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MORPHOLOGICAL OBSERVATIONS WITH SYSTEMATIC IMPLICATIONS ON SOME PALAEOZOIC RHYNCHONELLIDA FROM EUROPE, WITH SPECIAL EMPHASIS ON THE UNCILULIDAE

BY

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ABSTRACT

It is the aim of this publication to discuss some important morphological features of some Palaeozoic Rhynchonellida. Material has been investigated from Spain (Cantabrian Mountains), Czechoslovakia (mainly from the Barrandium), Germany (Eifel) France, Belgium and Gotland. Attention has been focused on the Uncinulidae, but representatives of other, related families have also been studied. Many of the given descriptions and interpretations can also be applied to other groups of Brachiopoda. A great number of the obtained data are used in a reconstruction of the phylogenetical tree of the Uncinulidae at the end of this publication. Using this some suggestions are made for a new classification of this family. The following topics are treated.

Chapter II. Microscopic shell structure. The shape and course of the fibres in the secondary shell layer and the shell mosaics on the inner shell surface have been given special attention. According to Williams (1956, 1965, 1966) each fibre has been secreted by one outer epithelial cell (fig. 11). Proceeding from this observation an attempt is made to reconstruct the movements and modifications in the outer epithelium during the formation of the shell (e.g. fig. 35, 36). In many instances these movements turn out to be unexpectedly complicated, but in general a certain regularity in the pattern can be discerned (fig. 21, Pl. IV, V, VII). In some cases these movements are demonstrated to be determined to a certain extent by increases and reductions in the size of the epithelial cells in certain areas of the shell (fig. 24, 28, 29, e.g.). An appropriate terminology is developed to describe and interpret the phenomena in question. The course, size and shape of the fibres are found to be very useful features in brachiopod systematics.

Chapter III. Marginal spines. The serial zigzag deflections in the commissures of young shells of most uncinulid species are known to convert at a certain growth stage into a combination of reduced zigzag deflections and a corresponding set of marginal spines. A morphological range can be framed from species with a well developed zigzag deflection and without marginal spines (e.g. *Estonirhynchia estonica*) to species with well developed marginal spines in combination with a completely rectimarginate commissure (e.g. *Kransia parallelepipeda*). Between these two extremes many transitions occur (cf. fig. 43, 44, 45, 46, 47). With the exception of a few species this morphological range appears to be in line with the succession of these fossils in time, so that it probably reflects a phylogenetical development. An attempt is made to analyse the function of the complex of marginal spines and zigzag deflections according to the principles put forward by Rudwick (1964) (with minor variations).
An examination of the structure of the marginal spines shows that they have been surrounded by the mantle and that the mantle border has extended along the whole or part of the spines as a closed fold (fig. 58, 60, 63, 65, 66, 67). The marginal spines which occur in *Hypothyridina cuboides* appear to be very different in many respects from those in the genuine Uncinulidae (fig. 68, 69).

Chapter IV. Articulation. The criteria introduced by Rudwick (1959) for the distinction between strophic and non-strophic shells are critically examined and some important corrections of his statements are made. In typically non-strophic species, such as *Kallirhynchia concinna* the presence of a dorsal palintrope is demonstrated (fig. 71, see also fig. 72 and 76). The distinction between strophic and non-strophic shells is evidently not so clear-cut as Rudwick suggests. Contrary to the expectations most of the Uncinulidae appear to be strophic. The hinge lines are only very short (fig. 73, 74, 75). *Plethorhyncha altera* and *P. diana*, however, appear to be perfectly non-strophic. The closure of the shell posterior to the hinge axis is a matter of great morphological and systematical interest. This function is mostly accomplished by a complex of elements of which the composition may vary greatly. In *Glossinulus* (*Glossinotoechia*) *latus* the following elements are involved: deltidium, lateral expansions of cardinal process, delthyrial margin, outer socket ridge, hinge line, squama, glotta. (fig. 78). An attempt is made to reconstruct the epithelium in the posterior part of the shell of *Sphaerirhynchia wilsoni* (fig. 79).

Chapter V. Phylogeny and the Classification of the Uncinulidae. An attempt is made to reconstruct the phylogenetical tree of this family on the basis of 17 characters which have been described for 24 uncinulid species studied. With the phenetic distances and the time intervals as starting points evaluations are made of the cladistic affinities between all the 24 species. This has been carried out by means of a computer. A rough estimation is made of the anagenesis on the base of the cladistic affinities and the phenetical distances. The suggested phylogenetical tree displays three main lineages which are subparallel and must have arisen after a radiation in the Upper Silurian (fig. 81). The original genus *Uncinulus* appears to consist of two groups of species which belong to entirely different lineages and which differ greatly in many characters. This is sufficient reason to erect the new genus *Kransia* (see Appendix). It is suggested that future classifications of the Uncinulidae should be more consistent with the phylogeny of this taxon.

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I INTRODUCTION

1. ACKNOWLEDGEMENTS

An occupation with less practical value than the study of the morphology and systematics of some uncinulid and related brachiopods from the Palaeozoic of Europe can hardly be conceived. In fact this work is not designed to be anything else but an example of one of the most amusing games I know. This game is called Pure Research. Since in the first instance a game never has any practical value and since, as we have seen, Pure Research is a game, Pure Research never has any practical value in the first instance. When it has a practical value in the second or in the third instance that is so much gained. However, it is even doubtful whether such will be the case with this publication.

With all the zeal and earnestness that are peculiar to the gamester I embarked upon this game. The continual uncertainty, the despair, the sleepless nights and also the incomparable joy in a moment of inspiration, all this is inherent to the pursuit of science, and, indeed, I have had my share of them. To be occupied in this way for some years with affairs which will almost certainly never influence world events is a rich experience allowed to only a few and it therefore tends to make one suitably grateful.

I wish to express my gratitude to all those who have contributed to the completion of this publication. Only a few of them can be acknowledged here.

I am most obliged to Dr. Jeannine Drot for her charming hospitality during a visit to the Institut de Paléontologie du Muséum national d'Histoire naturelle de Paris. Our cooperation was very fruitful and I had ample opportunity to take advantage of her admirable knowledge of the Palaeozoic Rhynchonellida. Some of her suggestions had a deciding influence on my work.

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2. PRELIMINARY REMARKS

Up to the present day the study of the Brachiopoda has practically been the monopoly of palaeontologists. This is undoubtedly due to the fact that the phylum had a most impressive development in the geological past and that it is now in decline, so that its representatives constitute only an insignificant part of recent marine faunas. Many invertebrate palaeontologists consider their subject as being only an auxiliary science of stratigraphy. As a result they are generally more interested in the identification of the fossil material than in a better understanding of the animals to which these remains belonged. This may explain the overwhelming abundance of systematic descriptions of fossil brachiopod faunas and the striking poverty in studies on other aspects of these intriguing animals, such as their morphology, physiology, or ecology. Some pioneer work in these fields was made in the second half of the nineteenth and the first decades of this century, and it is especially in recent years that an increasing interest in these subjects can be noticed.

It is the aim of this publication to contribute to this new development in the study of brachiopods. An attempt is made to describe and interpret some important features of fossil brachiopod shells. The attention has been focused on some Palaeozoic Rhynchonellida from Europe and more especially on representatives of the Uncinulidae. In the first place these fossils have been studied from the points of view of structural and functional morphology. Moreover, some preliminary inferences have been made on the phylogeny and the systematics of the Uncinulidae.

In the following two sections of this chapter some introductory remarks, mainly on the morphology of the brachiopods, will be made. Those characters which are relevant to this publication will be given particular attention. In the last three sections the species studied will briefly be remarked upon, the design of this study will be worked out in further detail, and the techniques will be described.

3. GENERAL CHARACTERS OF THE PHYLUM BRACHIOPODA

Brachiopods are marine, coelomate, unsegmented invertebrates, provided with an exterior bivalve shell. The two valves are bilaterally symmetrical but dissimilar, one is dorsal in position and is termed the brachial valve, the other is ventral and known as the pedicle valve. Brachiopod valves have often been compared with cones. Growth lines on the outer surface of the shell show indeed that each valve originated in a more or less prominent tip — the beak —, and grew radially from this point. As a rule a strong retardation of the growth has taken place in one — the posterior — direction, so that the posterior part of each valve is strongly reduced in comparison with the opposite — anterior — part.

The phylum is divided into two classes, the Inarticulata and the Articulata. The animals which form the subject of this study are representatives of the latter class. The Inarticulata will not be discussed here. The articulate brachiopods are inter alia characterized by the presence of a skeletal articulatory device, by means of which the shell can open and close. This device generally consists of two dorsally directed protuberances or teeth, which are symmetrically and posteriorly situated just inside the margin of the pedicle valve, and fit into correspondingly disposed grooves or sockets of the brachial valve (fig. 7). When the shell is closed the margins of both valves fit together properly so that the soft parts of the animal are completely isolated from the outside world, and a maximum of protection is provided. When the valves rotate about the hinge-axis — i.e. the straight line connecting the two actual rotation-points of the articulatory device — a narrow slit appears between the opposite valve margins. Through this slit the animal communicates with its environment: fresh sea-water, containing food and oxygen can be introduced and used sea-water, excretory products and other injurious materials can be removed. This slit can only occur anteriorly to the hinge-axis; posteriorly to this axis the closure is permanent. Primarily no shell growth takes place posteriorly to the articulation points in both valves. As a result a quadrangular opening exists between the articulation-points and the beaks (fig. 3), the ventral part being called delthyrium, the dorsal notothyrium. The aperture is closed by the body wall, which at this place is provided with a thick cuticular layer and forms a stalklike outgrowth, the pedicle, which

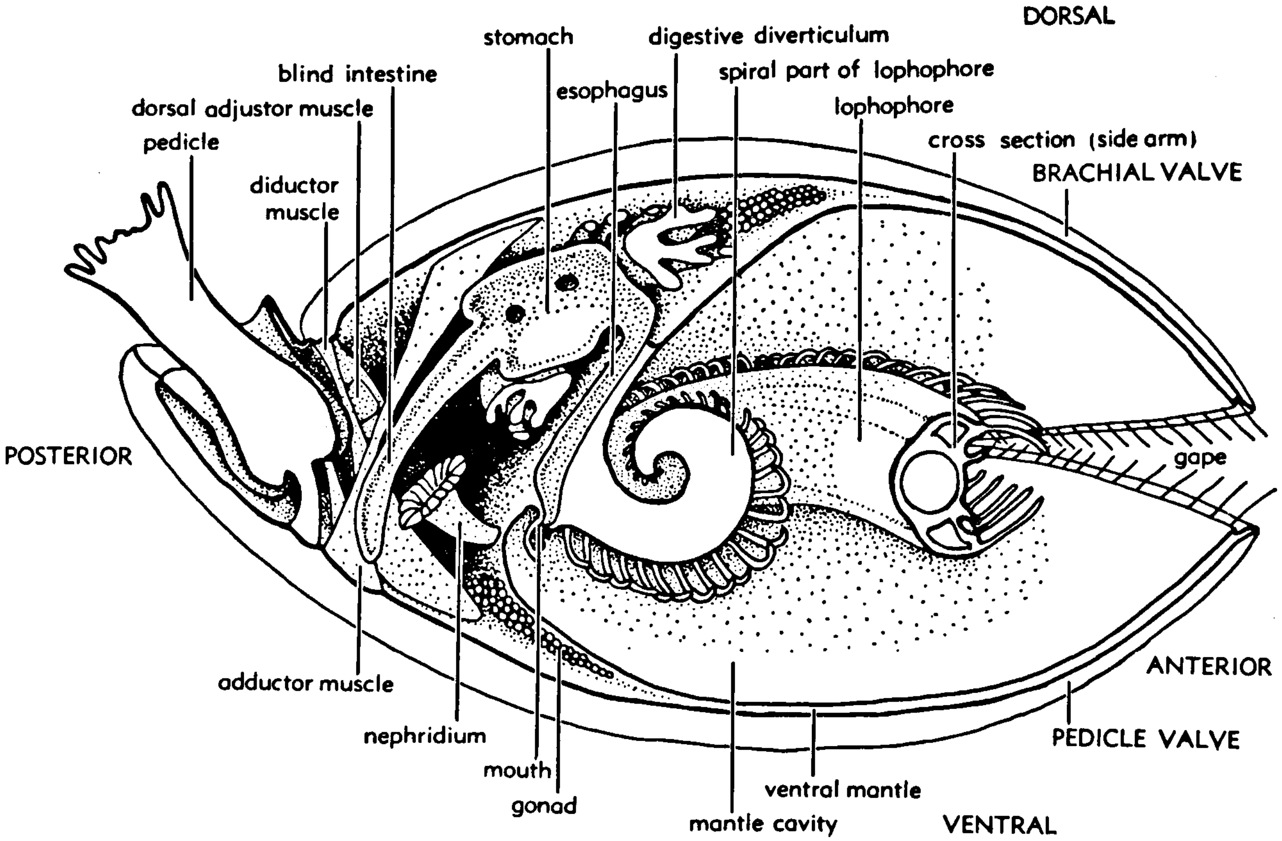

Fig. 1. Diagrammatic representation of principal organs of brachiopod typified by *Terebratulina*. (After Williams and Rowell, 1965).

generally protrudes through the delthyrium and serves to attach the animal to the substratum. Very commonly secondary outgrowths of the shell are formed which obturate the notothyrium and the delthyrium. They are called the chilidial and deltidial plates respectively. The body wall consists of three layers, an ectodermal epithelium, a connective tissue layer, and an internal, coelomic epithelium (peritoneum). In the ectodermal epithelium three distinctive zones can be distinguished: an outer, an inner, and a pedicle epithelium (Williams, 1956, Williams & Rowell, 1965) (fig. 1, 2). The outer epithelium lines the inner surface of the shell and is responsible for its formation. At the anterior valve margins the outer epithelium merges into a bilobed epithelial edge. Between the lobes there is a more or less pronounced mantle groove at the bottom of which new epithelial cells are produced. This narrow zone of cell proliferation is referred to as the generative zone.
The inner lobes constitute the edge of the inner epithelium. In the anterior part of the shell this epithelium is parallel to the inner valve surfaces and is separated from the outer epithelium by only a thin

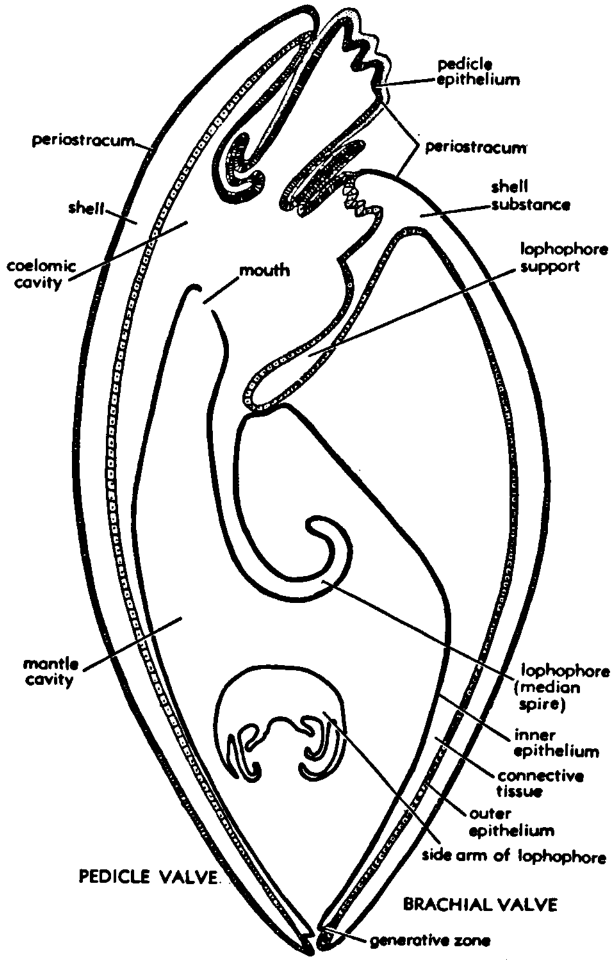

Fig. 2. Generalized representation of epithelium in terebratulids. (After Williams, 1956).

connective tissue layer. Thus, the inner surface of the anterior part of the shell is covered by a pair of blade-like extensions of the body wall, called mantles. Posteriorly to the mantles the inner epithelium runs transversely through the shell cavity, dividing the latter into the mantle cavity and the body cavity. The mantle cavity is in direct communication with the sea, whereas the body cavity is enclosed by the actual body wall, the surrounding ectodermal epithelia being internally lined with connective tissue and the coelomic peritoneum. It accomodates the muscles and the digestive, excretory and reproductive organs. The coelom is not restricted to the posterior part of the animal; it forms a complicated pattern of elaborately branching canals between the outer and inner epithelia of the mantles. The coelom also forms the centre of the lophophore, which consists of a pair of tubelike extensions of the anterior body wall (the brachia), placed symmetrically on either side of the mouth and projecting into the mantle cavity. The brachia are variously coiled and looped; they are provided with a longitudinal food groove which leads to the mouth and is bordered on one side by close rows of slender, flexible filaments. The entire surface of the inner epithelium is covered with cilia which induce a current in the mantle cavity. The rows of filaments on the brachia are arranged in such a way that they divide the slit of the gaping shell into one or more exhalant and inhalant apertures, and the mantle cavity into corresponding exhalant and inhalant chambers. Fresh sea-water enters into the inhalant chambers through the corresponding inhalant apertures, it then filters through the rows of filaments into the exhalant chambers from which it is pumped out through the exhalant apertures. In the filtering process the food is sieved out of the sea water and is then transported via the food-groove to the mouth. Moreover the lophophore may have a respiratory function.

The inner mantle lobes of both valves are fused at their intersections with the hinge axis. The parts of the commissure between these intersections and the delthyrio-notothyrial opening are referred to as the hinge line or the cardinal margin, depending on their being in line with the hinge axis or not. Here, the generative zone is flanked by two epithelial lobes each of which belongs to the outer epithelium of one valve (fig. 3).

The third zone of the ectodermal epithelium, the pedicle epithelium, primarily obturates the delthyrio-notothyrial aperture of the shell, at the border of which it merges into the outer epithelium. It forms a deep infold into the umbonal region of the pedicle valve, and from there it protrudes distally, constituting together with its thick, cuticular cover the outer wall of the pedicle.

In living articulate brachiopods three main muscle systems can be discerned. One or sometimes two pairs

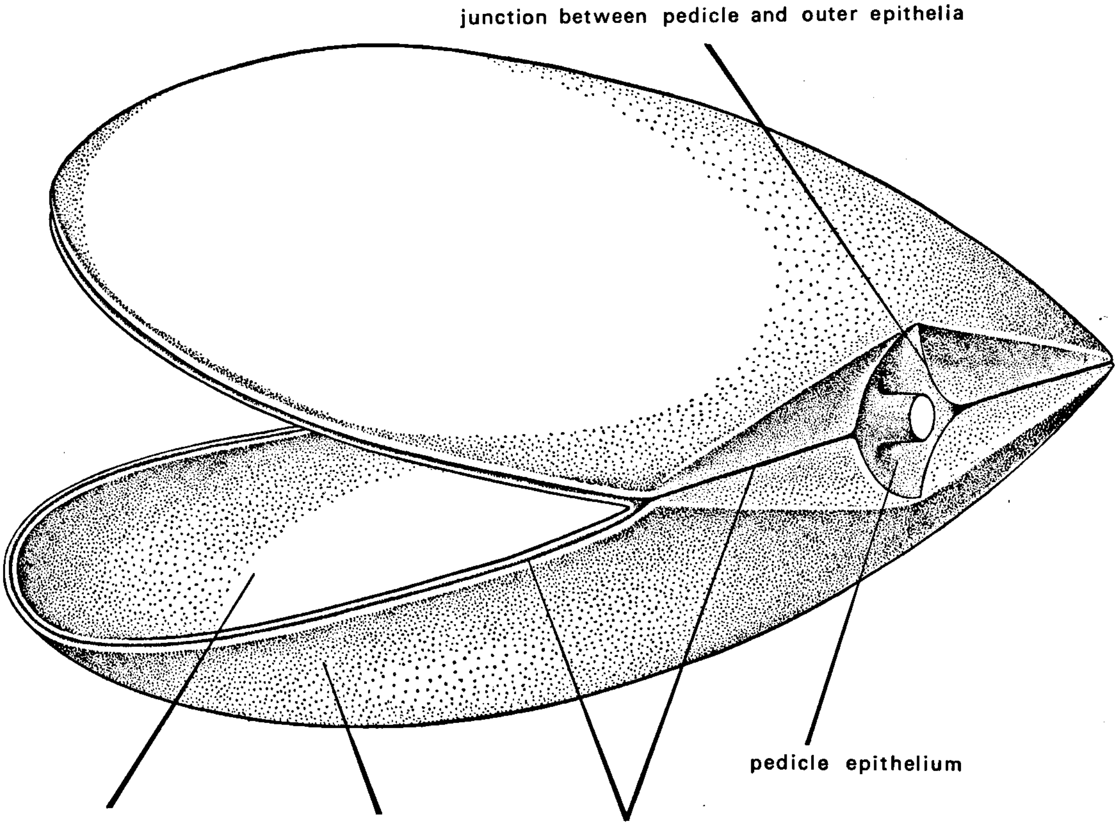

Fig. 3. Schematic representation of the outer, the inner and the pedicle epithelium and of the generative zones.

of diductor muscles serve to open the shell. They originate from the bottom of the pedicle valve and pass to the beak of the brachial valve, where they may be inserted in a special outgrowth of the shell — the cardinal process. The adductor muscles are responsible for the closure of the shell. They arise from two scars, located symmetrically on the pedicle valve; in the middle of the shell they bifurcate so that at the bottom of the brachial valve four symmetrically disposed scars occur. They lie for the greater part anteriorly to the hinge axis. Finally, one pair of dorsal and one pair of ventral adjustor muscles regulate the relative positions of the shell and the pedicle. They are fixed to the pedicle base and to the posterior parts of the brachial and pedicle valves respectively.

4. SOME ASPECTS OF THE BRACHIOPOD SHELL

The shell of an articulate brachiopod consists mainly of calcite and is the product of an additional growth process which is directly regulated by the outer epithelium. We have seen that this epithelium lines the inner surface of the shell, and regularly secretes new shell material against it. Only in a very few instances are existing shell deposits known to be removed by dissolution, so that broadly speaking one may argue that the animal loses its influence on a shell increment as soon as this has been secreted. In this way the outer surface of the shell can only grow at its edge, but for the rest the animal has no further influence on it. The growth of the outer shell surface is the result of a corresponding increase in size of the outer epithelium by the formation of new cells in the generative zone. The shell edge is displaced radially, the older commissures becoming growth lines, arranged concentrically around the beaks of both valves. In fact, these growth lines can very often be traced on the outer shell surface. This enables us to reconstruct the growth process of this surface. The growth in thickness of a valve is caused by the deposition of shell material on its inner surface; a process which is also regulated by the outer epithelium. The inner surface can be considered, therefore, as the final one of a series of growth surfaces which extend more or less parallel to each other (and thus to the inner surface), and appear at the outer surface as growth lines. In sections through the shell the growth surfaces are intersected. Very often such intersection lines can be traced. This enables us to reconstruct the growth process of the shell (fig. 4).

Anterior to the hinge axis the valve margins of a brachiopod shell fit closely together. Posterior to this line they constitute the delthyrial and notothyrial ridges and are free. In many shells the dorsal and ventral umbones are clearly opposite to each other, and lie on either side of the hinge axis. In other instances, however, the dorsal umbo may be tucked into the delthyrium and together with the notothyrial ridges be concealed by the deltidium. This is essentially the case in the Rhynchonellida. Laterally from the articulation points certain arcs of the growing valve edges may or may not be in line with the hinge axis. In the first case, this line constitutes a true hinge line; the sectors of both valves corresponding with these arcs are called interareas, and shells of this type strophic. In the second case, these arcs are generally curved and are not in line with the hinge axis, they constitute the cardinal margin, the homologues in both valves of the interareas are called palintropes, and shells of this type nonstrophic[1]. According to Rudwick (1959) the growth vector at any point of the growing edge can be appropriately resolved into three components, relative to the plane of symmetry and the commissural or normal plane (fig. 5): an anterior component, parallel with the intersection of both planes, acting anteriorly; a lateral component, acting perpendicularly to and away from the plane of symmetry, and a vertical component, perpendicular to the commisural plane, and acting towards the opposite valve [2]. Other useful terms which have been proposed by Rudwick are *zone, arc*

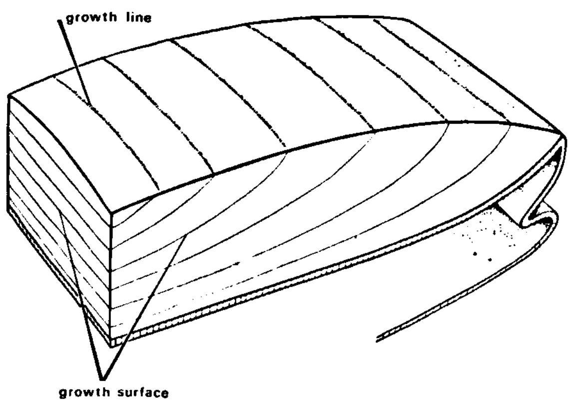

Fig. 4. The position of growth lines and growth surfaces in the shell.

