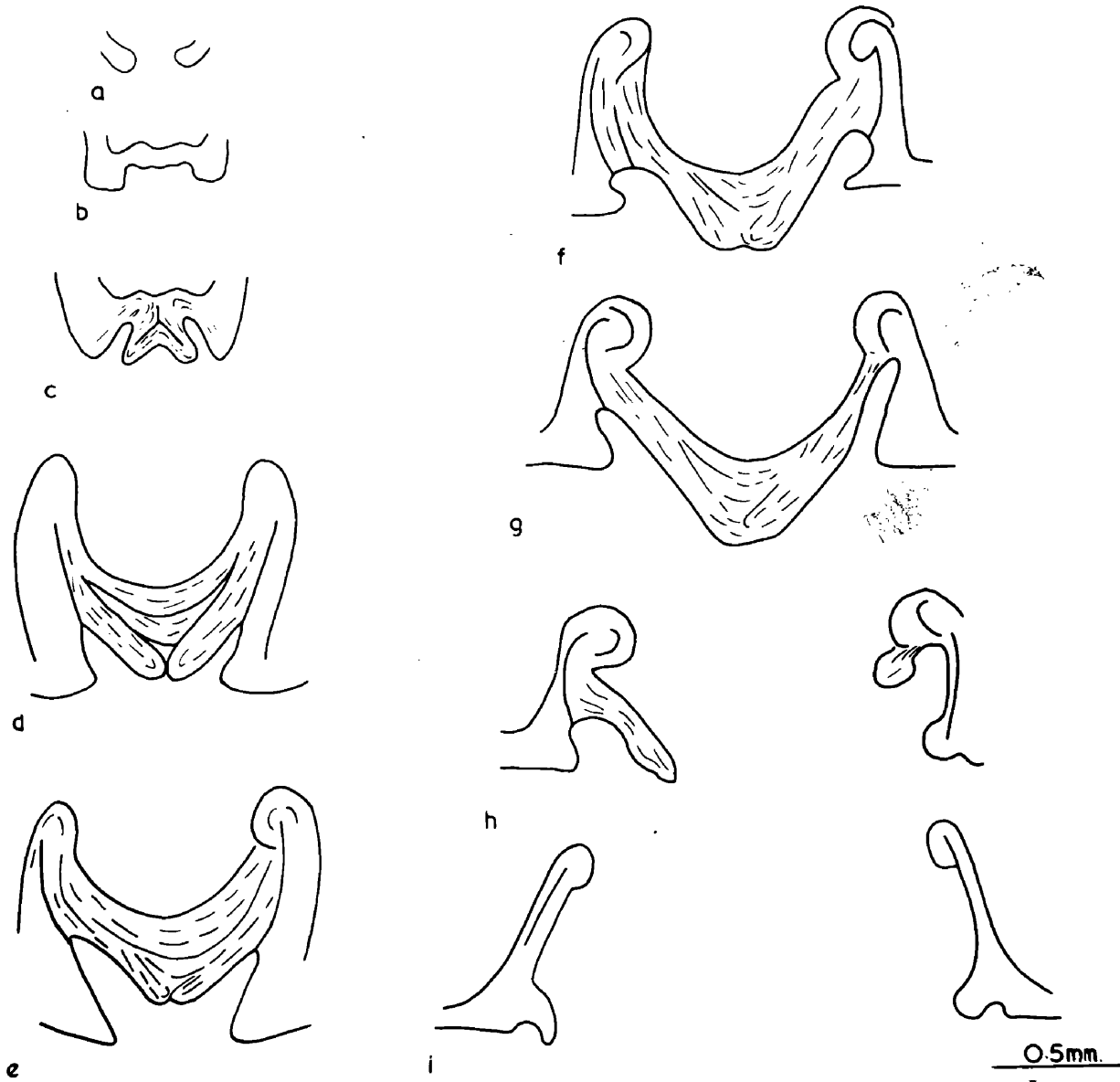


Fig. 14

Diagrammatic representation of the stages in the development of the delthyrial plate.

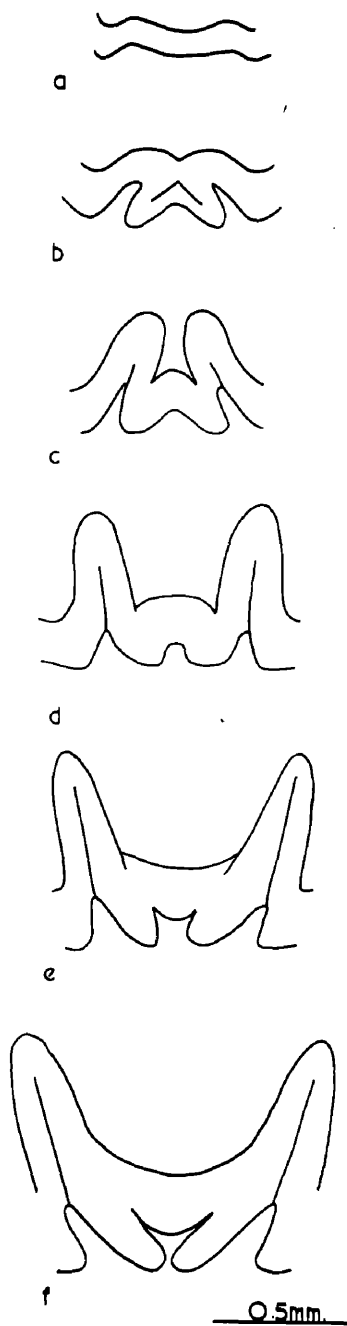
a Convex plate as in fig. 13b.

b Inverted Y stage as in fig. 13c.

c, d, e. Successive stages

f Modified U stage as in fig. 13d.

Fig.14



due in part to a variation in the form of the original plate along the length of the flange and in part to the variable development of shell layers around the initial plate. The initial form of the flange does not determine the form subsequently developed, for the same basic structure is found in flanges which are externally quite different.

d) The Delthyrial Plate

The apical part of the delthyrial plate is simply a slightly convex plate (figs. 12a, b, c, 13b). Anteriorly the plate becomes more complex (figs. 13c, d, e). With increasing width it becomes folded into an inverted Y-shaped structure (fig. 13c). Further increase brings the twin points of the Y together and a mass of fibrous calcite forms between them (fig. 13d). These points gradually lose their identity and the delthyrial plate becomes U-shaped (fig. 13e). The early stages in the growth of the delthyrial plate are shown diagrammatically in fig. 14. Anteriorly the delthyrial plate increases in size, protruding slightly above the level of the interarea (figs. 13f, g). The anterior margin of the delthyrial plate is concave, the lateral margins extending further anteriorly than the central part/

part (fig. 13h).

In one specimen 18 mm. in length the delthyrium is approximately 4 mm. in length and the delthyrial plate 1 mm. The anterior 0.5 mm. of the plate is U-shaped in section.

The delthyrial plate is formed by the oblique layer with, anteriorly, normal layer on the inner surface, never on the outer surface. The fibres lie parallel to the surface of the delthyrial plate (fig. 13g) and in general are normal to the length of the delthyrium.

The delthyrial plate lies between the dental flanges. The variable orientation of the flanges affects the relation between delthyrial plate and dental flanges. Posteriorly, where the dental flanges are convergent, the delthyrial plate is suspended between them (fig. 13b, c) but where the dental flanges are divergent the lateral parts of the delthyrial plate lie against the flanges (fig. 13d). Anteriorly the delthyrial plate is again suspended freely between the dental flanges (fig. 13g).

The relation between dental flanges and delthyrial plate is much more fully expressed in the internal structure. In the extreme apical part of the delthyrial plate the fibres are confluent with the fibres of the dental flanges (fig. 12a). There is no discontinuity in the shell structure/

ure between dental flange and delthyrial plate. They form a single structure and are only distinguished by their external form. At each successive stage anteriorly the delthyrial plate is, to a greater or lesser extent, distinct from the dental flanges.

Posteriorly the separation of the two structures is scarcely perceptible and is revealed only by the orientation of the fibres of the shell substance. The complete continuity of structure of the initial stage (fig. 12a) is not present anteriorly. The fibres of the outer part of the delthyrial plate are not in alignment with those of the outer part of the dental flanges, but merge into the fibres in the middle of the dental flange (fig. 12b). The succeeding stage (fig. 12c) is similar with in addition a lack of correspondence between the direction of the fibres and the surface of the delthyrial plate, the fibres in the outer part of the delthyrial plate being confluent with those of the dental flange, while those of the inner part of the plate are not in continuity with the flange. It is at this stage that the lateral parts of the delthyrial plate are fused to the divergent dental flanges. The plane separating the structures is clearly defined (fig. 12c).

Anteriorly, where the dental flanges become convergent, they/

they are more clearly distinguished from the delthyrial plate (fig. 12f). The delthyrial plate is attached to the inner edges of the dental flanges while the lateral parts of the plate are separated from the flanges by a deep groove. The structure of the dental flanges with their successive layers of shell material has already been described. The delthyrial plate is in continuity with the outermost layers of the flanges both on the outer and inner surfaces.

The change from the relatively continuous structure of dental flanges and delthyrial plate in fig. 12c to the separate structures in fig. 12f is a gradual one. The series of changes is shown in figs. 13d, e, f, g. The change in form is associated with the curving of the inner edge of the dental flange. The curving leads to the separation of the fine structure of the core of the dental flange from that of the delthyrial plate, so that the dental flanges and delthyrial plate emerge as distinct structures.

Towards the anterior margin of the delthyrial plate the dental flanges may be even more clearly delimited from the delthyrial plate (fig. 12h). In this case it is not merely the core of the dental flange which is structurally isolated, it is the core and several enveloping layers which are independent/

Fig. 15

Delthyrial plate with a complex arrangement of the fibres in the median part of the plate.

Fig.15

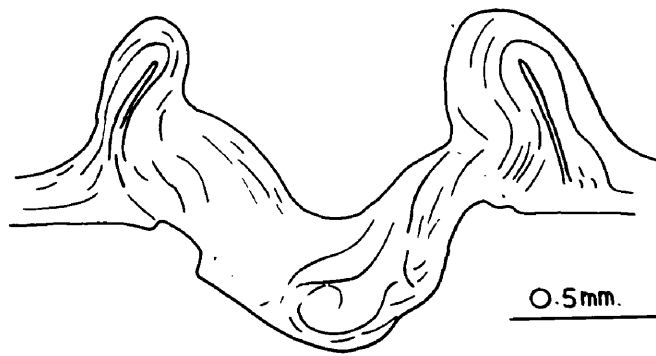
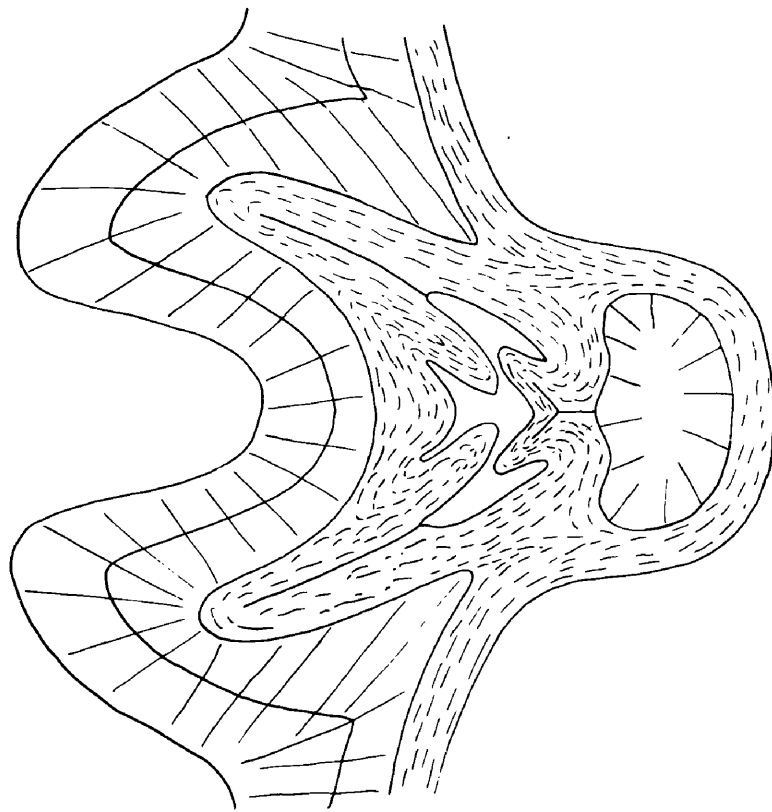


Fig. 16 Idealized transverse section of posterior part of the delthyrial region.

The section passes through the incurved umbo and thus several structures are duplicated. The inverted Y stage of the delthyrial plate is opposed by the modified U stage, the former is supported by convergent dental flanges and the latter by divergent flanges. The divergent flanges are enveloped by short dental plates but no dental plates are present in the umbonal section, the umbonal cavity being completely infilled.

Fig. 16



0.5 mm

dependant of the delthyrial plate. The delthyrial plate is in continuity with the outermost layers on the inner surfaces of the dental flanges.

The structure of the delthyrial plate itself is generally uniform but occasionally a discontinuity of structure is present along the median part of the plate (fig. 15). The fibres of the two parts of the plates are not confluent.

The development of normal layer on the inner surface of the delthyrial plate (fig. 12h and fig. 24a) will be discussed when the infilling of the delthyrial cavity is considered.

In the adult, curvature of the beak due to more rapid growth at the anterior margin causes structures formed at different parts of the delthyrium to be brought into contact, in opposition to each other. In one specimen (fig. 16) the inverted Y of the upper part of the delthyrial plate is brought into contact with the modified U- stage. The two inwardly directed points of the U- stage are accommodated between the outwardly directed points of the Y- stage and the two pairs of external grooves run together.

e) The Ventral Septum

All the structures so far described form in the delthyrial region. There are no plates on the floor of /

Fig. 17

The ventral septum.

- a Low, narrow septum close to umbo. The successive layers of the shell show the increasing height of the septum.
- b Septum present only in the later growth stages of the shell.
- c Low, broad septum some distance from umbo.
- d Longitudinal section showing the short distance which the septum extends from the umbo.

Fig.17

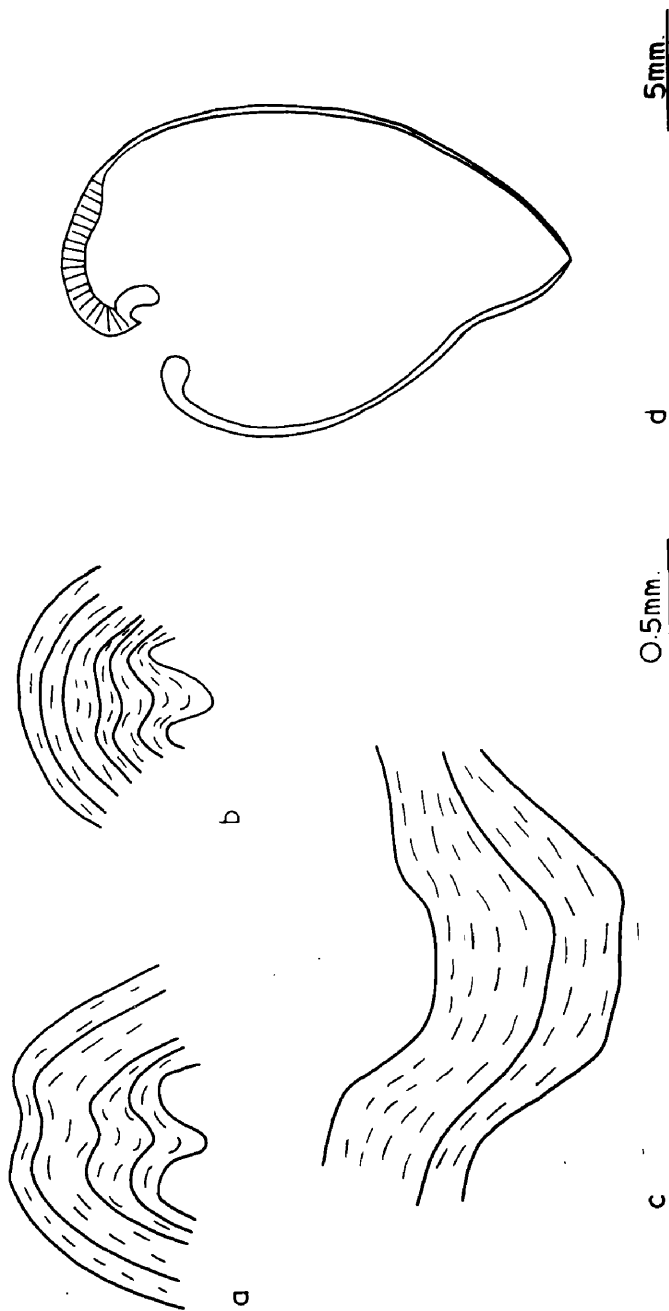


Fig. 18

The infilling of the umbonal cavity.

The longitudinal section, f, shows the position of the transverse sections a-e.

a Apex of valve infilled mainly with normal layer.

b Apex of valve infilled with oblique layer.

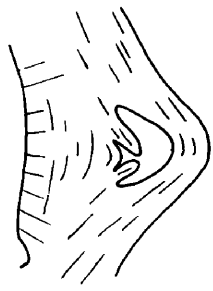
c, d, e, Open delthyrium of extreme apex and delthyrial plate which rises from floor of valve anteriorly (see fig. 11a).

Interval between sections

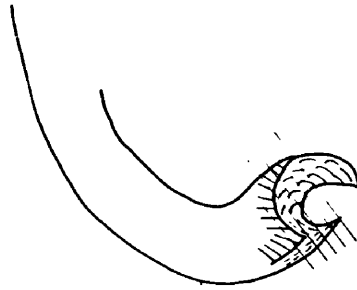
a-b 0.05mm. b-c 0.025mm.

c-d 0.025mm. d-e 0.025mm.

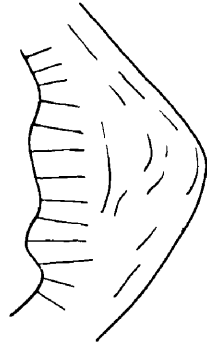
Fig. 18



c



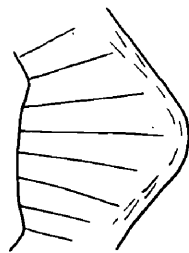
0.5mm.



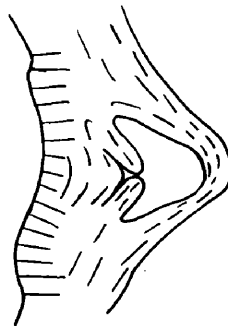
b



e



a



d

of the pedicle valve at or immediately anterior to the umbo. About 0.5 mm. from the umbo a septum develops. It is not a high partition, only a low ridge which extends at most a third of the length of the valve (fig 17 d). The posterior part of the septum is narrow (fig 17 a) but towards the anterior end it becomes much broader (17c). At all stages the crest is rounded. The septum may not be developed when the first shell layer is deposited, for several unfolded layers may be present immediately inside the lamellar layer (fig 17 b).

f) The Infilling of the Umbo.

The apex of the valve is a solid mass of calcite (fig 16). This is the material which is frequently referred to as "umbonal callus" and thereafter dismissed as a late stage infilling of no real significance. This attitude is quite unjustified for the apical infilling is as much a part of the shell as the outer layers. It is intimately connected with many of the internal plates.

