NOTES ON AN ORDOVICIAN ACROTRETACEAN BRACHIOPOD FROM THE OSLO REGION

VALDEMAR POULSEN

Pedicle valves of an unusual acrotretacean brachiopod from the Lower and Middle Ordovician of the Oslo region, Norway, are described with regard to morphology and shell structure. It is concluded that the inner layers, secreted at a late stage by the cells in the outer epithelium, are structurally different from the layers secreted by the same cells at an early stage when they were part of the proliferation zone. The unnamed acrotretacean is so far only known from two widely separated stratigraphical levels. A statistical evaluation of the material shows a significant difference between the early and late representatives.

The early Ordovician Ceratopyge Limestone (3aα) at Slemmestad, south of Oslo, contains numerous specimens of a very conspicuous acrotretacean brachiopod. The unusually high pedicle valves are mostly well preserved and show interesting structures in the apical region. Specimens were obtained by dissolving samples of the limestone in acetic acid followed by ultrasonic cleaning.

Dr Geörgy Hamar, Geological Institute, Blindern, Oslo, has found the same type of valve both in the Ceratopyge-Limestone and in the Middle Ordovician Ampyx Limestone (4aβ). The Middle Ordovician specimens are very similar in structure, but the pedicle valves are considerably lower than the ones from the Ceratopyge Limestone. In Hamar's opinion it is possible that the material known to date represents the first and last stage in an evolutionary line characterized by a gradual decrease in height of the pedicle valves.

If a gradual evolution can be ascertained, a simple biometric technique might eventually serve biostratigraphical purposes, thereby supplementing the evidence of conodonts and other fossil groups. Therefore the material has been tested statistically and a significant difference between early and late representatives has been found.

When the author became interested in the acrotretacean shell structure per se Dr Hamar kindly lent his material for study. A complete systematic treatment and discussion of the affinities of the acrotretacean will be pub-

lished by Hamar when sufficient material has been collected. Additional material, including the unknown brachial valves, and preferably from levels between the Ceratopyge Limestone and the Ampyx Limestone, is needed.

The electron micrographs were made in a Cambridge Stereoscan scanning electron microscope housed in the Geological Institutes of the University of Copenhagen.

Description of the pedicle valve

The pedicle valve is very minute, less than 2.0 mm high, acutely curviconical, with differential growth in anterior and posterior directions along the median axis. Due to mixoperipheral growth the pseudointerarea is procline, almost catacline in the early stages, whereas it is slightly apsacline in the adult stage.

Pseudointerarea is weakly developed, almost unmodified, as proparea and intertrough are absent; the only distinguishing character is a slight flattening which may be observed in the early stages. The pseudointerarea gradually becomes convex in later stages, so that the cross-section of the adult pedicle valve is almost perfectly circular.

The beak is nearly straight with a beak angle slightly above 20°. Pedicle opening is circular, situated in a collar-like extension of apex. If the pedicle opening has ever intersected the posterior margin, as in juvenile *Acrothele,* it must have been at a very early stage, and the posterior sector of the mantle almost immediately secreted shell material to form the non-indented ventral pseudointerarea.

Umbo is well defined; even at a fairly low magnification a more pronounced curvature of the ventral umbonal slope is quite conspicuous in many specimens. At higher magnifications the umbo is distinguished by a markedly scrobiculate surface which is absent in the adult stage.

The scrobiculation is formed by numerous, closely situated, almost perfectly round shallow pits with diameters ranging from 1 to 2.5μ. Irregularly spaced and smaller pits with diameters below 0.5μ are situated in the ridges separating the larger pits (plate 2, fig. 1B). The brachiopod protegulum is usually described as being smooth, but in this case the scrobiculation is quite distinct all the way up to the pedicle opening.

Several specimens show a marked constriction in the umbonal pseudointerarea at the boundary to the adult shell. Close to the constriction the scrobiculation tends to become effaced.

Biernat & Williams (1970) have observed a very similar structure in the protegulum of other acrotretaceans. They interpret the structure as moulds of a thin, highly vesicular periostracum. The absence of pits in the adult shell supposedly is due to the development of a thicker inner sealing membrane, masking the vesicular nature of the adult periostracum.

The surface of the adult shell is distinguished by closely situated growth lines which are slightly irregular. At inconstant intervals single growth lines may be more prominent.

Structure of the pedicle valve

Different sections were made in order to study the structure of the valves. Longitudinal sections to be studied under optical microscope and scanning electron microscope were made by a method developed by Hansen (1967). A valve is embedded in Lakeside 70 cement and ground to the median level through the umbo. The grinding is carried out under a binocular microscope using small frosted glass plates, with water as lubricant. In this way the continual change of level may be kept under constant surveillance.

Sectioned specimens to be studied under scanning electron microscope are then etched with a saturated aqueous solution of EDTA (ethylene-diamin-tetra-acetate) for three minutes. Specimens for optical microscope studies are ground to a level slightly above the median plane through the umbo and then turned over with the point of a heated needle. The grinding is continued from the other side until a suitable thickness is achieved.

The remaining part of the preparation of sections or entire specimens follows standard procedure.

Scanning electron micrographs (plate 5, figs. 1A–B) show that the pedicle valves consist of an outer layer and several inner layers which are structurally different from the outer layer.

Outer layer

The shell of phosphatic inarticulate brachiopods comprises a periostracum and irregularly alternating layers of calcium phosphate and organic material (chitin and protein).

The periostracum is secreted by a limited number of cells in the periostracal groove which is situated in the inner epithelium at some distance from the tip of the outer mantle lobe, see fig. 1B.