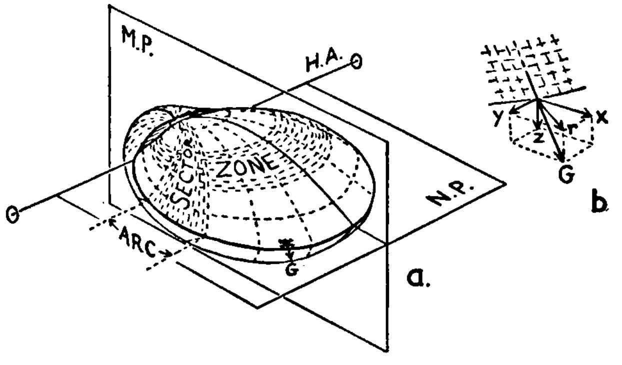

Fig. 5. (a) Perspective view of brachiopod shell. M.P.= median plane or plane of symmetry; N.P.= normal plane; H.A.= hinge axis; G= rate of growth at one point on dorsal valve edge. (b) Enlargement of same point on dorsal valve edge showing G resolved into component growth rates; r= radial; x= anterior; y= lateral; z= vertical. (After Rudwick, 1959).

[1] This description differs in some respects from the original analysis of Rudwick. This will be elucidated in chapter IV.

[2] The direction of a growth vector can only be unambiguously traced in the plane of symmetry. Elsewhere the only essential indications consist of radial ornaments, such as folds, costae or striae. See also note 23, p. 67.

and *sector:* "Considering first the whole of the growing edge of a valve, all the shell-material deposited during a certain period of growth may be termed a zone of the valve; thus a zone will be a strip of valve surface between any two growth lines or between one growth line and the final valve edge. A zone is a "cumulative" derivative of the whole growing edge. Secondly, any section of the growing edge may be termed an arc. The shell material deposited by an arc during the whole growth of the valve may be termed a sector; thus a sector will be a tract of valve surface radiating from the umbo...".

A sudden reduction of the anterior and lateral components to zero will cause vertical shell surfaces to be formed. This is in fact a very common phenomenon in uncinulids; it has been called geniculation (Williams & Rowell, 1965, p. H63), and here the corresponding vertical surface will be termed the *paries geniculatus* (= abgestutzte Vorder- und Seitenwände Hertha Schmidt's (1937)).

Radially arranged features of the shell surface e.g. costae are interpreted by Rudwick as deformations of a smooth shell surface, caused by corresponding local anomalies, deflections, of the commisure. He distinguishes between radial deflections (with an anomalous radial component), vertical deflections (vertical component is anomalous) and composite deflections (with an anomaly of both radial and vertical components). According to their position three types of deflections are distinguished: (1) median deflections, occuring singly, centred on the median plane; (2) paired deflections, occurring in pairs, symmetrically on either side of the median plane, and (3) serial deflections, which are numerous and similar.

The influence of all these deflections on the shell surface has often been described (e.g. Rudwick, 1959; Krans, 1965). As far as I know, however, this problem has not yet been treated in a more general way. The following theorem is an attempt to do just this. Let RST be a deflection, with a base RT, and an axis BAS. The direction BS is considered to be the direction of the deflection. Let fig. 6 represent a valve surface which is deformed by the deflection and rotates about RT. The line AQ runs parallel to the local growth vector of the shell surface, and the direction AQ corresponds with the direction of that vector. Let α be the angle between AQ and AS, and e the perpendicular from S on AQ; α is measured clock-wise from AS. Now e = AS sin α and is directly proportional to the elevation of the deformation above the shell surface. Two conditions are possible: either the outer shell surface faces upwards in fig. 6 (condition I), or it faces down (condition II). In both conditions e will be = 0 and no deformation will result when $\alpha = 0°$ or $180°$. In condition I e reaches its maximum value, giving rise to a rib of maximum height with $\alpha = 90°$; and e reaches its minimum value, giving rise to a groove of maximum depth with $\alpha = 270°$. In other words: when Q lies on the right side of BS in fig. 6, a rib will arise; when Q lies on the left side of BS a groove will result.

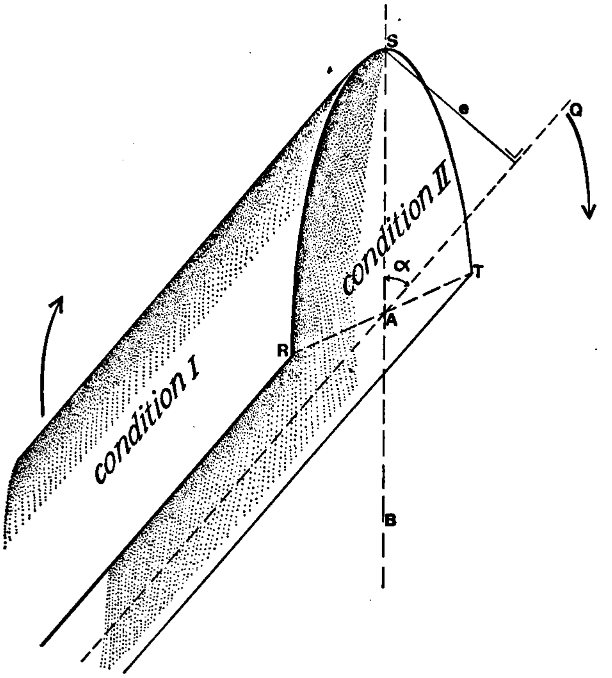

Fig. 6. Deformation of a valve surface by the deflection RST.

When condition II is fulfilled the situation is reversed. When Q lies on the right side of BS a groove will arise; when Q lies on the left side of BS a rib will result. The maximum and minimum deformations occur with $\alpha = 270°$ and $90°$ respectively.

In consequence of the sinusoid relation between α and e, a small increase or decrease of α from 0° or 180° will affect e maximally, and from 90° or 270° minimally. Both valves are deformed by the deflection, but in a different way. This difference is due in the first place to the fact that the outer valve surfaces make different angles with the plane of the deflection; secondly the valves each correspond with one of the two conditions described above, as a result of their opposite postition. Two possibilities are generally distinguished in this connection. When Q_1 and Q_2 of valve$_1$ and valve$_2$ respectively are situated on either side of BS, the same type of deformation will arise on both valves. This condition is known as opposite folding (Buckman, 1907). When however Q_1 and Q_2 lie on the same side of BS alternate folding will be the result, in which a fold in one valve corresponds with a groove in the other.

These considerations are, of course, only valid when the valves and the deflections lie in plane surfaces. On p. 51 the crenulate ribs which occur in many uncinulids are discussed. Here, indeed, the deflections lie in a strongly curved surface; the above arguments can nevertheless be used.

A very common feature in rhynchonellid brachiopods is the presence of a broad, dorsally directed median deflection, generally giving rise to a dorsal fold and a ventral sinus or sulcus. In addition, in most cases serial zigzag deflections are superposed on the medially

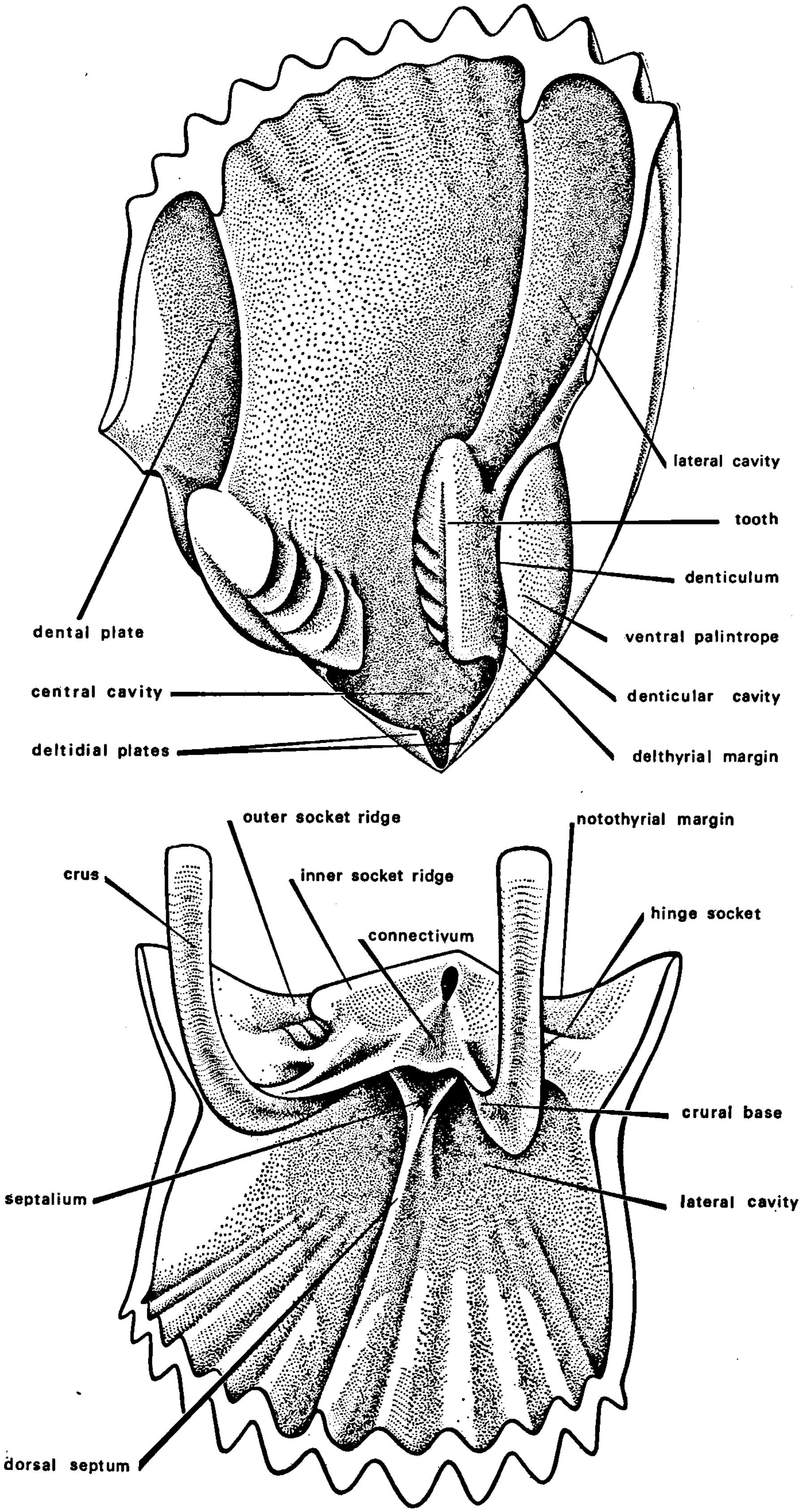

Fig. 7. *Trigonirhynchia pareti.* Three-dimensional reconstruction of the apical interior of its valves from serial sections. Pedicle valve above; brachial valve below.

deflected commissure, so that a pattern of radially arranged costae and grooves arises. All these deflections are of the composite type, but the vertical component predominates. As the shell is generally biconvex the grooves and costae alternate in both valves when the shell margin forms a sharp edge; in paries geniculati and other vertical surfaces the deformations are faintly or not developed.

In most uncinulids the originally simple zigzag deflections of both valves are modified in adult shells in such a way that the most prominent parts, which correspond with the grooves, project into the mantle cavity, giving rise to more or less developed marginal spines.

Most of the internal structures of the brachiopod shell originate in the apical regions and protrude from there into the shell cavity. They constitute a very diversified complex of features throughout the Articulata, but in this context it will be sufficient to point out only the structures which occur in the Uncinulidae and related genera. Most of them are very well developed in the Lower Devonian Spanish species *Trigonirhynchia pareti*, which, however, does not belong to the Uncinulidae itself. Nevertheless it will be taken here as an example.

Fig. 7 represents a three-dimensional reconstruction of the apical interior of its valves. The lateral edges situated between the ventral and dorsal beaks and the hinge axis are the delthyrial and notothyrial margins respectively. The delthyrium is partly obturated by very reduced deltidial plates, which in many uncinulids unite and form a solid deltidium, leaving only a tiny pedicle opening near the beak.

The articulatory device consists mainly of two nodular outgrowths of the inner surface of the pedicle valve, the hinge teeth, situated symmetrically at the anterior ends of the delthyrial margins, and of a pair of grooves, the dental sockets, at corresponding positions in the brachial valve. In fact, these sockets run along and just inside the notothyrial margins, but they are only functional at their anterior end, where they enclose the ventral teeth; more posteriorly they are commonly clogged with secondary shell materials. In a socket an outer and an inner socket ridge can be distinguished.

The hinge teeth are supported by vertically disposed dental plates, extending from the delthyrial margins to the bottom of the pedicle valve, and dividing the apical cavity into a central and two lateral cavities. In adult shells of many species the lateral cavities are filled up by secondary outgrowths of calcite, so that only the central apical cavity is present, bordered laterally by strongly thickened shell walls. The most prominent structures in the brachial valve are the crura: slightly divergent, rodlike protuberances, which at their base point anteriorly, and distally are bent in ventral direction. They are often provided with variously disposed longitudinal ridges. In recent representatives of the Rhynchonellida the crura are fixed at their distal ends to the anterior body wall, giving support to spirally curved brachia. At their base the crura are generally involved in other apical structures, where they only can be traced as a pair of ridges radiating from the dorsal beak, or in sections. These parts of the crura are known as the crural bases. Three pairs of shell plates which extend from the crural bases can generally be distinguished. One pair of these plates is directed dorso-medially; they are referred to as the crural plates and are fused at their intersection with the plane of symmetry. Thus, they form a spoon-shaped structure, the septalium, which is supported by a median, vertical ridge extending from the bottom of the dorsal valve, the dorsal median septum. A second set of plates is the outer hinge plates, which extend from the inner socket ridges to the crural bases. They are of variable breadth and sometimes can hardly be distinguished from the surrounding elements. According to their position relative to these structural elements a pair of lateral apical cavities and a septalial cavity are distinguished.

Finally, medially directed outgrowths of the crural bases may occur. These are the inner hinge plates and may unite, thus forming a connectivum, constituting a horizontal cover to the septalium. In many instances the connectivum is only developed between the anterior part of the crural bases, so that a narrow opening is left near the beak, bordered laterally by the reduced inner hinge plates. This opening very

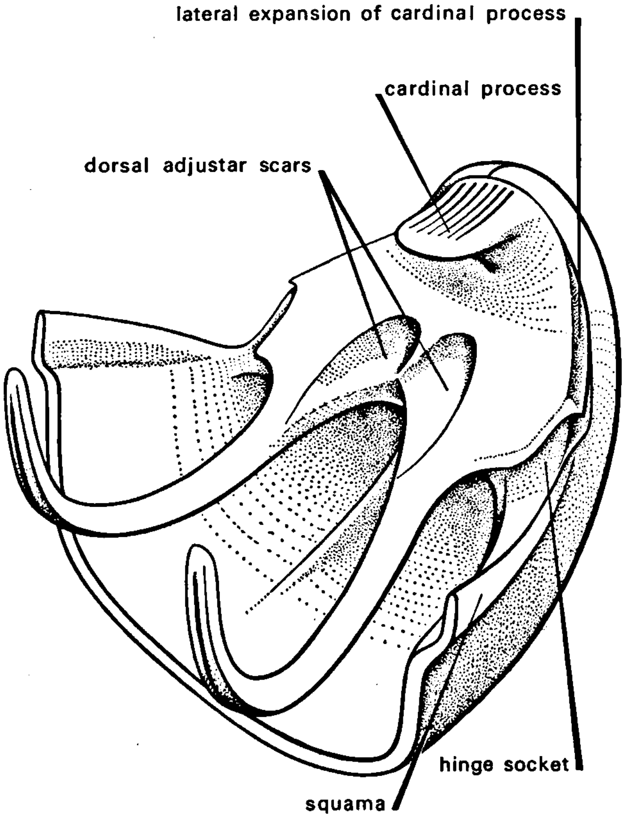

Fig. 8. *Glossinulus (Glossinotoechia) latus*. Three-dimensional reconstruction of the apical interior of the brachial valve from serial sections.

probably served as a passage to the main diductor muscles, which would then have been fixed to the underlying part of the septalium bottom. Possibly the accessory diductors might have had the reduced inner hinge plates as their base. In most Uncinulidae, however, a more or less pronounced cardinal process, provided with fine radial ridges on its ventral surface to which the diductors are attached, is developed.

In a specimen of *Glossinulus (G.) latus,* from the Lower Devonian of N. Spain, in which the cardinalia are beautifully exposed, I have observed a pair of muscle casts on the connectivum; this suggests that the connectivum has served for the attachment of the dorsal adjustors (for reconstruction see fig. 8).

In many Uncinulidae these structures have been secondarily thickened so that often they may even have lost their identity during ontogeny. Only the articulatory device, the crura and the cardinal process (if any) can always be identified; the hinge plates and the septalium are transformed into a thick horizontal platform, supported by a low and broad median septum.

All these inner shell structures have been lined and secreted by the outer epithelium throughout the life of the animal. They originated near the beak and then grew in size and thickness due to a differentially directed deposition of shell material by the corresponding parts of the epithelial membrane. Shell deposition at the distal ends of these structures will increase their size, whereas growth in thickness is affected by deposition on the more posterior parts of the structures. When the rate of the growth in size greatly exceeds the rate of the growth in thickness slender structures will arise, whereas massive structures will be the result of only slight differences in the growth rates. It is evident that all these structures will taper towards their distal end. Some important exceptions to this rule will be treated in the following chapter.

5. THE SPECIES INVESTIGATED

The species which have been considered in detail in this publication are listed below. Some remarks have been made incidentally on other species such as *Sicorhyncha trinacria tenuirostris* Havlíček, 1961, *Cupularostrum cantabricum* Westbroek, 1964, *Iberirhynchia santaluciensis* Drot and Westbroek, 1966, *Kallirhynchia concinna* (Sowerby, 1815) and *Rhynchopora nikitini* Tshernyshev, 1885. The chronostratigraphical positions of the species which occur in the list refer to the stages during which these species are known to have lived. The indications on the localities refer to the places from which the studied material has originated.

Material has been investigated from Spain (Cantabrian Mountains), Czechoslovakia (mainly from the Barrandium), Germany (Eifel), France (Normandy and Brittany), Belgium and Gotland. The collections which have been studied are kept in the following Institutions:

Spanish material:

(1) Geologisch en Mineralogisch Instituut der Rijksuniversiteit, Leiden, Netherlands.
(2) Rijksmuseum van Geologie en Mineralogie, Leiden, Netherlands.

Czechoslovak material:

(1) Narodní Muzeum, Prague.
(2) Ústřední Ústav Geologický, Prague.
(3) Muséum national d'Histoire naturelle de Paris, Institut de Paléontologie.

German material:

(1) Rijksmuseum van Geologie en Mineralogie, Leiden, Netherlands.
(2) Mineralogisch Geologisch Museum, Technische Hogeschool, Delft, Netherlands.
(3) Geologisch en Mineralogisch Instituut der Rijksuniversiteit, Leiden, Netherlands.

Material from Gotland:

(1) Mineralogisch Geologisch Museum, Technische Hogeschool, Delft, Netherlands.
(2) Rijksmuseum van Geologie en Mineralogie, Leiden, Netherlands.

Material from France and Belgium:

Mineralogisch Geologisch Museum, Technische Hogeschool, Delft, Netherlands.

Order RHYNCHONELLIDA Kuhn, 1949

Superfamily RHYNCHONELLACEA Gray, 1848

Family TRIGONIRHYNCHIIDAE McLaren, 1965

Trigonirhynchia pareti (De Verneuil, 1850), Upper Siegenian — Lower Eifelian, La Vid Formation, Cantabrian Mountains, Spain

Family UNCINULIDAE Rzonsnitskaya, 1956

Estonirhynchia estonica Schmidt, 1954
Upper Wenlockian — Ludlovian, Gotland

Sphaerirhynchia wilsoni (Sowerby, 1816)
Upper Wenlockian — Ludlovian, Gotland

Hebetoechia hebe (Barrande, 1847)
Ludlovian — Gedinnian, Bohemia

Hebetoechia nitidula (Barrande, 1879)
Siegenian — Emsian, Bohemia

Lanceomyonia tarda (Barrande, 1847)
Ludlovian — Gedinnian, Bohemia

Obturamentella lebanza (Binnekamp, 1965)
Siegenian, Lebanza Formation, Cantabrian Mountains, N. Spain

Markitoechia marki (Havlíček, 1956)
Emsian — Eifelian, Bohemia

Plethorhyncha altera (Barrande, 1879)
Gedinnian — Siegenian, Bohemia

Plethorhyncha diana (Barrande, 1879)
Gedinnian — Siegenian, Bohemia

Eucharitina eucharis (Barrande, 1847)
Siegenian — Emsian, Bohemia

Eoglossinotoechia cacuminata (Havlíček, 1959)
Ludlovian — Siegenian, Bohemia

Eoglossinotoechia mystica (Havlíček, 1961)
Ludlovian — Siegenian, Bohemia

Eoglossinotoechia sylphidea (Barrande, 1847)
Siegenian — Emsian, Bohemia

Glossinulus (Glossinotoechia) princeps (Barrande, 1847)
Siegenian — Emsian, Bohemia

Glossinulus (Glossinotoechia) henrici (Barrande, 1847)
Siegenian — Emsian, Bohemia

Glossinulus (Glossinotoechia) latus (Schumann, 1965)
Emsian, La Vid Formation, Cantabrian Mountains, N. Spain

Uncinulus subwilsoni (d'Orbigny, 1850)
Siegenian — Emsian. Specimens have been studied from la Baconnière (Mayenne, France), from the Néhou Formation (Cotentin, France), and from the Lebanza Formation, Cantabrian Mountains, N. Spain

Uncinulus pila (Schnur, 1851)
Siegenian — Eifelian
La Vid Formation, Cantabrian Mountains, N. Spain

Uncinulus maledictus maledictus (Barrande, 1879)
Emsian, Bohemia

Uncinulus orbignyanus (de Verneuil, 1850)
Eifelian, Santa Lucía Formation, Cantabrian Mountains, N. Spain

Uncinulus knjaspensis (Chodalevič, 1951)
Eifelian, Bohemia

Kransia parallelepipeda (Bronn, 1837)
Emsian — Givetian, Eifel (Germany)

Kransia primipilaris (v. Buch, 1834)
Eifelian — Givetian, Eifel (Germany)

Kransia goldfussii (Schnur, 1853)
Eifelian — Givetian, Eifel (Germany)

Kransia minor minor (Schnur, 1853)
Eifelian — Givetian, Moravia (Czechoslovakia)

INCERTAE SEDIS

Decoropugnax berenice (Barrande, 1847)
Ludlow, Bohemia

Corvinopugnax corvinus (Barrande, 1847)
Eifelian, Bohemia

Hypothyridina cuboides (Sowerby, 1840)
Frasnian, Belgium, Harz (Germany)

Broadly speaking the classification of the palaeozoic Rhynchonellida proposed by Schmidt and McLaren (1965) has been used in this book. There are however some significant deviations.

1. The Uncinulidae have not been divided into subfamilies. The division proposed by Schmidt and McLaren is unsatisfactory for reasons which will be explained in Chapter V.

2. *Eucharitina eucharis* has provisionally been included in the Uncinulidae. This is in accordance with the classification given by Havlíček (1961), who included this species in his Hebetoechiidae, which in turn form part of the Uncinulidae in the classification of Schmidt and McLaren. According to the latter authors *Eucharitina* must be grouped in the Eatoniidae. *Eucharitina* however has striking similarities with many genuine representatives of the Uncinulidae, although with none of the species studied could a very close relation be demonstrated. In fact the relation between the Uncinulidae and the Eatoniidae is a most interesting one. It should be studied in more detail in the future.