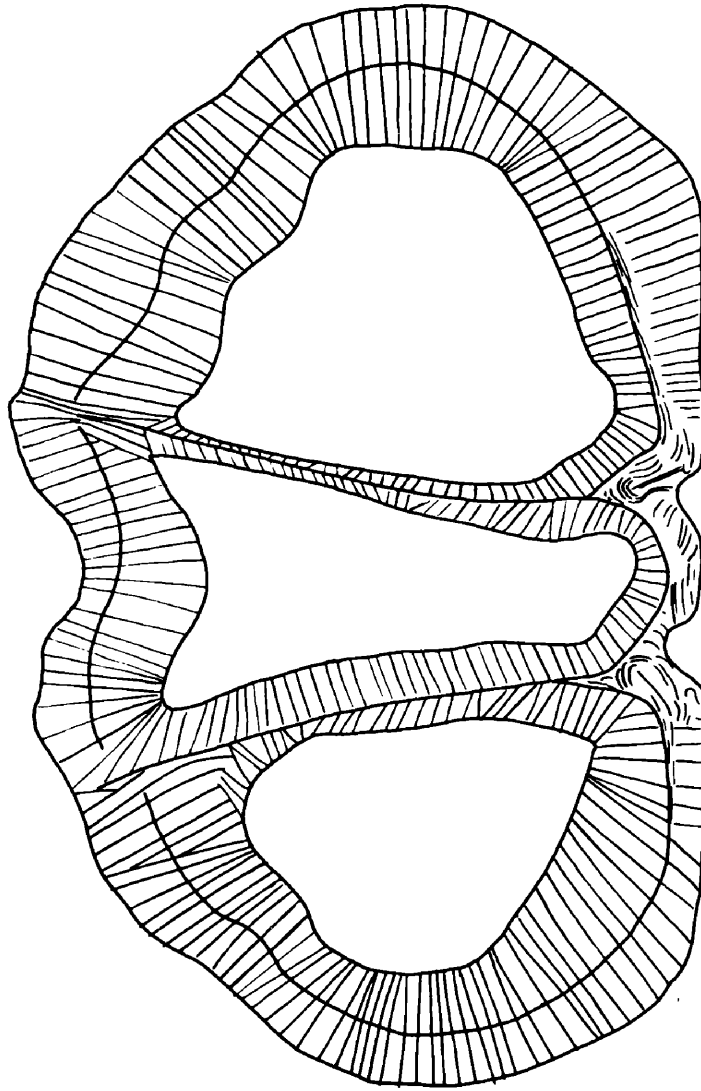
The main part of the infilling is prismatic calcite of the normal layer but it is encased in fibrous calcite of the oblique layer (figs 16, 18). The extreme apex of the incurved umbo consists entirely of oblique layer and is convex in transverse section with no delthyrial covering (figs 18d, e). Anteriorly (fig 18c) the oblique layer increases in thickness /

Fig. 19

Dental plates in transverse section.

The dental plates envelop the dental flanges and delthyrial plate.

Fig. 19



1mm.

Fig. 20

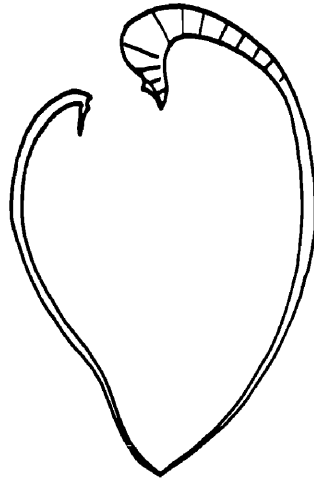
The extent and orientation of the dental plates.

a Longitudinal section passing through one plate.

b, c, d, Oblique transverse sections through the apex of the valve showing the parallelism of the dental plates, their position relative to the dental flanges, and the infilling of the three apical chambers.

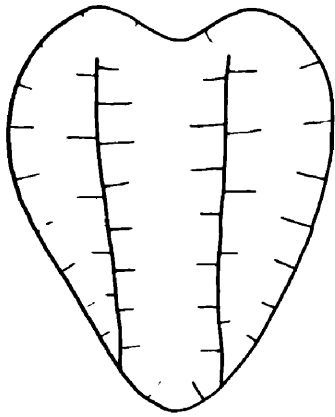
Interval between sections

b-c 1.2mm. c-d 0.8mm.

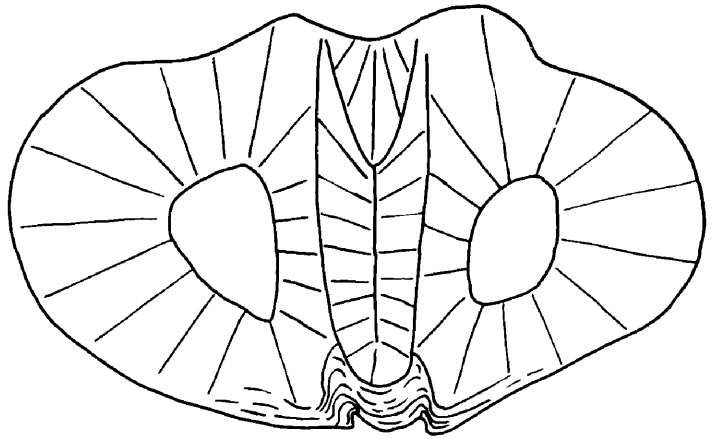


a

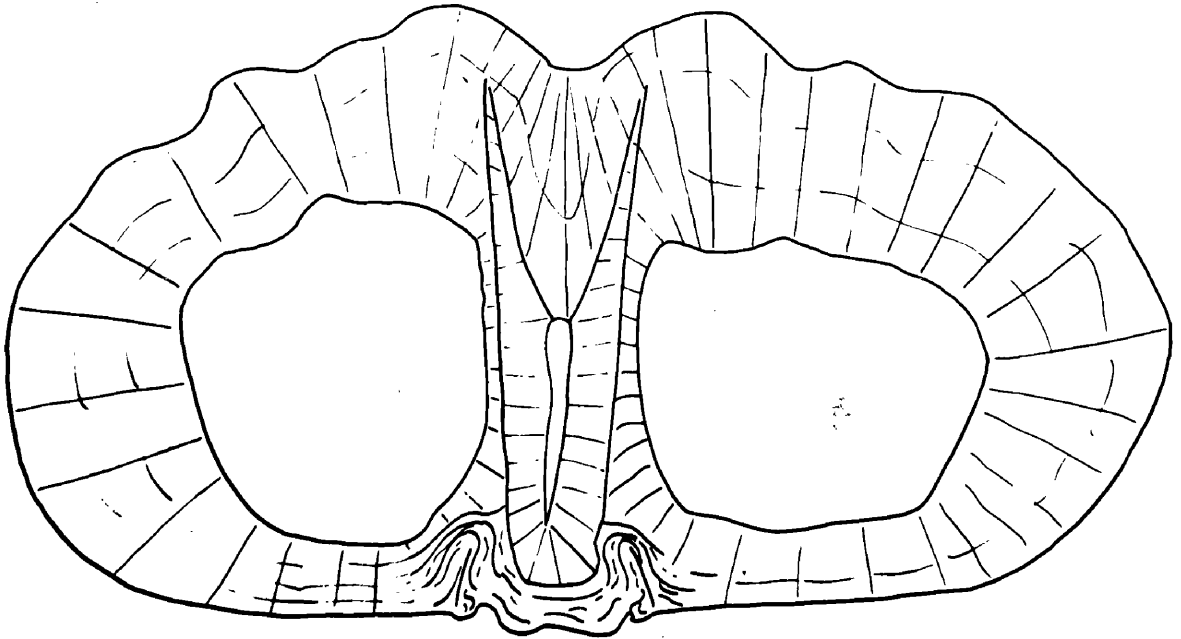
2mm



b



c



d

○ 5mm

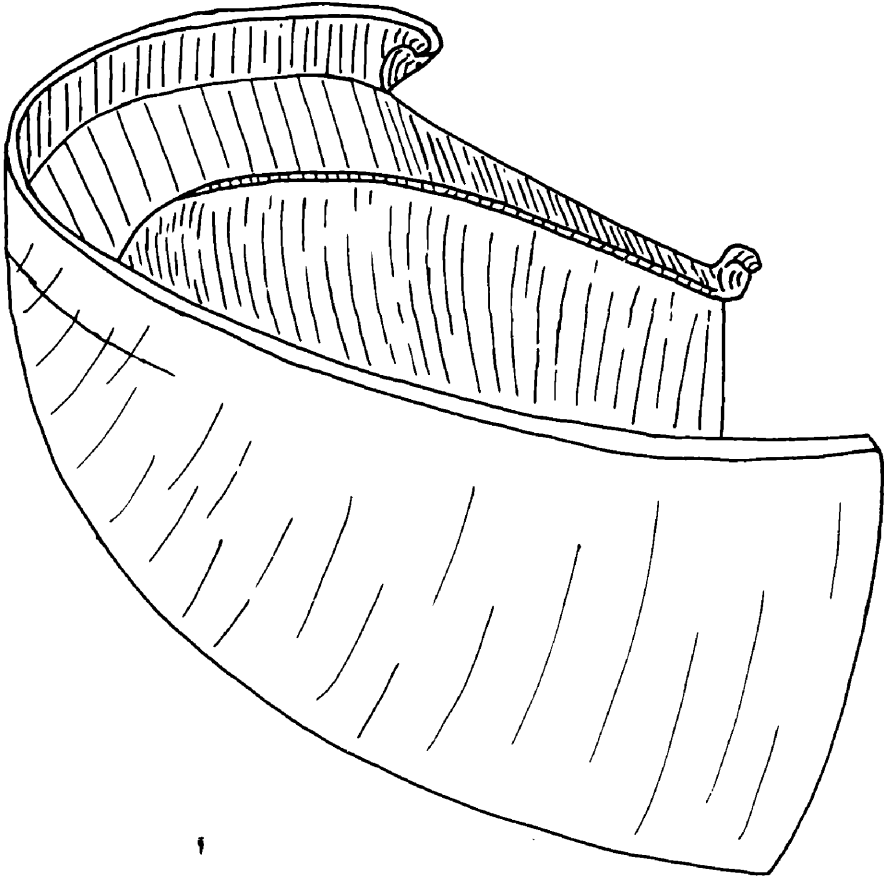
Fig. 21

Reconstruction of the apex of the pedicle valve showing the position of the dental plates.

The valve is cut along the sagittal plane.

The dental plates are parallel posteriorly and diverge along the margins of the delthyrium. They do not extend to the umbo.

Fig. 21



thickness until it fills the internal cavity and closes the delthyrium. The oblique layer becomes restricted to the outer layer and the internal part is composed of normal layer at a short distance from the apex (fig 18 a).

g) The Dental Plates.

The dental plates are two almost parallel vertical plates in the posterior part of the valve. They are of variable length, frequently extending no further than the highest part of the curve of the valve, but occasionally extending some distance along the floor of the valve (fig 20 a). They may be no more than low ridges in the apical region (fig 16).

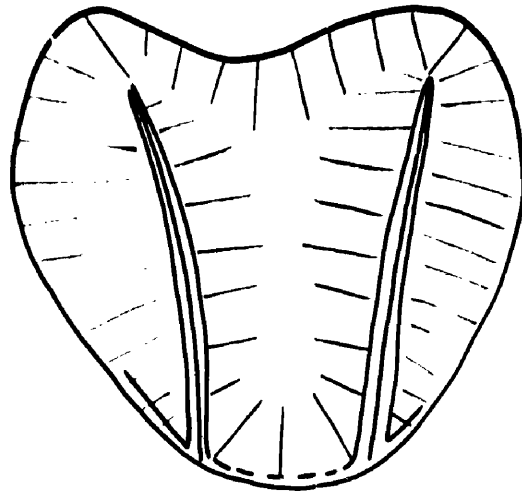
The dental plates extend along the margins of the delthyrium, posteriorly from the teeth (fig 21), but since the delthyrial margins converge towards the umbo, whereas the dental plates remain more nearly parallel (fig 20b,c,d), the plates are more widely spaced than the posterior margins of the delthyrium. The dental plates never reach the umbo (fig 16) but form two sub-parallel vertical plates which cross from the palintrope to the floor of the valve some little distance anterior and lateral to the umbo (figs. 21, 25b).

In detail therefore the relation of the dental plates to /

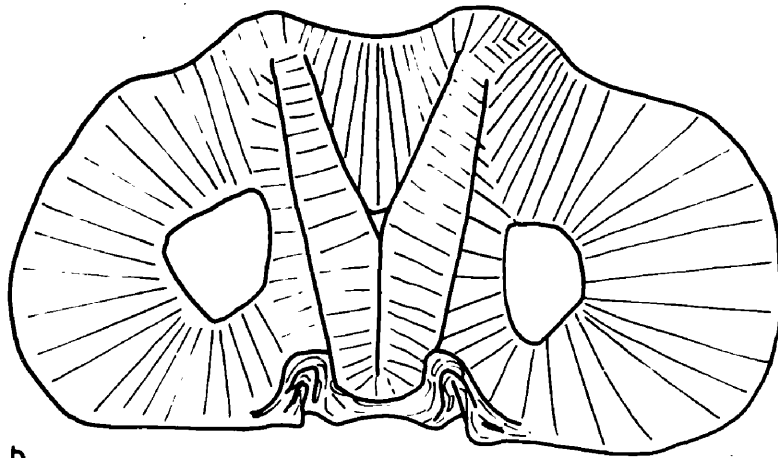
Fig. 22

Variable thickening of the dental plates.

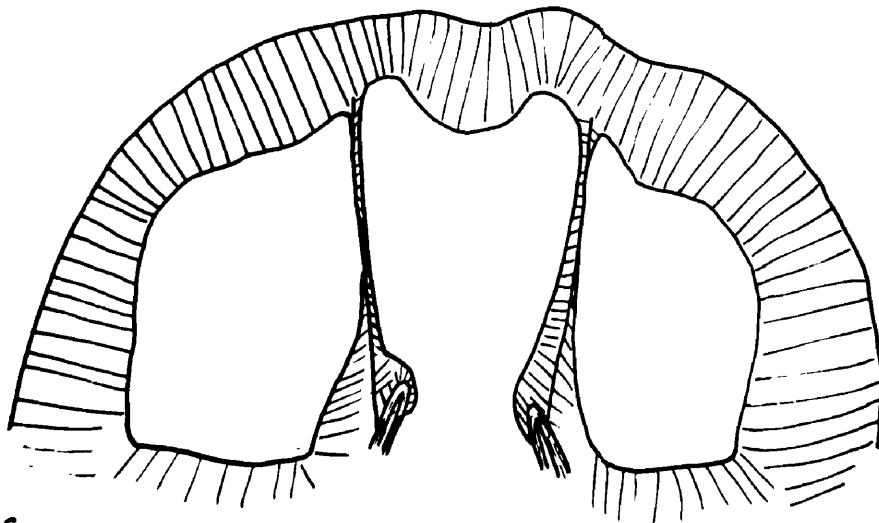
- a Trace of early formed dental plates within the later thickening of the plates which completely fills the apex.
- b Dental plates much thickened. Three small apical chambers remain. Ventral septum enclosed by dental plates.
- c Dental plates thin.



a



b



c

1mm

to the other parts of the valve appears to be extremely complex. While the dental plates may form immediately over the dental flanges so that the flange then appears to be simply the core of the dental plate (figs. 16, 19, 22 b) the dental plates may equally well develop lateral to the dental flanges (fig. 22 c).

The dental plates divide the apex of the valve into three chambers. The two lateral have been termed the umbonal cavities and the median the delthyrial cavity. The term delthyrial cavity is perhaps rather misleading, for the cavity extends on either side of the apical part of the delthyrium and is therefore not wholly delthyrial.

The dental plates are formed almost entirely of normal layer (fig. 19). Each plate is made up of two parts, the surface separating the two parts appearing in cross-section as a well defined line. Thin sections show that the calcite crystals do not cross this line and are frequently at different angles on the two sides. In contrast to this marked division within each plate is the continuity of structure in the material lining the three cavities.

The umbonal cavities are simple in form depending only on the length and thickness of the dental plates and the thickness/

thickness of the shell wall. The normal layer is continuous from the shell wall to the dental plate, with only a minor discordance in the shell structure at the junction, between the dental plate and the floor of the valve (fig.19).

The delthyrial cavity is more complex since it is flanked not only by the dental plates but also by the ventral septum, the dental flanges and the delthyrial plate (fig. 20c). A continuous sheet of normal layer covers the floor of the valve, where it forms the ventral septum, extends across the delthyrial cavity, where it forms one side of each dental plate and continues across the delthyrium where it forms the inner layers of the delthyrial plate. The apex of the delthyrial cavity is occupied by the umbonal infilling already described (fig. 20b). The normal layer of the infilling is continuous with the normal layer lining the sides of the delthyrial cavity.

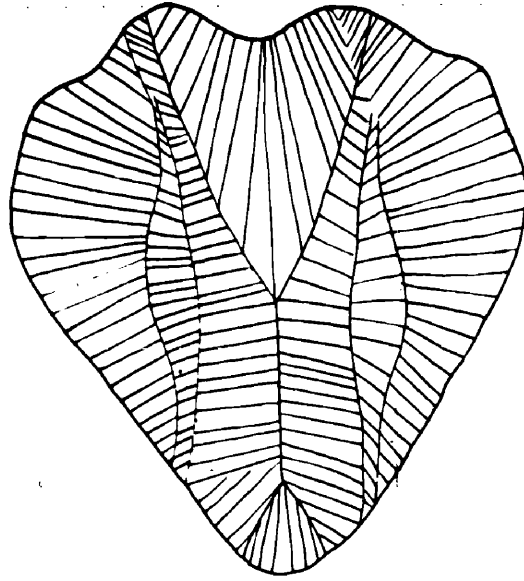
The dental plates and the shell walls may be so greatly thickened that the umbonal and delthyrial cavities are infilled in the apical region. The trace of the lines of junction within the dental plates remains (fig. 22a). In other cases the dental plates are not much thickened, and while deposition has continued on one side of the plate it may have stopped on the other (fig. 22c).

The growth of normal layer in the delthyrial cavity tends/

Fig. 23

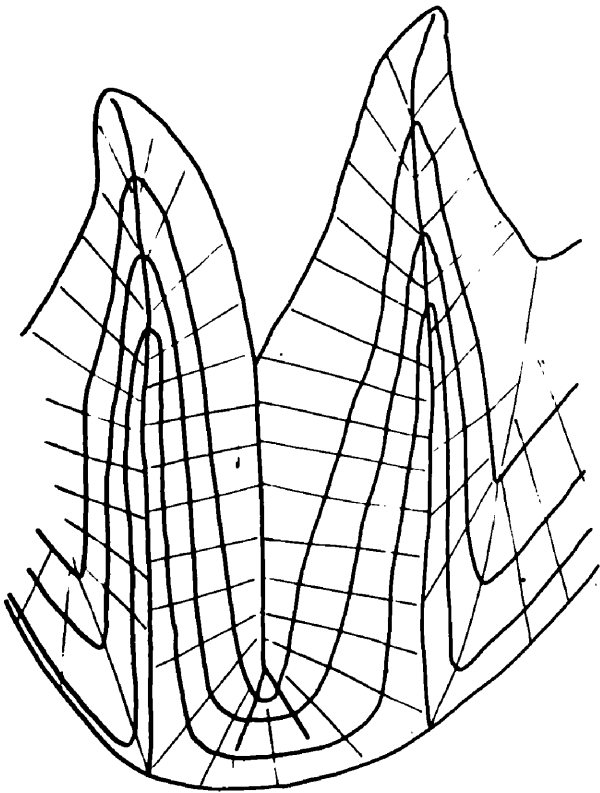
The relation between the dental plates and the septum.

- a Section through the incurved umbo passing twice through the septum. The dental plates on either side of the septum in contact with the septum.
- b Transverse section through the dental plates showing the septum completely enclosed by the growth of the dental plates.
- c&d Two earlier stages in the development of septum and dental plates as shown by the growth lines in fig. b.

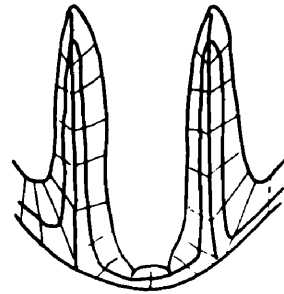


a

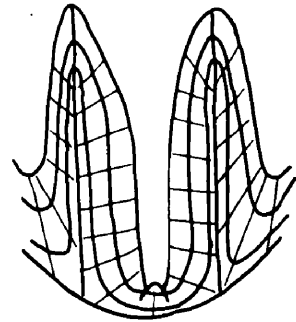
1mm.



b



c



d

0.5mm.

tends to cover pre-existing structures - the dental flanges, the delthyrial plate, and the ventral septum. In the case of ventral septum, where the dental plates are not greatly thickened the septum remains as a distinct structure, but frequently the dental plates are sufficiently developed to lead to the incorporation of the ventral septum in the dental plates. This is always found in the apex of the valve where the ventral septum forms a wedge, triangular in section, between the bases of the dental plates (figs. 22b, 23a). It is possible to reconstruct the stages in the envelopment of the ventral septum by use of the growth lines on the normal layer (fig. 23b, c, d). The individual layers are continuous from dental plate to ventral septum.