A

← PHOSPHATIC LAYER

← ORGANIC LAYER

B

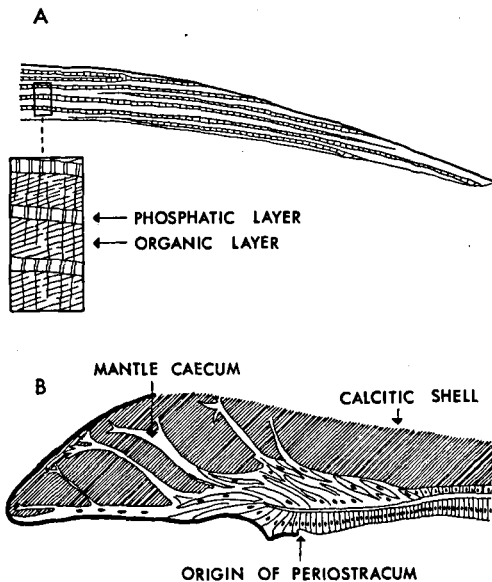MANTLE CAECUM

CALCITIC SHELL

ORIGIN OF PERIOSTRACUM

Fig. 1. A: Diagrammatic section through the brachial valve of recent *Lingula* showing punctae in organic and phosphatic layers (slightly modified after Williams & Rowell, 1965). B: Section through the mantle margin in recent *Crania* showing mantle caeca (modified after Blochmann, 1892).

At the tip of the lobe a physiological change occurs within the migrating epithelial cells, and alternating phosphatic and organic layers are deposited instead of the periostracum. The ability of the cells of the outer epithelium to secrete either organic or phosphatic material possibly reflects the response of the outer epithelium to some unknown physiological requirements of the animal. The thickness of the shell layers is governed by the number of cells involved in secretion at the mantle adge.

Several specimens from the Ampyx Limestone (plate 2, figs. 3–4) have suffered natural abrasion in such a way that the fabric of the shell may be studied. It appears that the outer layer of the pedicle valve consists of hollow, very closely situated tubes with rectangular cross-sections. Normally one would expect the tubes to be filled up with phosphatic material during diagenesis, but this has not happened in the present case.

The tubular structure of the outer layer was possibly dependent upon the shape of the secretory cells in the proliferation zone of the outer epithelium. An alternation of larger (higher) and smaller cells might result in the observed structure, if calcium phosphate was secreted along the entire free periphery of the larger cells, and organic material in a narrow strip on the free upper surface of the intervening smaller cells.

Inner layers

The major part of the interior of the pedicle valves may be occupied by secondarily formed layers which are structurally different from the outer layer.

Scanning electron micrographs (plate 5) show thin, widely spaced phosphatic lamellae. They are connected by a large number of round "pillars" at right angles to the lamellae. The transverse lamellae are more closely spaced laterally, turning forwards and becoming almost parallel to the outer layer which is smoothly joined by the lamellae. Mesially the lamellae turn in posterior direction and join to form a wide pedicle tube.

In recent *Lingula* the phosphatic shell bands are traversed by punctae which, due to their small diameter, probably represent cytoplasmic strands rather than mantle caeca as in *Crania*, see fig. 1.

The punctae are very conspicuous in the phosphatic bands in the lingulid shell, whereas they are almost invisible in the organic bands. Comparable structures are known in a few other inarticulate brachiopods and were most likely widespread among extinct groups.

The thin phosphatic inner layers in the author's material from pedicle valves cannot represent anything but primary phosphatic bands, and accordingly the empty spaces between the phosphatic bands may be interpreted as the sites of former organic bands. The "pillars", which connect the individual phosphatic bands, are here regarded as phosphatic moulds of punctae originally present in the organic bands.

Thin sections of *Acrotreta socialis* v. Seebach from the early Middle Cambrian of Bornholm (plate 7) show a very similar structure, but in this case the wide bands consist of phosphatic material which has a strongly fibrous fabric, the fibres being almost normal to the thin intervening phosphatic bands.

The fibrous layers have previously been regarded as primary phosphatic bands separated by thin organic layers without a fibrous structure. The Norwegian material indicates that the thin bands, on the contrary, are the original phosphatic bands, and that the organic bands constituted the bulk of the inner layers.

The first step in the diagenesis must have been the deposition of calcium phosphate in the punctae of the organic layers; subsequently the organic material was decomposed and carried away in solution. The disappearance of organic material was not followed by any noticeable precipitation of calcium phosphate or deposition of sediment from the embedding matrix. The space between the phosphatic bands must have been effectively sealed off along the outer layer and the pedicle tube by a final precipitation of calcium phosphate in punctae or in other openings in the primary phosphatic parts of the shell.

However, it cannot be excluded that the "pillars" represent a primary structure deposited to reinforce the widely spaced phosphatic bands.

Shell growth in the adult stage

Increase in height of the pedicle valve was accomplished by addition of material to the outer layer along the entire anterior periphery of the shell. The zone of proliferation was situated on the external side of the outer mantle lobe just behind the tip of the lobe. Layers of organic material were quite subordinate compared to the phosphatic layers.

Migration of the epithelial cells according to a "conveyor-belt" system resulted in an increasingly posterior position of cells which no longer belonged to the proliferation zone. Simultaneously these cells became "dormant". At a later stage the forward migration of the soft parts was accompanied by reactivation of the "dormant" cells of the outer epithelium which secreted the partitions in the posterior part of the shell. By then the secretory behaviour of these cells had changed considerably, the organic bands being predominant.

Material

The pedicle valves from the Lower Ordovician Ceratopyge Limestone (about 30 specimens) are in most respects identical to those from the Middle Ordovician Ampyx Limestone (about 20 specimens), the only verified difference being the height:diameter ratios.

Despite the fact that at present representatives are unknown from intervening stratigraphical levels, there can be no doubt that the late population descended from the stock in the Ceratopyge Limestone. Common acrotretacean genera are associated with both populations and are known from other parts of the Ordovician sequence (see for instance Brögger, 1882). It is possible that the origination of an anomalous acrotretacean is to be regarded as the response to a drastic change in the environment, as indicated by the lithology of the Ceratopyge Limestone.

Corresponding brachial valves have not been identified.

Figured specimens are in the type collection of the Mineralogical Museum of the University of Copenhagen.

Measurements

Types of growth representing transitions between holoperipheral and mixoperipheral patterns are common among some inarticulate brachiopods. How-

Fig. 2. Enlarged outline drawings of two acrotretacean pedicle valves. A: specimen from the Ceratopyge Limestone. B: Specimen from the Ampyx Limestone. Arrows show series of height:diameter measurements.
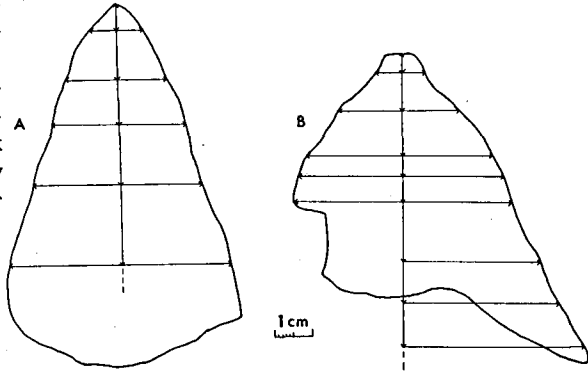
ever, the acrotretacean pedicle valves described in the present paper are unusually high and therefore an analysis of the relative growth rates was carried out.