3. *Decoropugnax, Corvinopugnax* and *Hypothyridina* have been considered as genera *incertae sedis* because the position of these genera relative to the existing families is far from understood. Havlíček (1961) includes these genera in the family Hypothyridinidae Rzonsnitskaya, which, in turn, he considers as belonging to the Superfamily Rhynchonellacea Schuchert. The Uncinulids, on the other hand, are grouped in the Superfamily Camarotoechiacea. The main difference between these two superfamilies is considered by Havlíček to consist of the absence or presence of a dorsal median septum.
For Schmidt and McLaren the main criterion for classification of these genera is the development of a cardinal process. These authors have grouped *Hypothyridina,* and *Decoropugnax* in the Hypothyridininae which they assign to the family Uncinulidae. *Corvinopugnax* is placed in the Pugnacidae. Classifications which are based on so few characters often have little predictive value and are not very reliable sources of information on phylogenetic relationships. The systematic position of these controversial genera is therefore far from understood.

The generic assignment of the species studied has generally been accomplished according to the most recent state of affairs in the literature. Here, too, some remarks must be made.

1. *Obturamentella lebanza* certainly does not belong to *Uncinulus* as has been suggested by Binnekamp (see Chapter V). The assignment of this species to *Obturamentella* is also questionable, but it certainly makes more sense.

2. The generic division of the stock comprising *Eoglossinotoechia* and *Glossinulus* is unsatisfactory, in spite of the emendations which have been recently proposed by Schmidt and McLaren (1965). A revision of the classification of this group is very disirable but beyond the scope of this publication. The generic names therefore have been given here in accordance with the works of Havlíček (1961) and Schmidt and McLaren (1965).

3. One new genus is erected, viz. *Kransia*. This genus comprises a number of mainly Middle Devonian species which were formerly assigned to *Uncinulus*, such as "*Uncinulus*" *parallelepepidus*, "*U.*" *primipilaris* and "*U.*" *goldfussii*. The differences with representatives of the genuine genus *Uncinulus* appear to be very significant (see Chapter V). A further discussion of the genus *Kransia* is given in the Appendix.

6. THE DESIGN OF THIS PUBLICATION

The main intention of this publication is to discuss some important morphological features of these animals which up to now have not been studied in sufficient detail. Many of the given descriptions can also be applied to other groups of Brachiopoda. In the end some suggestions will be made on the phylogeny and the classification of the Uncinulidae.

Some aspects of the microscopic shell structure of the species studied are described in detail. An attempt is made to explain the observed phenomena. This is often possible by means of a dynamic interpretation of the structures, i.e. by considering the structures as the result of shell growth.

From the jutting crests of the zigzag-deflected commissure of most Uncinulidae marginal spines project into the mantle cavity and may form a more or less developed grille situated in the opening of the shell. A functional analysis of these structures is given. A systematic description of the marginal spines in the species investigated reveals that an evolutionary development has taken place from an unspined zigzag deflection in Silurian species to a rectimarginate shell with very long spines in Middle Devonian species. Some cases of a homoplastic formation of marginal spines are discussed.

The statements by Rudwick (1959) on the growth of the exterior features of the hinge are subjected to a critical examination. It appears that no clear-cut distinction exists between strophic and non-strophic shells. The mechanism of the articulation and the closure of the posterior part of the shell are examined and compared in a considerable number of species. An attempt is made to reconstruct the position of the outer epithelium in the posterior part of the shell.

Many of the data which are obtained in the preceding chapter can be considered as new characters to be used in systematics. In the enclosure at the end of this publication short descriptions based on these characters and on some others from the literature are given in tabular form of all the uncinulid species studied. The tabulated data have been worked out numerically with the aid of the computer. On the ground of the correlation factors which thus are obtained some suggestions are made as to the phylogeny of the Uncinulidae. Some systematic implications are discussed.

7. TECHNIQUES

The internal structures of the shells have been studied in serial sections. Peels have been prepared of these sections by using 3 mm thick acetophane. Drawings of the sections and of the peels were made by means of the Wild M5 binocular microscope and the Wild M20 microscope; these instruments were provided with a drawing tube after Treffenberg.

For the preparation of three-dimensional reconstructions of the internal structures of the brachiopods an important technical improvement has been developed. The enlarged drawings of the sections are copied on to thin glass plates which are then mounted on an appropriately sized block in such a way that the spaces between the glass plates correspond with the distances between the sections and that the drawings on the plates are appropriately situated relative to each other. Stereophotographs are made of this arrangement from all desired points of view. These stereophotographs were taken with a Nikon Photomatic slr. camera, provided with a tele-lens and mounted on a Novoflex Gastel Apparatus (sledge). From these photographs the three-dimensional reconstructions can often easily be drawn by means of a stereoscope. Pl. IX, fig. 6a and b shows a set of such stereophotographs. The corresponding reconstruction is represented in fig. 55. By the application of this relatively simple technique the amount of time and toil involved in the reconstruction of the interior of brachiopod shells is considerably reduced.

The photographs which are reproduced in the Plates have been made partly with a Nikon Photomatic slr. camera (for small magnifications) and partly with a Leitz Ortholux microscope (for high magnifications).

II ON THE STRUCTURE AND GROWTH OF THE SHELL

1. INTRODUCTION

The microscopic structure and the growth process of the articulate brachiopod shell are subjects which have tended to be seriously neglected for a very long time in palaeontology. In the second half of the nineteenth century and the first decades of this century they have been given some rather sporadic consideration, e.g. by Carpenter (1843, 1855), King (1867), van Bemmelen (1882), Blochmann (1908), and Leidhold (1920, 1925). Although these authors have revealed many important features of the shell structure, their results and methods were only very limitedly applied in palaeontologic research.

In recent times, however, new attention has been given to these problems. It is in the first place Williams, who, in a number of admirably erudite and original publications, has given a new impetus to the study of these subjects (Williams, 1956, and 1966, Williams and Rowell, 1965). His observations on the intimate relation between the shell and the outer epithelium, and on the exact process of shell growth certainly will constitute the base of many further detailed investigations. The works of Cloud (1942), Vandercammen (e.g. 1959), Krans and Binnekamp (1965), Schumann (1965), and especially Krans (1965) are further examples of this increasing interest. These new developments in the study of brachiopods will certainly have important consequences. An increase of our knowledge of the growth and microscopic structure of all parts of the shell will not only give a better insight into the animal as a whole, but will also yield new criteria for the comparison between different species and for the discernment and interpretation of homoplasy, a phenomenon which, as is well known, is very frequent throughout the phylum. Finally all this will have important bearings on the study of the evolution and classification of these animals.

2. WILLIAMS's THEORY ON THE GROWTH OF BRACHIOPOD SHELLS AND AN IMPORTANT IMPLICATION

According to Williams the inner and outer epithelia mainly grow at their junction, the generative zone, which is situated at the bottom of a circumferential groove dividing the mantle edge into an inner and an outer lobe respectively (fig. 9). In this zone new epithelial cells are produced. After its formation a cell

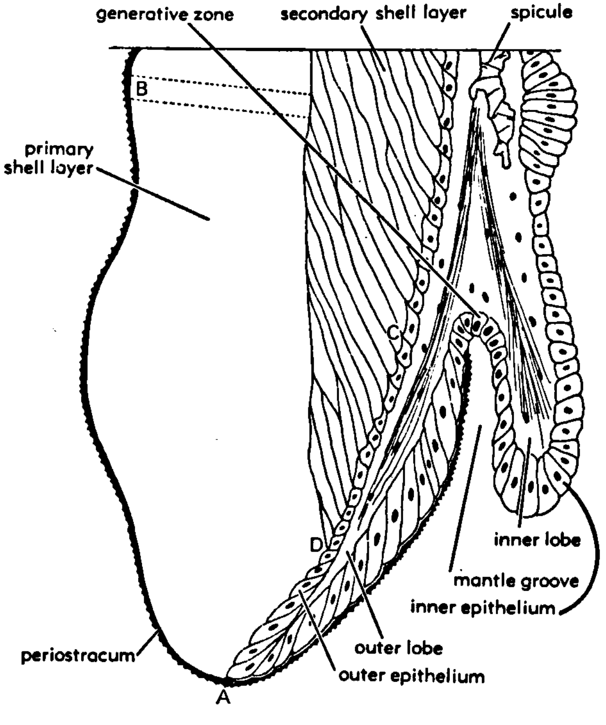

Fig. 9. Section through the mantle margin of an articulate brachiopod. (After Williams, 1956, slightly modified).

migrates towards the tip of either the outer or the inner lobe by the formation of new cells behind it and is incorporated into the outer or the inner epithelium respectively. The cells at the inner surface of the outer lobe are columnar in shape. They secrete the outermost layer of the shell, the periostracum, which consists entirely of protein, envelops the whole shell, and is never preserved in fossils. At the tip of the outer lobe the cells start the deposition of finely fibrous calcite at their outer surface and so become separated from the periostracum by a gradually thickening calcareous layer. At this stage the cells are still columnar in shape. The long axes of the fibres are normal to the shell surface. No organic traces have been found in this layer. This type of calcite deposition only occurs along the edge of the outer lobe. Consequently the periostracum is internally lined by a thin but continuous, exclusively calcareous sheet, the primary layer.

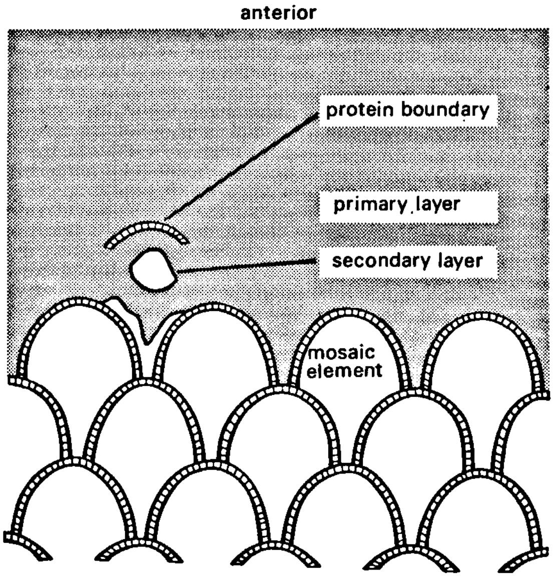

Fig. 10. Diagrammatic internal surface view of the junction between the primary and secondary layers of the articulate brachiopod shell. (After Williams, 1966).

As growth proceeds and the mantle edge is displaced radially, the process of shell deposition of the originally marginal cells undergoes an important change, while new cells are brought into a position to be involved in the formation of the primary layer. At this stage the cells become cuboidal and begin secreting protein along their exterio-anterior boundary and calcite along the rest of their outer surface. The protein-secreting boundary of a cell is arc-shaped and anteriorly convex, the bases of the arc being fixed to the front of the protein boundaries belonging to the cells immediately behind (fig. 10). In this way elongated, subparallel calcite fibres are formed, each of which is related with one cell of the outer epithelium, lengthens during its growth, and is enveloped in a continuous sheath of protein (Williams, 1966)[3]. See Plate III, fig. 1 and 2. This type of shell secretion is consistent, apart from some minor variations, over the whole inner shell surface, with the exception of the narrow strip at the valve edges where the primary layer is secreted. The resulting deposits constitute the secondary layer, which makes up the bulk of the shell[4].

The structure of the primary and secondary shell layers is commonly well preserved in fossils. The protein sheaths in the secondary layer have disappeared of course but the fibres they enveloped can in general be easily distinguished.

In many thick-shelled Uncinulidae the normal fibrous structure of the secondary shell undergoes an important modification by which the posterior part of the shell comes to consist mainly of thick calcite prisms, of which the c-axis is perpendicular to the inner surface and generally also to the outer surface. Pl. II, fig. 4; Pl. VII, fig. 2. Most of the apical structures are generally covered with a thick sheet of this 'prismatic' layer. Alexander (1948) first described this layer from the Pentameracea, while Dunlop (1962) found it in *'Spirifer' trigonalis* and called it the "columnar layer". Williams considers the prismatic layer to be a particular modification of the secondary layer; the difference being that in the prismatic layer there is no protein secretion by the epithelial cells. The prismatic layer, however, should not be confused with the myotest, as Williams does (Williams and Rowell, 1965); cf. § 15[5].

The principle involved in secondary shell growth as depicted above is that each fibre forms the trajectory along which the corresponding epithelial cell has travelled during the period it was engaged in the formation of the secondary layer. As a result the fibres run from the inner surface of the primary layer to the inner surface of the shell (fig. 11). An exception to

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[3] The assumption by Williams that every fibre of the secondary layer has been deposited by only one epithelial cell constitutes the starting-point of many of the following considerations. We should not forget, therefore, that Williams has in fact repeatedly postulated this allegation but has never proved it. It remains to be seen whether this statement is the result of careful and direct observations of the phenomenon in question, or of an intelligent speculation e.g. based only on examination of brachiopod shells (this would appear to be the case from his 1966 paper). In any case it conflicts with the observations of van Bemmelen, who drew a thin connective tissue layer between the epithelium and the protein boundaries in a longitudinal section through the decalcified shell of 'Waldheimia cranium' (van Bemmelen, 1882, Fig. 8). Van Bemmelen's observation may, however, be due to poor preparation of the animals.

[4] Not all fibres originate at the valve edges; they may also arise by inframarginal cell division in the outer epithelium. This type of fibre and cell proliferation is known to occur even abundantly in the formation of the internal apical structures of the shell.

[5] Copper (1967) has observed that the prisms are structually continuous with the fibres. I have not studied the prismatic layer in sufficient detail to verify this most interesting statement.

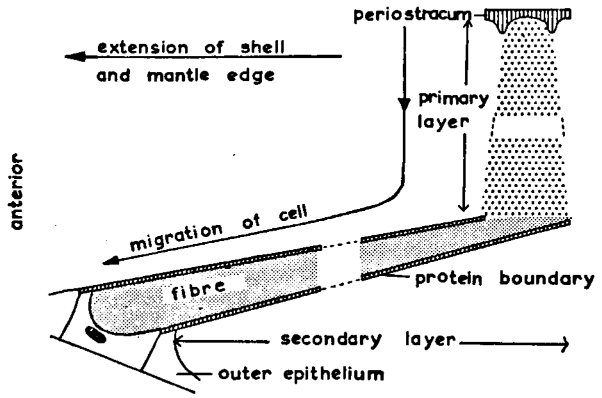


Fig. 11. Diagrammatic longitudinal section showing the trajectory along which an epithelial cell has travelled during the period it was engaged in the formation of the three layers of an articulate brachiopod shell. (After Williams, 1966).

this rule is constituted by the fibres which have orginated by inframarginal division of the outer epithelial cells; but these too will invariably run towards the inner shell surface.

The course of a fibre may be very erratic. Nevertheless, the course of all fibres in a considerable part of the shell generally follows a similar, often complicated pattern. In other words: the trajectory of the shell-secreting epithelial cells may be complicated, but is often comparable in considerable parts of the epithelium.

It is obvious that a close scrutiny of the shape and course of the fibres is of paramount importance for the understanding of shell growth and structure. Moreover, the fibres provide a key to the study of the behaviour of the epithelium during the process of shell growth. Finally, since striking differences in these phenomena can be observed in different species, these investigations are obviously of great systematic value. However, surprisingly little attention has been given to these problems: as far as I know only Williams and Krans have dealt with the subject in some detail. This neglect may be due to the fact that nearly every attempt to describe and to interpret correctly these phenomena meets with serious difficulties, which are partly of a geometrical and technical character and partly due to our still imperfect knowledge of the process of shell deposition by the outer epithelium in living brachiopods. Thus, although the problems involved are very attractive and fascinating, their treatment mostly results in a deceptive amount of time-consuming fancy.

3. THREE TECHNIQUES AND SOME PRELIMINARY RESULTS

Three techniques have been used for the investigation of the fibres:

1. the examination of shell mosaics;
2. the examination of chips of the secondary shell layer and of the surfaces which are uncovered by these chips.
3. the examination of the fibres in sections through the shell, especially in acetate peels.

(Sub 1). At the inner surface of the secondary layer the extremities of the fibres and their protein sheaths are arranged into a so-called shell mosaic, which is of course strongly related to the pattern of shell-secreting cells in the outer epithelium, or more precisely to that of those parts of the cell surfaces which face the interior of the shell. In recent and subrecent shells this mosaic can easily be studied in collodion peels of the inner shell surface (Williams, 1965). In fossils this method can only be applied when the internal mould is so soft that it can easily be removed (Leidhold, 1920). In Palaeozoic fossils, however, this is only exceptionally the case. Here, well preserved internal moulds may sometimes locally display a cast of the mosaic, but in many instances very good results were obtained by grinding the fossils parallel to their surface at the spot where the mosaic was to be observed till the inner shell surface was just exposed, and then making an acetate peel of the ground surface. Some of the results are shown in pl. I and II. In some species, such as *Uncinulus pila* and *U. subwilsoni*, only traces of the mosaic were obtained by applying this technique; in others *(Uncinulus orbignyanus, Eoglossinotoechia sylphidea, Glossinotoechia lata, Eucharitina eucharis, Markitoechia lebanza* and *Decoropugnax berenice)* the results were poor to reasonable, whereas in *Spaerirhynchia wilsoni, Hypothyridina cuboides, Kransia parallelepipeda, Eoglossinototoechia mystica, Glossinotoechia henrici,* and *Hebetoechia hebe,* the mosaic was reasonably to well exposed.

In principle the outline of any mosaic element is determined anteriorly by the convexly arcuate protein boundary of the corresponding epithelial cell, and posteriorly by the similarly arranged protein boundaries of the cells immediately behind. The corresponding pattern has been designated by German authors with the appropriate, although somewhat militaristic, term "Schuppenpanzerstruktur" (fig. 10).

It is a well known fact that the mosaic may undergo considerable changes during growth, partly due to modifications of the outwardly facing surfaces of the secreting cells and partly to changes in the process of deposition. In the first place the epithelial cells as well as the mosaic elements will increase in size during growth. This is revealed immediately by comparison of the elements near the commissure with those more inwardly situated. In a well preserved specimen of *Sphaerirhynchia wilsoni* I found that the mosaic elements very near the commissure have a diameter of 10 μ and more posteriorly of 40 μ; a linear increase of 4 × !

Another type of mosaic deformation occurs at the muscle bases; here, the pattern is often blurred, problably by the reduction of the protein secretion, so that a finely granular shell layer may be deposited (myotest of Krans, 1965; see also Krans and Binnekamp, 1965, Williams, 1966, Williams and Rowell, 1965). We shall see below, however, that this disposition is somewhat different in many of the rhynchonellid species studied in this paper.

Finally, van Bemmelen (1882) and also Blochmann (1908) have shown that the mosaics of *Gryphus vitreus* and of *Hemithyris psittacea* become extremely irregular in the older parts of the shell. It is not improbable that this pattern would correspond with the gross, so called prismatic layer, which very often occurs in great quantities in uncinulid shells.

The typical "Schuppenpanzerstruktur" is only rarely displayed in the mosaics shown in pl. I and II (e.g. in *S. wilsoni, E. eucharis, E. mystica).* More commonly the elements have a rhomboidal or polygonal outline. In some species, such as *Hypothyridina cuboides,* these features are so consistent as to constitute a typical character of the species; in others, however, they are merely local modifications of a much more variable pattern.

All these modifications should be studied more closely in recent as well as in fossil brachiopods. Ideally, the entire shell mosaic of a species should be carefully described in order to be useful in systematics. This, however, would be extremely laborious if not impossible. Leidhold has pointed out that in spite of the local variations which may occur in the mosaic of one shell the pattern displays enough consistency in front of the muscle bases and at some distance of the commissure to be usable in systematics. His argument is sustained by Williams (1966) as well as by my own observations. In uncinulid brachiopods the mosaic near the frontal border of the paries geniculatus has been found to be fairly constant in one specimen as well as within one species. Therefore most of the mosaics figured in pl. I and II have been taken in this region. Thus, although adequate caution has to be exercised in drawing too drastic inferences from the sparse data obtained, I believe that some general statements can safely be made. The results are given in enclosure I.

An important observation on the mosaics is that the longest diagonals of the elements have always been found to be more or less coincident with the projections of the longitudinal axes and thus of the direction of growth of the fibres on the inner shell surface. When the growth of a fibre changes in direction a corresponding modification occurs in the orientation of the related mosaic element. In mosaics with a typical "Schuppenpanzerstruktur" the direction of growth corresponds with the convex arcs of the elements.

(Sub 2) In the nineteenth century it was already known that the brachiopod shell chips easily along planes of minimum resistance, the position of which is largely determined by the stacking of the fibres. It is very easy to produce such flakes by cutting the shell with a razor-blade, and with the help of a binocular it is possible to make them in whatever thickness and direction desired (fig. 12). They can be studied under the microscope in incident light and when very thin in transmitted light, and often reveal invaluable data about the stacking and shape of the fibres involved. It is often useful to make stereoscopic microphotos; these can be obtained by photographing the object in different places of the field. When the fibres are of average coarseness enlargements of some 400 times are found to be the most appropriate (Pl. III, fig. 7 and 7 a; Pl. IV, fig. 3).

The shell surfaces uncovered by the chips can be studied under the binocular and display sometimes beautifully the relation between the local shell form and the course of the fibres (Pl. III, fig. 3 and 4; Pl. IV, fig. 1, 1a, 2, 2a; Pl. V).

This technique can be applied almost exclusively for the study of the outer structure of the shell. As far as I know this has not been done before.

The shape of a fibre is a function of the outline of its mosaic element and of the angle between its longi-

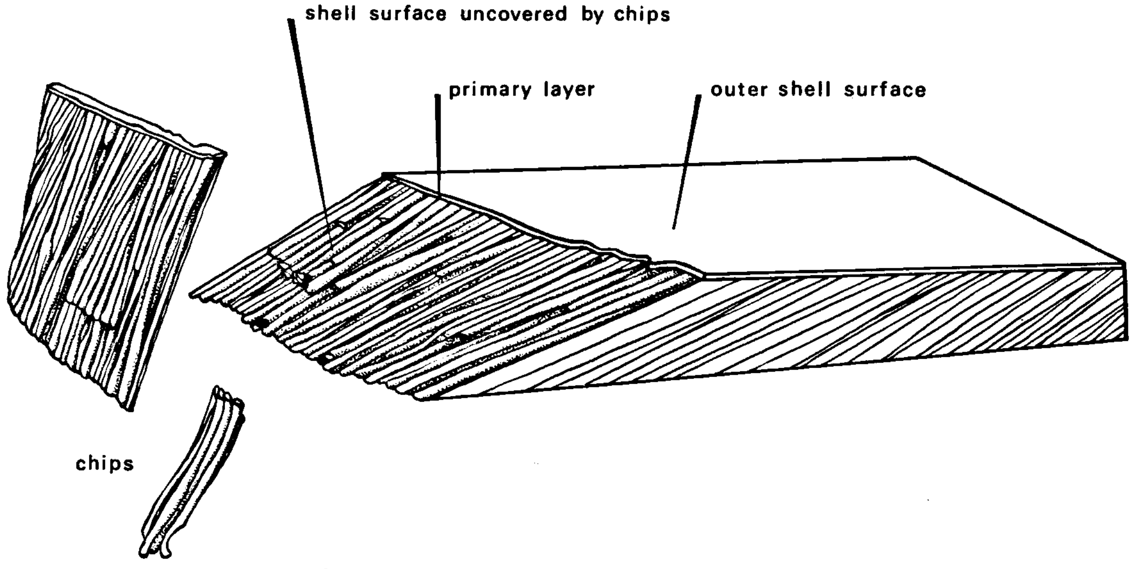


Fig. 12. Chips of fibres of the secondary shell layer.

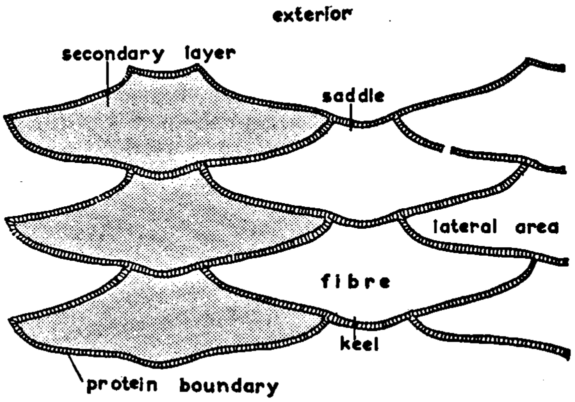


Fig. 13. Diagrammatic transverse section showing the relationship between fibres of the secondary layer of an articulate brachiopod shell. (After Williams, 1966).