The outer part of the delthyrial plate is formed by the oblique layer. This part has already been described. The inner surface is frequently covered by normal layer (figs. 16, 20c, d). The normal layer is continuous with the normal layer of the dental plates. Apically the normal layer on the delthyrial plate and the dental plates is sufficiently thick to close the delthyrial cavity (fig. 20c). Anteriorly the normal layer decreases in thickness and at the margin of the delthyrial plate no normal layer is present.

The/

Fig. 24

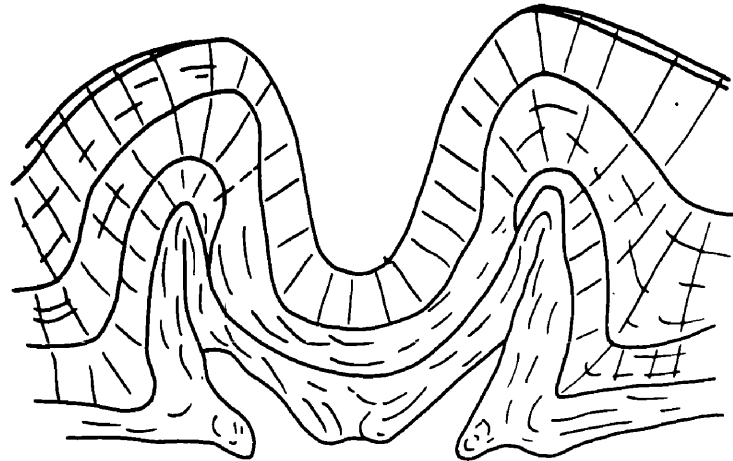
The internal thickening of the delthyrial plate.
Three transverse sections from one specimen.

Interval between sections

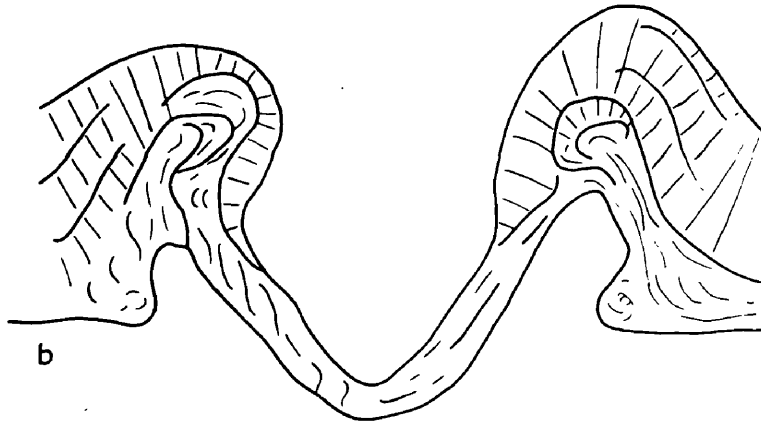
a-b 0.35mm. b-c 1.25mm.

- a The delthyrial plate is thickened by successive layers deposited on the inner surface. These layers are continuous with those of the short dental plates which envelop the dental flanges.
- b The delthyrial plate consists of one layer only. The normal layer does not extend across the delthyrium. The dental plates are not separable from the dental flanges.
- c No delthyrial plate, neither oblique nor normal layer extending across the delthyrium. The normal layer on the inner surface of the dental flanges extends round the inner edges of the flanges.

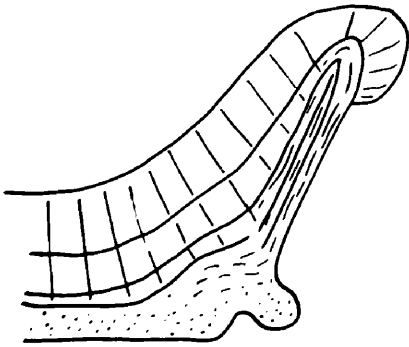
Fig. 24



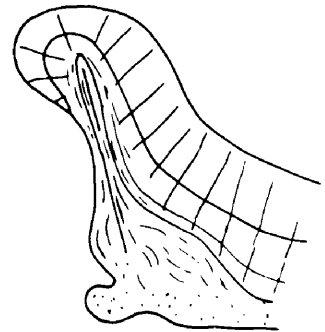
a



b



c



○ 5mm

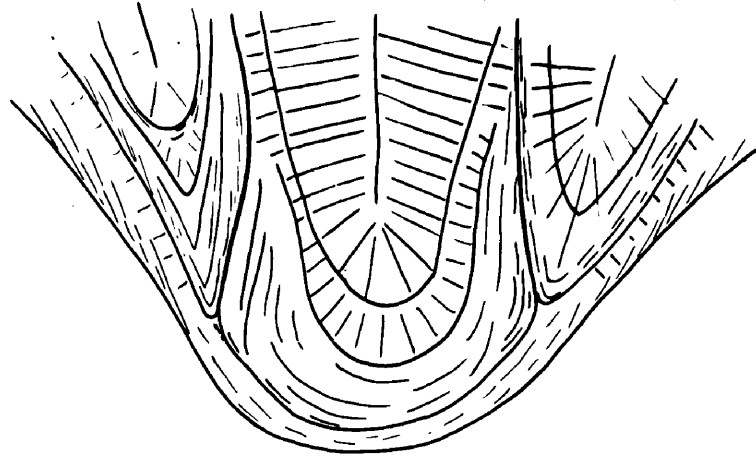
Fig. 25

The secondary development of the dental plates

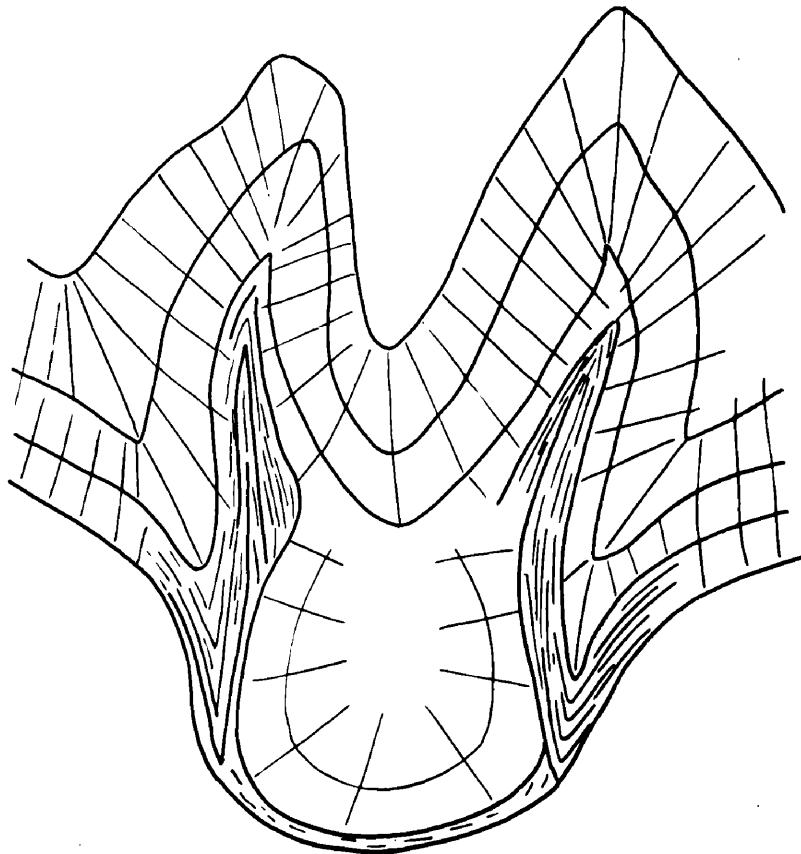
a Transverse section in the apex of the valve passing through the dental plates and the three completely filled apical chambers.

A thin film of shell separates the dental plates from the exterior. The median plane of the plate does not reach the exterior of the shell.

b Transverse section passing through the incurved umbo. The umbonal cavity is infilled and no dental plates are present within it. The structure of the dental plate extends on either side of the umbonal infilling, showing that the dental plates do not extend to the apex of the delthyrium but cross from the delthyrium to the floor of the valve on either side of the umbonal cavity.



a



b

0.5mm.

Fig. 26

The initiation of the dental plates.

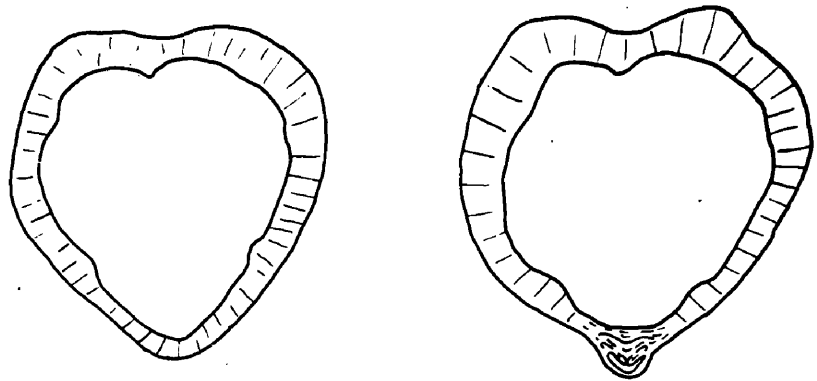
A series of transverse sections through a **small** specimen.

Interval between sections

a-b 0.205mm. b-c 0.125mm.
c-d 0.20mm. d-e 0.30mm.

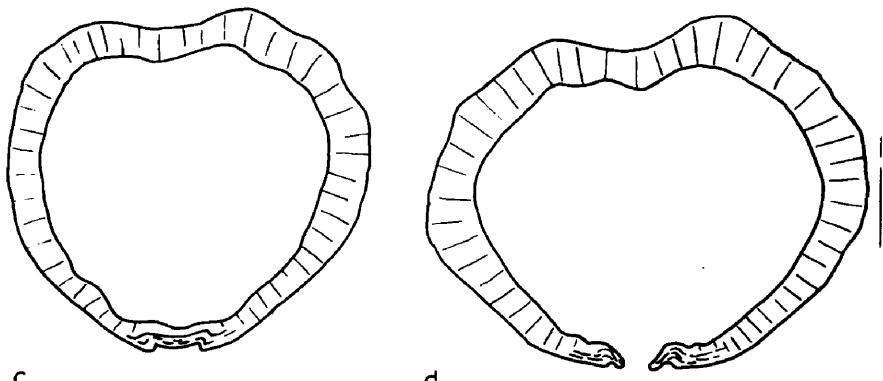
- a Four small projections on the inside of the valve, two on each side, are the incipient dental plates, at this stage very low ridges.
- b, c & d Two similar small projections on either side of the delthyrium. Dental flanges present.
- c The delthyrium bounded by dental flanges with no dental plates.

Fig. 26



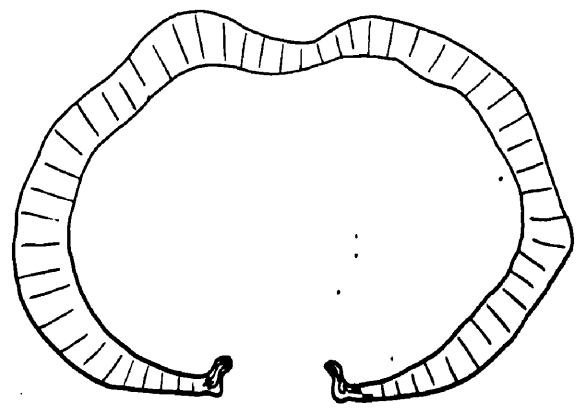
a

b



c

d



e

1mm.

The thinning of the normal layer of the delthyrial plate is shown in fig. 24. The continuous sheet of normal layer (fig. 24a) becomes discontinuous (fig. 24b) and finally disappears a short distance from the margin of the delthyrial plate.

ii) THE BRACHIAL VALVE.

The brachial valve is smaller and less convex than the pedicle valve and the beak is only slightly incurved. The palintrope, low compared with the ventral interarea, is divided by the notothyrium which is bounded by dental sockets and erural plates. The internal structures of the brachial valve are not as complex as those of the pedicle valve.

a) The Notothyrium

The notothyrium is as broad as the delthyrium but not having the same height it forms a widely obtuse angle at the umbo. The apex of the notothyrium is occupied by the cardinal process (fig. 27).

b) The Dental Sockets

The dental sockets are the dorsal counterparts of the dental ridges. They are two plates attached to the inner surface of the palintrope along the notothyrial margins/

Fig. 27 A reconstruction of the apex of the brachial valve.

The structures illustrated are as follows:--

pits along the hinge line

dental sockets and crural plates bordering the notothyrium

crura attached to the dental sockets

cardinal process at the apex of the notothyrium

Fig. 27

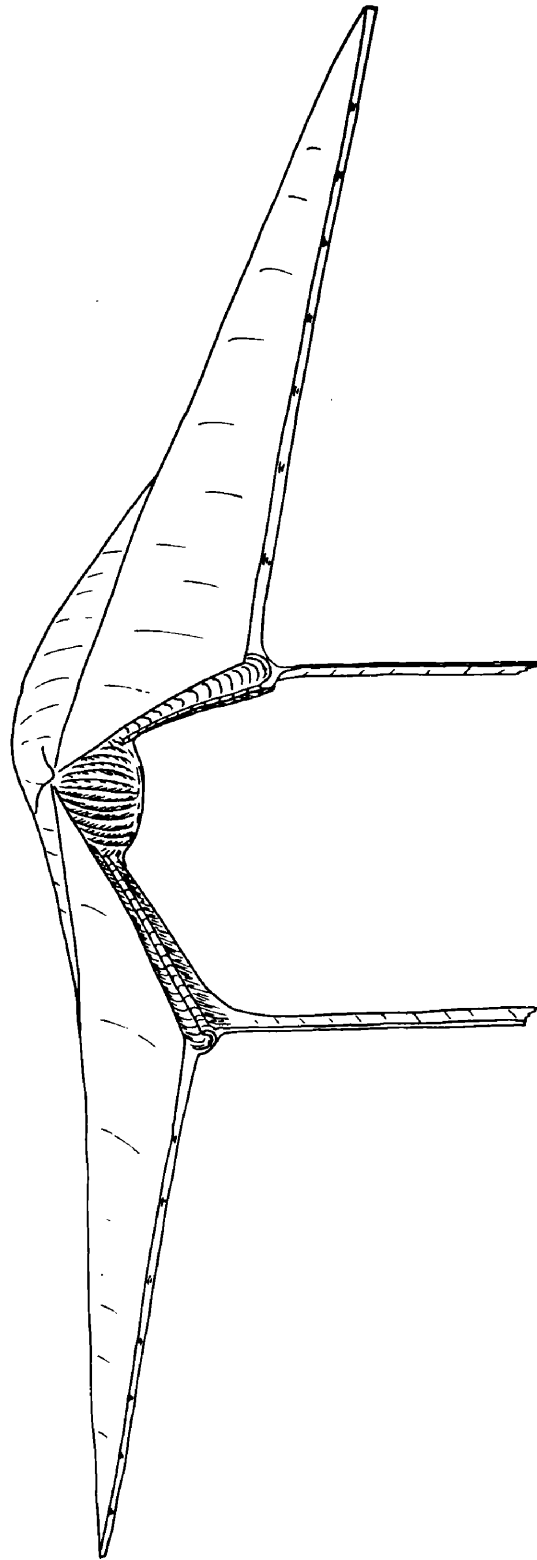
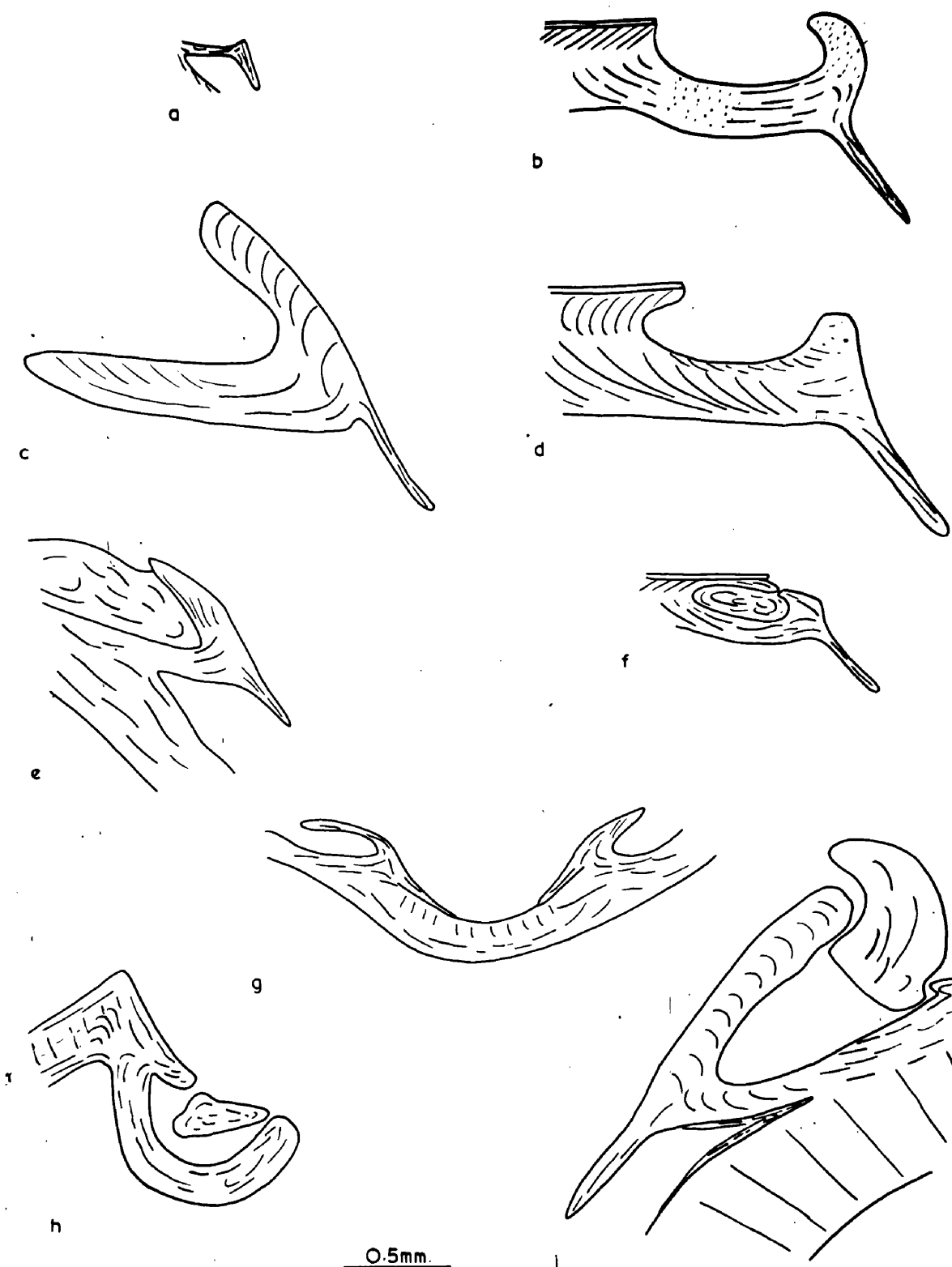


Fig. 28

The dental sockets and crural plates.

- a T.S. Small dental socket with no socket ridge in a young individual. Crural plate attached.
- b T.S. Concave dental socket with well developed socket ridge attached to the dorsal palintrope. The crural plate extends from the convex surface of the socket.
- c T.S. The functional dental socket with prominent socket ridge and slender crus.
- d T.S. The palintrope overhanging the socket in the manner of an outer socket ridge.
- e T.S. The dental socket attached to the floor of the valve infilled by later shell secretion.
- f T.S. The extension of the lamellar layer of the palintrope across the infilled dental socket.
- g T.S. The crural plates fused to the floor of the valve.
- h L.S. Tooth in socket. Palintrope overhangs the socket
- i T.S. Tooth in socket. Two concave surfaces on the tooth accommodate the socket ridge and the palintrope.



margins. They are not present at the apex of the notothyrium but appear at about 0.1 mm. from the umbo and extend to the anterior margin of the palintrope, projecting a little distance into the pedicle valve.

The dental sockets, elongated along the notothyrial margins, are not flat plates but are curved towards each other on either side of the notothyrium (fig. 27). The sockets small and shallow at the posterior end become larger and deeper anteriorly (fig. 28). The concave surface of the socket is turned up along its inner edge into a socket ridge. This socket ridge is not developed posteriorly but with increasing depth of socket it becomes more prominent and more strongly curved.