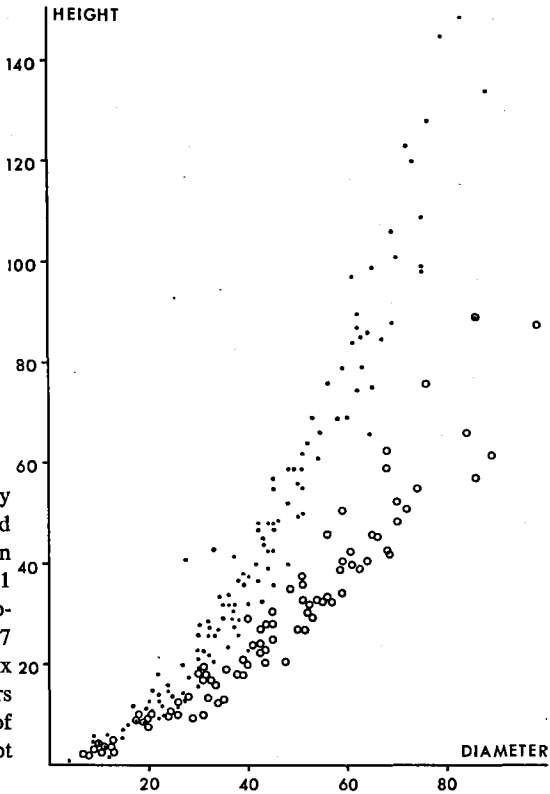The majority of the valves are less than 1 mm high and for practical

Fig. 3. Scatter plot on ordinary coordinate paper of height and diameter in mm measured on enlarged outline drawings of 31 pedicle valves from the Ceratopyge Limestone (dots) and 17 pedicle valves from the Ampyx Limestone (circles). A few pairs of measurements with heights of more than 150 mm are not shown.
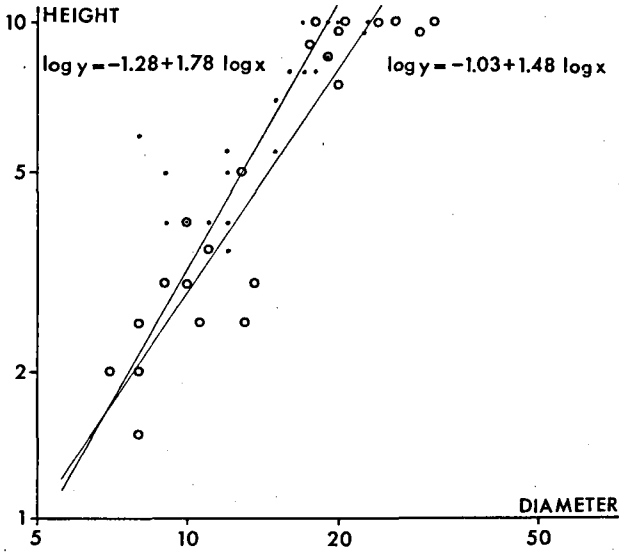
20*

Fig. 4. Scatter plot on graph paper with logarithmic vertical and horizontal scales of the measurements presented in fig. 3. Height-diameter pairs with heights of more than 10 mm in enlarged outline drawings are omitted. A considerable overlap is evident.
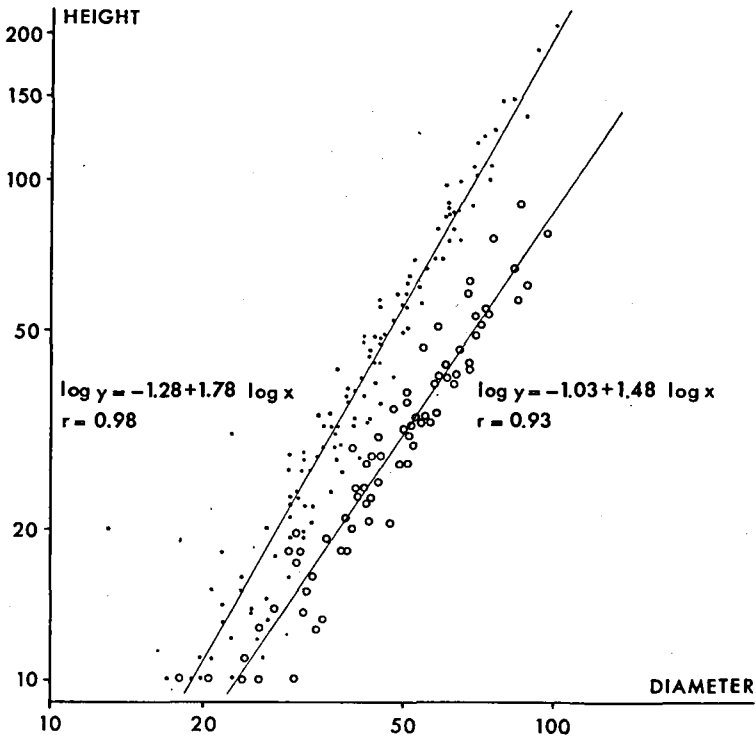

Fig. 5. Scatter plot on graph paper with logarithmic vertical and horizontal scales of the measurements presented in fig. 3. Height-diameter pairs with heights of less than 10 mm in enlarged outline drawings are omitted.

reasons the height:diameter ratios were measured on enlarged camera lucida drawings of the shell outlines (see fig. 2).

The pedicle valves were drawn in dorsal view in order to cancel any undue influence of shell curvature upon the measurements. Several specimens are broken anteriorly and in these instances the diameter was obtained by doubling the radial distance to the preserved side of the shell.