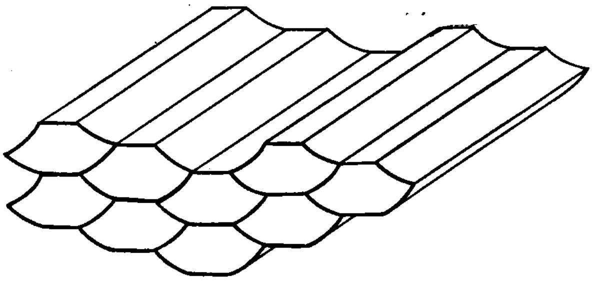


Fig. 14. In chips fibres often look much narrower than they really are.

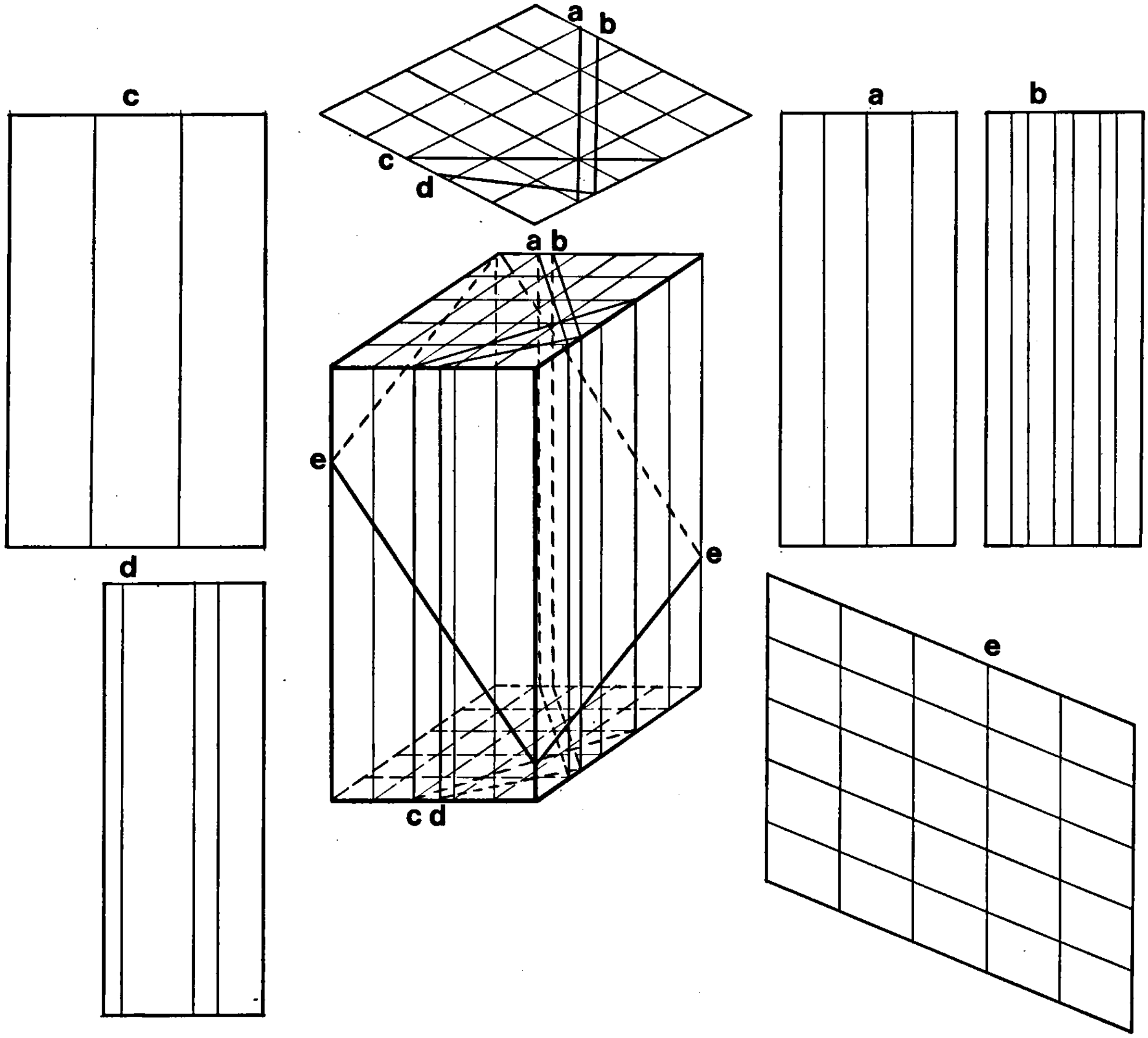


Fig. 15. Some sections through a bundle of fibres. The size of a fibre cannot simply be evaluated from random sections.

tudinal axis and the inner shell surface. Williams (1966) has demonstrated that transverse sections through a bundle of fibres related with a "Schuppenpanzerstruktur" show a typical pattern of more or less rhomboidal elements with lateral areas, saddles and keels (fig. 13)[6].

When chips of fibres of this stacking are studied under the microscope one can very easily make mistakes as to the breadth of the fibres, which often look much narrower than they really are (fig. 14). Fibres related with a rhomboidal mosaic show a pattern of flattened rhombs in transverse sections. Here, the danger of underestimation of the breadth of the fibres in chips is reduced.

(Sub 3) Sections through the shell often give valuable information about the fibres. Especially acetate peels of serially ground surfaces have been used with much profit (see also Krans, 1965). This method is disadvantageous in so far that the sections are generally oriented according to the overall shape of the shell, and thus will cut at random through the fibres (Pl. III, fig. 1, 2). Some of the difficulties have been seen which may arise when evaluating the dimensions of the fibres in chips. The same difficulties are met with in the interpretation of sections through the fibres in acetate peels of ground surfaces but here they are a bit more complicated.

In the following preliminary analysis for the sake of convenience the fibres will be compared with very elongated prisms which constitute a parallelogram in cross section. Fig. 15 represents a number of possible sections through a bundle of such fibres. The great variation displayed may illustrate the danger involved in the uncritical evaluation of the actual shape and dimensions of the fibres after random sections. However, the following general statements can be made in order to grasp the possibilities which nevertheless exist here.

1) A normal section through a fibre is the section with the smallest possible surface and dimensions.

2) A random section through a fibre will always constitute a parallelogram; the shortest distance possible between two opposite sides of such a parallelogram is always shorter than the longest diagonal of a normal section through the same fibre.

Proof[7]

Let ABCD, a normal section through the prism, be a parallelogram, and AC (= d) be the longest diagonal through that section (fig. 16). Then ∠ ABC (= ∠ φ) is obtuse, and cos φ < 0 . AB = a; BC = b.

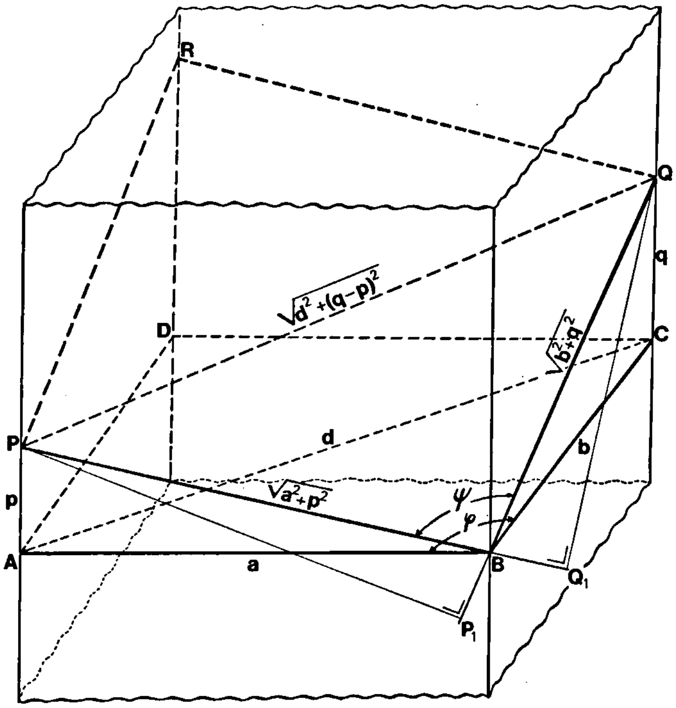


Fig. 16. A random and a normal section through a fibre.

ABCD is chosen in such a way as to have one angular point (B) in common with a random section PBQR. AP = p, QC = q. PB = $\sqrt{a^2+p^2}$, BQ = $\sqrt{b^2+q^2}$, and PQ = $\sqrt{d^2+(q-p)^2}$. The perpendicular from P on BQ is PP_1, or h_p, and from Q on PB is QQ_1, or h_q; ∠ PBQ = ψ. $h_p = \sqrt{a^2+p^2}\sin\psi$; $h_q = \sqrt{b^2+q^2}\sin\psi$.

Suppose $h_p < h_q \longleftrightarrow a^2+p^2 < b^2+q^2$ . . . . . (1)

$$PQ^2 = PB^2 + BQ^2 - 2\,PB\,.\,BQ\cos\psi$$

$$2\,PB\,.\,BQ\cos\psi = PB^2 + BQ^2 - PQ^2$$

$$\cos\psi = \frac{PB^2 + BQ^2 - PQ^2}{2PB\,.\,BQ}$$

$$h_p^2 = PB^2\sin^2\psi = PB^2\left[1 - \frac{(PB^2 + BQ^2 - PQ^2)^2}{4\,PB^2\,.\,BQ^2}\right]$$

$$h_p^2 = PB^2 - \frac{(PB^2 + BQ^2 - PQ^2)^2}{4\,.\,BQ^2}$$

$$h_p^2 = a^2 + p^2 - \frac{[a^2 + p^2 + b^2 + q^2 - d^2 - (q-p)^2]^2}{4\,(b^2+q^2)}$$

$$d^2 - h_p^2 = d^2 - a^2 - p^2 + \frac{(a^2 + b^2 - d^2 + 2\,pq)^2}{4\,(b^2+q^2)}$$

$$(b^2+q^2)\,(d^2 - h_p^2) = (b^2+q^2)\,(d^2 - a^2 - p^2) + \frac{(a^2 + b^2 - d^2 + 2\,pq)^2}{4}$$

$$d^2 = a^2 + b^2 - 2\,ab\cos\varphi$$

$$(b^2+q^2)\,(d^2 - h_p^2) = (b^2+q^2)\,(b^2 - 2\,ab\cos\varphi - p^2) + \frac{(2\,ab\cos\varphi + 2\,pq)^2}{4}$$

$$(b^2+q^2)\,(d^2 - h_p^2) = (b^2+q^2)\,(b^2 - p^2 - 2\,ab\cos\varphi) + (ab\cos\varphi + pq)^2$$

Suppose $\cos\varphi = -\,\Theta$, where $0 < \Theta < 1$

---

[6] As the convex arcs of the elements correspond with the direction of growth of the fibres, one would expect the convex protein boundaries to face towards the exterior in transverse sections. This, however, is in contradiction to the statements by Williams (see his fig. 6 = our fig. 13), and to my own observations. I have no explanation for this.

[7] I wish to express my profound gratitude to Dr. L. M. de Haan, 's-Gravenhage, for providing the following elegant proof to this theorem.

$$
\begin{aligned}
(b^2 + q^2)\,(d^2 - h_p^2) &= (b^2 + q^2)\,(b^2 - p^2 + 2\,ab\Theta) + \\
&\quad + (pq - ab\Theta)^2 \\
&= (b^2 + q^2)\,(b^2 - p^2) + \\
&\quad + 2\,ab\Theta\,(b^2 + q^2) + p^2q^2 - \\
&\quad - 2\,abpq\,\Theta + a^2b^2\Theta^2 \\
&= b^4 - b^2p^2 + b^2q^2 + \\
&\quad + ab\Theta\,(2\,b^2 + 2\,q^2 - 2\,pq) + \\
&\quad + a^2\,b^2\,\Theta^2 \\
&= b^2\,(b^2 - p^2 + q^2) + \\
&\quad + ab\Theta\,(2\,b^2 + 2\,q^2 - 2\,pq) + \\
&\quad + a^2b^2\Theta^2 \quad \ldots\ldots\ldots \quad (2)
\end{aligned}
$$

$$a^2 + p^2 < b^2 + q^2 \quad \ldots\ldots\ldots\ldots\ldots\ldots \quad (1)$$

$$b^2 - p^2 + q^2 > a^2 > 0$$

$$
\begin{array}{r}
a^2 + p^2 > b^2 + q^2 \quad \ldots\ldots\ldots \quad (1) \\
b^2 + q^2 - 2\,pq = b^2 + q^2 - 2\,pq \\
\hline
0 < a^2 + b^2 + (p - q)^2 > 2\,b^2 + 2\,q^2 - 2\,pq
\end{array}
$$

The three terms of (2) all appear to be positive, thus:

$$
\begin{aligned}
(b^2 + q^2)\,(d^2 - h_p^2) &> 0 \\
d^2 - h_p^2 &> 0 \\
d^2 &> h_p^2
\end{aligned}
$$

$$\boxed{d > h_p}$$

Quod erat demonstrandum.

(3) Only if the shortest distance between two opposite sides in a random section through a fibre is longer than the longest diagonal in a random section through another fibre, can one positively compare the size of both fibres, in so far as their longest diagonals in normal sections are concerned. This diagonal will certainly be longer in the first fibre than in the second one.

Proof

Let h_1 be the shortest distance in the random section, and d_{n1} the longest diagonal in a normal section through the first fibre; let d_2 be the longest diagonal in the random section, and d_{n2} idem in the normal section of the second fibre.

$$
\left.
\begin{array}{l}
\left.\begin{array}{l} h_1 > d_2 \\ d_2 > d_{n2} \end{array}\right\} \; h_1 > d_{n2} \\
\\
h_1 < d_{n1}
\end{array}
\right\} \; d_{n1} > d_{n2}
$$

Conversely, the size of fibres cannot be compared explicitly in random sections which do not conform to this condition Consequently, in sections 1 and 2 the size of the corresponding fibres cannot be compared; the same holds for sections 2 and 3; however, d_{n3} is longer than d_{n1}, d_1 being shorter than h_3 (fig. 17).

(4) In some cases it might be of interest to compare the size of the mosaic elements of different fibres which are only known from random sections. We have seen before (p. 16) that the long diagonal of a mosaic element is in line with the projection of the longitudinal axis of the fibre on the inner shell surface. When the angle α between this projection and the actual fibre axis is very small (and this is normally the case), the longest diagonal of a normal section through the fibre will be equal to the shortest diagonal of the mosaic element. In this case it is possible to compare the shortest diagonals of two mosaic elements in random sections, provided that these sections conform to the conditions stated under 3.

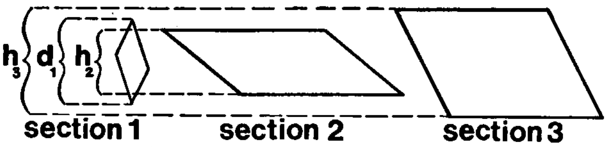


Fig. 17. Comparison of random sections through three different fibres.

However, the orignally shortest diagonal of the normal section will increase in length with *a*, and when *a* exceeds a certain minimum (which depends on the shape of the mosaic element) this diagonal will exceed the orginally longest diagonal in length and the comparison will be more complicated, if not impossible. As α is known to be generally fairly small, this will rarely be the case. Moreover, as the diagonal of the random section which corresponds with the longest diagonal of the mosaic element is often directed normally to the inner shell surface and connects the saddles and the keels (see p. 18) the situation can generally be adequately analysed.

(5) A special problem arises regarding the longitudinal sections through the fibres, of which some examples are shown in fig. 15. Here, the diagonals are extremely elongate and cannot serve adequately in the comparison in shape between the fibres. Depending upon their orientation very thin and very wide longitudinal sections through a bundle of fibres can be obtained. One can only argue that the longest diagonal of the normal section will be minimally as long as the width of the section exposed. Comparisons between the size of the fibres in normal sections are however not possible on this basis.

(6) Although great caution must be observed in interpreting the dimensions of the fibres in random sections, the difficulties can be considerably reduced when the orientation of the sections relative to the fibres is known. Tangential sections through the shell which in addition cut longitudinally through the fibres will generally be parallel with the shortest diagonals of the mosaic elements (and thus generally with the longest diagonals of the normal sections). On the contrary longitudinal sections through the fibres which are perpendicular to the shell surface will be parallel to the longest diagonals of the mosaic elements (and to the shortest diagonals of the normal sections).

It is also often obvious in non-longitudinal sections how these are oriented relative to the fibres. When two bundles of fibres are known to be dissected at the same angle one may, with due reserve, draw conclusions as to the normal sections. A thorough and critical analysis of the situation is therefore an essential condition for the study of the size of the fibres in random sections.

Finally, I want to repeat here that the above conclusions are only valid for fibres which display a parallelogram in normal sections. The question is, therefore, often even more complicated.

4. FIVE QUESTIONS. A MODEL OF THE EPITHELIUM

In the following account an attempt will be made to describe and interpret the course, shape and size of the fibres of the secondary shell layer in the light of a number of concrete examples. For each example five successive questions will be posed.

1. What are the course, shape, size, and mosaic of the fibres?
2. Which changes and movements of the epithelial cells lie at the root of these features?
3. Do these changes and movements occur with any regularity; and if so, what rules can be established? In the framework of this question an attempt will also be made to compose a comprehensive model of the outer epithelium which will include all the properties recorded for it.
4. What is the cause of these changes and movements?
5. What is their function?

Only very rarely an answer can be given to the last two questions.

With reference to the third question it will be attempted to compose at first a provisional model of the outer epithelium, based on the data available at this stage.

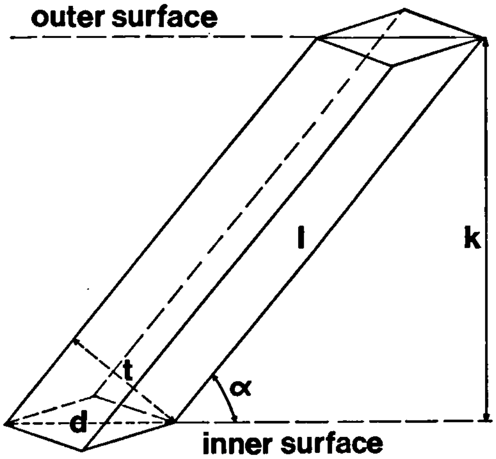
The outer epithelium is a cellular membrane, one cell in thickness. It grows in extent by addition of new cells at its border, whereas locally inframarginal cell division may occur. It is known that the outer epithelium is responsible for the secretion of the shell, according to the principles given by Williams. The study of the shell mosaics has already shown that the mosaic elements and thus the cell surfaces facing the exterior are very variable in size and shape, in one specimen as well as in different species. The longest diagonals of the mosaic elements and of the corresponding cell surfaces have invariably been found to correspond with the direction of the cell migration during growth.

5. THE STRUCTURE OF THE FIBRES

Williams (1966) has argued that the surfaces of the cells which are directed towards the shell are concave. This statement corresponds with the observations made by Krans on the structure of the fibres in spirifers (Krans, 1965, p. 84). These fibres display a ladder-shaped structure in longitudinal sections, with arcuate rungs, the convex sides of which face the youngest end of the fibre. Krans has interpreted this phenomenon as being caused by discontinous calcite secretion of the corresponding epithelial cells. This is also a very general feature in the rhynchonellids studied. See e.g. Pl. IX, fig. 3.

6. RELATION BETWEEN THE SHAPE, SIZE AND POSITION OF THE FIBRES IN THE SHELL

In fig. 18 the relation is shown between the thickness *(t)* and the length *(l)* of a fibre, and the angle α between the fibre axis and the inner shell surface. When d is the longest diagonal of the mosaic element t decreases in length from d to 0, and l increases from k to ∞ with α decreasing from 90° to 0°. Thus, the larger the angle α, the shorter and thicker the fibres; the smaller the angle α, the longer and flatter the fibres in shells of equal thickness. Long (and thus flat) fibres are related to mobile; short (and thus thick) fibres to non-mobile epithelial cells. See also p. 31: the septum *S. wilsoni*. It is very striking that in all the species investigated the fibres related to a gross mosaic belong to the short and thick type, and that those related to a fine mosaic are long and flat. It is of course dangerous to generalize on this statement, which is in fact based on only a few data. More observations are needed on the subject.



$$l = \frac{k}{\sin\alpha}\,;\ t = d\sin\alpha$$

Fig. 18. The relation between the thickness (*t*) and the length (*l*) of a fibre, and the angle *a* between the fibre axis and the inner shell surface.

With respect to the model of the epithelium it may be concluded, with due reserve, that large cells are less mobile than small ones.

7. THE LENGTH OF THE FIBRES

In a specimen of *Trigonirhynchia pareti* the length of a considerable number of fibres located along a radial line in the shell has been measured. These measurements have been plotted in fig. 19 against the distance between the loci of origin (i.e. the outwardly pointing tips of the fibres) and the commissure. The length of the fibres appeared to increase very rapidly within a short distance from the commissure, and then to remain nearly constant up to the beak. From this one may conclude that the growth rate of the fibres and the shell-secreting activity of the epithelial cells reach their maxima near the commissure and then decrease rapidly till they come almost to a standstill in the rest of the shell. No further exact measurements have been made in other shells, but other more preliminary observations on shells of many species strongly suggest that this phenomenon (although probably not exclusive) is very common among brachiopods. It is only in the very posterior part of the shell that the growth of protruding inner elements may give rise to a local renewal of fibre growth.

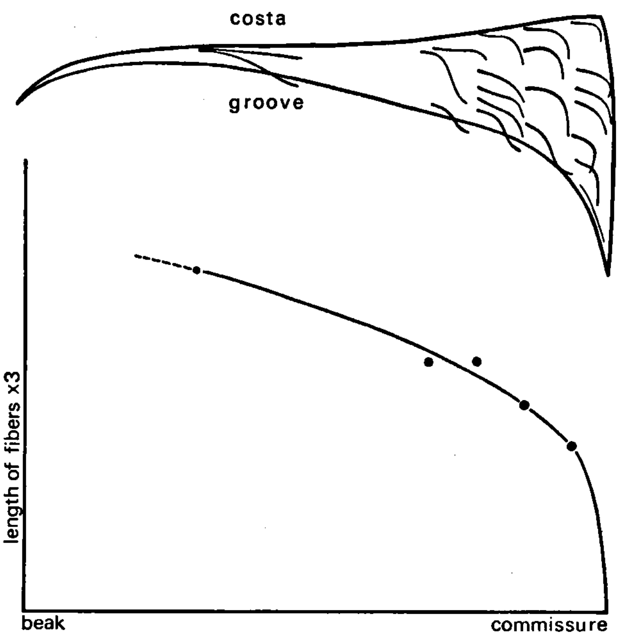


Fig. 19. *Trigonirhynchia pareti.* The length of the fibres and their distance from the commissure.

8. MUTUAL MOBILITY OF THE CELLS

Plate IV, fig. 3, represents a close-up of some fibres in a tooth of the Jurassic species *Kallirhynchia concinna.* Some of these fibres which originally lay against each other are slightly divergent, whereas the underlying or overlying fibres fill up the space arising between them. When translating this phenomenon into terms of epithelial cell movements it must be considered that fibres which lie side by side were secreted by cells which also lay side by side, and that fibres situated at some distance from each other were secreted by cells which lay at least at this distance from each other. So, when fibres which originally lay side by side diverge it must be concluded that the corresponding cells were also divergent; and when the originally underlying and overlying fibres are inserted between the divergent ones, then the corresponding cells, which must have lain behind and in front of the separate cells, must also have been inserted between these.

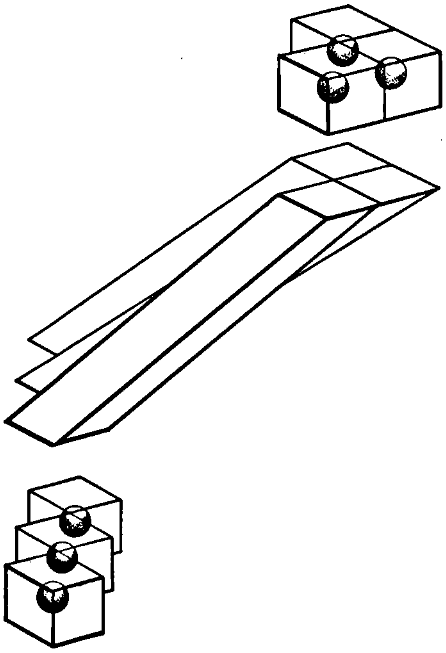


Fig. 20. Divergence of the fibres and concomitant divergence of epithelial cells.