The opposite margin of the socket is formed by the overhanging edge of the palintrope. This also increases in width anteriorly. It functions as an outer socket ridge (fig. 28d, h), but it is not strictly part of the dental socket, and has a distinct structure.

The dental sockets and palintrope are formed by the oblique layer. The surface of the palintrope is in addition covered by the lamellar layer which extends to the edge of the notothyrium (fig. 28b). Within the socket the fibres are arranged longitudinally, curving down across the floor and into the socket ridge (fig. 29i). Those in the palintrope/

Fig. 29

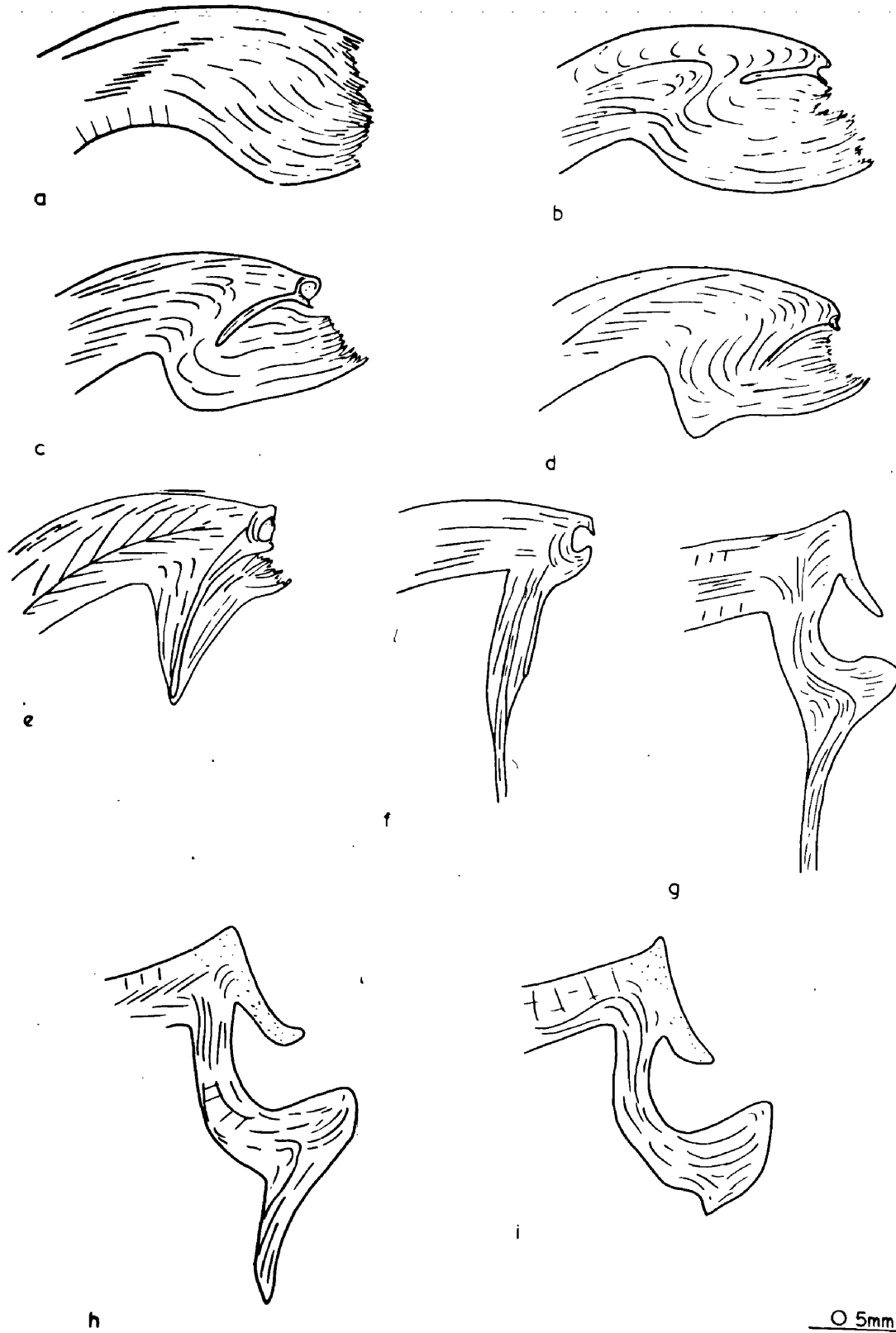
The cardinal process and the crural plates.

A series of longitudinal sections from one specimen.

Interval between sections

a-b	0.10mm.	b-c	0.10mm.
c-d	0.10mm.	d-e	0.10mm.
e-f	0.30mm.	f-g	0.39mm.
g-h	0.13mm.	h-i	0.19mm.

- a Sagittal section. The ventral surface of the cardinal process is highly irregular with the ends of the fibres. This is the area of muscle attachment.
- b The earliest dental socket and crus enclosed by the later growth of the cardinal process.
- c, d, e. The change in orientation of the crural plate relative to the surface of the shell. The crural plate and dental socket enclosed by the cardinal process.
- f The crural plate almost free from the cardinal process.
- g The dental socket close to the anterior margin of the notothyrium is large. The descending lamella is attached to the convex surface.
- h The dental socket with the overhanging palintrope and a small part of the descending lamella.
- i The functional dental socket.



trope on the other hand lie along its width and are inclined inwards, away from the notothyrium (fig. 28b). There is consequently a sharp change in the orientation of the fibres at the junction between palintrope and socket (figs. 28b, d).

c) The Crura and Crural Plates

The crura are attached to the convex surface of the dental sockets (fig. 27). In direction, the width of the crus corresponds with the notothyrial margin. The direction is maintained as the crura descend in parallel fashion from the socket almost to the anterior margin of the shell. These are the descending lamellae. Near the anterior they are rotated into a single vertical plane before giving rise to the spiralia. The descending lamellae measure about 0.75 mm. in width. There are 11-12 coils in the spires of specimens 20 mm. in length. The descending lamellae and the spires are composed of fibrous calcite of the oblique layer (fig. 29g).

Extending along the length of the convex inner surfaces of the dental sockets are two inclined plates. They vary in width from 0.3 mm. at the posterior end to 1.3 mm. at the anterior end. They also vary in inclination. At their posterior end they project dorsally from the under side of the dental sockets (fig. 29b) but this/

but this inclination gradually changes along the length of the sockets till they are directed anteriorly (fig. 29c-f).

Anteriorly these plates are continuous with the crura. They are crural plates, the remnants of the crura formed during growth. The descending lamellae are resorbed with growth but the crural bases remain to form the crural plates. The fibres of the oblique layer are elongate across the width of the crural plates.

d) The Cardinal Process

The cardinal process is of the striate form typical of spiriferids. Situated under the umbo at the apex of the notothyrium it is attached dorsally to the shell wall and laterally it envelops the abandoned dental sockets. It is knob-like in shape with the lower surface a smooth curve and the upper ventral surface striate (fig. 27). The posterior part is level with the palintrope while the antral part projects above it.

The cardinal process is formed by the oblique layer, the dorso-ventrally elongated fibres curving slightly to the contour of the process (fig. 29a). The fibres are arranged longitudinally in plates which can be traced through the substance of the process (fig. 30).

Posteriorly/

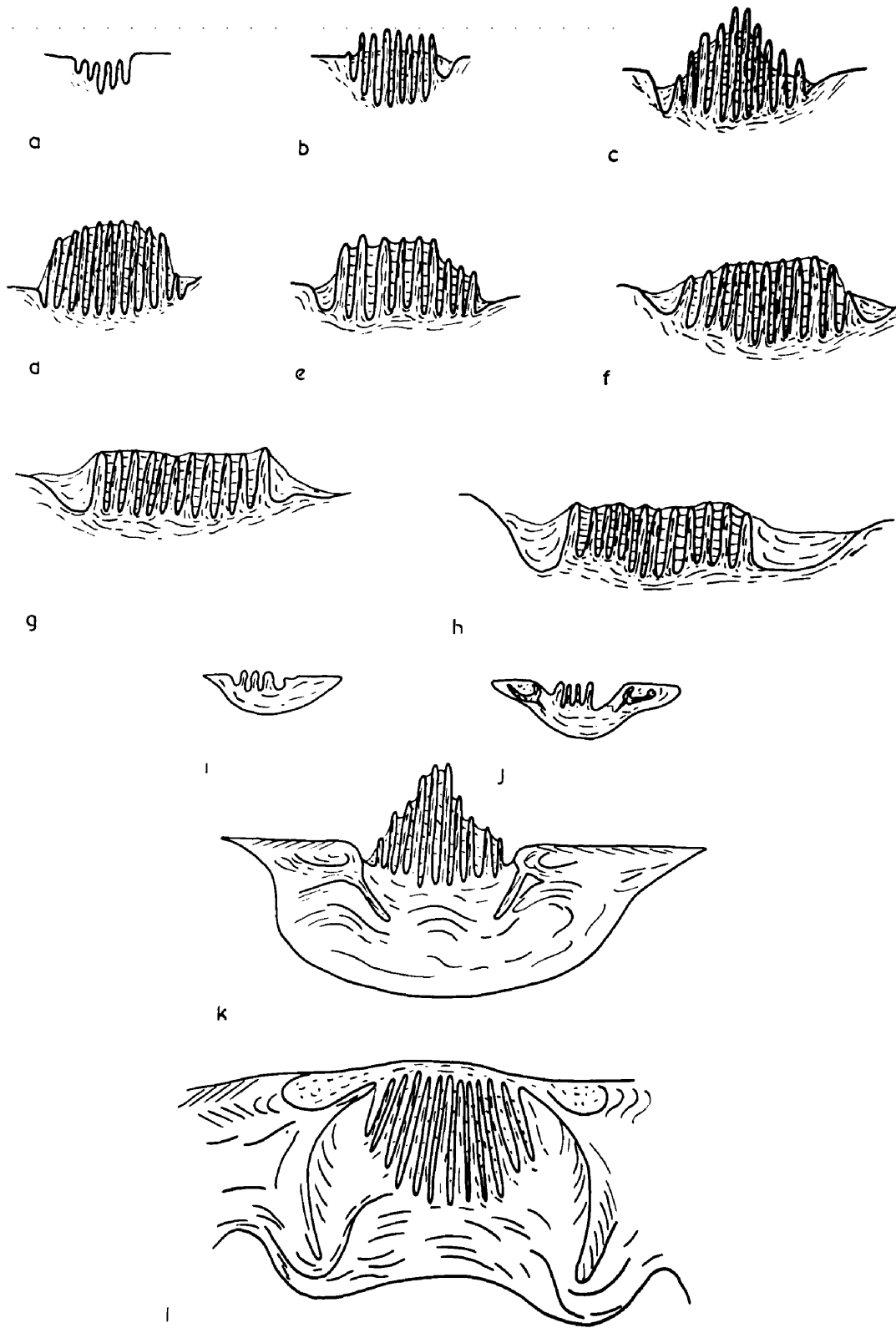
Fig. 30

The cardinal process in transverse section.

Interval between sections

a-b	0.12mm.	b-c	0.08mm.
c-d	0.05mm.	d-e	0.05mm.
e-f	0.05mm.	f-g	0.10mm.
g-h	0.03mm.		

- a-h A series of sections from one specimen showing the increase in the number of plates within the process with growth. Sections b-e in which the plates project from the surface of the process represent the surface of muscular attachment.
- i, & j Sections showing the small cardinal process of a young individual.
- k The cardinal process with the dental sockets and crural plates on either side. The growth of the cardinal process has enveloped the crural plates. The apex of the valve is thickened so that the cardinal process is attached to the floor of the valve.
- l Growth lines indicate the stages in the envelopment of the crural plates. The material infilling the grooves in the cardinal process is continuous with that filling the dental sockets.



0.5mm

Posteriorly there are two or three plates but the number increases with the width of the process until there are about fourteen (fig. 30 a-h). The median plates project further from the notothyrium than the lateral plates.

For the greater part of their length these plates are buried in fibrous calcite formed between the plates and it is only on the upper ventral surface that they form the ridges which give the striate appearance to the process. The ends of the fibres in these ridges are free. This is the surface of muscular attachment.

The cardinal process is attached dorsally to the shell wall and laterally to the posterior ends of the dental sockets. In the median plane (fig. 29a) there is very little break between the structure of the cardinal process and the shell wall. On either side of this, the structure of the cardinal process is controlled by the presence within the process of the crural plates (fig. 29 b-e). The fibres of the cardinal process curve around these plates. Posteriorly where the crural plate is inclined at a low angle to the shell surface there is a sharp change in direction of orientation of the fibres from the shell wall to the cardinal process (fig. 29b). Anteriorly this angle is increased (fig. 29d).

Posteriorly/

Posteriorly the whole crural plate is contained within the structure of the cardinal process (fig. 29 b,c,d fig. 30 j,k,l) and may be buried at a considerable depth within the shell. Anteriorly however the burial is not complete (fig. 29e).

The abandoned dental sockets are also enclosed in the cardinal process (fig. 30 j,k,l). The fibres of the shell material follow the curvature of the socket. This calcite is in continuity with that filling the spaces between the plates of the cardinal process (fig. 30l). In some specimens the lamellar layer also develops across the former socket (fig. 30k).

VIII. THE DEVELOPMENT OF THE SHELL

Three lines of evidence are used in tracing the development of the internal structures of the shell. Direct evidence is derived from a comparison of young and old specimens. Secondly, the sequence of development can be proved in some parts of the shell where later structures are superimposed on early structures without any resorption of the previous shell substance. Finally, the prismatic calcite of the normal layer shows growth lines which illustrate the form of particular parts of the shell at successive stages in growth.

i) THE DEVELOPMENT OF THE PEDICLE VALVE. (Fig. 37)

At the earliest observed stage of development the pedicle valve is convex with an open delthyrium, no interarea and no internal septa. It consists of lamellar layer and a thin development of oblique layer on the inner surface of the valve.

Growth proceeds anteriorly with the formation of lamellar layer and oblique layer, the oblique layer increasing in thickness away from the umbo. In addition, the oblique layer spreads from the floor of the valve, close to the umbo, across the apical cavity to the delthyrium/

delthyrium, in this way initiating the infilling of the umbo and forming the delthyrial plate with its flanking dental flanges (fig. 11a). Once the apical cavity is floored over by oblique layer the infilling of the umbo proceeds, consisting in large part of normal layer.

a) The Development of the Delthyrial Plate.

The delthyrial plate is formed of oblique layer and normal layer, but without lamellar layer. The lamellar layer on the interarea does not extend on to the delthyrial plate, but terminates at the grooves adjacent to the dental ridges. The absence of lamellar layer on the delthyrial plate is taken to indicate that the delthyrial plate was enveloped by the mantle during life: that the delthyrial plate is an internal rather than an external structure (Williams 1953, p. 280).

The delthyrial plate does not result from the simple fusion of two mantle flaps extending from either side of the delthyrium, but is formed within a fold of the mantle which originates on the floor of the valve close to the umbo, extends from the floor across the apical cavity to the delthyrium and then folds back on itself to the floor of the valve. The mantle completely covers the outer surface of the delthyrial plate at all stages of growth, extending/

extending from inside the shell across the delthyrial plate to the delthyrial margins. (fig. 37a)

The delthyrial plate grows anteriorly. There is no indication of any subsequent thickening of the delthyrial plate on the outer side, though the plate remains covered by the mantle. Internally there is further deposition on the inner surface of the delthyrial plate, part of the general apical infilling (figs. 20 c,d).

The sides of the delthyrial plate grow in advance of the central part so that the anterior margin of the plate is deeply indented (fig. 10). The directions of growth on the two sides of the plate thus tend to be opposed. Along the median part of the delthyrial plate there is in some cases an irregularity of structure, the normal regular orientation of the fibres is lacking and instead they form complex folds (fig. 15). This structure is due to the change in the direction of growth of the fibres along the median line.

b) The Development of the Dental Flanges.

The dental flanges are not covered by lamellar layer and are, like the delthyrial plate, internal structures. They result from secretion by two mantle folds which extend along the delthyrial margins, advancing along/

along the dental ridges a short distance from the cardinal margin. Anteriorly, where the structure is not complicated by the delthyrial plate, the double plate of the dental flange clearly indicates its formation within a mantle fold (fig. 12e). This initial plate grows by the addition of further layers of shell material particularly on the inner surface (fig. 12g). Posteriorly however, the development of the dental flanges is to a greater or lesser extent related to the development of the delthyrial plate.

The continuity of structure between the dental flanges and the delthyrial plate at the apex of the delthyrium is such that it is concluded that they formed at one time as a single structure (fig. 12a). But it is only at this initial stage that they formed simultaneously. At each successive stage the dental flanges formed before the corresponding part of the delthyrial plate, with the result that in the adult the dental flanges extend almost to the teeth whereas the delthyrial plate only partly covers the delthyrium. The anterior growth of the delthyrial plate lags behind the advance of the dental flanges.

These conclusions on the difference in anterior growth rate of the dental flanges and delthyrial plate based/

based on the relative development of these structures in the adult are supported by a study of the internal structures of the plates themselves. It has been shown (p.40) how the delthyrial plate by successive stages becomes separated from the dental flanges. It is concluded that this gradual isolation of the dental flanges reflects the steadily increasing time lag between the formation of the dental flanges and the delthyrial plate. Certainly, anteriorly there is considerable deposition around the core of the dental flanges before the formation of the delthyrial plate, which indicates an interval between the initiation of the dental flanges and the formation of the delthyrial plate.

The explanation in terms of the mantle probably is that posteriorly the lateral mantle folds in which the dental flanges are formed are joined together by the anterior growth of the mantle pocket which secretes the delthyrial plate. The mantle forms a continuous sheet covering the inner surface of the valve. This sheet is raised in two folds along the delthyrial margin and folded back into a pocket at the apex of the delthyrium. When this sheet is complete shell material is secreted in a continuous layer around the inner surface of the shell,

over/

over the dental flanges and across the delthyrial plate (fig. 37b). Anteriorly however, the shell material is only continuous from the inner surface to the dental flanges, there being no delthyrial plate. The part of the mantle forming the delthyrial plate advances slowly, with the secretion of the delthyrial plate across the delthyrium some time after the formation of the flanking dental flanges. (fig. 37c)

c) The Development of the Dental Ridges.

The dental ridges are not present quite so close to the apex of the delthyrium as the dental flanges, but as the tooth normally extends beyond the dental flange it is possible that the dental ridges are initiated at much the same time as the dental flanges. The dental ridges are formed within and covered by the same mantle fold which secretes the dental flanges. The thin layer of calcite which extends from the dental flange to cover the surface of the dental ridge (fig. 11b) and fill the groove between these two structures is also deposited by this mantle fold when the tooth ceases to be functional.

d) The Development of the Ventral Septum.

While all the structures just described are forming at the delthyrium the ventral septum is formed by a slight folding of the mantle on the floor of the valve/

valve. The layer of unfolded calcite which is frequently present under the septum shows that the septum does not form until there has been some growth in thickness of the shell (fig. 17b).

e) The Development of the Dental Plates.

When first formed the delthyrial cavity is lined by oblique layer but as the thickening of the shell proceeds normal layer is deposited. With the thickening of the shell the mantle is withdrawn from the umbo, and at the same time the mantle undergoes a change in form. Two invaginations develop in the mantle and within these mantle folds the dental plates are formed. The presence of these mantle folds is deduced from the structure of the dental plates. The dental plates are double structures, each side of a plate being formed by secretion from one side of a fold. The dental plates and the surrounding shell wall increase in thickness with growth and there is a corresponding decrease in the size of the three apical chambers.

Like the ventral septum, the dental plates develop after the thickening of the shell has proceeded to some extent (fig. 25 a.b). Indeed, in some cases growth lines can be traced from the dental plate round the delthyrial/

delthyrial cavity and across the septum (fig. 20d and 23 b,c,d) showing that the dental plates form simultaneously with the septum. In other cases the dental plates form later than the septum and may bury it completely (fig. 23, a).

The relative ages of the dental plates and the other internal structures can be deduced in two ways. In the first place young specimens having dental flanges, dental ridges and a delthyrial plate, as well as a ventral septum, are found to have no dental plates showing that the dental plates are of later formation than any of the other internal structures. In the second place the shell itself records the sequence of events in its formation. If by the growth of the dental plates a structure becomes buried, then the dental plates are of later formation than that structure. If however the shell material of the dental plates forms a continuous layer with the shell material of another structure then these two structures are contemporaneous.