When height and diameter measured in 31 specimens from the Ceratopyge Limestone and 17 specimens from the Ampyx Limestone are plotted on ordinary coordinate paper (fig. 3) the scatter plot distinctly indicates a curvilinear relationship, and an overlap of the early growth stages of the two populations involved is equally conspicuous.

As the curvilinear relationship is suggestive of allometric growth, the same data were plotted on graph paper with logarithmic vertical and horizontal scales (figs. 4 and 5).

In this case the scatter plot demonstrates a linear relationship, and the Y intercept and the steep slope of the row of points show the presence of positive allometric growth.

Statistical procedure

Height-diameter pairs with heights of less than 12 mm, as measured in the enlarged outline drawings, are not considered in the statistical treatment of the data, as the juvenile part of the pedicle valve of the two populations displays a morphology which is markedly different from that of the adult shell. Even small errors introduced in the making of the camera lucida drawings will seriously affect the measured growth ratios of the early stages.

The allometric growth evidenced by the rectilinear relationship of the scatter plots in the logarithmic graphs (figs. 4 and 5) indicates that the suitable regression equation is:

$$\log y = \log b + k \log x$$

(b = Y intercept, log b = log y when x = 0. k = a constant).
k may be obtained from the equation:

$$k = \frac{\Sigma \log x \log y - \frac{1}{n} (\Sigma \log x \ \Sigma \log y)}{\Sigma (\log x)^2 - \frac{1}{n} (\Sigma \log x)^2}$$

(n = number of pairs of measurements).
When k is known log b may be obtained from the equation:

$$\Sigma \log y = n \log b + k \Sigma \log x$$

A standard computer programme for an *Olivetti P 203* was used for 83 pairs of measurements on the population from the Ceratopyge Limestone and 71 pairs on that from the Ampyx Limestone.

The regression equation for the growth pattern of the population from the Ceratopyge Limestone was computed as:

$$\log y = -1.28 + 1.78 \log x$$

and the growth pattern of the population from the Ampyx Limestone as:

$$\log y = -1.03 + 1.48 \log x$$

For the population from the Ceratopyge Limestone the coefficient of correlation was computed as $r = 0.9767$, which for 81 degrees of freedom ($n - 2$) corresponds to a probability value of less than 0.1 %. For the population from the Ampyx Limestone r was computed as: $r = 0.9268$, while the probability value thus is slightly larger than for the former population.

The standard error $s_{\log y \log x}$ computed for the two equations is 0.0652 and 0.0790 respectively. Thus the zones of $\pm\ s_{y \cdot x}$ around the regression equations are fairly narrow with a limited overlap in the region with $y \leq 10$.

The difference observed in the scatter plots and the regression equations may be analysed further by testing the properties of the reduced major axes.

The slopes of the two separate reduced major axes can be compared by using the equation:

$$Z = \frac{k_C - k_A}{\sqrt{s_{k_C}^2 + s_{k_A}^2}}$$

(Z = the statistic. k = slope, or growth ratio. s_k = standard error of slope. C = population from the Ceratopyge Limestone. A = population from the Ampyx Limestone).

From this equation Z is calculated as $Z = 2.52$. This value corresponds to a probability of about 1.0 %, indicating that the difference in slope is significant.

The difference in slope, even if considered significant, is slight and therefore the positional difference, or difference in initial growth index (Y intercept) is tested. In order to do this the vertical distance between the two reduced major axes is tested at a selected x value (x_0). For reasons stated above measurements on the enlarged camera lucida drawings involving heights below 12 mm have been left out of consideration in the statistical treatment of the data. Accordingly, a suitable x_0 is chosen from the combined

samples as the smallest x value at y = 12 mm. With x_0 = 17 mm the vertical distance between the reduced major axes is: $\log y_C - \log y_A = 0.1694$.

For the test use is made of the equation:

$$Z = \frac{\log x_o (k_C - k_A) + (\log b_C - \log b_A)}{\sqrt{s_{k_C}^2 (\log x_o - \log \bar{x}_C)^2 + s_{k_A}^2 (\log x_o - \log \bar{x}_A)^2}}$$

(Z = the statistic. x_0 = 17 mm. $\bar{x}$ = mean of x. k = slope. b = Y intercept. s_k = standard error of slope. C = population from the Ceratopyge Limestone. A = population from the Ampyx Limestone).

Substituting the computed values in the equation, it is found that Z = 4.1666. Referring to Z tables a difference $\log y_C - \log y_A > 0.1694$ at x_0 = 17 mm can only be expected in about 0.01 % of the instances, and it is concluded that the observed positional difference is statistically significant.

The two populations concerned are widely separated in time and according to the tests they might well be considered as separate species. However, the criteria for distinction of species among some groups of inarticulate brachiopods may need revision, and more samples are needed from intermediate parts of the stratigraphical column.

Such supplementary material may very likely show a growth pattern intermediate between that of the two populations discussed here. If that is the case, the acrotretacean may eventually be regarded as one species in an evolutionary line with steadily decreasing height of the ventral valves.

Dansk sammendrag

En ordovicisk acrotretid brachiopod karakteriseret af en usædvanlig høj ventralskal beskrives. Den juvenile del af skallen inclusive protegulum har en markant grubet overflade (tavle 1, fig. 1 B-C og fig. 2 B), mens den postlarvale del af skallen er præget af enkle tilvækstlinier (tavle 1, figur 1 A og 2 A).

Indre lag, som udfylder apicalenden, har en karakteristisk struktur tydende på en primær alterneren mellem tynde fosfatiske lag og tykke lag af organisk materiale (tavle 5). De tykke lag har hidtil været anset for primært fosfatiske, og de tynde lag skulle repræsentere de organiske lag; men det norske materiale viser, at det forholder sig omvendt. Søjle-agtige bindeled mellem de tynde fosfatlag tydes som diagenetisk udfyldte kanaler i det oprindelige organiske lag. I det foreliggende tilfælde er hulrummene efter det forsvundne organiske materiale ikke sekundært udfyldt af fosfat, som det ellers er normalt hos acrotetiderne (tavle 7). Søjlerne kan dog muligvis være primære støtteelementer.

Tilhørende dorsalskaller er ikke identificeret.