The phenomenon is represented in fig. 20, which is incorrect, however, in so far as the shape of the fibres and cells is concerned. To prevent confusion the fibre overlying the separating ones has not been drawn; it would have been cut into two pieces by the underlying one during the process of its insertion. The same is true for the corresponding cells. In fact any divergence of fibres and cells must be concomitant with drastic transformations of all the cells and fibres involved.

This divergence of the fibres was found to be a most common phenomenon; in fact it can be traced more or less distinctly in any brachiopod shell. In *Trigonirhynchia pareti* it is very pronounced in the costae. Here, bundles of fibres originating at the very ridge of the costae spread out fan-wise towards the inner shell surface (fig. 21; pl. V). This phenomenon will be treated more extensively below.

Regarding the model of the epithelium it may be concluded that the cells display a considerable mutual mobility.

9. SOME NEW TERMS

The following preliminary considerations may serve for a better understanding of the next sections. In this connection it is necessary to introduce some new terms.

The entire complex of properties, or a reduced number of these properties, on which attention is focused at a given moment is called the *modality* of (a), (b) and (c) respectively, where (a) is the process of shell growth at a certain place of the inner shell surface and during a very short interval of time; (b) is the corresponding part of the outer epithelium during the same interval of time, in so far as these properties influence the process of shell growth; and (c) is the part of the shell secreted by (b) during this time interval.

Any coherent part of the outer epithelium in which the modality is equal, and different from its surroundings is termed an *epithelial unit.* The identity of an epithelial unit may be preserved during a part of or during the whole period of growth of the shell. It is possible, however, that an epithelial unit is constituted continuously by different cells during the period of its existence. For instance, the part of the epithelium involved in the formation of the primary shell layer clearly consitutes a very stable epithelial unit during the whole growth of the shell, but different cells continuously form part of it.

An epithelial unit may be divided into minor, subordinate units when more properties are taken into account in the definition. Thus, the part of the

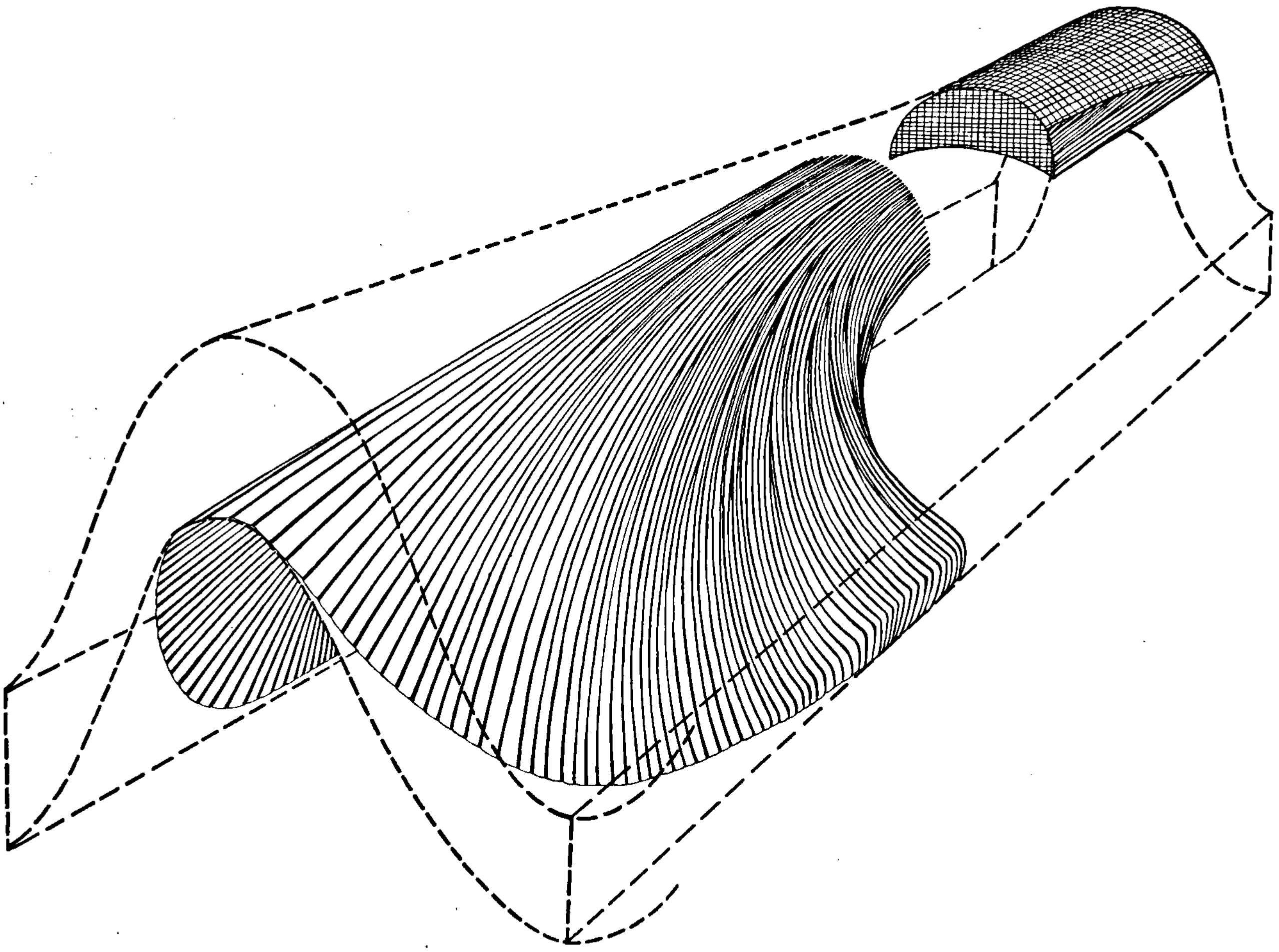


Fig. 21. The course of a bundle of fibres in a costa of *Trigonirhynchia pareti.*

epithelium involved in the formation of the secondary layer clearly constitutes an epithelial unit which, however, may be divided into a number of smaller units when attention is focused on properties such as the dimensions and shape of the epithelial cells, the direction of migration of the cells, the rate of shell secretion, the relative amount of protein secreted, etc. Finally, one may consider the individual epithelial cells as elementary epithelial units.

The whole outer epithelium, at a given moment of growth, can be considered to consist of a number of epithelial units which are bounded to each other by more or less sharp *epithelial unit boundaries.* Any change occurring in this pattern during growth will be called a *modification.* This term includes the changes which the cells undergo when migrating from one unit to another.

The part of a shell which is secreted by an epithelial unit is homogeneous, and differs from its surroundings in modality [8]. It will be termed a *shell unit.*

The whole shell can be considered to consist of a number of shell units, which are bounded to each other by more or less sharp *shell unit boundaries.* These boundaries constitute the record in the shell of both the epithelial unit boundaries during their entire development and the different modifications the epithelial unit pattern has undergone [9].

Shell units and shell unit boundaries and their respective modalities constitute the primary data available for the palaeontologist since they are directly provided by the fossil record. Using these primary data an attempt will be made to reconstruct the process of shell growth by applying the five successive questions formulated on p. 20. Here however the second question will be: "which epithelial units can be distinguished, how did they develop during the process of shell growth, where were they located, which modifications took place?"

The location of the different shell units and their boundaries in the shell are matters of extreme im-

---

[8] In this connection it may be useful to repeat what has already been suggested in the definition of the term modality, namely, that an epithelial unit is only characterized by proporties which influence the process of shell growth.

[9] In some epithelial units no shell secretion takes place; others are even known to dissolve already existing shell structures. No actual shell units correspond to these epithelial units. One might also consider these shell units to be superficial and negative respectively.

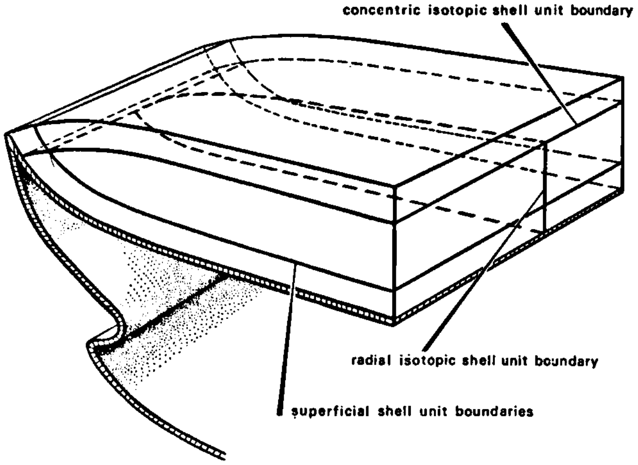


Fig. 22. The situation of different types of shell unit boundaries in the shell.

portance for their interpretation. The following types may be preliminarily distinguished (fig. 22).

1. *Isotopic* shell units and shell unit boundaries are the records of isotopic epithelial units and epithelial unit boundaries respectively [10]. The latter are characterized by the fact that they display a certain consistency during the whole or part of the shell growth process, and are localized during their entire existence on approximately the same positions in the growing outer epithelium. This constancy in position may be realized variously; it may e.g. mean a constant distance from the growing valve edge. Whether an epithelial unit or unit boundary is isotopic or not does not depend on its shape and position at a certain moment of its existence, but only on the trajectory along which it travels during its entire existence.

An epithelial cell migrating across an isotopic epithelial unit boundary undergoes a corresponding modification. Thus, in so far as isotopism is concerned, the modality of a cell is determined at any moment by its position in the growing outer epithelium. Isotopic epithelial units and epithelial unit boundaries characterized by a constant position in the overall growing epithelium can be radially and concentrically arranged. The corresponding shell units and their boundaries must be perpendicular and parallel respectively to the outer shell surface. All transitions occur. These shell units and boundaries invariably intersect the growth surface of the shell (Introduction, p. 6, Fig. 22). Isotopism is found to be by far the most common feature in brachiopod shell growth.

2. Shell units, epithelial units and unit boundaries that are non-isotopic are in the following account referred to as *anisotopic*. The *superficial* shell unit boundaries constitute a very special type. These occur along growth surfaces in the shell and must have originated as a result of simultaneous and momentary modifications of the corresponding parts of the outer epithelium. The inner surfaces of growth lamellae are an example (see e.g. Krans, 1965, p. 87—89, especially his fig. 14). For the rest it is not easy to find examples of anisotopism in brachiopod shells.

As a matter of fact this classification is of a most preliminary nature, due to the fact that the investigation of this subject is still in its infancy. At a later stage, when more factual data in respect of this matter will be available, further improvement can be made.

10. THREE IMPORTANT FEATURES IN BRACHIOPOD SHELLS

Attention is turned once more to the classical figure by Williams of a radial section through a brachiopod valve near the commissure (fig. 9). Here, some important shell units and shell unit boundaries are shown. First, there is the boundary between the periostracum and the primary shell layer. This boundary corresponds with the epithelial unit boundary between the protein-secreting epithelial unit, i.e. the inner surface of the outer mantle lobe, and the calcite-secreting epithelial unit located marginally on the outer surface of the outer lobe. The second shell unit boundary displayed is the transition from the primary into the secondary shell layer, corresponding in the epithelium with the boundary between the unit secreting pure calcite and the unit depositing calcite fibres enveloped in protein sheaths. Both these shell unit boundaries are clearly of the concentric isotopic type, as they are parallel to the outer shell surface and intersect the growth surfaces and the inner shell surface. The epithelial unit boundaries are very consistent and their location is rather constant during the whole growth of the animal. Different cells continuously form part of the epithelial units and migrate from one unit to another, undergoing an isotopic modification when passing an epithelial unit boundary.

The third important feature is the obliquely anterior direction of the fibres of the secondary shell layer. As shown in the figure, this phenomenon characterizes the entire part of the secondary shell layer displayed. Thus, the part of the shell with this modality constitutes a shell unit which is bounded by the primary shell layer, and the shell unit boundary is of the isotopic type. The following observations may help to explain this phenomenon.

During its formation each part of the inner periostracal surface must have been situated on the inner surface of the outer mantle lobe, where it was attached to the outer epithelial cells responsible for its secretion. Each of these cells has left a cast on the periostracum, so that its inner surface is pitted, each pit corresponding with an epithelial cell (Williams, 1966, Williams and Rowell, 1965). It may be concluded from this that in the inner surface of the outer mantle lobe the position of the cells in relation to each other as well as to the periostracum is already more or less established. At a later stage in the development these cells

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[10] It is very difficult to find appropriate terms for these concepts. Again and again I found that the terms I proposed had synonyms. *Isotopic* and *anisotopic* have at least the relative advantage of being synonymous with well-known terms of a very remote discipline so that confusion is excluded. As far as I know no homonyms exist.

contribute to the formation of the primary and secondary shell layers, and gradually become removed from the periostracum they once secreted. As far as the secondary layer is concerned, the trajectory along which the cells have travelled can be reconstructed, from the course of the fibres. It can be assumed therefore, that the cell which was situated on the inner periostracal surface at B in fig. 9 at the moment of the animal's death will have been located at C approximately. All the cells which lay between A and B on the periostracal inner surface are now found between A and C. This means a radial shortening of the corresponding epithelium of AB minus AC. This is indeed a considerable shortening and is obviously related to the anterior direction of the fibres. Therefore it can be assumed that the actual shortening process is localized at a place where the fibre growth changed direction. As suggested by fig. 9 this conversion must take place between A and D, thus during the period when the cells are involved in the formation of the primary layer, or at the transition primary — secondary layer. The latter possibility is by far the most probable. According to Williams, the cells convert at this stage from a columnar to a cuboidal shape; this, in connection with the radial reduction of the cell size, suggests a reduction of the volume of the cells in this area. Unfortunately, there is not enough factual evidence resulting from investigations on recent brachiopods on this subject. A reduction in volume of epithelial cells, however, is certainly not an exceptional phenomenon.

The anteriorly directed migration of the cells is a most consistent feature among brachiopods. In some instances this modality can be traced in large areas of the inner shell surface (Pl. III, fig. 3, 4, 5 and 6); in others, however, it only occurs in a narrow zone just inside the growing valve-edge; (i.e., anteriorly directed fibres are only found in a thin layer just below the primary layer). Behind this zone the growth pattern changes again as a result of one or a set of other modifications.

Thus, the following conclusions can be drawn in regard of the model of the outer epithelium.

1. The periostracum, the primary shell layer, and the secondary shell layer are separated from each other by isotopic shell unit boundaries.
2. The transitionary surface between the primary and secondary shell layers also constitutes a concentric isotopic shell unit boundary as far as the obliquely anterior direction of the fibres in the secondary layer is concerned. This phenomenon is related to an anterior migration of the outer epithelial cells involved in the formation of the secondary layer, and is probably caused by the occurrence of radial shortening of these cells which occurs simultaneously with the transition in secretion from primary to secondary shell material.

11. THE COURSE OF THE FIBRES NEAR THE COMMISSURE IN *GRYPHUS VITREUS*

It has been seen (p. 15) that the mosaic elements (and the adherent epithelial cells) often increase in size away from the commissure. The question which then arises is: how does this affect the direction of migration of the cells and the resulting course of the fibres involved? Fig. 23 represents a radial section showing, at some distance from the primary-secondary shell unit boundary, a concentric isotopic epithelial and shell unit boundary which separates a unit with small cells from one with larger cells. It is evident that with this increase in size a reduction of the radial component in the direction of the migration of the cells is correlated.

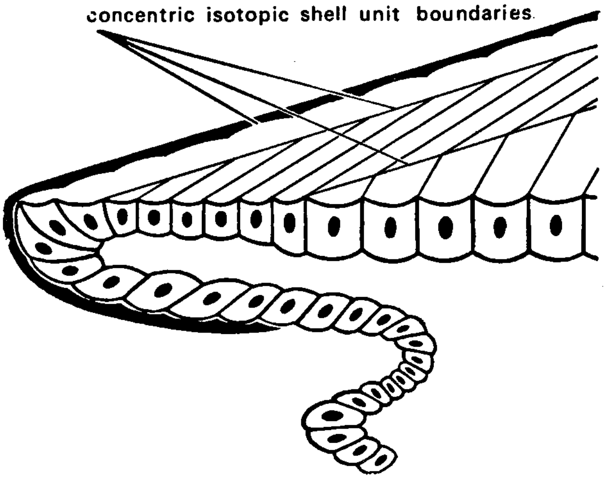

Fig. 23. Correlation between reduction of radial component of fibres and increase in cell size along concentric isotopic epithelial unit boundary.

Fig. 24 is a reproduction of a figure by van Bemmelen (1882, fig. 1), and represents the shell mosaic of the valve edge of *Gryphus vitreus*. The periostracum and the primary and secondary shell layers are clearly shown. Indeed, an increase in size of the mosaic elements away from the commissure is displayed. In addition, a concomitant rotation of the long axes of the elements appears to have occured. The axes of the small elements are directed radially and more posteriorly those of the larger elements are parallel to the commissure. This rotation of the axes of the elements implies a corresponding rotation of the migratory direction of the epithelial cells, and of the course of the fibres. Thus, the migration is purely radial near the primary layer; the radial component decreases rapidly posteriorly and is at the same time replaced by a perpendicular component. As has been seen above a decrease in the radial component is correlated with an increase in the size of the cells *in radial section.* In the shell illustrated in fig. 24 radial sections would be parallel to the longest diagonal of the elements near the primary layer, and to the shortest diagonal in the elements further behind. Consequently, the shortest diagonal in the elements further behind must be longer than the longest diagonal in the elements near the primary layer. In the figure of van Bemmelen this seems indeed to be the case. This rotation and the corresponding increase in

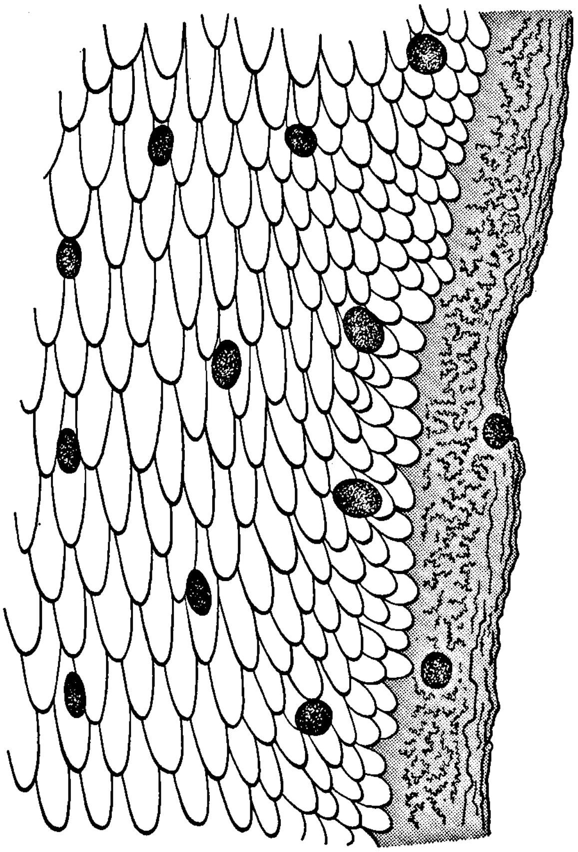

Fig. 24. Interior surface of valve of *Gryphus vitreus*, at commissure, with periostracum, primary layer and shell mosaic of secondary layer. (After Van Bemmelen, 1882).

size of the mosaic elements is most probably governed by concentric isotopism. This course of the fibres parallel to the commissure (and at some distance to it) has very often been observed in the fossil Rhynchonellida studied. The question which can now be posed is: where are these epithelial cells going? The discussion of the following two examples may serve as an answer.

12. THE COURSE OF THE FIBRES IN A SPECIMEN OF *SICORHYNCHA TRINACRIA TENUIROSTRIS* (HAVLÍČEK, 1961)[11] (Pl. IV fig. 1, 1a, 2, and 2a)

In this specimen the course of the fibres is beautifully displayed in a considerable part of the shell. In the pedicle valve a broad sulcus is developed which ends in a slightly protruding tongue. This sector forms a depression in the shell; the growth rate has been greater here than in the surrounding parts of the shell. The fibres which originated in the median sector of the sulcus grew exclusively towards the anterior. Those which originated more laterally are radially arranged near the primary layer and are then bent in the direction of the median sector of the sulcus. This sector is therefore an area of concentration of the fibres, and the underlying epithelial unit must be one of concentration of the cells. In the brachial valve the situation is quite different. Here, the sector corresponding with the ventral sulcus, the saddle, is characterized by a relatively small growth rate, whereas the growth rate was maximal in both antero-laterally directed sectors. Here, too, the fibres converge towards the sectors of maximum shell growth and diverge away from the sectors of minimum growth, i.e. the (postero-) lateral shell borders and the median sector of the saddle, after having grown for some distance in exactly radial directions away from their origin. A reconstruction of the directions of migration of the epithelial cells in both valves is given in fig. 25. A number of epithelial units can be distinguished and are indicated in the figure. They and their boundaries are of the isotopic type. This is inferred from the position of the corresponding shell units and their boundaries. The concentrically and radially arranged epithelial unit boundaries correspond with shell unit boundaries which are parallel and perpendicular to the outer shell surface respectively.

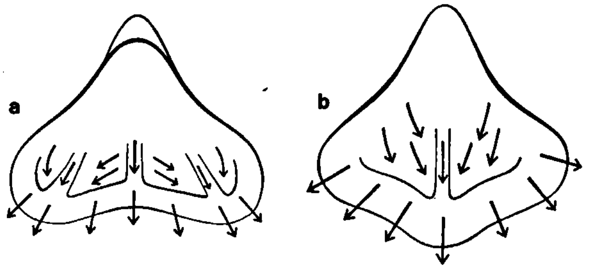

Fig. 25. Isotopic epithelial units and epithelial unit boundaries in a specimen of *Sicorhyncha trinacria tenuirostris* (Havlíček, 1961). The arrows indicate the direction of migration of the epithelial cells.

In connection with section 11 it may be concluded that in considerable parts of the shell a similar rotation of the migratory direction of the cells occurs: along certain concentric isotopic epithelial unit boundaries which are situated near the commissure the direction changes from radial to more or less parallel to the commissure. This deviation takes place in the direction of sectors with maximum superficial shell growth. In these sectors themselves the cells migrate only in radial direction. They are sectors of fibre and cell concentration. In sectors of minimum superficial shell growth the cells also migrate in radial direction. These sectors, however, behave as areas of fibre and cell dispersion.

This phenomenon, of which only a few examples can be treated here, is nevertheless a strikingly general property of rhynchonellid shells. Examination of the course of the fibres demonstrates again and again that they are directed radially near the outer shell surface and then deviated towards sectors of maximum superficial shell growth. The above conclusive statement can, therefore, be added to the model of the outer epithelium. Exceptions occur indeed but in general

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[11] Koněprusy Limestone, Bohemia; Mneinan. Muséum d'Histoire Naturelle, Laboratoire de Paléontologie, Paris, no. B 4791.

they can be easily explained. For instance, along the commissures of gerontic specimens aberrations are often observed, but these may be due to a stagnation in shell growth during the ultimate stages of ontogeny. Another important type of exception is described in § 14.

13. THE COURSE OF THE FIBRES IN THE COSTAE OF *TRIGONIRHYNCHIA PARETI*

In this species the deviation of the fibres is extremely well developed. The shell has very high and steep costae. These costae act as sectors of fibre and cell dispersion, and the intervening grooves as sectors of fibre and cell concentration. The higher the costae, the sharper the deviations. However, although the costae are rather faint in the posterior part of the shell the deviations there are also very clearly shown.

In accordance with the general rule formulated in connection with the previous example, the sectors of concentration and dispersion correspond with those of maximum and minimum superficial shell growth respectively [12].

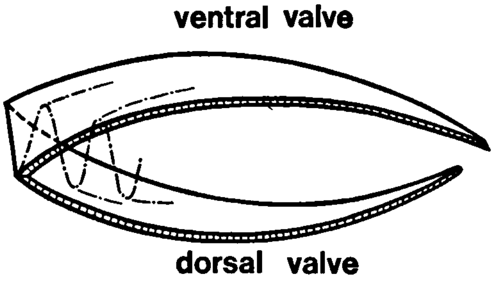

Fig. 26. *Trigonirhynchia pareti*, young specimen. The difference in growth rate between costa and groove is very small.