This second principle has already been used to show that the septum and dental plates may form contemporaneously or that the dental plates may form later. The same conclusion is reached about the delthyrial plate. Posteriorly the delthyrial plate is formed before the dental plates but anteriorly they are contemporaneous.

The/

The relation between the dental flanges and the dental plates is more complex. Since the dental plate grows over the dental flange it is clear that it is of later formation. But the dental flange may also be regarded as an early stage in the development of the dental plate - an immature dental plate not sufficiently developed to reach the floor of the valve. However the correspondence between the dental plate and the dental flange is not precise. Posteriorly the dental plates are more widely spaced than the dental flanges (fig. 22c); and anteriorly, while the dental plates frequently develop on top of the dental flanges (figs. 19, 20c, 22b, 16) and splay out along the delthyrium (fig. 24), the dental plates are in some cases more closely spaced than the dental flanges (fig. 20d).

The transformation of the dental flange into the dental plate is not merely a question of a gradual increase in the width of the dental flange until it reaches the floor of the valve. It is an abrupt change. In some specimens the change occurs immediately after a marked pause in growth indicated by a prominent growth line in the shell. (figs. 19, 20d)

As another source of information on the development of/

of the dental plates young specimens may be examined, specimens in which the dental plates are weakly developed. In these the dental flanges are present along the delthyrial margins (fig. 26 d). Posteriorly the inner edges of the dental flanges are concealed by subsequent deposition in the apical cavity and the delthyrium is closed by the delthyrial plate (figs. 26 b,c) but anteriorly, from the stage at which the dental flange develops a turned-over edge, the inner edges of the dental flanges are free and the delthyrium is open (fig. 26 c).

The dental plates in these young specimens are very low ridges which extend, parallel to each other, from the delthyrium across the ceiling of the apical cavity to the floor of the valve (fig. 26 a). At the delthyrium they correspond in width to the free dental flanges, but there is progressively less correspondance as they are traced posteriorly.

The ridges are uniformly low, from which it is concluded that growth begins simultaneously along their length rather than from a point. Though the dental plates extend further along the delthyrium at a later stage, a large part of the length of the dental plate is initiated at one time.

The/

The subsequent growth of the dental plates consists of an increase in height of the ridges to form two complete partitions, an increase in the thickness of the plates and an anterior prolongation of the plates. The direction of anterior growth is dependant on the pre-existing structures. The dental plates continue in parallel fashion as long as the dental flanges are suitably placed to support the dental plates (fig. 21). This means that the dental plates are situated either directly over the cores of the dental flanges or between the cores of the dental flanges and over the outer layers of the flanges. However, anteriorly there is no structure in this position in the delthyrium, especially where the delthyrial plate is not present, and the dental plates follow the direction of the dental flanges and splay out on either side of the delthyrium. The dental plates are here inseparable from the dental flanges. Thus, after their initial formation the dental plates become more closely related to the dental flanges until the two structures become a unity.

A reconstruction of the form of the mantle during the development of the dental plates may be attempted. (fig. 37d) On the initiation of the dental plates there are two parallel invaginations in the mantle in the apical cavity. These/

These are continuous with the mantle folds enveloping the dental flanges, the two folds meeting at a point on the delthyrial margin. Posteriorly from this point there is no mantle fold along the delthyrial margin, for shell deposition in the apical cavity has covered the earlier formed structures. There is only one pair of mantle folds. It appears that at no time during growth are there two separate mantle folds for the formation of dental flanges and dental plates. The fold which secretes the dental flange grows into the fold which secretes the dental plate. Therefore, though the development of dental flange into dental plate is not simply an increase in size the dental flange is in effect an early stage in the development of the dental plate.

ii) THE DEVELOPMENT OF THE BRACHIAL VALVE.

Since the valve is composed very largely of oblique layer it is more difficult to establish the stages of growth in the brachial valve. Some of the early structures are buried within later formed structures and these can be distinguished. Otherwise it is necessary to examine young specimens.

The earliest stage in the development of the brachial valve/

valve which can be seen is one without internal plates, the lamellar and oblique layers forming a slightly convex shell. Growth proceeds with increase in the overall size of the valve and in the thickness of the shell. At the same time the oblique layer fills the umbo and the formation of the cardinalia is initiated.

a) The Development of the Dental Sockets.

The dental sockets, composed entirely of oblique layer are internal structures formed within two mantle folds which extend along the notothyrial margins on the inner surface of the palintrope. They are to be compared with the dental ridges in the pedicle valve.

The only change which takes place in the dental sockets with growth is that the later formed parts are larger than the earlier with deeper sockets and more prominent ridges. There is no indication of successive layers of deposition on the dental sockets so there is apparently no increase in the size of any part of the socket once it is formed. The enveloping shell material bears no relation to the structure of the sockets.

b) The Development of the Crura and the Crural Plates.

There is continuity of structure between
the/

the dental sockets and the crural plates, the fibres of the two merging with each other with no abrupt break. From this it is concluded that the crural plates are formed simultaneously with the dental sockets. They are secreted by the same mantle folds which secrete the dental sockets.

For a similar reason it is concluded that the crura form simultaneously with the adjacent parts of the crural plates. The crura are formed within lobes of the mantle which form as offshoots of the mantle folds enveloping the dental sockets and crural plates. These lobes also secrete the spiralia.

However the earlier-formed descending lamellae of the crura are not preserved and there is no trace of any but the last stage in the development of the spires. Only the crural plates remain as traces of the early formed crural elements. It is concluded that the spires and the descending lamellae are continually resorbed and grown again.

The early formed crural elements are inclined at low angles to the present shell surface whereas the latest are vertical. This does not however reflect any change in the position of the crura during growth, but is merely a/
a/

a reflection of the developing curvature of the valve.

As in the case of the dental sockets the crura do not increase in thickness after formation. The only subsequent growth of shell material around the crura is either part of the cardinal process or else part of the apical infilling. By growth of the shell wall the crural plates may become fused to the floor of the valve. (fig. 28g)

c) The Development of the Cardinal Process.

The cardinal process lies at the apex of the notothyrium where no dental sockets are present. It may therefore be initiated earlier than the dental sockets but it seems more probable that the sockets and cardinal process are of contemporaneous formation, the dental sockets being anterior to the cardinal process. During its subsequent growth the cardinal process extends around the earlier formed but now abandoned dental sockets and crural plates in the posterior part of the notothyrium. In this respect the cardinal process is of later formation.

Unlike the dental sockets and crural plates the cardinal process has a complicated development. The structure is modified during growth. A series of phases in development can/

can be recognised. Since the anterior part of the cardinal process is the most recently formed it shows the youngest stages of development. The posterior part shows the later stages. In this way the development can be traced.

The cardinal process forms as an extension of the oblique layer from the apex of the valve into the notothyrium. At the umbo the structure of the cardinal process is continuous with that of the shell wall (fig. 29a) though clearly defined dorsally by a flexure of the fibres of the oblique layer. Anteriorly the structure of the cardinal process abuts against the dental sockets and crural plates on both sides of the notothyrium. It is concluded that the cardinal process develops simultaneously with the oblique layer of the shell wall but some time later than the dental sockets and crural plates against which it is deposited. The development of the cardinal process is comparable with the development of the delthyrial plate.

As growth proceeds the continuity of structure between the cardinal process and the shell wall is maintained, the shell wall increases in thickness while the cardinal process grows anteriorly. The anterior growth results in the burial of the dental sockets and crural plates within the cardinal process (fig. 30i). First a thin layer is deposited around the convex surface of the dental sockets, then it/

it extends to the crural plates and finally there is complete envelopment of the plates. When this stage is reached the inner part of the cardinal process is in continuity with the lateral parts of the shell wall. Any further deposition leads to the infilling of the apical cavity (fig. 30k). The anterior growth of the cardinal process thus not only results in the closure of the apex of the notothyrium but also results in the smoothing out of the irregularities of the inner surface of the apical region and eventually the infilling of the apical cavity.

As the cardinal process grows anteriorly it increases in width and in depth. The increase in width is achieved by the introduction of additional plates in the cardinal process, while the increase in depth is achieved by the increase in length of these plates. This results in the cardinal process projecting further into the notothyrium.

While the plates of the cardinal process increase in length the hollows between the plates are continually infilled, so that though long plates are present, in no specimen are there deep hollows between the plates. The infilling of the hollows takes place simultaneously with the lengthening of the plates, thus keeping the grooves relatively shallow.

There/

There is one further aspect of the development of the cardinal process. Just as the crural plates and dental sockets are covered internally by the cardinal process, so externally the dental sockets become infilled. The oblique layer which develops in the sockets is in continuity with that filling the grooves on the surface of cardinal process, showing that this outermost layer forms at one time, extending across the notothyrium from one dental socket to the other (fig. 30i). When the sockets are completely infilled the lamellar layer extends across them from the palintrope to the edge of the cardinal process. The posterior part of the sockets is thus hidden both externally and internally.

In summary, the development of the cardinal process consists firstly of the extension of the oblique layer across to the notothyrium and the establishment of the cardinal process between the sockets and crural plates; secondly, the anterior and lateral growth of the cardinal process enveloping the structures on both sides of the notothyrium; thirdly the extension of the plates of the cardinal process and finally the infilling of the grooves on the surface of the cardinal process accompanied by the infilling of the dental sockets on either side of the cardinal process.

In the formation of the cardinal process the mantle extends/

extends from the apex of the valve to the notothyrium and folds back on itself to the floor of the valve. The outer part of this mantle fold is itself highly convoluted, a series of vertical infoldings corresponding with the longitudinal plates of the cardinal process. During growth the mantle is withdrawn from the deeper parts of the cardinal process depositing fibrous calcite between the plates and at the same time lengthening the plates. This is the specialised mantle of the diductor muscle.

On the inner surface the mantle fold enveloping the cardinal process joins together the two mantle folds in which the crural plates are formed and makes a complete lining around the apex of the valve. As the cardinal process grows over the crural plates the mantle folds disappear posteriorly.

On the outer surface the mantle covers the cardinal process and extends laterally over the dental sockets to the edge of the palintrope. With growth this also is modified as the mantle retreats from the dental sockets and the lamellar layer extends to the margin of the cardinal process.

IX. THE ARTICULATION OF THE VALVES

i) THE TEETH AND DENTAL SOCKETS.

The principal articulation is between the teeth and the dental sockets, the two structures being moulded to fit into each other. The tip of each tooth is curved laterally (fig. 10) so that the teeth are directed towards each other on either side of the delthyrium, and it is the curved tips of the teeth which rest in the sockets (fig. 28i). The sockets in their turn fit around the teeth, the socket ridges resting on the inner surface of the teeth. There are two concave surfaces on either side of the tooth, the inner one on which the socket ridge articulates and an outer one on which the dorsal palintrope articulates. These surfaces correspond with the two grooves which define the dental ridge, the outer one along the delthyrial margin and the inner one along the base of the dental flange.

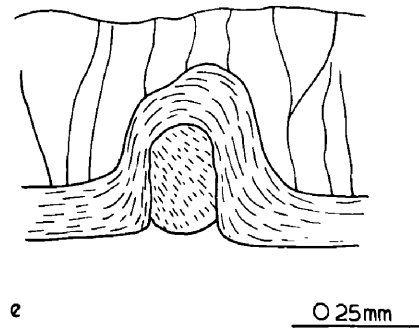
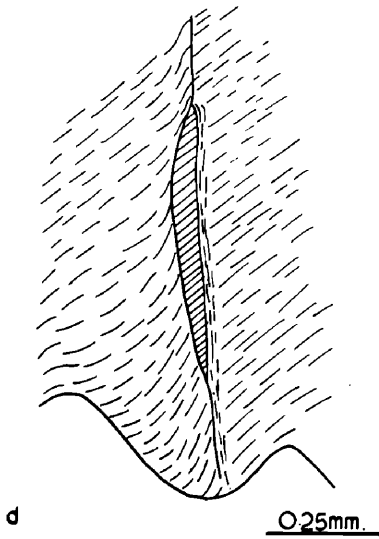
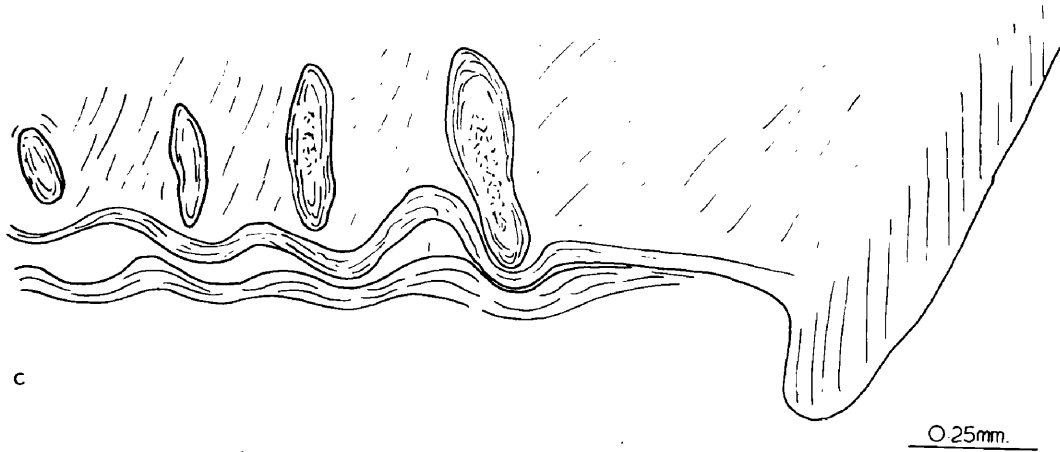
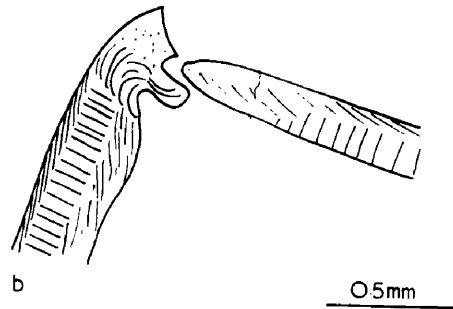
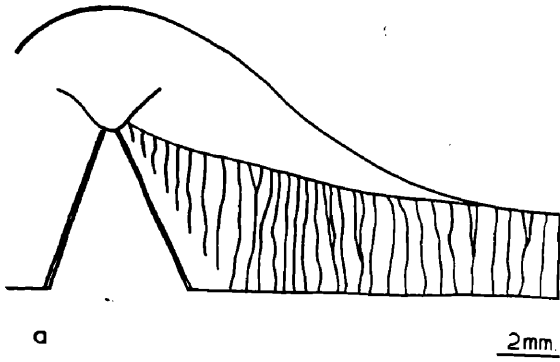
With growth both teeth and sockets are modified. The sockets become infilled with later formed shell material. The teeth on the other hand are partly resorbed. As the shell grows the curved tip of the tooth is continually being resorbed leaving only the part which forms the dental ridge.

ii)/

Fig. 31

Denticles and pits.

- a The ventral inter-area showing the sinuous denticle tracks, occasionally fusing and the area with no denticles bordering the delthyrium.
- b Longitudinal section of a denticle in a pit
- c Oblique section passing through the ventral inter-area and the dorsal palintrope showing oblique sections of four denticles and the four corresponding pits. A tooth is also present
- d Longitudinal section of a denticle enclosed in the substance of the inter-area. The fibres are inclined away from the delthyrium which is to the right of the section.
- e Transverse section of a denticle enclosed in the oblique and normal layer of the inter-area.



ii). THE DENTICLES AND PITS.

Additional articulation is provided by a series of pits and denticles which develop along the length of the hinge. They form on the edge of the interarea, the pits in the brachial valve and the denticles in the pedicle (fig. 31 b,c). In a specimen 35 mm. in width there are about 25 on each side of the delthyrium. The pits and denticles are not normally visible in a complete specimen (pl. VII) but associated with the denticles there are vertical striations on the interarea and these are preserved on most specimens (fig. 31a, pl. VII).

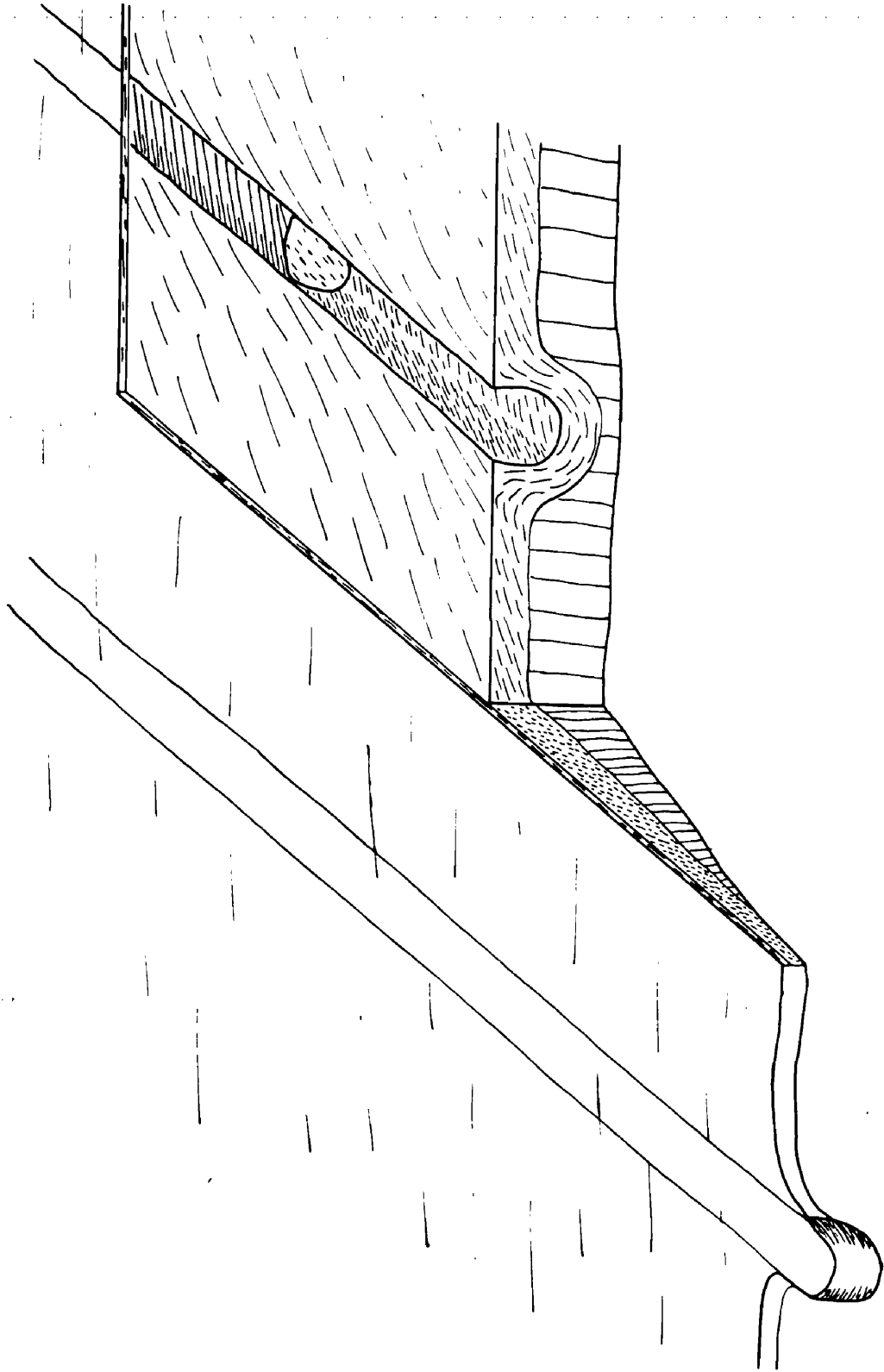
The striations, more or less vertical in direction, are sinuous lines irregularly spaced on the interarea. On either side of the delthyrium there is a band on which no striations are developed. Though essentially vertical the striations are not strictly parallel and adjacent striations may fuse anteriorly. They never split anteriorly.