Den ydre skal kan i enkelte slidte eksemplarer (tavle 2, 3 og 4) ses at være opbygget af langsgående hule rør med rektangulært tværsnit. Den ejendommelige struktur kan

eventuelt afspejle de skaludskillende epitelcellers form. Strukturen kunne opstå ved en alterneren mellem høje og lave celler, idet fosfat da udskiltes langs hele den frie overflade af de høje celler. På grund af materialets særlige bevaringstilstand er rørene ikke blevet diagenetisk udfyldt af fosfat.

Materialet stammer fra Ceratopyge-kalken (nedre Ordovicium) og Ampyx-kalken (mellem-Ordovicium) i Oslofeltet. Ventralskallerne fra Ampyx-kalken er relativt lavere, og en statistisk behandling af materialet viser, at forskellen ikke kan skyldes tilfældigheder ved indsamling af materialet. Eksemplarerne fra de to niveauer kan betragtes som to adskilte arter; men da der ikke kan iagttages andre forskelle, er det muligt, at materialet repræsenterer yderpunkter i en udviklingslinie karakteriseret af en jævn aftagen af skalhøjde. Et kendskab til formerne i mellemliggende stratigrafiske niveauer må være en forudsætning for en egentlig systematisk beabejdelse.

Institut for almen Geologi
Østervoldgade 5–7
DK-1350 København K, Denmark
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Table 1. Heights (H) and corresponding diameters (D) measured in mm on enlarged camera lucida drawings (×180) of acrotretacean pedicle valves from the Ceratopyge Limestone at Slemmestad and Killingen, Oslo region.

Slemmestad								Killingen	
H	D	H	D	H	D	H	D	H	D
7.0	15.0	23.0	31.0	4.0	10.0	9.5	22.5	15.0	24.0
20.0	27.0	44.0	43.0	13.5	25.0	19.5	32.0	33.5	34.0
32.0	35.0	69.0	53.0	27.5	41.0	43.0	44.0	48.0	42.0
48.0	45.0	97.0	61.0	33.0	43.0	64.0	52.0	55.0	45.0
69.0	60.0					89.0	62.0		
		1.5	12.0	4.0	10.0	120.0	73.0	10.0	20.0
11.0	21.0	26.0	32.0	15.0	21.0	148.5	83.0	21.0	30.0
27.5	32.0	37.5	40.0	26.0	30.0	183.0	93.0	36.5	38.0
40.0	41.5	59.0	49.0	34.0	36.0	205.0	101.0	52.0	48.0
55.0	51.0	76.0	56.0						
		99.0	65.0	6.0	8.0	10.0	23.0	8.0	17.0
12.0	17.0	123.0	72.0	16.0	24.0	33.0	40.0	23.0	31.0
28.0	30.0	145.0	79.0	29.0	37.0	50.0	51.0	38.0	39.0
41.5	37.0			36.5	42.0	75.0	65.0		
57.0	45.0	5.5	15.0			99.0	75.0	5.0	9.0
		16.0	30.0	3.5	12.0	134.0	88.0	12.0	26.0
11.0	20.0	29.0	38.0	14.0	22.0			32.0	36.0
17.5	28.0	42.5	45.0	28.5	32.0	22.0	32.0	48.5	46.0
27.5	37.0	66.0	54.5	47.0	42.0	43.0	44.0		
		84.5	62.0	62.0	51.0	61.0	54.0	5.0	12.0
8.0	16.0	101.0	70.0	85.0	63.0	79.0	63.0	12.0	23.0
13.0	22.0							27.0	34.0
19.0	30.0	8.0	18.0	4.0	9.0	23.0	31.0	44.0	43.0
26.0	38.0	20.5	33.0	10.0	17.0	45.0	43.0		
32.5	42.5	40.0	48.0	18.0	22.0	64.0	52.0	11.0	25.5
				32.0	40.0	84.0	61.0	22.0	32.0
26.0	33.0	4.0	11.0	49.5	50.0			32.0	37.0
47.0	45.0	8.5	19.0	74.5	62.0			48.0	44.0
69.0	58.0	14.5	27.0	88.0	69.0				
98.0	75.0							4.0	12.0
		13.0	20.0	5.5	12.0			13.0	27.0
29.0	35.0	23.0	30.0	19.0	32.0			22.0	33.0
59.0	48.0	36.0	39.0	39.0	44.0			31.0	37.0
87.0	62.0	59.0	51.0	56.0	50.0				
106.0	69.0	79.0	59.0	86.0	64.0			1.0	4.0
128.0	76.0			109.0	75.0			10.0	19.0
								23.5	36.0

Table 2. Heights (H) and corresponding diameters (D) measured in mm on enlarged camera lucida drawings (×180) of acrotretacean pedicle valves from the Ampyx Limestone at Ildjernet, Oslo region.

H	D	H	D	H	D	H	D
2.5	13.0	5.0	13.0	3.5	11.0	2.5	10.5
7.5	20.0	15.0	32.5	9.5	20.0	10.0	20.5
17.0	31.0	27.0	50.0	21.0	39.0	19.5	31.0
30.5	45.0	32.5	55.0	33.0	51.0	28.0	45.0
37.5	51.0	39.0	58.5	42.5	60.5	36.0	51.0
59.0	68.0	55.0	74.0	52.5	70.0	46.0	56.0
76.0	76.0	66.0	84.0	57.0	86.0	50.5	59.0
89.0	86.0	77.5	98.0			62.5	68.0
				3.0	13.5		
3.5	11.0	3.5	11.0	13.0	35.0	3.0	10.0
10.0	26.0	10.0	20.5	27.0	51.5	12.5	26.0
18.0	38.0	24.0	41.0	42.0	68.5	19.0	35.5
20.5	47.5	40.0	61.0	61.5	89.0	23.5	41.0
34.0	59.0	48.5	70.0			29.0	40.0
40.5	64.0			1.5	8.0		
		9.5	29.0	10.0	24.0		
10.0	31.0	12.5	34.0	16.0	33.5		
18.0	39.0	20.5	43.5	24.0	42.5		
32.0	52.5	32.5	57.0	32.5	54.0		
40.5	59.0	39.0	62.5				
51.0	72.0	45.5	66.0	2.0	7.0		
				10.0	18.0		
3.5	11.0	2.5	8.0	18.0	31.5		
12.5	26.0	9.0	17.5	28.0	43.5		
23.0	43.5	18.0	30.0	33.5	56.0		
29.5	53.0	27.0	42.5				
42.5	68.0	35.0	48.5	4.0	10.0		
				13.5	32.0		
2.0	8.0	3.0	9.0	22.5	42.5		
11.0	24.5	8.5	19.0	32.5	55.0		
20.0	40.0	13.5	28.0	45.5	65.0		
30.5	52.0	25.0	45.0	54.0	74.0		
		33.0	54.0				

Plate 1

Fig. 1. Acrotretacean pedicle valve (MMH no. 11024) from the Ceratopyge Limestone, Slemmestad. 1A: Lateral view. Scanning electron micrograph (SEM) × 37. 1B: Posterior view. SEM × 330. 1C: Boundary between juvenile and adult shell, lateral view. SEM × 330.