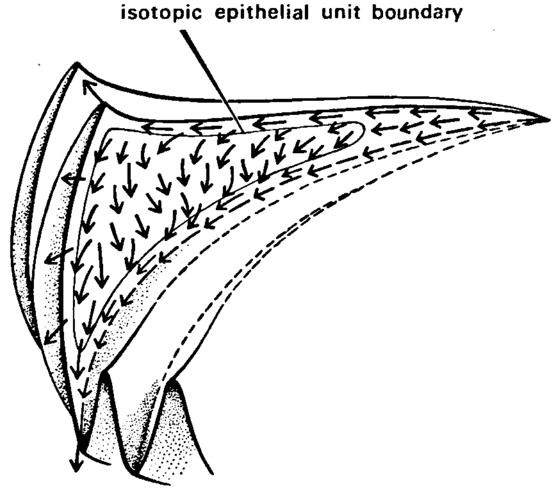

Fig. 27. Isotopic epithelial units and epithelial unit boundaries in the flank of a costa of *Trigonirhynchia pareti*. The arrows indicate the direction of migration of the epithelial cells.

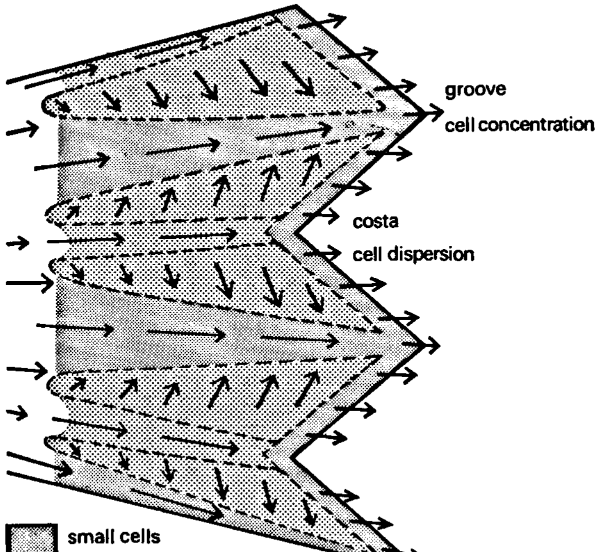

Fig. 28. Correlation between cell size and direction of migration of the cells in costae of *Trigonirhynchia pareti*. Isotopic epithelial units and their boundaries are indicated.

The course of the fibres is demonstrated in a set of photographs on pl. V, and in fig. 21. Fig. 27 represents a reconstruction of the underlying movements in the epithelium. The different epithelial units are indicated. Their boundaries are of the isotopic type, and vary from sub-radial to concentric in position. In principle, the pattern is similar to that in *Sicorhyncha trinacria tenuirostris* (§ 12).

The question which now arises is: what determines this process of concentration and dispersion? It cannot merely be derived from the overall geometry of the shell, and is probably due to changes in the epithelium itself. One specimen of this species provided a nearly ideal internal mould of a groove and the flanks of two adjacent costae close to the commissure. A latex peel of this produced data which are invaluable for the solution of this problem (see fig. 28, and pl. VI fig. 1a, b. c, and d). In this peel there is only a very local display of a true shell mosaic; generally pieces of the fibres have remained attached to the internal mould, and these parts are exposed in the peel. The breadth of these fibre tips is well exposed and corresponds with the shortest diagonals through the mosaic elements. So the size of the elements (or at least their breadth) can be easily compared. In the bottom of the groove the elements appear to be much smaller than in the flanks. This area of reduction in size of the elements begins at some distance from the commissure and broadens gradually in posterior direction. Away from this area as well as from the commissure itself the size of the elements increases rapidly in the flanks and on the crests of the costae. The areas of concentration

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[12] However, in young specimens the differences in growth rate must be very small, as shown in fig. 26. Nevertheless, it has been seen that the deviations also occur in these parts of the shell. Thus, the deviations here seem to be related to differences in the vertical component along the growing commissure rather than to differences in growth rate.

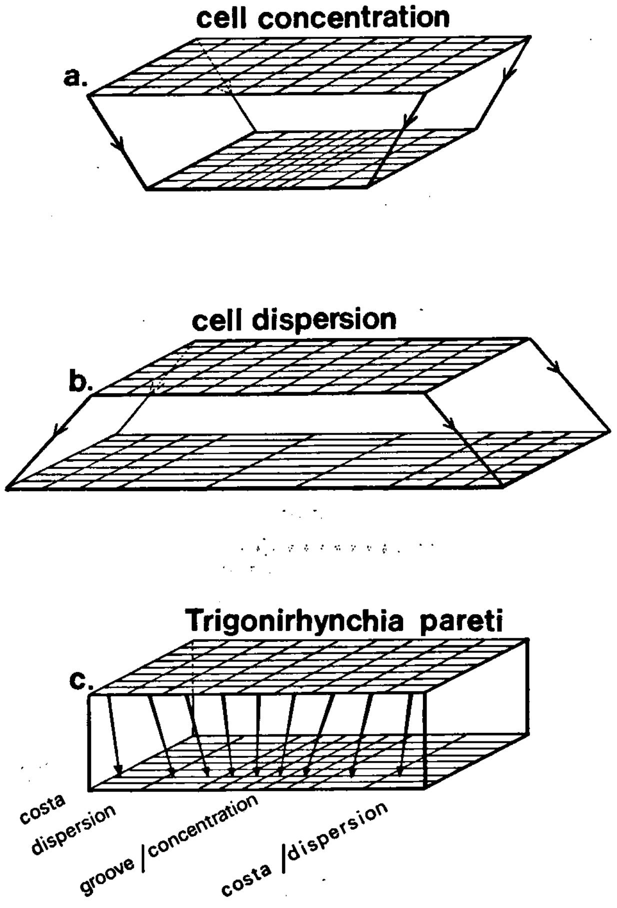

Fig. 29. Correlation between local reduction (a) and increase (b) in size of epithelial cells and the direction of their migration. c: The situation in *Trigonirhynchia pareti* simplified as a combination of (a) and (b).

obviously coincide with the areas of reduction in cell size, and the areas of dispersion with those of increase in cell size.

In fig. 29 the relation between changes in size of the fibres and their migration is demonstrated in three cases. Fig. a shows the effect that a reduction in size of the cells in a narrow strip has on the adjacent epithelium. The cells will obviously migrate towards the centre of the area of reduction and the whole epithelium displayed will decrease in size correspondingly. The reverse is shown in fig. b: here, in a similar strip of epithelium an increase in size of the cells occurs. The epithelial cells migrate away from the centre of the strip and the whole epithelium displayed increases in size. The mechanism operating in the costae and grooves of *T. pareti* in so far as the radial parts of the epithelial unit boundaries are concerned is represented in a slightly simplified way in fig. c: the overall size of the epithelium in question remains roughly constant during growth, and strips of reduction and of increase in cell size alternate. The first are sectors of cell concentration and the second of cell dispersion. The actual situation in the fossils is even somewhat more complicated by the fact that the areas of reduction and increase constitute epithelial units, between which the boundaries are of the isotopic type and make acute angles with the radial directions. Consequently, the areas of reduction are wedge-shaped, their thin ends are radially directed; they move through the epithelium following the growing shell edge (fig. 28).

Unfortunately, the relation between the deviations and the size of the cells could only be established in *G. vitreus* and in *T.pareti.* In the other cases of deviations investigated no data concerning the size of the mosaic elements could be obtained. Nevertheless, the relation described will be included, although with due reserve, in the model of the outer epithelium.

It should be pointed out here that as yet no reference has been made to the inframarginal cell division as a factor affecting the course of the fibres. Indeed, as will be shown below, the occurrence of this phenomenon can often be demonstrated in the apical shell structures but more anteriorly it is only identified with difficulty. It is probable, however, that areas of intense inframarginal cell division will tend to increase in size, and will have the same effect on their surroundings as areas of increase in cell size.

14. THE COURSE OF THE FIBRES IN *CORVINOPUGNAX CORVINUS* (Pl. VI, fig. 2, 3)

In this species very pronounced costae and grooves occur, comparable with those in *T. pareti.* One would expect therefore the fibres to be similarly disposed in both species. This, however, proves to be only partly the case. In *Corvinopugnax corvinus* the fibres are radially arranged over their entire length, and they even show a slight concentration towards the costae (this also is the case in the exterior parts of the fibres in *T. pareti).* The deviation which is so beautifully developed in *T. pareti* has not been observed here. It is only in girontic specimens that very incipient deviation may locally occur. Moreover, the fibres of both species differ in dimensions: those of *T. pareti* are thin and elongated and their mosaic elements are small; the fibres of *C. corvinus* are very stout and short, and their mosaic elements are very coarse. This is in full agreement with the statements in section 6. With reference to section 7 the difference in the course of the fibres in *C. corvinus* and *T pareti* may now be explained as being caused by the fact that the less mobile and thick cells of *C. corvinus* stopped depositing shell material before being entangled in the concentration-dispersion mechanism which operated with such spectacular results in *T. pareti.* According to this assumption, the pattern of epithelial units and their boundaries would in principle be similar in both species, but those units and boundaries which are related to the process of deviation would be only virtually present in *C. corvinus* as a result of the premature stop in shell secretion. The occasional presence of an incipient deviation is a strong argument in favour of this idea.

There are indications that these results can be considered to apply to large groups of brachiopods, e.g., the spiriferid *Kozlowskiella esquerrai* displays exactly the same phenomena as *T. pareti:* very pronounced costae and grooves, and fine and elongated fibres, with similar deviations. This is an interesting case of homoeomorphism. On the other hand, species with coarse fibres never display pronounced deviations.

15. THE MYOTEST. Pl. VII, fig. 2 and 3

Krans (1965) showed in his account of the morphology of Devonian spirifers from Spain that a modification in the process of secondary shell growth occurs at the places of insertion of the muscles. Williams and Rowell (1965) also dealt with the matter. Krans found that at these places a finely granular non-fibrous layer is deposited. It is often coloured black and can be traced in the shell over considerable distances. He called this layer the myotest. In the rhynchonellids studied I have only observed myotests in species with very thick tests, such as those belonging to *Uncinulus* and *Kransia.* In many other species the shell is so thin that no clearly differentiated myotest could be discerned. The structure of the rhynchonellid myotests differs somewhat from the one Krans has found in spirifers in that it is not granular, but finely fibrous, the fibres being much finer and the structure much more blurred than they normally are in the fibrous secondary shell. (Pl. XIV, fig. 6). These myotests are generally accompanied by a strongly developed prismatic layer. Both layers are then very clearly differentiated.

The myotest is generally best developed in the ventral valve; here, the marks of the diductors and the adductors leave beautiful traces in the shell. Krans has already shown that the myotests of most muscles run from the beak, near the outer shell surface anteriorly towards the actual muscle marks at the inner shell surface. (See also Krans & Binnekamp, 1965). This corresponds with the trajectory of the muscles during growth. The boundaries of these myotests are therefore isotopic shell unit boundaries.

16. THE COURSE OF THE FIBRES IN *UNCINULUS PILA, U. ORBIGNYANUS,* AND RELATED SPECIES

In some Uncinulidae, such as *Uncinulus pila* and *U. orbignyanus,* the course of the fibres has a most typical pattern which has been described by Schumann as "vielschichtiger Schalenbau". Indeed, when sectioned, the shell of these species seems to be built up of layers, with the orientation of the fibres being similar within each layer and different in adjacent layers (Pl. VII, fig. 1, 2, and 3). Shell surfaces from which chips have been removed enable the phenomenon to be described somewhat more clearly [13]. The fibres appear to have started by growing towards the anterior for some distance and to have been secreted along complicated trajectories which may be compared with spirals. In large parts of the shell these trajectories are similar so that layers of equally arranged fibres arise. The stratification is best developed at some distance from the paries geniculatus and somewhat anterior to the main muscle areas. From there radially the layers decrease in thickness till they become hardly distinguisable, however they extend undisturbed into the paries geniculatus. More posteriorly, the spirals become gradually weaker, and the fibres nearly straight. Even more posteriorly, in the area of the muscle casts, the fibrous secondary shell layer merges into the prismatic layer. Here, the stratification is vague and can be traced in radial sections as faint, dotted lines running towards the umbo.

The number of strata varies greatly, even in shells of equal size and exterior shape. In some shells only one or two strata have been found, in others up to 15. The first shells are thin, the others very thick. Strongly and poorly stratified shells have been collected next to each other in one and the same population, so that an ecological or evolutionary explanation of the difference becomes highly improbable. Since the strongly stratified shells exceed the others greatly in number, not only in one locality, but in my whole collection, the difference can hardly be an expression of sexual dimorphism. To me the most plausible explanation is that a thickening of the test and deposition of most of the strata occur in the final stages of ontogeny, when the shell has nearly reached its ultimate size. In other words: the growth in thickness of the test reaches its maximum rate at a fairly late stage in ontogeny, and is effected by deposition of secondary shell material with a layered appearance.

Since the stratification is practically parallel to the outer as well as to the inner shell surfaces it is very difficult to identify the types of shell unit boundaries between the layers. Their being parallel to the outer shell surface in radial sections is an argument in favour of isotopism, but a position parallel to the inner shell surface suggests that the boundaries are of the superficial type, two conditions which correspond with quite different modes of shell secretion.

Two arguments against the isotopism of the boundaries can be urged. In the first place it is very difficult to conceive an isotopic boundary nearly parallel to the inner shell surface, extending over a large part of the shell and bounding a pair of shell units which were deposited when the shell had nearly reached its maximum size. The corresponding epithelial unit boundary would have had to move rapidly from behind in radial direction till it reached the anterior and anterolateral commissural area. This, in fact, is in contradiction with the principle of isotopism.

Such a process of formation of the boundaries in question would, however, not correspond with the superficial condition. When this is the case the shell unit boundaries have no relation with epithelial unit boundaries, but with momentary and simultaneous changes in the epithelial unit pattern. This would imply that all epithelial cells involved in the formation of the stratified shell had travelled simultaneously along similar spirally shaped trajectories (fig. 30). Both these anisotopic explanations are possible and no

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[13] Unfortunately no good photographs could be obtained of the phenomena observed.

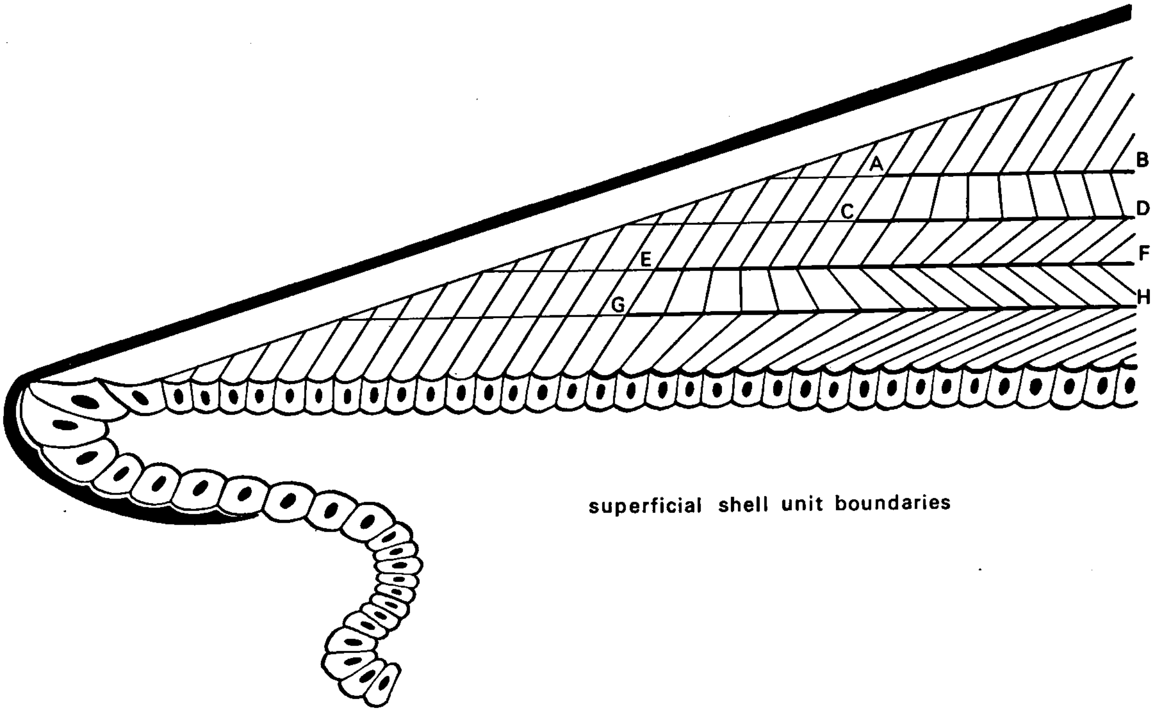

Fig. 30. The stratified shell structure, considered as a result of sudden changes in size of clusters of epithelial cells and concomitant changes in the direction of migration of the cells behind. Superficial condition.

argument favouring one more than the other can definitely be given at this stage.

The second argument against isotopism in the formation of the layers lies in the fact that the boundaries clearly intersect the myotest of the ventral diductors (Pl. VII, fig. 3). As this myotest is bounded by isotopic shell unit boundaries, the intersecting boundaries between the shell strata can hardly be so.

It may thus be concluded that the boundaries are most problably of the anistopic type. It is not yet known whether they correspond with momentary changes in the pattern of epithelial units (superficial condition — see fig. 30), or with epithelial unit boundaries which moved relatively quickly through the epithelium in radial direction. Further research on this intriguing little problem has to be carried out before it will be more fully understood. It may then well turn out that the stratification is the result of yet another type of growth.

The stratified shell structure has been observed in some species with a very thick test, and a fine shell mosaic. It is well developed in *Uncinulus pila, U. orbignyanus,* and *U. knjaspensis.* In *Uncinulus subwilsoni* the shell does not display such a beautifully stratified structure; here, too, the course of the fibres is very complicated, but instead of being arranged in a stratified pattern, the structure is much more chaotic, and difficult to describe (Pl. VII, fig. 4). This is also the case in some parts of the shell of *Eucharitina eucharis.* In *Kransia* the course of the fibres is simply radial without many complications, although the test may attain a considerable thickness. The shell mosaics in this genus are very coarse. This, again, may serve as an argument for the lack of mobility of large epithelial cells.

In any case, all these phenomena can contribute to an improvement in the systematics.

17. THE INTERNAL APICAL PROTUBERANCES OF THE SHELL

The structure and growth of the internal apical protuberances of the shell constitute a fascinating but most complicated subject. Not all the phenomena involved can be treated here; the discussion, therefore, will be confined to two important and characteristic examples: first, the dorsal median septum of a number of species will be treated, and next the growth and structure of a dental plate and tooth of a single specimen of *Trigonirhynchia pareti* will be studied by means of a series of sections parallel to the normal plane. It may, however, be of interest to preface the treatment of these examples with some more general considerations. All the elements concerned have been lined with and secreted by the outer epithelium throughout the life of the animal. Generally they originated near the beak and then grew in size and thickness by a differential deposition of shell material by the corresponding parts of the epithelial membrane. Shell deposition at the distal ends of these structures has increased their size, whereas growth in thickness will have been caused by deposition on more posterior parts of the structures. When the rate of growth in size greatly exceeds the rate of growth in thickness slender structures will arise, whereas massive structures will be the result of only slight differences in growth rate.

The relative position occupied by all these structures in the shell cavity remains much the same throughout the growth of the shell. The term isotopism can also be appropriately applied here for the designation of this constancy in relative position. The whole complex of apical elements can be divided into a number of shell units, each with a different growth rate and direction, their common boundaries being shell unit boundaries which correspond with epithelial unit boundaries the relative position of which is constant during growth. Here, too, the position of a cell in the epithelium is determinant for its secretory activity.

Two types of internal apical structures can be distinguished. Structures of the first type extend from the beak into the shell cavity. In a cross section through such a structure the core is the oldest part and represents the distal end at an earlier stage of growth, whereas the surrounding shell material has been deposited afterwards. Towards the beak the core of the structure becomes progressively older, as shell materials have been deposited around it over an increasingly longer period. Most of the structures concerned belong to this type.

Structures of the second type do not extend from the beak, but project in a non-radial direction from another structure into the shell cavity. The teeth of the rhynchonellid shell (most probably not those of spirifers), the spiralium of spirifers and the connectivum of many Trigonirhynchiidae, are examples (fig. 31, a, b, and c). In principle, the process of growth of these structures may be considered to be isotopic or anisotopic. Isotopism would imply that structures had moved radially from the beak and had conserved their shape and their size and position relative to the whole growing shell during the entire process. This means that shell deposition must have taken place continuously along their anterior surface and simultaneously dissolution along their posterior surface. An anisotopic mode of growth can hardly signify anything else than that the structure was secreted once and for ever at a relatively late stage of growth, and in non-radial direction, so that shell dissolution did not occur or hardly so.

As the teeth are very obviously of the isotopic type, there can be hardly any doubt as to their growth according to the secretion-dissolution mechanism [14]. The same applies to the spiralium of spirifers, although the matter is here somewhat more complicated, as has been demonstrated by Krans (1965). Finally, the connectivum has also been found to be an isotopic structure at least in *Trigonirhynchia pareti* and in *Ptychomaletoechia cf. gonthieri* from the Crémenes Limestone in Spain (Westbroek, 1964). Here, the connectivum is well developed in very young specimens (fig. 32, e.g.).

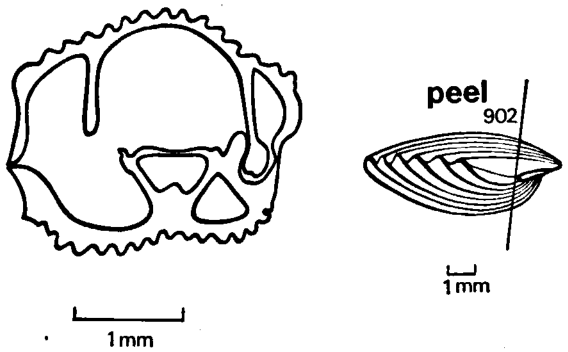

Fig. 32. Very young specimen of *Trigonirhynchia pareti*. Connectivum is well developed.

18. THE DORSAL MEDIAN SEPTUM

When the structure of this septum in a number of species is compared, it appears to be rather variable. Two extremes were found. The first one is exemplified by *Kransia parallelepipeda*. In a specimen from the Ahrdorfer Schichten (Eifel) a septum was found only

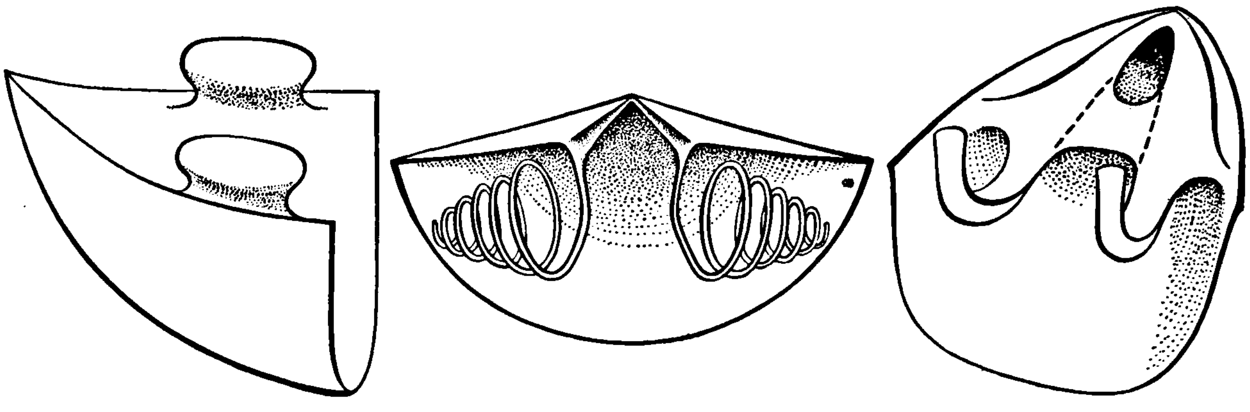

Fig. 31. Internal apical shell structures which do not extend from the beak, but project in a non-radial direction from another structure into the shell cavity. (a) teeth of rhynchonellid shell; (b) spiralium of spirifer; (c) connectivum of Trigonirhynchiidae.

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[14] On p. 34, and 69, respectively, two other arguments in favour of this conclusion are urged.

about 30 μ thick (Pl. 9, fig. 1). A section parallel to the normal plane displayed a central granular layer of about 10 μ thick, which ran medially through the whole septum and was flanked on both sides by a very thin fibrous layer, the fibres of which originated at the granular layer and extended in anterolateral direction. Pl. IX, fig. 2, taken from a specimen from the Rommelsheimer Schichten (Eifel) presents the same picture, but here the septum is much thicker.