The striations are related to the denticles for they correspond in position to them, each striation terminating in a denticle. On well preserved specimens there are no striations, the lamellar layer forming a complete sheet over the interarea. Accordingly, the striations either represent/

Fig. 32

A reconstruction of the ventral interarea showing denticles. The lamellar layer is removed from part of the inter-area, to show the fibres of the oblique layer and the denticle enclosed by the oblique layer. The normal layer thins towards the hinge line.

Fig. 32



represent canals just below the surface (Yanishevsky 1935) or the moulds of some rod-like structures which are exposed when the lamellar layer is removed. Young (1884) considered the structures to be formed by recrystallised aragonite.

If the structures were either infilled canals or recrystallised aragonite it might be expected that they would differ in their micro-structure from the rest of the shell. In fact the denticles and the material infilling the striations are composed of fibrous calcite of the oblique layer. The only distinction is in the arrangement of the fibres (fig. 31 d).

A bundle of fibres extends posteriorly from each denticle. The anterior end of the bundle forms the denticle while the remainder is incorporated in the substance of the interarea (fig. 32). The structures are comparable with the dental ridges since they are the successive growth stages of the denticles, the "striations" are no more than the moulds of these denticle tracks.

The denticles are buried with growth by the advancing margin of the interarea. The fibres of the oblique layer of the interarea are orientated across the width of the shell at a distinct angle to the fibres of the denticles (fig. 31 d). They wrap around the inner and lateral surfaces/

surfaces of the denticles, embedding them (fig. 31c).

The outer surface of the denticles is covered by the anterior growth of the lamellar layer on the surface of the interarea.

When the interarea is not too greatly thickened the denticle tracks form ridges on the inner surface. Further thickening obscures these ridges and the inner surface becomes smooth. The shell material immediately covering the denticles is oblique layer but the major part of the thickness is normal layer (fig. 31e).

The pits are negative features. They are formed by the undulations of the fibres of the oblique layer of the dorsal interarea (fig. 31c). Occasionally the track of the pits is preserved on the area as a slight hollow.

The denticles grow by the progressive elongation of the bundles of fibres. The direction of growth remains virtually constant, the denticle tracks being parallel. No explanation can be found for the occasional coalescence of adjacent denticles. As the hinge elongates new denticles form at the margin. The addition of denticles at the extremities is slightly offset by the loss of denticles bordering the delthyrium as that structure increases in width and prevents the further growth of the innermost denticles.

The denticles project into the brachial valve causing undulations/

undulations of the mantle along the hinge line. The pits develop in these mantle grooves.

X. THE MICRO-STRUCTURE OF THE SHELL OF

SPIRIFER BROCKLEYENSIS

It has already been noted that the shell is composed of three types of shell material, the lamellar layer, the oblique layer and the normal layer (fig. 9a). The lamellar layer forms a thin film over the entire surface of the shell, while the oblique layer and normal layer make up the remainder of the shell.

i) THE RELATION OF NORMAL LAYER TO OBLIQUE LAYER.

There is a regular distribution of the two layers. The internal structures are always formed by the same shell layer. The teeth, dental ridges, dental flanges and cardinalia are invariably formed by the oblique layer, while the greater part of both the dental plates and the ventral septum is formed by the normal layer. There is variation in the degree of development of the layers in individual cases but their relative distribution in the apical plates and cardinalia is invariable.

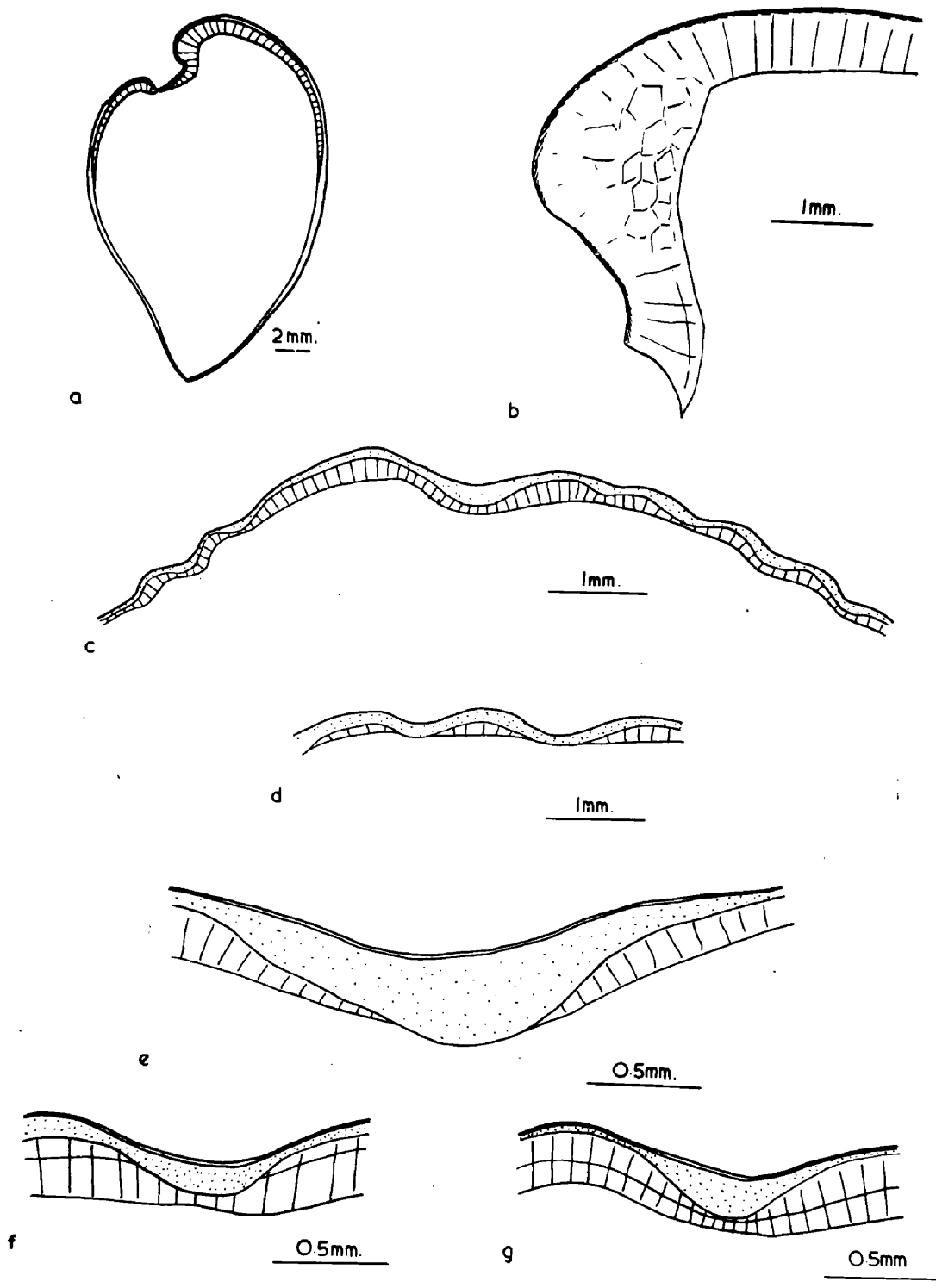
In other parts of the shell there is also a regular distribution of the two layers. Much of the shell is formed by the oblique layer which extends over the whole shell beneath the lamellar layer. At the umbones the oblique layer is thin but it increases in thickness anteriorly.

Absence/

Fig. 33

The normal layer and its relation to the oblique layer.

- a Longitudinal section showing the general distribution of the normal and oblique layers.
- b Longitudinal section of the apex of the ventral valve showing the normal layer of the umbonal infilling.
- c T.S. Normal layer in the posterior part of the pedicle valve of a young individual.
- d T.S. Anterior prolongations of the normal layer in the grooves on the inner surface of the shell, beneath the ribs.
- e T.S. Normal layer flanking the oblique layer of the ventral sulcus.
- f T.S. Normal layer overlapping the oblique layer of the sulcus
- g T.S. Normal layer thinning against, then overlapping the oblique layer of the sulcus.



Absence of the oblique layer from any part is considered to be due to imperfect preservation, for in no case where the lamellar layer is intact is the oblique layer missing. It is most frequently lost at the umbones where there is in any case only a thin layer over the normal layer.

In contrast to the lamellar and oblique layers which are present from umbo to anterior margin, the normal layer is confined to the posterior region (fig. 33 a,b). It is internal to the oblique layer, the two being distinctly defined with no gradation from one to the other. It is concluded that the normal layer forms later than the oblique layer, a distinct break occurring between the secretion of the two layers.

However, normal layer is found in shells which are not fully grown, showing that its development is not merely a late stage, gerontic phenomenon (fig. 33c). Deposition of normal layer is begun when the shell is neanic. In immature specimens the distribution of normal and oblique layers is the same as in the adult shell, the normal layer being confined to the apical part of each valve. Deposition of the two types of shell material occurs concurrently, the oblique layer forming anteriorly while the normal layer is forming posteriorly. Both layers thus increase in areal extent/

extent as the shell grows, but the normal layer never expands to cover the whole of the inner surface of the shell.

The oblique and normal layers also increase in thickness with growth but there is some difference between them in this respect. While the normal layer continues to increase over its whole surface and in the adult becomes so thick that it completely fills the apical cavity, the oblique layer cannot grow in thickness after the normal layer is deposited over it. At all stages of growth the thickest development of oblique layer is found immediately anterior to the area of the normal layer. In the young shell the oblique layer grows to no great thickness before it is covered by normal layer with the result that the oblique layer in the posterior part of the adult is thin, very much thinner than the normal layer of the same part.

The oblique layer, growing anteriorly, parallels the valve margin. Forming immediately under the lamellar layer it reflects all the undulations of the surface of the shell. The ribs and furrows, fold and sulcus are reproduced in the oblique layer. The development of the normal layer is quite different.

The anterior margin of the normal layer is not parallel to the margin of the valve. Long prolongations of the normal layer extend anteriorly along the ribs, separated by/

by the hollows between the ribs which are entirely composed of oblique layer. The result is a smoothing of the undulations on the inner surface of the shell (fig. 33d). It is only when the costal grooves are filled by normal layer that normal layer grows over the intervening ridges and forms a complete sheet on the inner surface of the valve. Subsequent growth of the normal layer is growth in thickness accompanied by further anterior growth along the ribs.

The fold and sulcus can be regarded as larger equivalents of ribs and furrows and as would be expected the fold has a high proportion of normal layer in it whereas the sulcus is formed almost entirely of oblique layer (fig. 33e). The normal layer in the fold extends from the umbo for a considerable distance. The normal layer is present only in the posterior part of the sulcus of the larger specimens and in no part of the sulcus of the smaller specimens.

The mode of growth of the normal layer is well illustrated in the region of the sulcus. The sulcus consists of a ridge of oblique layer flanked by normal layer, which rests on it (fig. 33e). The growth lines show that successive layers terminate against the sulcus (fig. 33f), or even thin out as they approach the sulcus (fig. 33g) until eventually/

Fig. 34

The interlayering of normal and oblique layers.

a L.S. showing two interlayerings of oblique and normal layer

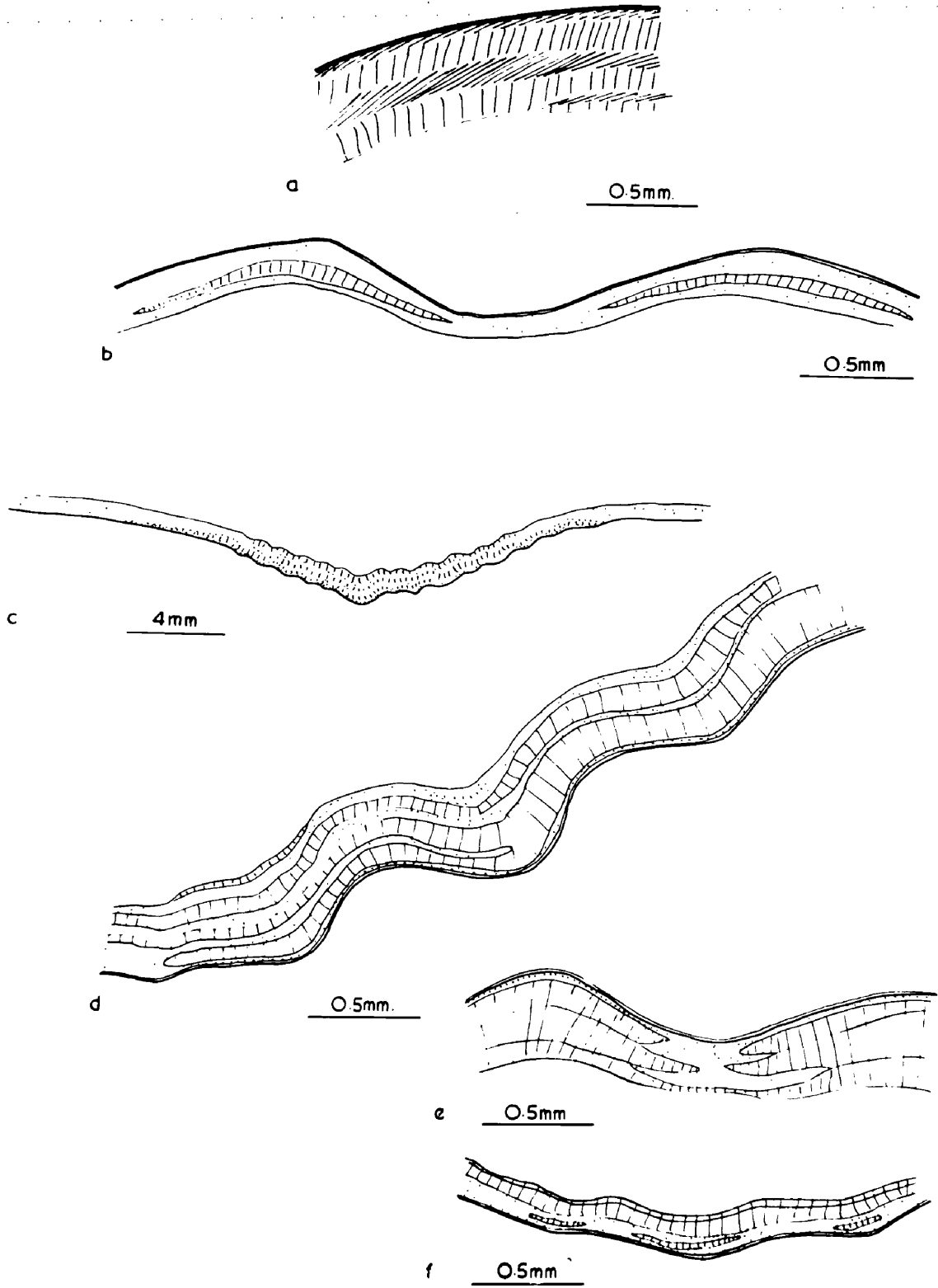
b T.S. showing two "lenticles" of normal layer in oblique layer

c T.S. showing a series of interlayerings

d Enlargement of part of fig. c showing four oblique and four normal layers.

e T.S. of ventral sulcus showing interdigitation of oblique and normal layers

f T.S. of dorsal fold of same specimen showing lenticles of normal layer.



eventually the normal layer reaches the level of the ridge and overlaps the oblique layer completely.

The normal layer thus differs from the oblique layer in its pattern of development. While the shell may be regarded as growing by the deposition first of lamellar layer, then of oblique layer and finally of normal layer, each increasing the thickness of the shell, it should also be recognised that the normal layer is not merely a variant of the oblique layer, a different type of material secreted in the posterior part of the shell at a later stage. The oblique layer conforms to the shape laid out by the lamellar layer, but the normal layer neglects this pattern and fills in the undulations on the inner surface of the shell.

ii) THE INTERLAYERING OF THE NORMAL LAYER AND THE OBLIQUE LAYER.

While the normal layer is usually internal to the oblique layer and can be regarded as secondary, in some cases this is only partly true for the two layers are found interlayered (fig. 34a, pl. XIII a). The sequence of shell layers from the outer surface is then lamellar layer, oblique layer, normal layer, oblique layer, normal layer. The outer normal layer is then secondary with respect to the outer oblique layer but not with respect to the inner oblique layer/

layer.

The interlayering does not extend over the whole shell but is quite limited in extent. It is not however restricted to any one part of the shell and may be found wherever normal layer is present. The limitation in extent is in a longitudinal direction, the interlayering not extending more than 5 mm. There is no limit to its lateral extent. While it may reach from one side of the shell right across to the other (fig. 34c) it may however be incomplete. Fig. 34b shows a specimen in which the normal layer appears only as lenticles in the oblique layer. In this case the inner oblique layer develops in that part of the shell where the normal layer extends anteriorly in the costal grooves, not forming a complete layer over the outer oblique layer.

Several alternations of normal and oblique layer may occur in the one shell (fig. 34d) but this is rare.

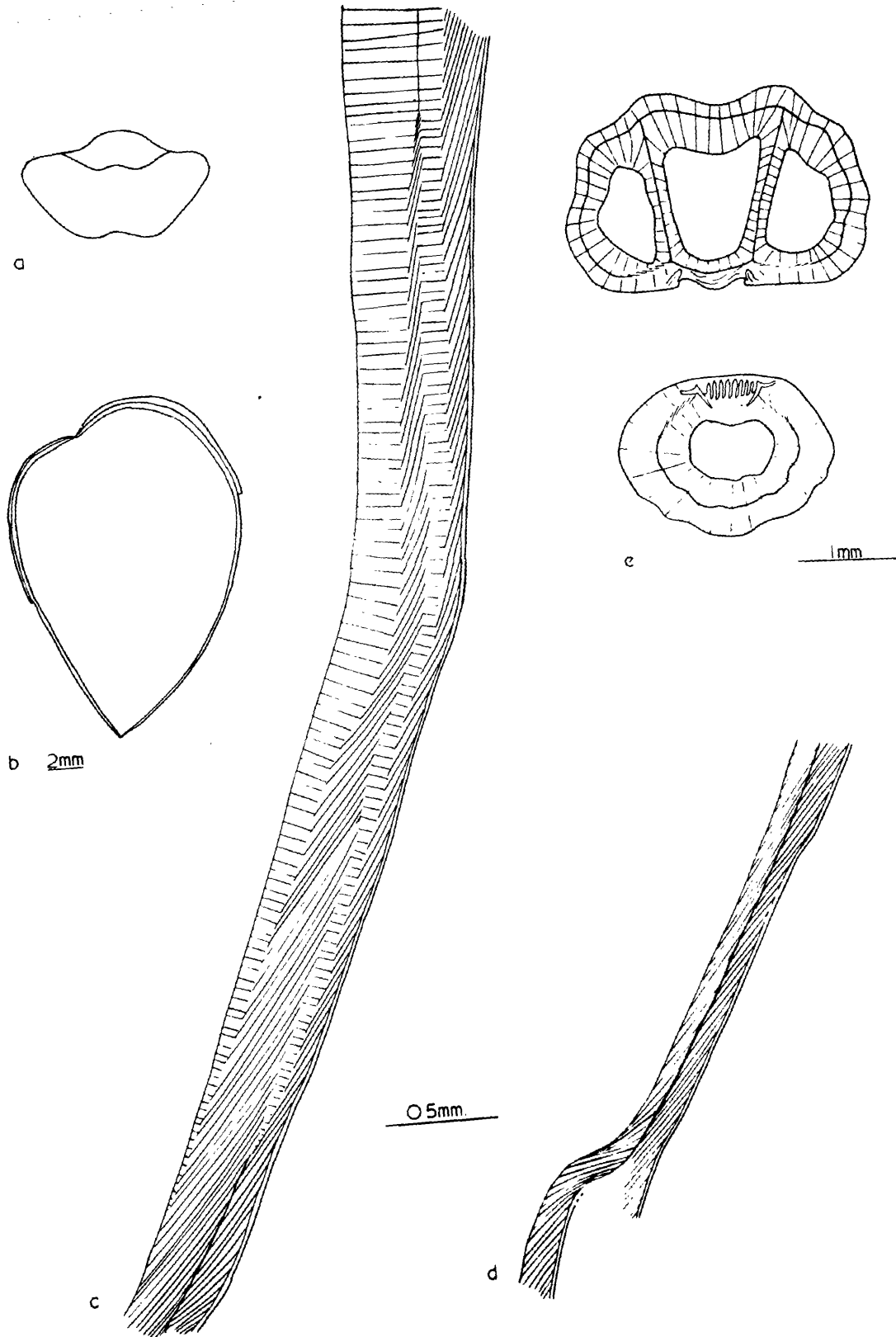
The interlayering of the two types of shell material shows that it is possible for oblique layer to form over normal layer in certain circumstances. The particular circumstances are appreciated when the interlayering is studied in relation to the structure of the other parts of the shell.