Fig. 2. Acrotretacean pedicle valve (MMH no. 11025) from the Ceratopyge Limestone, Slemmestad. 2A: Dorsal view. SEM × 102. 2B: Dorsal view of umbonal region showing constriction and effacement of the juvenile scrobiculation at the boundary to the adult shell. SEM × 286.

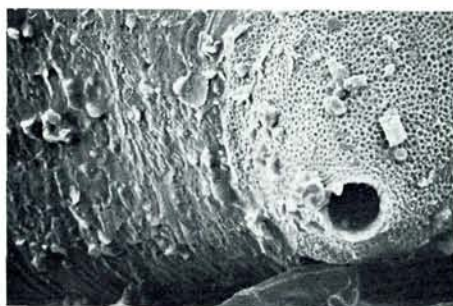Bull. geol. Soc. Denmark, vol. 20, 1971. POULSEN
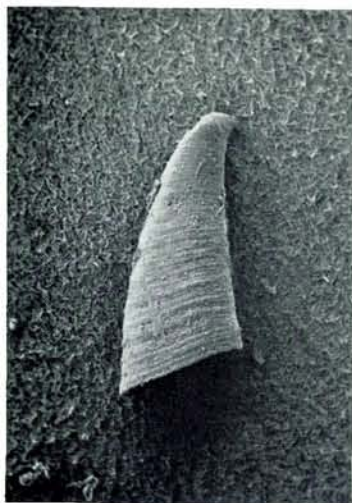
Plate 1

1 A

2 A

1 B

1 C

2 B

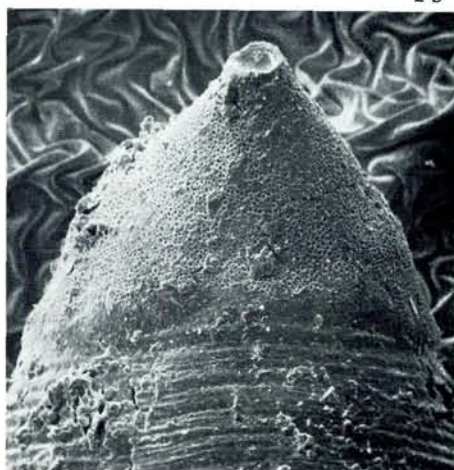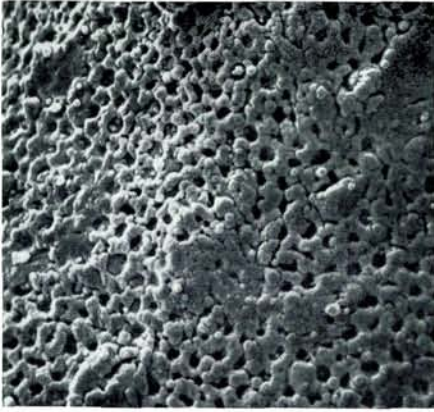## Plate 2

Fig. 1. Shell surface of juvenile part of the specimen figured on plate 1, fig. 2. 1A: SEM × 1470. 1B: SEM × 3570.
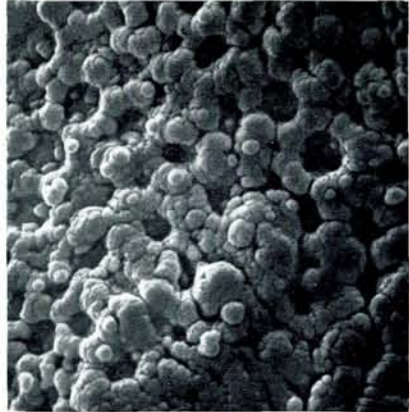
Fig. 2. Oblique dorsal view of acrotretacean pedicle valve (MMH no. 11026) from the Ampyx Limestone, Ildjernet. SEM × 127.

Fig. 3. Dorsal view of slightly abraded acrotretacean pedicle valve (MMH no. 11027) from the Ampyx Limestone, Ildjernet. SEM × 117.
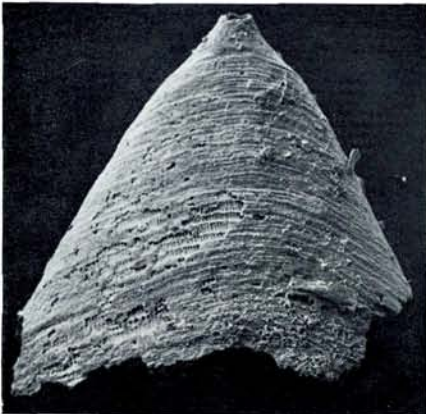
Fig. 4. Dorsal view of abraded and broken acrotretacean pedicle valve (MMH no. 11028) from the Ampyx Limestone, Ildjernet. SEM × 134.