A similar phenomenon in the dental plates of a number of spirifers such as *Brachyspirifer rousseaui* has been discussed by Krans (1965). His interpretation of the phenomenon is as follows. The septum (or dental plate) was secreted in a fold of the outer epithelium, which was enlarged by inframarginal cell division. This cell division was concentrated in a very narrow zone (probably not more than the width of one cell), situated medially along the entire anterior edge of the fold. The cells situated in this zone have secreted the mediotest; the cells which are derived from them by division have deposited the flanking fibres (Fig. 33).

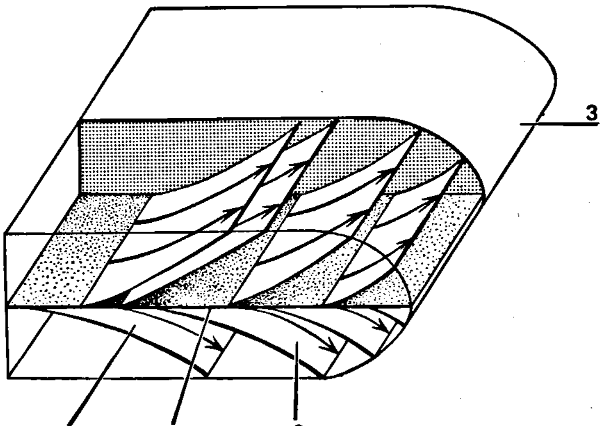

Fig. 33. Growth of tooth plate and formation of mediotest. The arrows indicate the direction of fibre growth. 1= mediotest; 2= surfaces in which the fibres are situated; 3= zone of epithelial growth where the mediotest is formed, (After Krans, 1965).

The boundaries between the mediotest and the adjacent fibrous material can without any doubt be considered as isotopic shell unit boundaries. Krans considered the mediotest to be made up of fibres. It is, however, much more likely to be of a granular nature, since a considerable number of sections taken at different angles through one and the same mediotest in *Kransia parallelepipeda* never displayed anything else. The mediotest shows close affinity with the primary shell layer, in structure as well as in genesis: both are of a granular structure and related to a zone of intense cell proliferation. In the interpretation of the structure of the marginal spines (p. 52) it will sometimes be difficult to decide which of the two is being dealt with. Perhaps the problem is only academic. Research on recent brachiopods may in the future give a decisive answer on the subject. This type of growth of the septum is confined to the relatively early stages of its development, when increase in length prevails. Later, when it chiefly grows in thickness, the original blade-like septum is generally covered with a thick layer of prismatic material. The carinate cells loose their generative potential, and the mediotest is only present in the core of the septum. The age at which this conversion takes place is very variable, even within one species.

The other extreme in structure of the septum is found e.g. in *Sphaerirhynchia wilsoni.* A section parallel to the normal plane shows all fibres to be more or less parallel to the plane of symmetry (Pl. IX, fig. 3). The median fibres are much thicker than the lateral ones (as the fibres are all cut in the same way by this section their thickness can be compared fairly well). A section perpendicular to the plane of symmetry and to the normal plane confirms this impression, whereas the longest diagonals in the sections through the fibres appear to be of similar length here. This phenomenon is obviously related to the fact that laterally the angle between the fibres and the inner shell surface is very small, whereas medially it can be as large as 90° (fig. 34). This structure, therefore, constitutes a beautiful illustration of section 6, where the dependence of the thickness of the fibres on their angle with the inner shell surface was discussed. From this it may be inferred that the septum of *S. wilsoni* was secreted by a fold of the outer epithelium which grew by inframarginal cell division occurring evenly over the entire surface of the fold, and not, as in *K. parallelepipeda,* exclusively in the carinate zone. Nevertheless, here also the medium zone of the septum differs from the flanks, and the casual observer (who e.g. only studies polished surfaces in incident light) may not notice the elementary difference between the septa of *K. parallelepipeda* and *S. wilsoni.* This difference, however, is most certainly of great system-

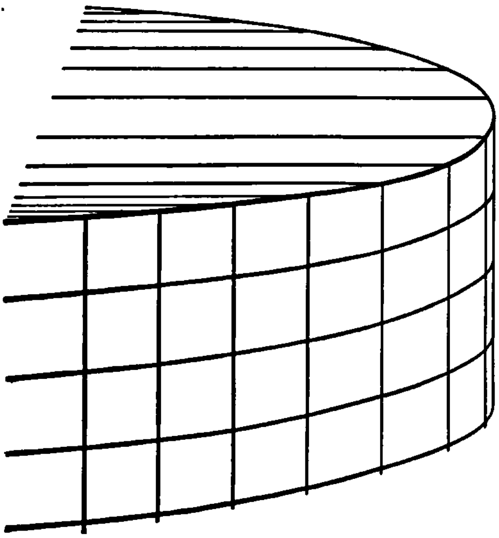

Fig. 34. Carinate part of septum in *Sphaerirhynchia wilsoni.* Mosaic elements are represented by squares. The median fibres are thick, the lateral ones flattened.

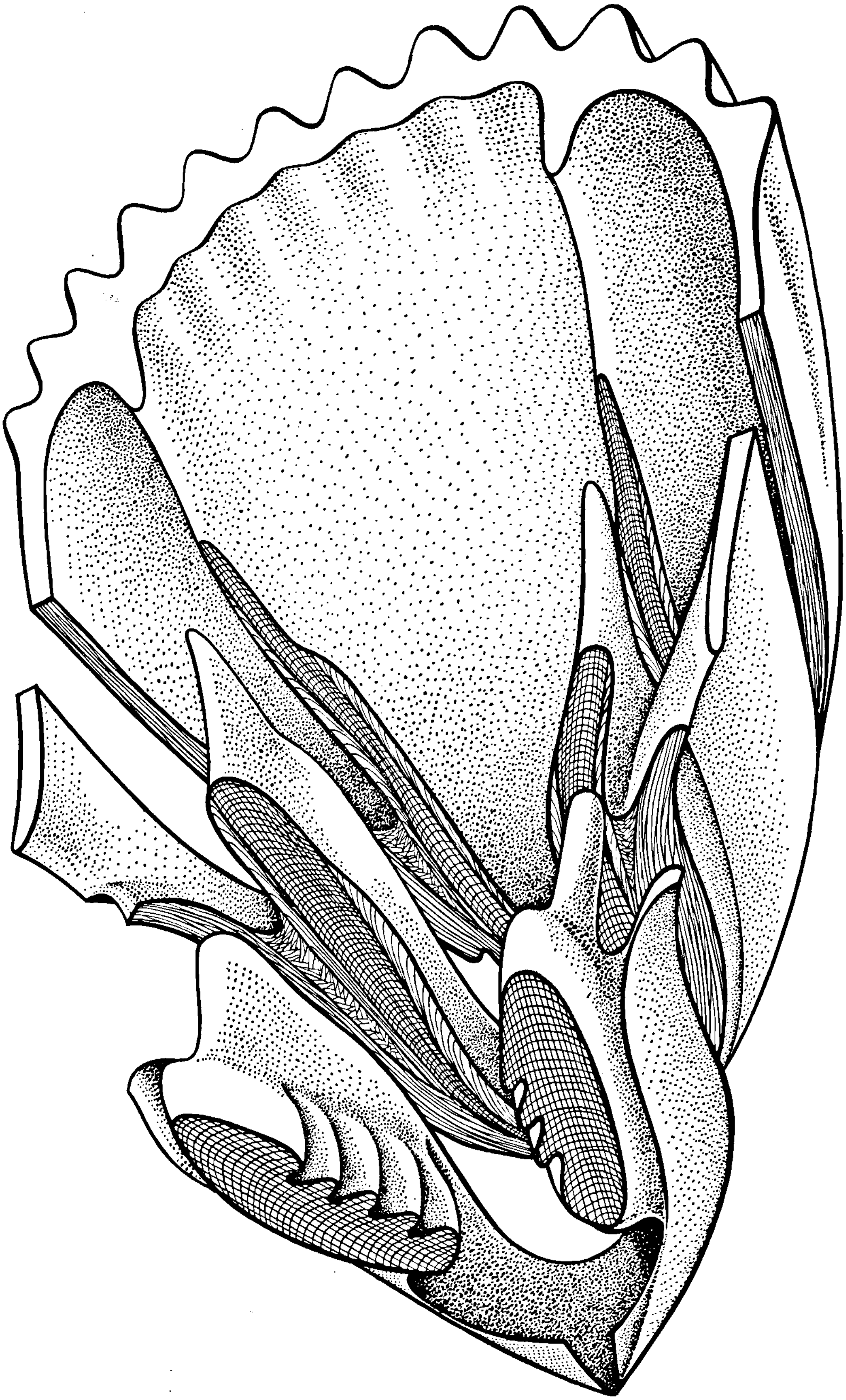

Fig. 35. *Trigonirhynchia pareti*. Block diagram of apical part of ventral valve. Shell units and shell unit boundaries.

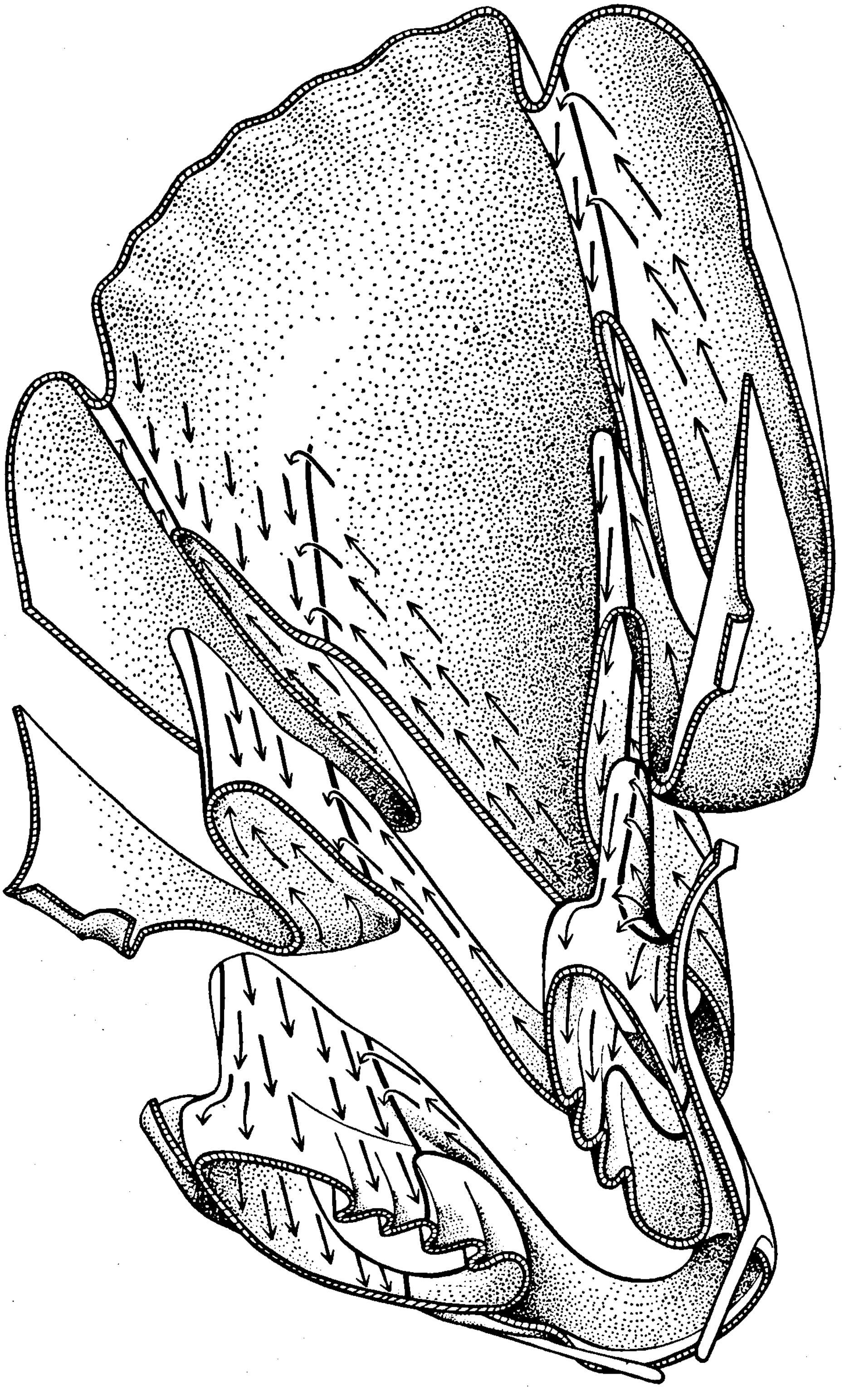

Fig. 36. Reconstruction of epithelium surrounding part of shell represented in fig. 35. Arrows indicate cell migration. Epithelial unit boundaries represented by thick lines.

atic value. I have never observed any intraspecific variation in this respect, although I have often checked many specimens of a species. In many species transitions between these two septal structures occur. The description of this character for each of the investigated uncinulid species can be found in enclosure I; see also Pl. IX, fig. 4.

19. A DENTAL PLATE AND TOOTH OF *TRIGONIRHYNCHIA PARETI* (Plate VIII)

This section deals with the structure and growth of a dental plate and tooth in one particular pedicle valve of *Trigonirhynchia pareti*. The primary data of these observations are provided by a series of sections parallel to the normal plane. Fig. 35 shows a block diagram of the whole structural complex, a reconstruction based on these sections [15]. Apart from the overall shape, the course of the fibres has been indicated. Fig. 36 gives a reconstruction of the surrounding outer epithelium, on which the direction of the cellular migration has been indicated. In the first instance three different shell and epithelial units can be distinguished. The first shell unit involves the medial core of the dental plate and the entire tooth. The outcrop of this unit forms an area consisting of (1) the anterior edge of the dental plate, (2) the anterior part of the dental plate surface which faces the plane of symmetry just ventral of the tooth, and (3) a very narrow strip along the lateral dental plate surface. In this shell unit the fibres are directed dorsally, and consequently the epithelial cells involved have migrated in the same direction. The remaining two shell units are situated in the more posterior part of the dental plate on either side of its medial core. The fibres are directed anteriorly, and the cells involved must have migrated in the same direction. The shell unit boundaries concerned are all of the isotopic type.

It has already been seen that for reasons of isotopism the teeth of the Rhynchonellida are likely to have grown by secretion along their anterior surface and to have been dissolved posteriorly, so that their nodular appearance could be maintained during growth (p. 30). In this context another argument in favour of this viewpoint can be urged. In transverse sections through their posterior part the teeth invariably constitute isolated semi-circular patches consisting of fibres of which both ends terminate on the inner shell surface. As fibres normally run from the outer to the inner surface, the fibres in question are most likely cut off from their base by resorption (see pl. IX, fig. 5). A third argument will be given on p. 69. A fourth epithelial unit can consequently be distinguished: it lines the posterior surface of the tooth and is responsible for its dissolution.

It can now be concluded that the growth of the tooth and dental plate proceeds as follows. Along the anterior and lateral surfaces of the tooth secretion of fibres has taken place by cells which have come from its base and from that part of the anteromedially facing surface of the dental plate which is situated above, thus ventral of it. As the anterior surface of the tooth becomes displaced anteriorly, and as the surrounding cells which are responsible for this displacement migrate perpendicular to it, a constant supply of these cells is indispensable. This explains why the fibres in the core of the dental plate are directed dorsally: they have contributed to the supply of the cells in the tooth at a younger stage of growth, i.e. when it was situated closer to the beak.

Along its posterior surface the tooth is dissolved by the surrounding epithelium. Here, no further supply of cells from more ventrally situated parts of the structural complex is necessary, so that the cells of the posterior part of the dental plate migrate in anterior direction, where in turn they may supply the more anteriorly situated part of the dental plate from which the cells are continuously withdrawn by the tooth. The same thing occurs on the surface of the dental plate which constitutes the inner wall of the lateral apical cavity. Here, the cells cannot move directly towards the tooth, being prevented in doing so by the bottom of the lateral apical cavity. They therefore move anteriorly till they have reached the edge of the dental plate. From there they can migrate directly towards the tooth.

The epithelial fold enveloping the whole structure obviously increases in size during growth. This can only be explained by inframarginal cell division. This division however is not limited to a special area in the epithelium, as it is in the septum of *Kransia parallelepipeda:* no mediotest has been met with. Most probably, the division takes place in the larger part or the whole of the epithelium concerned, while moreover cell supply from the surrounding epithelium may occur. The mode of growth of the whole structure, as described above, implies that all shell and epithelial unit boundaries concerned are of the isotopic type, even the boundaries of the epithelial unit involved in the dissolution of the tooth. The whole phenomenon constitutes a strikingly complex example of isotopism.

It remains to be seen whether the growth of the tooth-dental plate structural complex always takes place according to the above principles. No further research on this problem has yet been made. Anyhow, the fibres of the teeth in all the rhynchonellids investigated are invariably dorsally directed.

20. CONCLUSIONS

Summarizing, the following conclusions can be drawn with regard to the composition of the model of the outer epithelium which was proposed on p. 20.

The outer epithelium is a cellular membrane one cell thick. It grows in extent by the addition of new cells at its border, whereas locally inframarginal cell division

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[15] For a better insight into the structure the other tooth and dental plate have also been drawn. The data on the structure of these elements have not been obtained by observation, but are simply the reflected image of the symmetrically situated tooth and socket which actually have been studied.

occurs. The outer epithelium is responsible for the secretion of the shell, according to the principles described by Williams. The study of the shell mosaics has shown that the mosaic elements, and thus the exteriorly facing surfaces of the cells, are very variable in size and shape, in one specimen as well as in different species. The longest diagonals of the mosaic elements and of the corresponding cell surfaces correspond with the direction of the cell migration during growth.

The calcite secretion by the epithelial cells involved in the formation of the secondary layer is discontinuous. Large cells are generally found to be less mobile than small ones.

It is very probable that the shell-secreting activity of the epithelial cells is generally maximal near the commissure, decreasing rapidly towards the posterior. The cells often display a considerable mutual mobility. The epithelial units involved in the formation of the periostracum, the primary and the secondary layers have common boundaries referred to as isotopic epithelial unit boundaries. The general anterior direction of the migration of the cells near the commissure is probably due to a reduction in size of the epithelial cells when they form the primary layer.

At some distance from the commissure a subsequent increase in the size of the cells may occur. In many instances this is found not only to result in a reduction of the anterior component of the migration, but also in a rotation of the migratory direction, which generally becomes parallel to the commissure. The cells, then, move generally away from sectors of slow superficial shell growth — which act as sectors of cell dispersion — towards sectors of maximum growth in which as a result cell concentration occurs. In one case a sector of the last type was shown to behave as a sector of cell size reduction. The whole phenomenon can clearly be described as isotopic. The epithelium situated at the places of muscle intertion often secretes a type of secondary shell which is slightly different from the normal fibrous and prismatic material. The shell layers forming this myotest are bounded by isotopic shell unit boundaries.

In some species with very thick shells the cells migrate along spirally shaped trajectories in such a way as to result in a stratified shell. The shell unit boundaries concerned are most probably of the anisotopic type, although the exact mechanism of growth is not yet known.

All the internal apical structures of the shell which have been studied appear to be the result of an isotopic growth. A great many epithelial units can be distinguished. Some of them are found to be involved in shell dissolution, others in excessive cell proliferation, etc.

Isotopism is obviously a factor of paramount importance in the shell growth of the Brachiopoda studied. Only two examples of anistopism were found — growth lamellae, and the stratified shell of some Uncinulidae. This frequency of isotopism is without any doubt related to the generally gnomonic growth of accretionary structures [16]. Although these two terms — isotopic and gnomonic — naturally apply to the same type of features, they should not be confused. The theory of gnomons is connected with the overall shape of a feature, whereas isotopism relates to the position throughout the growth of a definite part of an accretionary structure in relation to the whole. The following example may illustrate this difference.

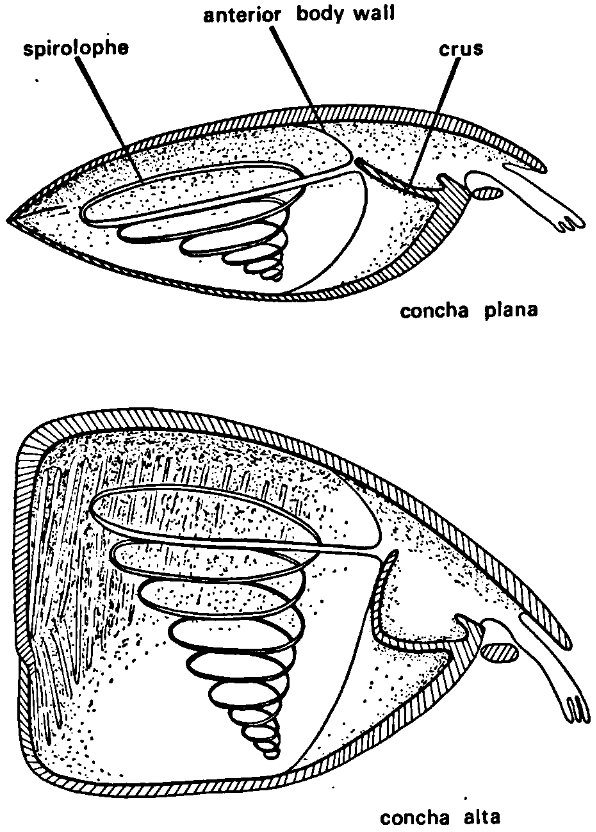

Fig. 37. Growth of crus in uncinulid shell is isotopic but not gnomonic.

The geniculation which occurs in most of the Uncinulidae typically is a non-gnomonic feature: it clearly constitutes a divergence from the logarithmic spiral form of the ideal brachiopod shell (Rudwick, 1959, Fig. 41, Fig. 37). Before geniculation sets in the shell grows mainly in radial direction. It remains very flat, and the height of the shell cavity remains very small in relation to the length. In recent representatives of the Rhynchonellida the lophophore is a spirolophe and both spirals are directed dorsally. At their base, on the anterior body wall, the spirals are attached to the tips of the crura. It can safely be assumed that the situation was the same in the Uncinulidae. The geometry of the shell of these animals suggests that the spirolophe grew mainly in

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[16] See W. d' Arcy Thompson, 1961, p. 185: "each successive increment of growth is similar, and similarly magnified, and similarly situated to its predecessor, and is in consequence a gnomon to the entire pre-existing structure".

the horizontal plane before geniculation, the whorls becoming increasingly wider and the number of whorls remaining relatively reduced. The crura are straight and directed radially. After geniculation the shell grows only in height, as does the shell cavity. The brachia will grow mainly vertically by an increase in the number of whorls. The tips of the crura which remain attached to the base of the largest and most ventrally situated whorl will be situated constantly at a similar relative distance from the inner surface of the ventral valve and from the anterior border of the shell. Simultaneously with geniculation the growth of the crura therefore will change from radial to ventral. Indeed, the crura display a sharp corresponding bend in radial sections. The growth of the crura is therefore non-gnomonic, since a definite change in form occurs. However, the constantly similar position of their distal ends in the whole shell suggests their growth to be isotopic.

Finally, attention should be given to the slight suspicions expressed on p. 14, relative to the postulations by Williams that every fibre of the secondary layer has been deposited by only one epithelial cell, an assumption which constitutes the base of most of the above considerations. In this connection it has to be stated that none of my observations contradicts this starting point. I consider this fact as an indirect argument in favour of the allegation of Williams.

III. THE MARGINAL SPINES

1. FUNCTIONAL ANALYSIS OF ZIGZAG DEFLECTIONS

All the species treated in this paper show a pattern of radially arranged costae and grooves of which the prominence and appearance vary greatly. Undoubtedly, costate surfaces are very frequent and spectacular features in brachiopod shells and it is therefore not surprising that they have been the subject of a considerable number of more or less evolved functional interpretations.