Consider the case where two series are present, an outer/

Fig. 35

- a External view of specimen with one prominent growth line.
- b Longitudinal section of this specimen showing the corresponding internal growth line.
- c, d Detail of micro-structure of L.S. showing interlayering of oblique and normal layers, growth lines in normal and oblique layers and the external growth line with the interruption of the lamellar layer.
- e Transverse sections through the apices of both valves showing the growth line in the normal layer and the thin film of oblique layer interlayered with the normal layer in the inter-areas.

Fig. 35



outer and inner normal layer (fig. 35c, and pl. XIII a). When traced posteriorly the inner oblique layer thins out and the outer and inner normal layers are separated only by a growth line. Similarly when traced anteriorly the outer normal layer thins out and the outer and inner oblique layers come together separated only by a surface of discontinuity, a growth line in the oblique layer. When traced further the outer oblique layer dies out giving rise to a step on the profile of the shell. This step is a growth line on the external surface of the shell (fig. 35d).

It is therefore evident that the interlayering of normal and oblique layers is to be correlated with a pause in the growth of the shell. The pause which produces a prominent growth line on the exterior also affects the internal secretion of the shell (fig. 35 a,b).

The specimen from which the section in fig. 35c is cut shows such a growth halt (fig. 35a). The discontinuity of structure produced by the break in growth can be traced as a growth line in the substance of the shell (fig. 35b). Similar interlayering of normal and oblique layers can be recognised in the transverse section of the interareas of both valves (fig. 35e pl. XII b). The pause in growth is thus recorded in all parts of the shell, though in different/

different ways. Three types of modification can be recognised.

The first type occurs posteriorly where the growth pause is recorded as a discontinuity in the normal layer. Immediately anterior to this a thin film of oblique layer may be found along the growth line. This development leads to the second type in which normal layer occurs interlayered with oblique layer. Here normal layer was present before the growth pause but on the resumption of growth oblique layer was deposited. In that part of the shell where no normal layer was present before the pause in growth the third modification is found. Oblique layer is deposited over oblique layer, the surface separating the two being visible in longitudinal section (fig. 35d).

The result of the growth pause is therefore the resumption of the deposition of oblique layer in those areas of the shell posterior to the margin in which oblique layer had already been deposited and in which normal layer may also have been deposited. In the latter case interlayering of normal and oblique layers results.

The pause in growth may occur at any stage and produces different results accordingly. At an early stage normal layer extends across the inner surface of the beak of the pedicle valve, with the exception of the internal ridge of the/
the/

the sulcus. In the brachial valve it is present only in the ribs. A pause in growth at this stage thus produces rather different effects in each valve. In the pedicle valve the pause is marked by a growth line in the normal layer and an extension of the oblique layer from the sulcus to overlap on to the normal layer on either side. The central part of the sulcus is covered by normal layer later (fig. 34e). In the brachial valve the oblique layer deposited after the growth pause rests on the earlier formed oblique layer and on the normal layer of the ribs. A complete cover of normal layer forms later (fig. 34f).

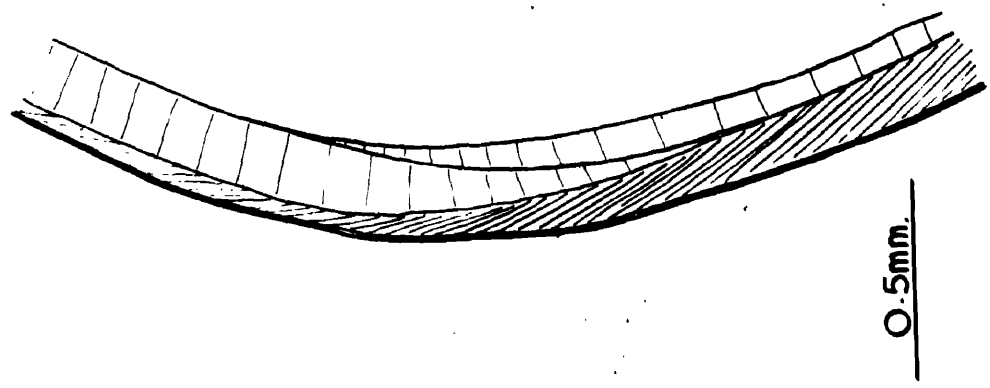
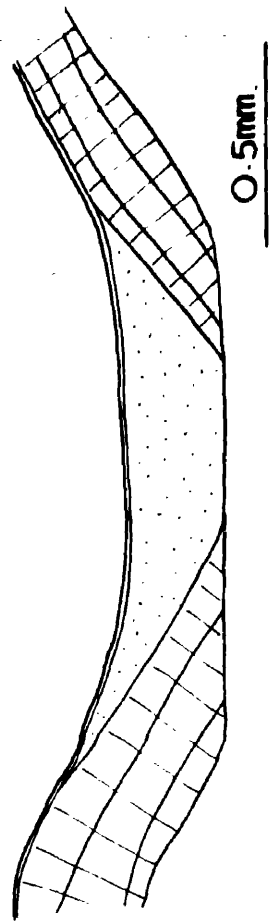
When the growth pause occurs at a later stage a complete layer of normal layer is present in both valves beforehand and then interlayering is present across the complete width of the shell. There will however, be an area anterior to this where the anterior prolongations of the normal layer in the costal grooves form lenticles in the oblique layer.

The late-stage intermittent growth often found in larger specimens does not cause any considerable interlayering. The duplication of the oblique layer close to the anterior margin is usual in this area. Posteriorly these late growth pauses are recorded as growth lines in the/

Fig. 36

- a A film of normal layer thinning out posteriorly, its formation related to muscle attachments.
- b Resorption of normal and oblique layers in the ventral sulcus.

Fig. 36



the normal layer.

There may be several distinct pauses in growth. Each pause is recorded at the beak but only the later ones are recorded in the anterior part. Thus transverse sections cutting through parts of the shell of different ages show a variable number of growth breaks (fig. 34c). The median part is older and shows more pauses than the younger lateral parts.

iii) MUSCLE ATTACHMENT.

In all cases so far described the normal layer has been found to extend anteriorly, from the apex of the umbo. There is an additional development of normal layer, in some cases, in the central part of the inner surface of the valves. This dies out posteriorly as well as anteriorly and is associated with the attachment of the muscles (fig. 36a).

There is also evidence of resorption of shell material on the floor of the pedicle valve in the area of the sulcus (fig. 36b). It may be that this too is related to muscle attachment.

iv) THE MODE OF FORMATION OF THE OBLIQUE LAYER AND THE NORMAL LAYER.

The oblique and normal layers differ greatly in structure/

structure and it has already been shown that they differ in their pattern of development so it seems probable that they are deposited by different parts of the mantle.

Williams (1956 p. 246) shows that the secondary (= oblique) layer forms at the mantle edge and increases in thickness with growth. The secretion of the oblique layer is intracellular. The normal layer, so completely different in structure, cannot be formed in the same manner. Each fibre of the oblique layer has a corresponding epithelial cell. The difference in size of the fibres of the normal layer shows that a modification of the mantle takes place before the secretion of the normal layer. That is to say, the mantle in the posterior part of the shell differs from that in the anterior part of the shell. Williams (1956 p. 250) considers that the normal layer is formed by extracellular secretion as opposed to the intracellular deposition of the oblique layer.

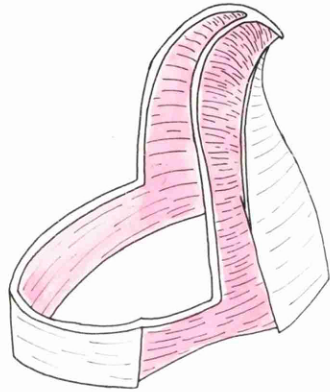
Since the normal layer is confined to the posterior of the shell, it may be that there is some relation between the normal layer and the viscera. Yet in most brachiopods, and even in many spiriferids, no normal layer is developed so a genetic relation between viscera and normal layer seems improbable.

The/

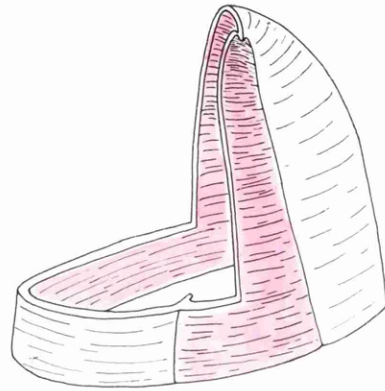
Fig. 37 Reconstructions of the apex of the pedicle valve.

The mantle is shown coloured pink.

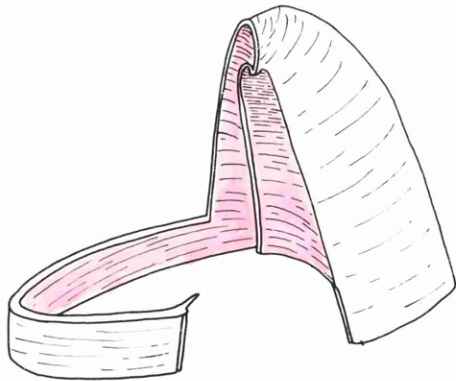
- a The delthyrial plate arising from the floor of the valve.
- b The dental flanges developing in two mantle folds on either side of the delthyrial plate.
- c the dental flanges growing along the delthyrial margins in advance of the delthyrial plate.
- d The initiation of the dental plates as two low ridges in the apex of the valve.



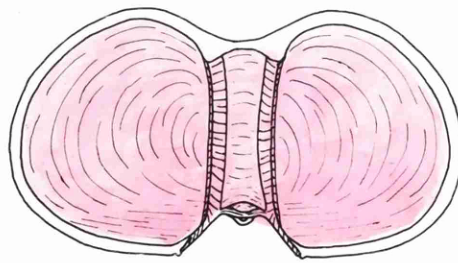
a



b



c

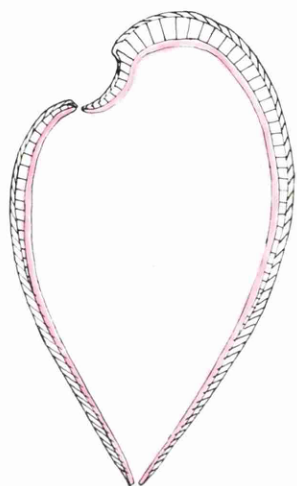


d

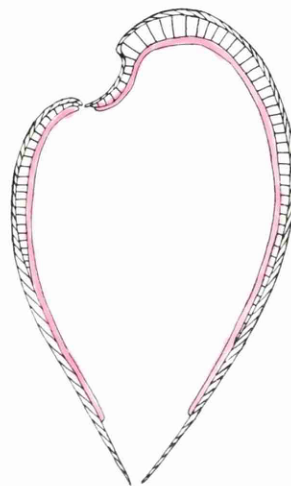
Fig. 38. The development of interlayering in the shell.

The mantle is shown in pink.

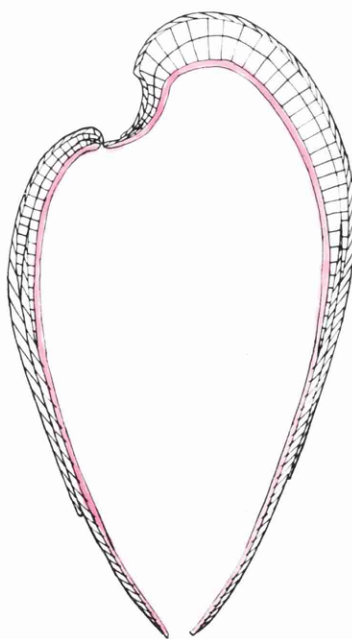
- a The shell before a growth halt, the mantle is in its normal position.
- b The shell during a growth halt, the mantle is retracted.
- c The shell after a growth halt, interlayering present in the shell, the mantle normal again.



d



b



c

The mantle which secretes the oblique layer appears to be different from the mantle which secretes the normal layer. The mantle is modified posteriorly. Yet the interlayering of the two shell layers appears to suggest that the same part of the mantle secretes both types of material. If this were so, the mantle would be required to change in structure repeatedly to give the complex interlayering of the shell. The interlayering, however, only develops after a growth halt and the deposition of oblique layer on normal layer would appear to result from a contraction of the mantle which brings that part of the mantle responsible for the secretion of oblique layer over an area in which normal layer was deposited before the growth halt. (fig. 38)

Since the secretion of the oblique layer is intracellular a contraction of the mantle of the type envisaged would cause disruption of the epithelial cells. This is apparently borne out by the complete lack of correspondence of the fibres of the oblique layer across the growth line (fig. 35d).

In a similar way, the extracellular secretion of the normal layer is demonstrated by the continuity of crystal structure across the growth lines of the normal layer (pl. XI b)/

(pl. XI b). It does not imply absence of contraction of the mantle in the posterior region, since the crystals would develop in optical continuity even if the mantle had moved as long as secretion is extracellular.

The amount of contraction of the mantle is variable depending probably on the duration of the growth pause. The amount of contraction is measured by the length of the zone of interlayering which it produces. It does not exceed 5 mm.

It is not known whether the retraction of the mantle so affects the epithelial cells that they are incapable of further secretion. If this were so, the contraction of the mantle would not be measured by the length of the zone of interlayering alone. The contraction would have to be sufficient to bring the generative zone, close to the edge of the mantle, into the shell in a position corresponding to the posterior end of the inner oblique layer - a contraction of 8 mm.

It is concluded that the oblique layer and normal layer differ in their mode of formation and that there is a corresponding difference in the structure of the mantle which deposits the two layers. The initial shell growth on the inner surface of the lamellar layer is of oblique layer/

layer while the secondary thickening of the shell is of normal layer. The oblique layer therefore is the deposit of the advancing mantle while the normal layer is the deposit of the static one.

XI. ACKNOWLEDGEMENTS

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Plate I

Spirifer brockleyensis

Holotype

a dorsal view

b ventral "

c posterior "

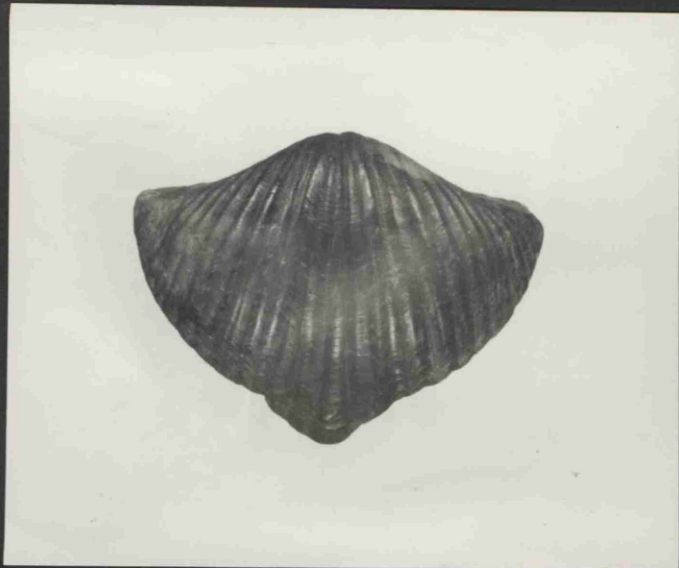
d anterior "

e side "

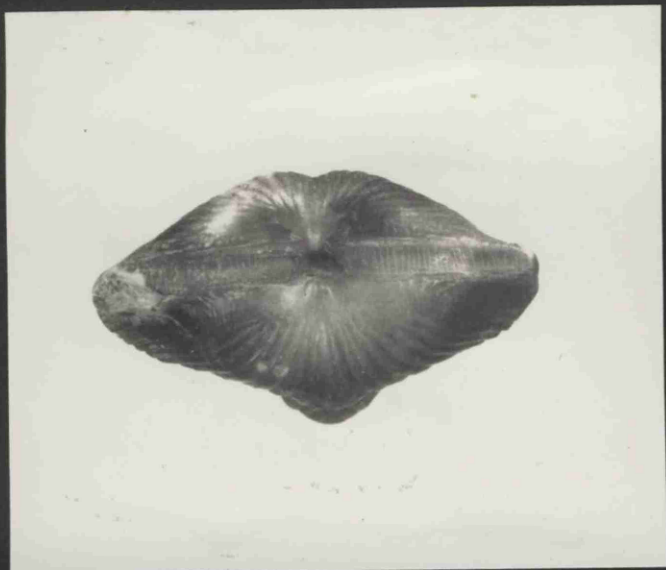
All $1\frac{1}{2}$ times
natural size



a



b



c



d

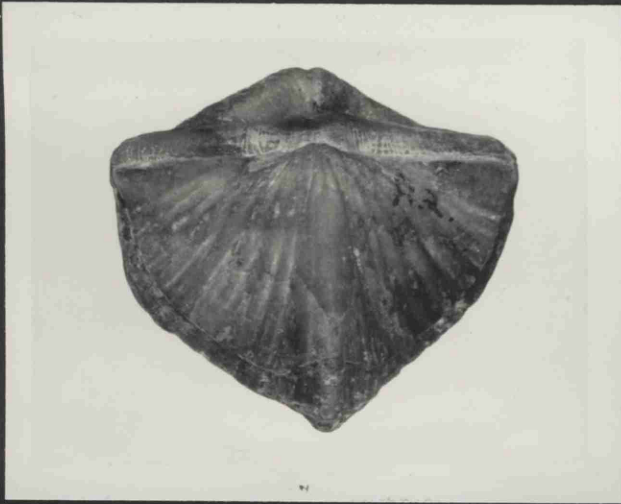


e

Plate II

Spirifer brockleyensis

- | | | | |
|---|-------------|-------------|--------------------------|
| a | Specimen AI | dorsal view | |
| b | " | " ventral " | |
| c | " | " side " | All $1\frac{1}{2}$ times |
| d | Specimen A7 | dorsal view | natural size |
| e | " | " ventral " | |
| f | " | " side " | |



a



b



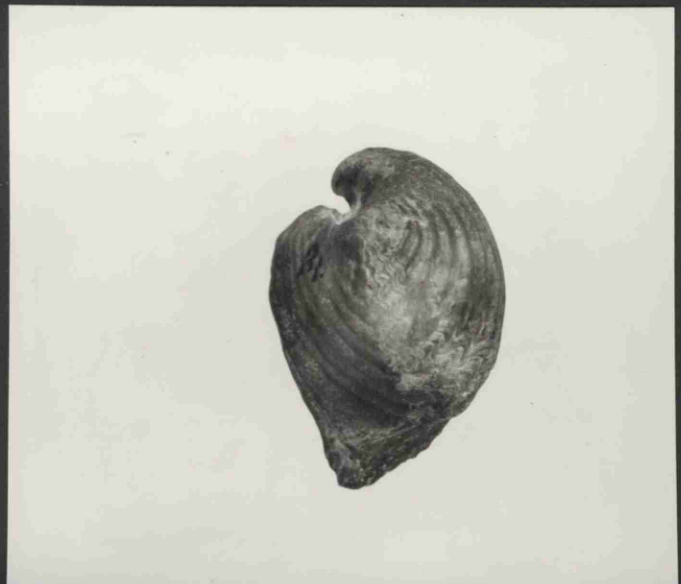
c



d



e



f

Plate III Spirifer brockleyensis

a	Specimen	B1	dorsal view	
b	"	"	ventral "	
c	"	"	side "	All $1\frac{1}{2}$ times
d	Specimen	C2	dorsal view	natural size
e	"	"	ventral "	
f	"	"	side "	