1 A

1 B

2

3

4
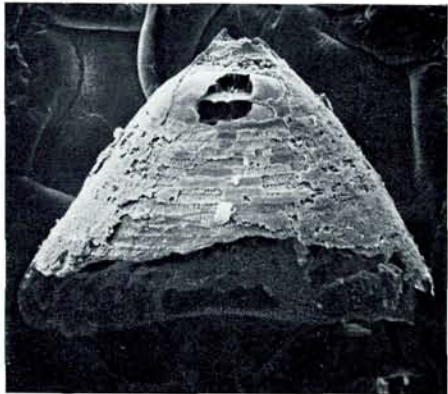
Plate 3

Fig. 1. Abraded pedicle valve from the Ampyx Limestone figured on plate 2, fig. 4. 1A: Oblique frontal view of adult shell surface. SEM × 1000. 1B· Frontal view of same. The specimen shows that the outer wall consists of layers of longitudinal isolated tubes with rectangular cross-sections. SEM × 1000.
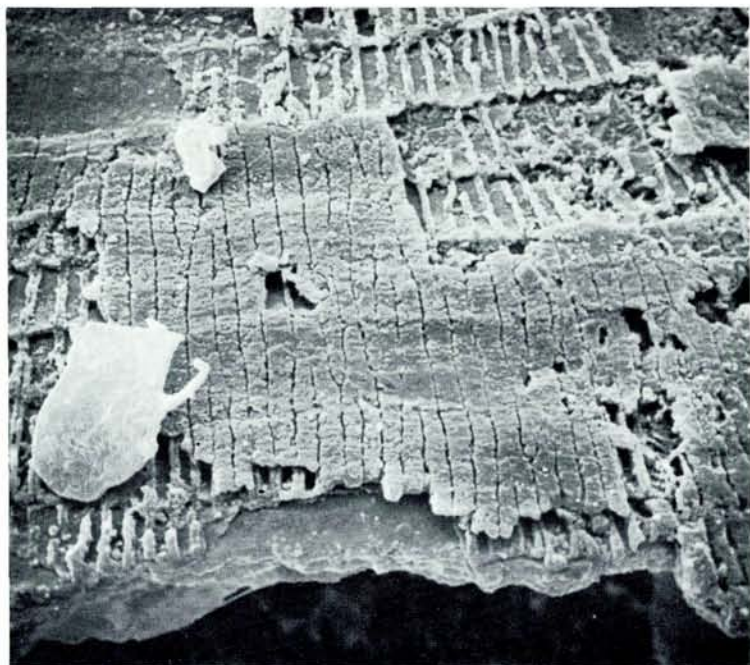
1A

1B
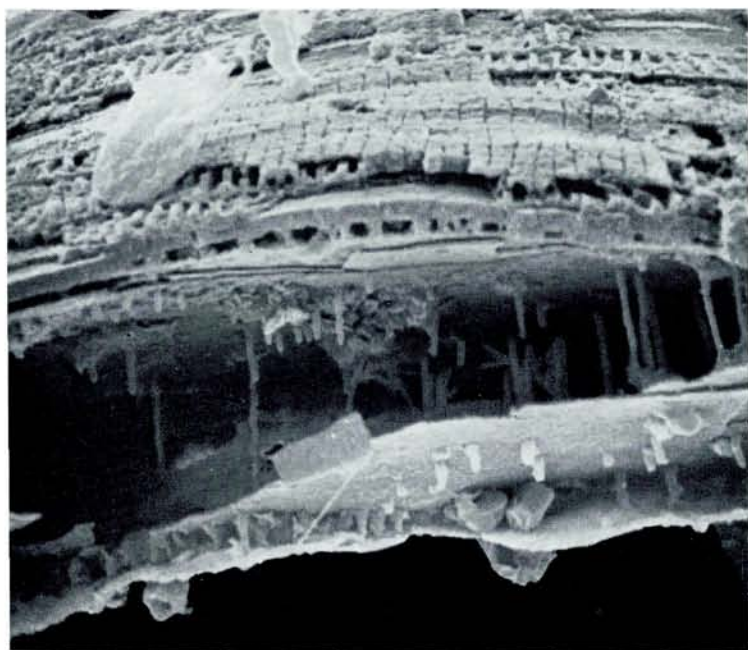
Plate 4

Fig. 1. Dorsal view of adult shell surface in the specimen figured on plate 2, fig. 4. SEM × 2100.

Fig. 2. Oblique frontal view of adult shell surface in the specimen figured on plate 2, fig. 3. SEM × 1085.

1

2

Plate 5

Fig. 1. Broken acrotretacean pedicle valve (MMH no. 11029) from the Ampyx Limestone, Ildjernet. 1A: Dorsal view showing inner layers and "pillars" connecting the primary phosphatic bands. SEM × 210. 1B: Detail of same. SEM × 525.
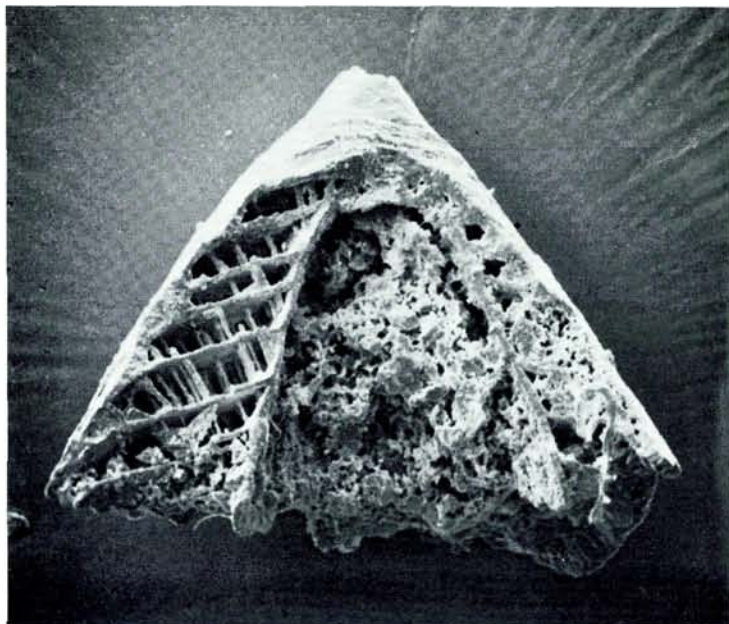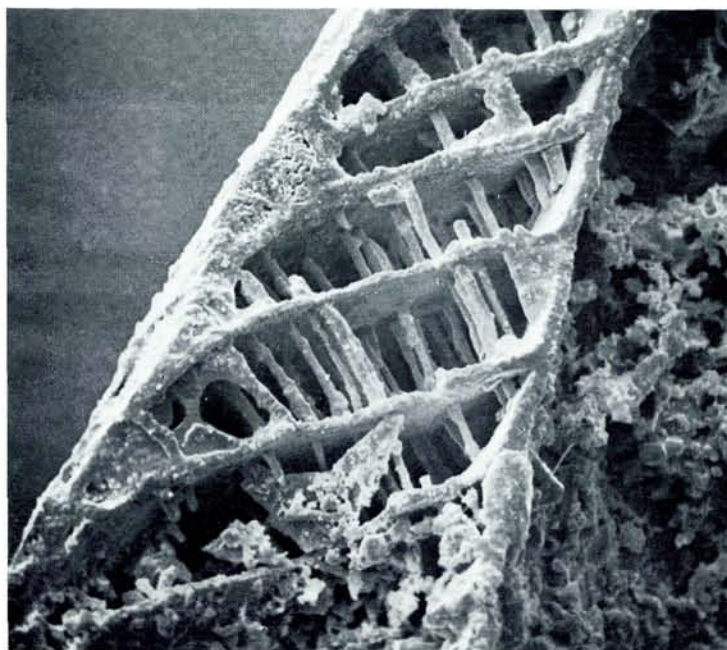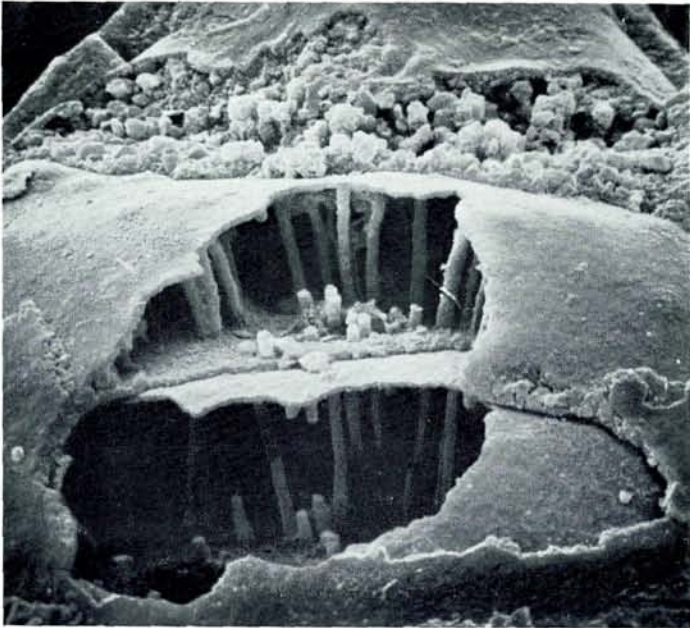
1 A