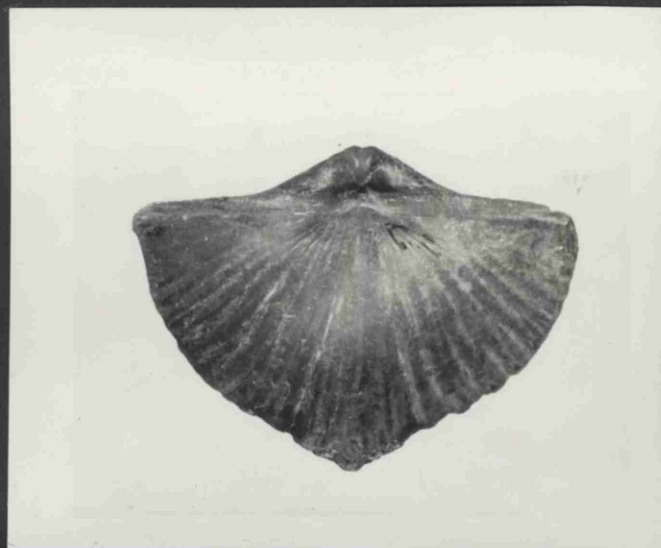
a



b



c



d



e

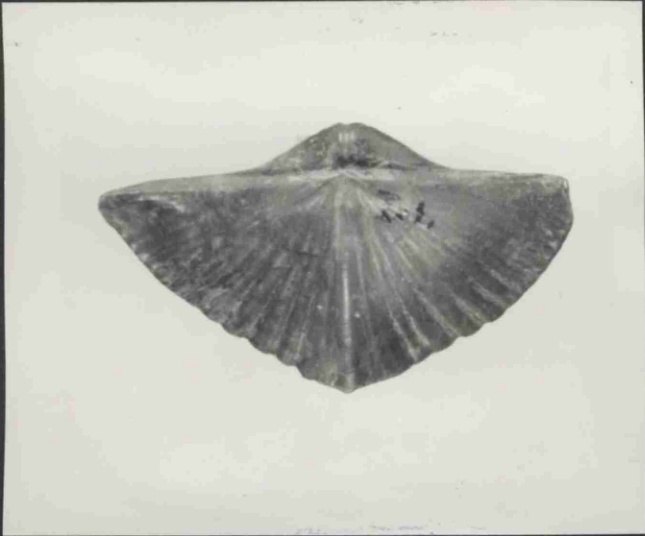


f

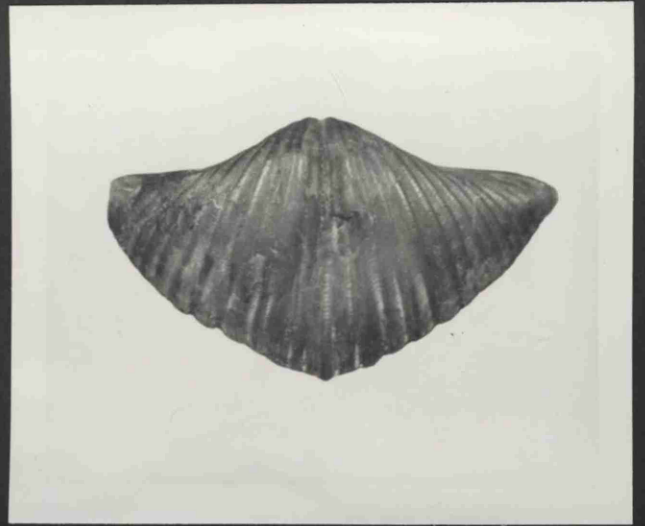
Plate IV

Sprifier brockleyensis

- | | | | | |
|---|----------|----|-------------|----------------------------|
| a | Specimen | D1 | dorsal view | |
| b | " | " | ventral | " |
| c | " | " | side | " all $1\frac{1}{2}$ times |
| d | Specimen | F1 | dorsal view | natural size |
| e | " | " | ventral | " |
| f | " | " | side | " |



a



b



c



d



e

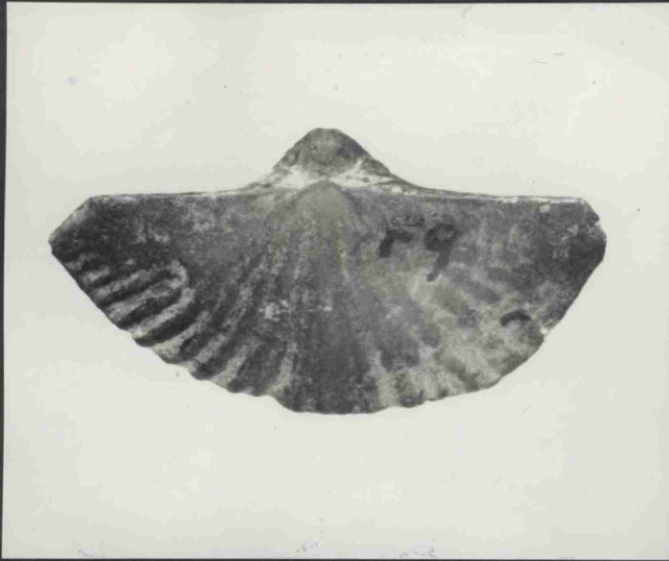


f

Plate V

Spirifer brockleyensis

- | | | | | |
|---|----------|----|-------------|---------------|
| a | Specimen | F9 | dorsal view | |
| b | " | " | ventral | " |
| c | " | " | side | " All 3 times |
| d | Specimen | I2 | dorsal view | natural size |
| e | " | " | ventral | " |
| f | " | " | side | " |



a



b



c



d



e



f

Plate VI

Spirifer brockleyensis

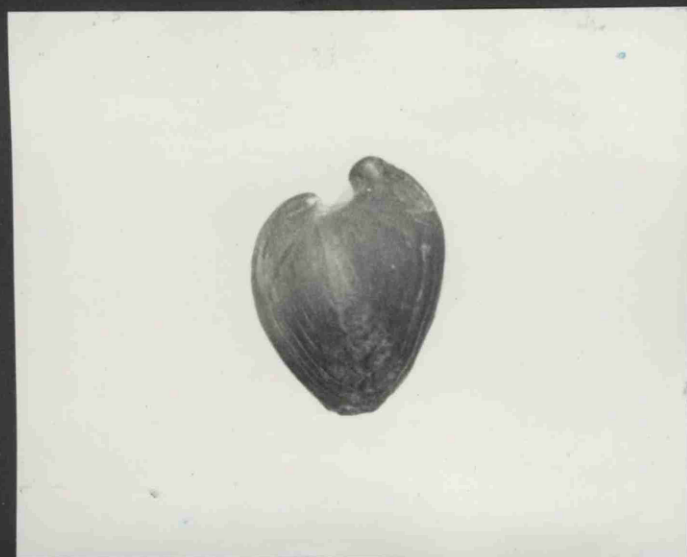
a	Specimen	G13	dorsal view	
b	"	"	ventral	"
c	"	"	side	" All 3 times
d	Specimen	G19	dorsal	" natural size
e	"	"	ventral	"
f	"	"	side	"



a



b



c



d



e



f

Plate VII

Spirifer brockleyensis

- a Specimen J1 dorsal view
- b " " ventral "
both showing prominent growth lines
- c Specimen K5 posterior view
showing denticles on hinge line
- d Specimen B2 posterior view
showing striations on inter-area
- e Specimen F3 ventral view
showing many fine growth lines
- f Specimen A3
showing fine longitudinal striations
on median rib of sulcus

All ~~1~~ times natural size.



a



b



c



d



e



f

Plate VIII

Photograph of cellulose peel showing detail
of the micro-structure of shell; oblique
and normal layers cf. fig. 25a. X50

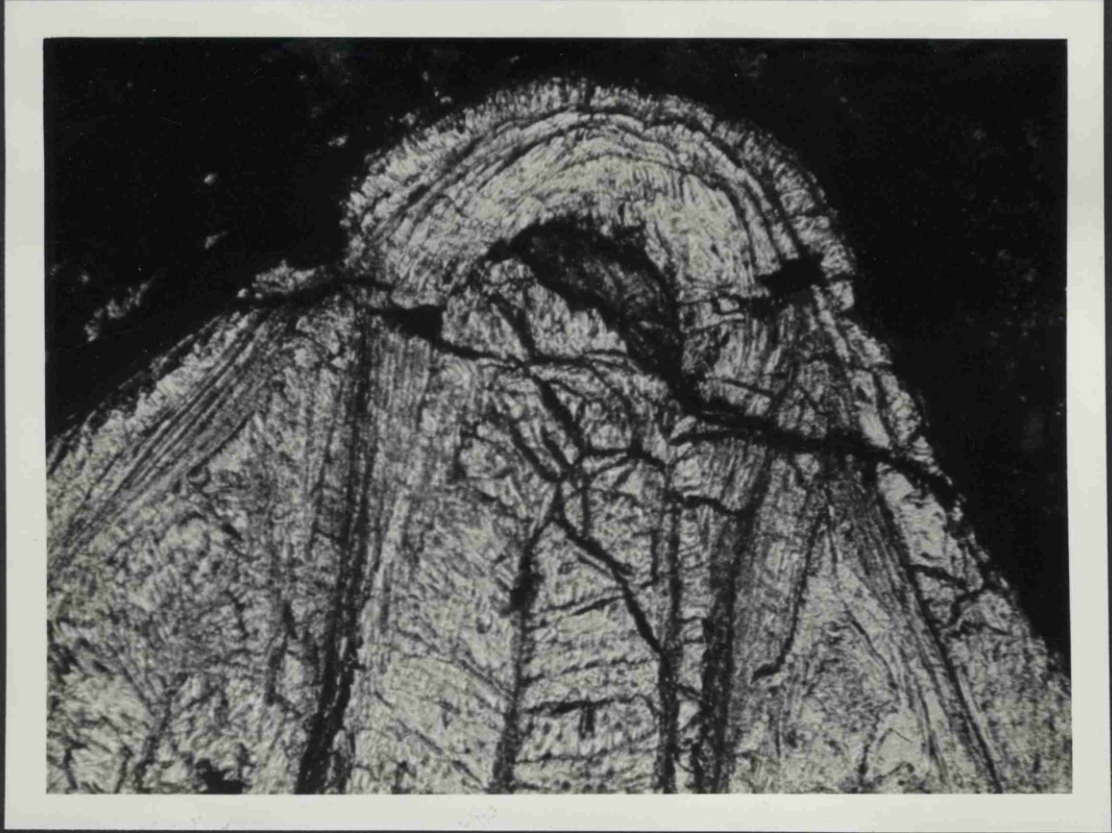
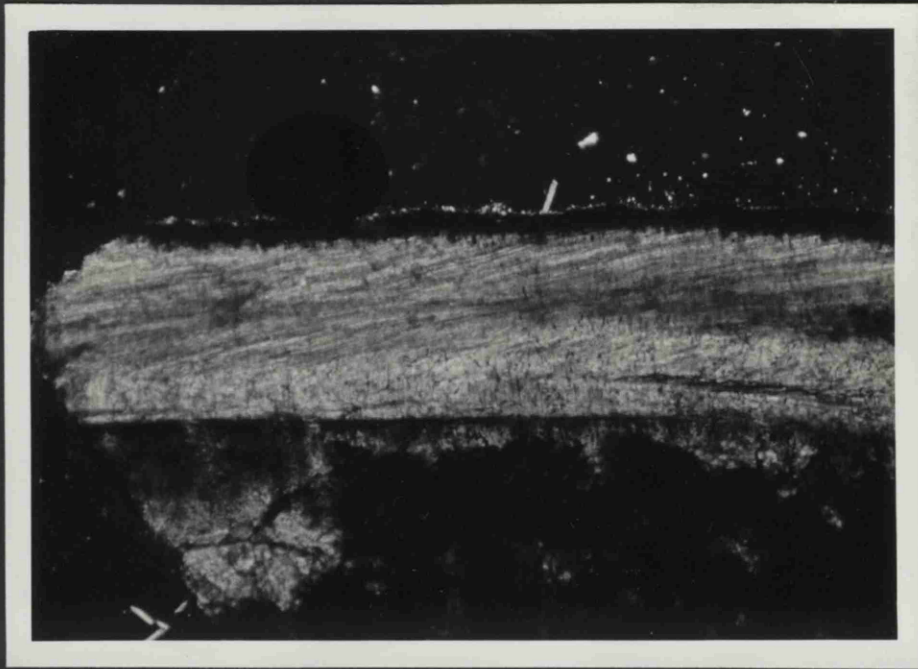


Plate IX

a L.S. Oblique layer

X45

b L.S. Oblique layer with two interlayerings
of normal layer. Lamellar layer on
external surface. X35



d



b

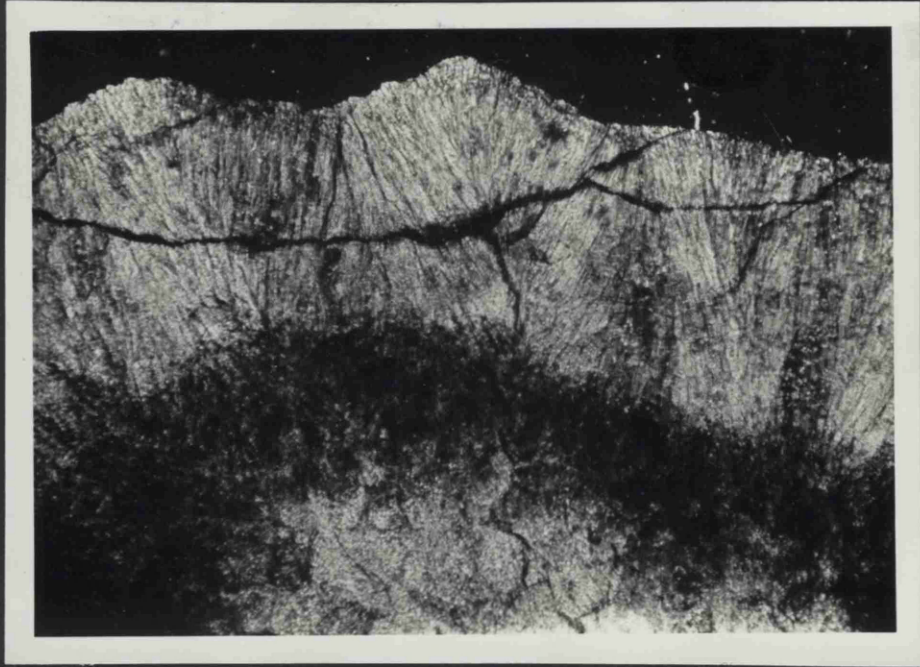
Plate X

a T.S. Normal layer

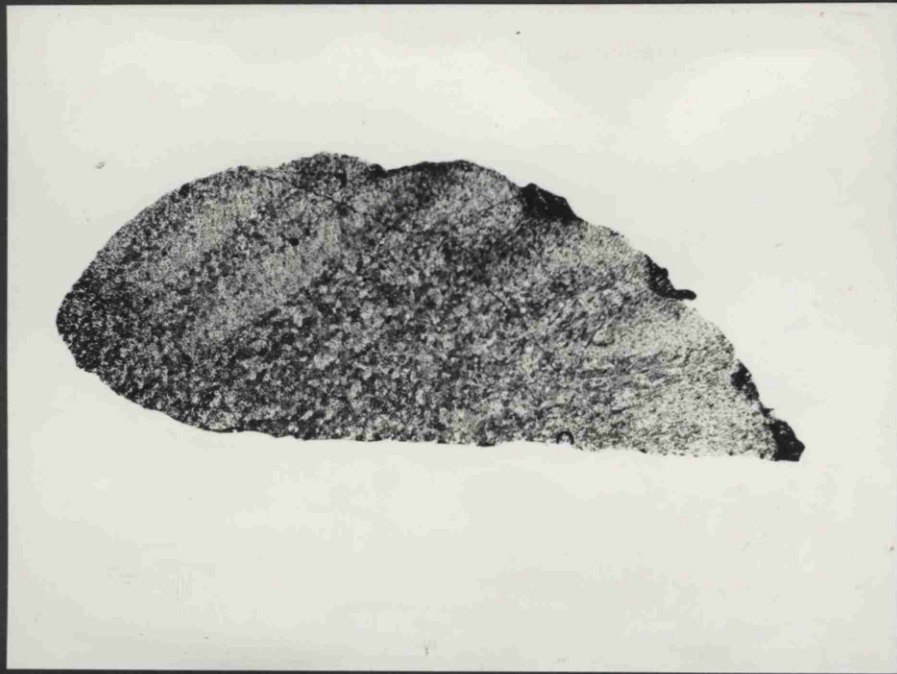
X33

b Tangential section - Normal layer

X11

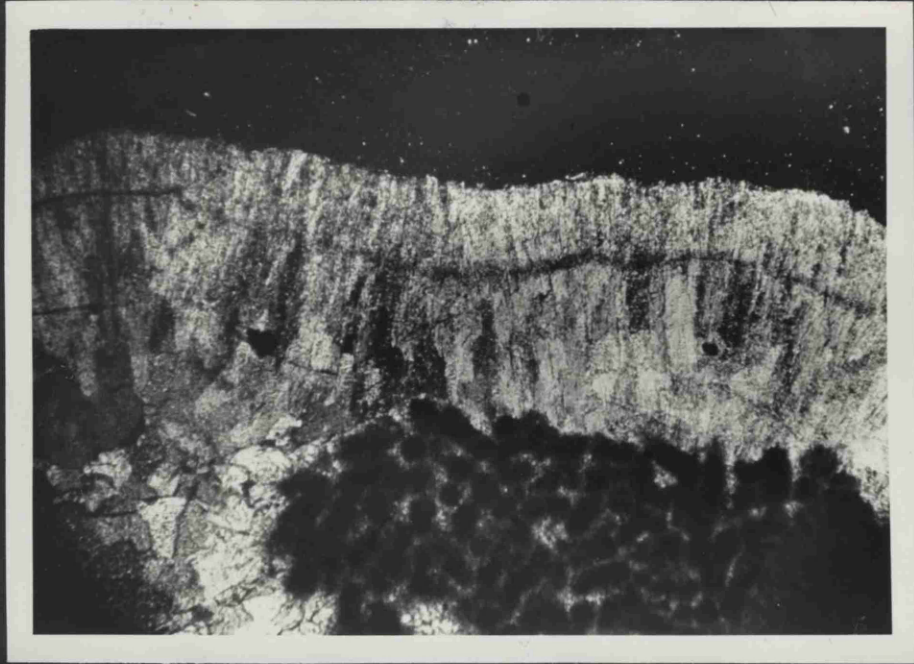


a

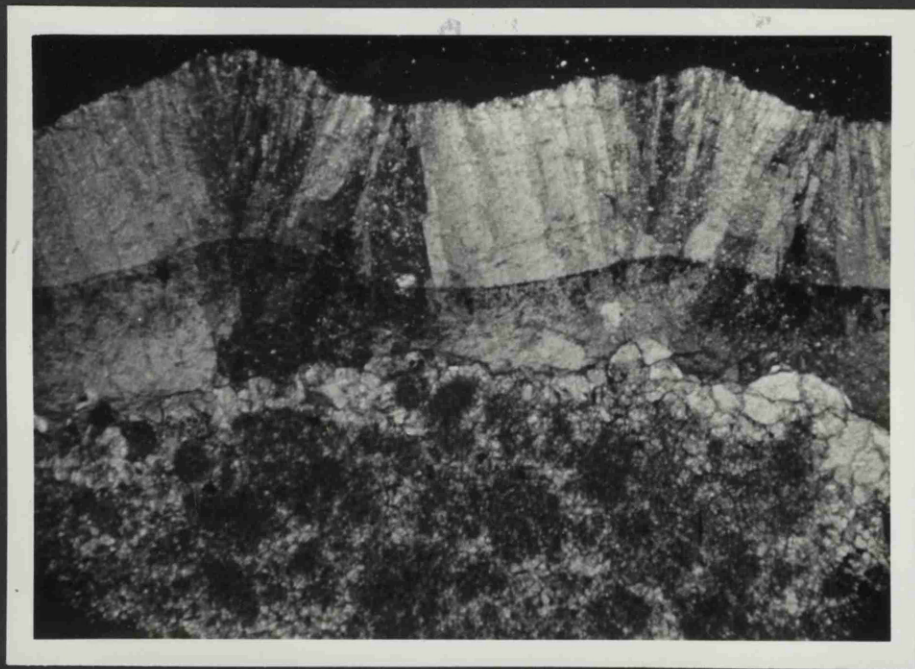


b

Plate XI a L.S. Normal layer with growth line X35
 b T.S. Normal layer with growth line X35



a



b

Plate XII

- a L.S. Ventral inter-area showing lamellar,
oblique and normal layers X40
- b T.S. Ventral inter-area with dental flange
delthyrial plate and dental plates X



a



b

Plate XIII

- a L.S. Lamellar layer on exterior. Two inter-layered series of oblique and normal layers X40
- b L.S. Lamellar layer on exterior, interrupted at external growth line. Oblique layers showing internal growth line. X25



d



b