1 B

Plate 6

Fig. 1. Detail of broken and abraded pedicle valve figured on plate 2, fig. 4.
1A: Dorsal view of curved inner layers and connecting "pillars". SEM ×
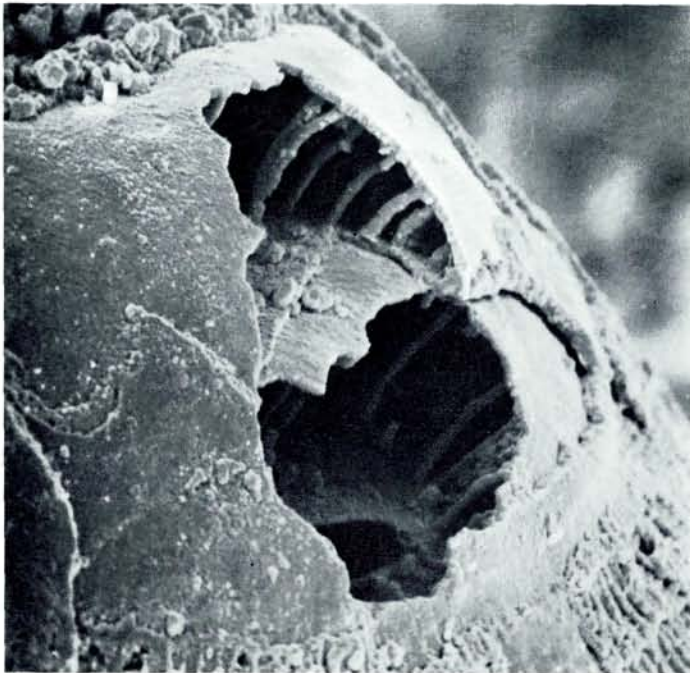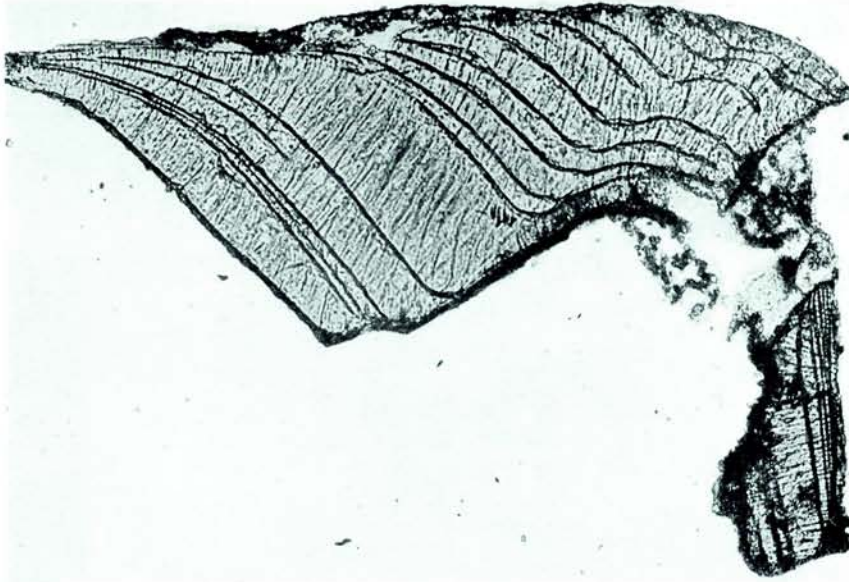1000. 1B: Oblique lateral view of same. SEM × 1050.

1A

1B

Fig. 1. Pedicle valve of *Acrotreta socialis* v. Seebach (MMH no. 11030) from the early Middle Cambrian of Bornholm. 1A: Median section. Optical microscope, polarizer only. × 175. 1B: Same, crossed nicols. × 175. The shell is recrystallised to a certain extent, but the primary structures are only destroyed in a narrow marginal zone. Thick layers showing a fibrous texture are believed to be primary organic bands replaced by calcium phosphate during diagenesis.

1 A

1 B