It was Herta Schmidt, who, in 1937, pointed out that the function of the costae must be sought primarily in the serial zigzag deflections of the commissure which, in fact, are responsible for their formation. The zigzag deflections clearly constitute a modification of a pair of most essential features of the brachiopod shell: the valve edges, which surround the opening by which the animal communicates with its environments. Ac-

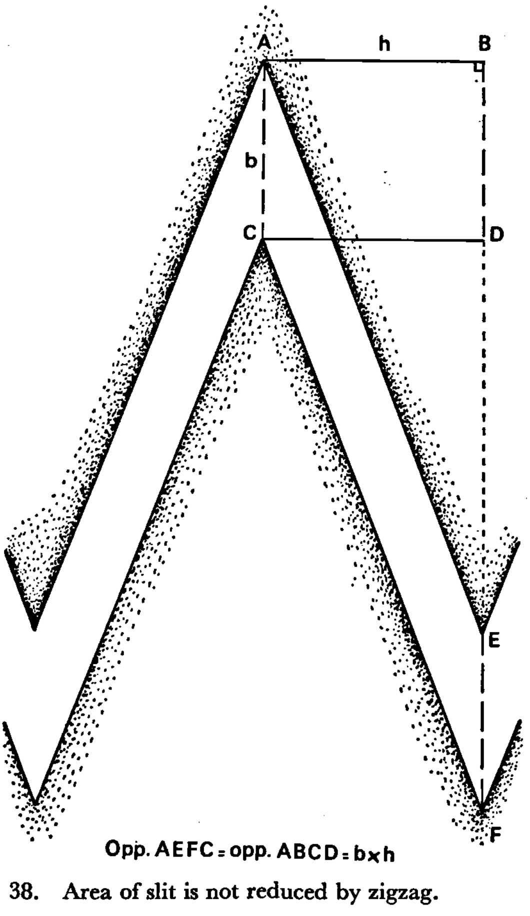

Fig. 38. Area of slit is not reduced by zigzag.

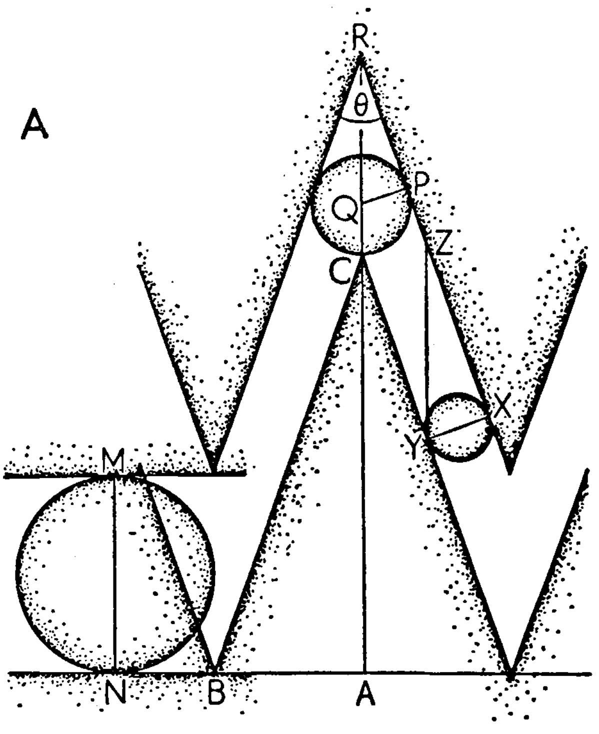

Fig. 39. Portion of "ideal" protective zigzag slit, showing spherical "particles" passing through flanks of slit (diameter XY), crest of slit (diameter PQ), and undeflected slit of same gape (diameter MN). Width of slit 33 per cent of gape; degree of protection (MN/XY= 3) is equal to relative amplitude of zigzag (BC/AB). (After Rudwick, 1964).

cording to Schmidt, then, the zigzag deflection does not affect the area of the slit between the valve edges at any degree of opening, but reduces the distance between the edges (fig. 38). The risk of entry of "harmful particles" — which in Schmidt's interpretation are for the sake of convenience represented by small spheres — is therefore likewise reduced, and consequently the zigzag deflection is interpreted as a protective device.

This hypothesis of Herta Schmidt has been further developed and partly modified by Rudwick (1964). The general methodology of functional interpretations of fossils, as formulated by Rudwick, is as follows: "first, the demands of a postulated function are analysed; from this analysis is derived a structural specification (the paradigm) which would give maximal efficiency for the function; finally, the functional interpretation is tested by comparing this specification with the observed structure of actual fossil specimens". Rudwick shows the relative amplitude of the zigzag (= BC/AB, in fig. 39) to be equal to the degree of protection of the slit (= MN/XY), so that "the degree of protection depends only the "strength" of the zigzag, and not on the extent to which the valve edges gape apart; it can therefore be determined even for fossil brachiopods". Herta Schmidt has already shown that through the crests of the deflections larger particles can pass than through the flanks. Rudwick considers the crests as "localized anomalies in an otherwise uniform degree of protection, represented by the particles passing through the flanks. This justifies using the latter, i.e. the width of the slit, for defining the degree of protection".

The paradigm for a protective zigzag deflection will combine the following specifications, according to Rudwick (fig. 40):

1. the deflections will be axial, "since the valve edges separate, not on a linear course, but by rotation around the hinge-axis";

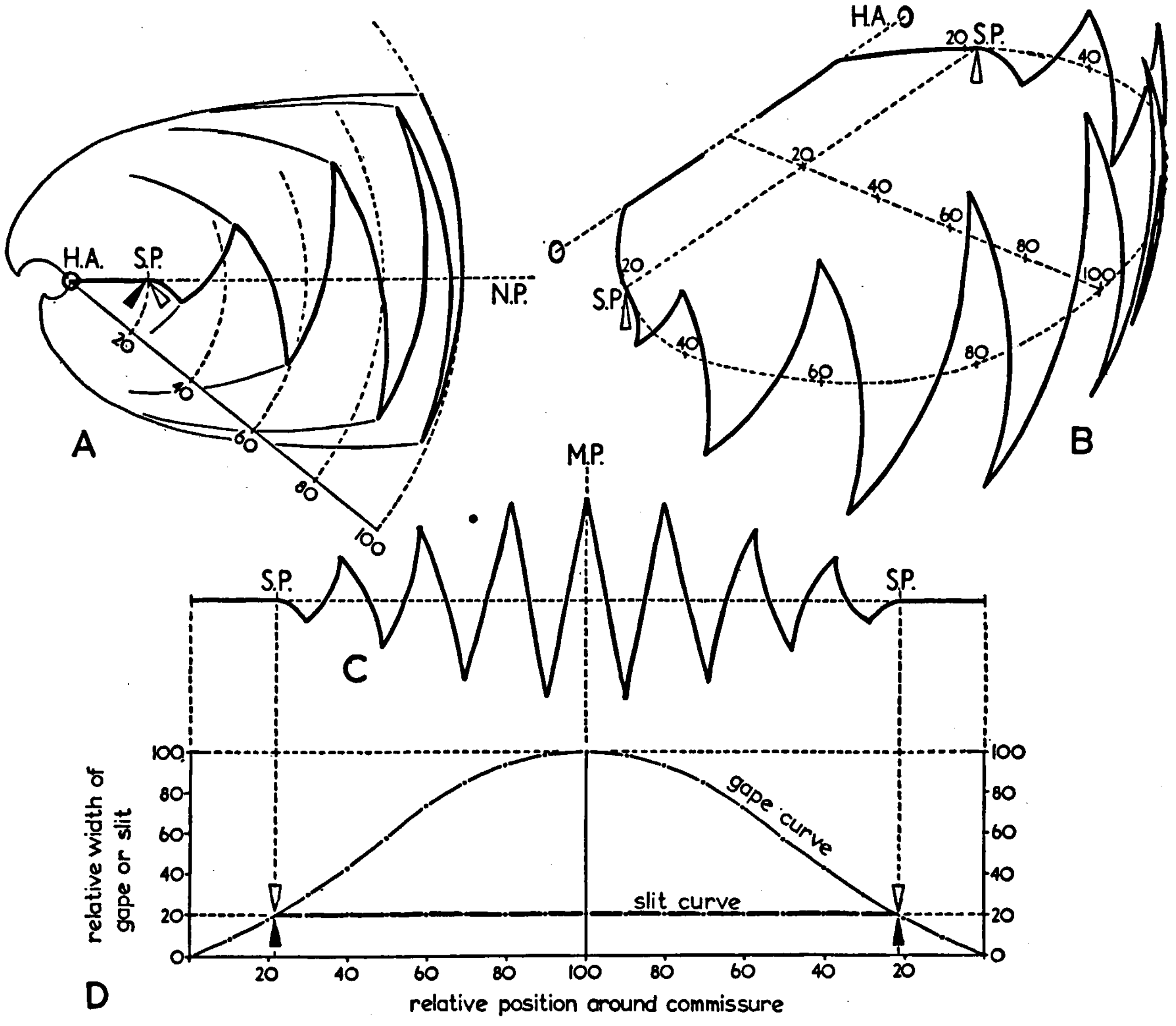

Fig. 40. Paradigm for protective zigzag deflection on commissure of subcircular plan. (After Rudwick, 1964).

2. sharp crested;
3. of large relative wavelength, i.e. of low crestal number, to avoid the deleterious effect of the crests;
4. "of high relative amplitude and straight flanks anteriorly"; and
5. "of appropriately graded relative amplitude and flank curvature laterally and posteriorly". This is a result of the decrease in gape (vertical distance separating the valve edges) in posterior direction towards the hinge axis. "At one particular suppression point (S.P.), the relative amplitude will fall to unity..., and the zigzag deflection will therefore die away. Between the suppression point and the hinge axis the commissure will be undeflected, and the slit necessarily less than the standard width".

In actual brachiopods the zigzags show a definite approach to the paradigm, and consequently Rudwick interprets these deflections as protective devices, just as Schmidt had done previously, but his arguments are better.

Nevertheless, the opinions of Schmidt and Rudwick in relation to the exact mechanism of protection by the zigzag-deflected valve margins are widely divergent. Schmidt considers the slit to be a straining device, sorting the approaching particles into two classes on the basis of their size, rejecting one class and accepting the other. Rudwick, on the other hand, has pointed out that the mantle-edges, which line the valve edges, are highly sensitive to tactile and chemical stimuli and to light. Indeed, their borders are richly supplied with nerve endings. "A simple reflex nerve circuit from the mantle-edges causes the shell to be snapped shut in response to stimuli (Rudwick, 1961). Hence, any modification of the form of the mantle-edges can be considered as a possible modification of this protective system". Thus, the zigzag-deflected valve-edges are rather a warning than a straining protective system. This also means that the brachiopod is protected against much smaller harmful particles than Schmidt's hypothesis implied. In principle, therefore, the question is not concerned with the size of the largest particles able to pass through the slit, but with the degree to which the slit is controlled by the mantle-edges, According to Rudwick, this has no influence on the paradigmatic specification, which therefore can still be expressed in terms if idealized spherical particles.

It is necessary at this point in the argumentation to introduce two new terms. The *local degree of control* by the mantle-edge at a certain point of the slit is the reciprocal of the distance from that point to the nearest point of the mantle border. The *overall degree of control* is the reciprocal of half the distance between the mantle-edges in a small section of the slit [17]. Thus, in a slit of which the degree of protection is ideally graded, the overall degree of control is constant. In fig. 41 a, b, c, and d a pair of zigzag-deflected valve margins is shown at four different degrees of opening. In each slit a set of lines has been drawn connecting points which lie at equal distances from the nearest mantle border, and thus with equal local degree of control, and the distances between these lines are constant. The areas between these lines are shaded in such a way that the darkness of the shading increases as the local degree of control decreases. Thus a most differentiated picture is obtained of the local degree of control at any point of the slit, as well as of the overall degree of control. Such drawings will be termed here *control diagrams.* The degree of protection is represented in the corresponding gape curves and slit curves.

When the gape is small, as in fig. 41 a, the overall degree of control is very high, although somewhat lower in the crests than in the flanks. The slit is mainly controlled by the flanks and the deleterious effect of the crests is localized in very small triangles and is therefore very reduced. The degree of protection amounts to 3 in the flanks and to 2 in the crests. With increasing gape, as in fig. 41 b and c, the overall degree of control decreases proportionately, in the flanks as well as in the crests. The maximum and minimum values of the degree of protection remain 3 and 2 in the flanks and in the crests respectively. However, the reach of the crestal anomalies rapidly increases at the expense of the reach of the flanks, as is shown in the slit curves. The control diagrams also show an increase in crestal influence: the absolute as well as the relative size of the anomalous triangles increases. When the gape increases still further, the maximum value of the degree of protection decreases, whereas the minimum value remains constant (fig. 41 d). The original "crestal anomalies" dominate the picture, in so far as the degrees of protection and overall control are concerned. The shading of the slit, however, shows that areas of actual "crestal anomaly" remain relatively reduced. The degrees of protection and overall control therefore give a slightly exaggerated picture of the "crestal anomalies". Finally, with very large gapes, the original minimum value of the degree of protection in the crests (= 2) is reduced. It may be concluded that with increasing gape the degree of protection of the undeflected commissure (= 1) is increasingly approached. The crestal parts of the slit can only be considered as local anomalies when the gape is small. This also means that the grading of the degree of protection decreases with increasing gape. Rudwick has noticed in this respect that "as a warning device, a zigzag slit would have been most important in the early stages of reopening of the shell".

2. MARGINAL SPINES — GENERAL CONSIDERATIONS

In nearly all the representatives of the Uncinulidae marginal spines occur: they are slender, elongated

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[17] It might be more accurate to define the degree of control as the square of these values. However, as we are not interested in this account in the exact value, but only in the relative increases or decreases of the degree of control, there is little point in going further into this problem at the moment. The above definitions are most convenient for our purpose.

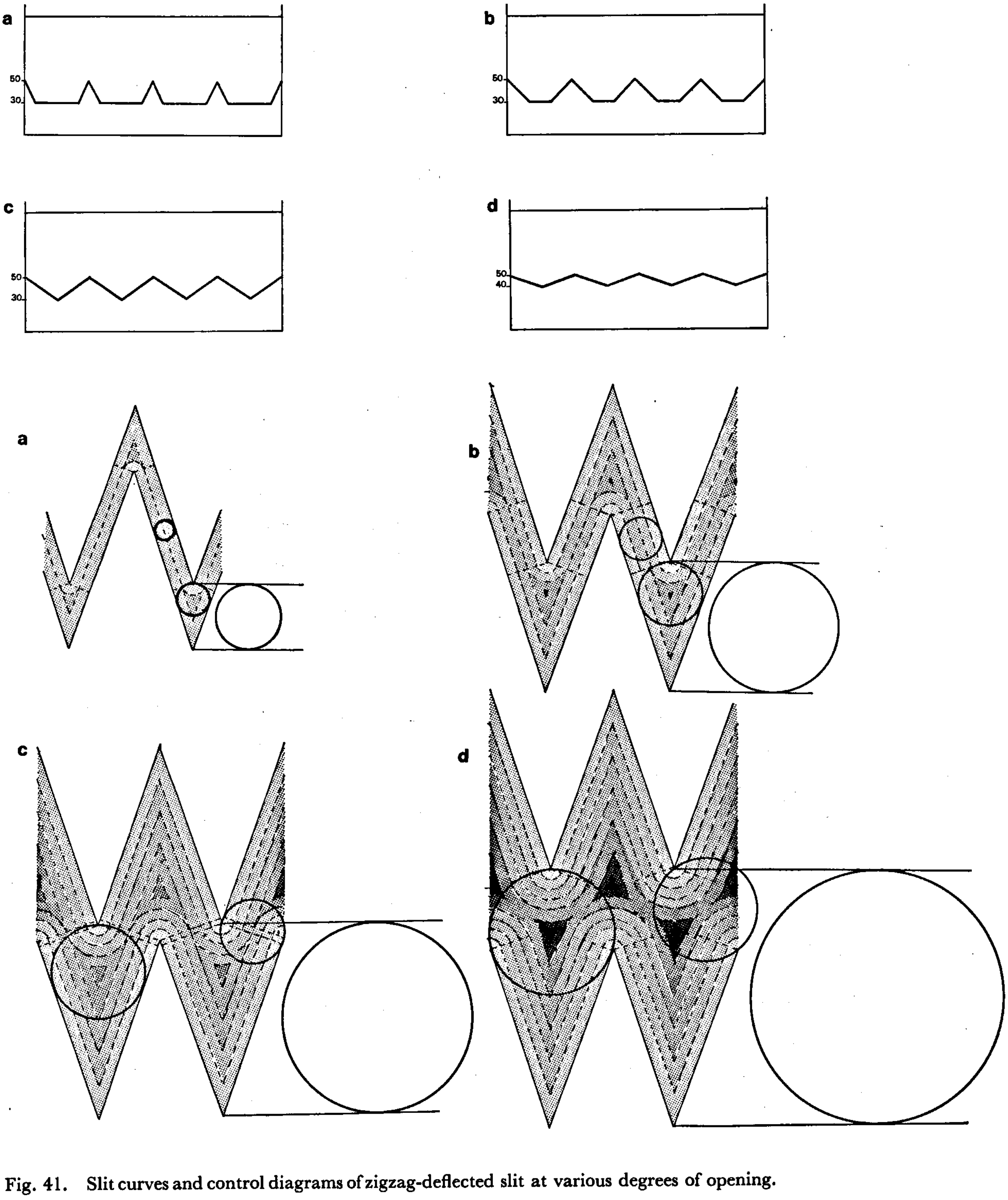

Fig. 41. Slit curves and control diagrams of zigzag-deflected slit at various degrees of opening.

outgrowths of the shell, forming continuations of the jutting crests of the zigzag-deflected valve margins and thus of the grooves of the shell surface, and they project into the mantle cavity where they lie just behind the inner surface of the opposite valve. These marginal spines, which were discovered by Herta Schmidt in 1937, certainly form interesting modifications of the zigzag deflected valve margins. When the shell is opened the spines form local barrages in the slit, running between the corresponding crests in both valves. An analysis of their structure (see p. 52) reveals that the spines have been enveloped by the mantle, so it can be assumed that they have had the same sensitive potential as the mantle-edges along the zigzag-deflected commissure. Consequently, the spines may not have performed a straining function, as Schmidt supposes, but must be considered as a modification of the warning protective device constituted by the zigzag deflections.

The fact that the spines are continuations of the grooves of the shell surface has important consequences (fig. 42). As growth proceeds the bases of the spines become incorporated in the overall shell structure, and the spines themselves grow distally. Thus the marginal spines can be considered to be "advanced outposts" of the shell. Hence, the position of the spines is to a large extent determinant for the direction in which the shell will grow in the future. It is known that they project into the mantle cavity and lie close to the inner surface of the opposing valve. In consequence of this, they can occur only in shells where the valves make angles of 180° or more at the commissure. Indeed, wherever marginal spines occur the adjacent shell walls are invariably vertically disposed.

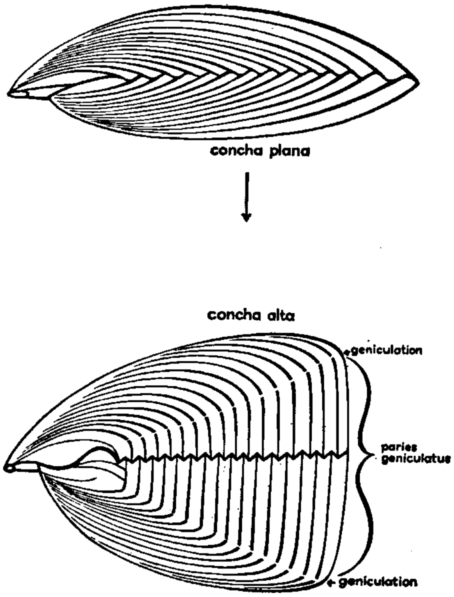

Fig. 42. Geniculation in uncinulid brachiopod.

Brachiopods with such vertical walls can only grow in thickness and not in length. Consequently, marginal spines can only occur in the post-brephic stage of ontogeny, when the growth in length is already fully completed. Hence, brephic shells are flat and grow in length, whereas post-brephic shells are thick and grow in thickness. The process of conversion in growth direction from mainly radial to vertical is called *geniculation* (Williams and Rowell, 1965). Here three

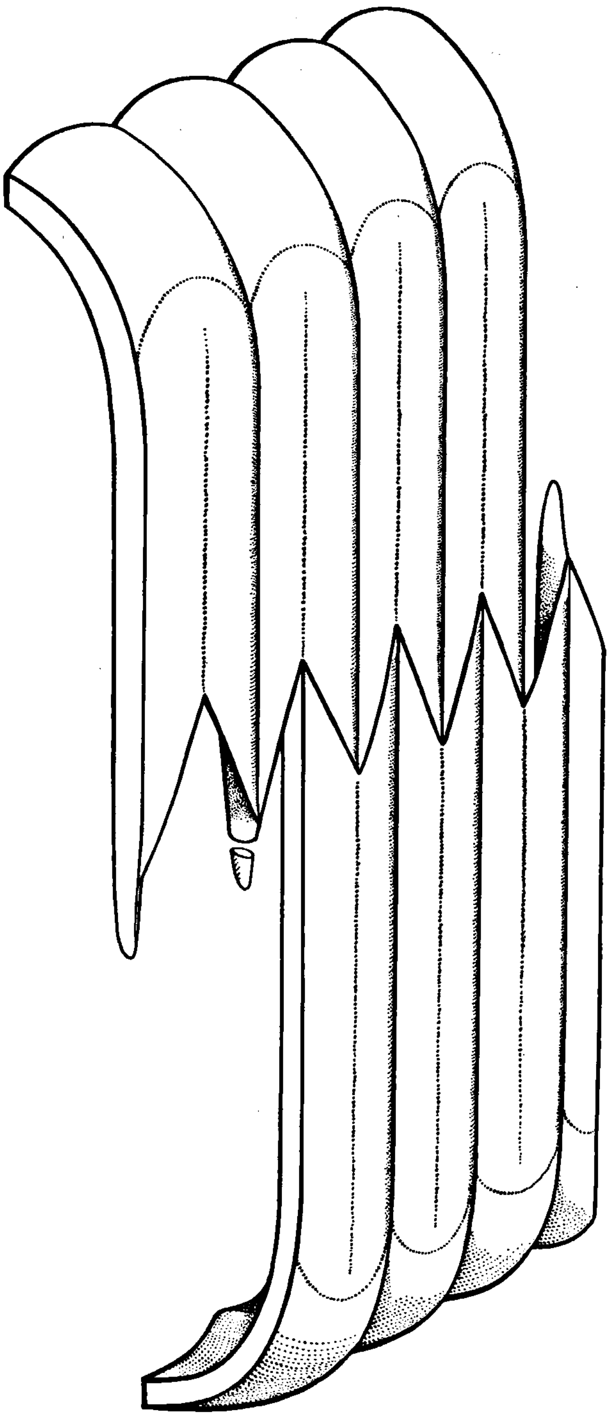

Fig. 43. *Sphaerirhynchia wilsoni*. Part of the paries geniculatus and marginal spines (reconstruction from serial sections). Type A.

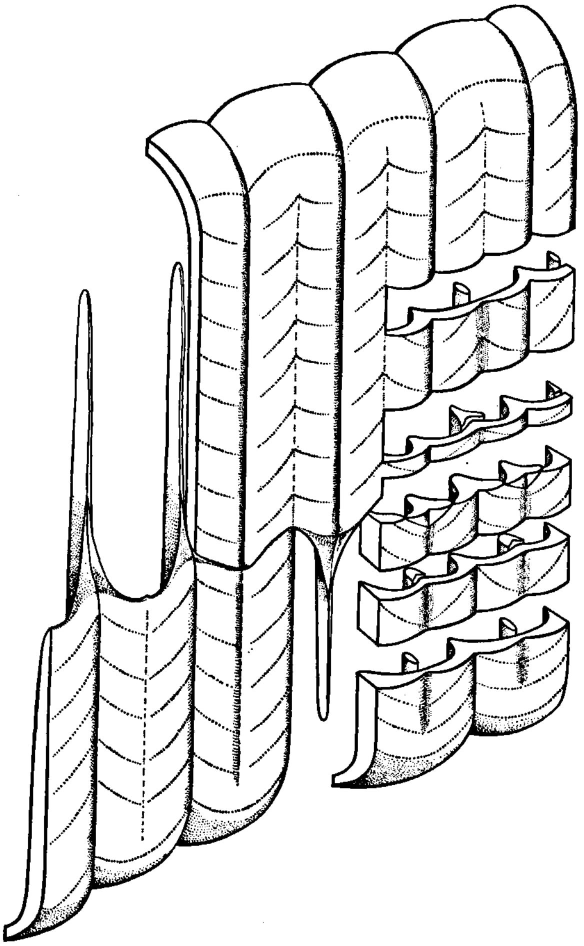

Fig. 44. *Glossinulus* (*G.*) *latus.* Part of the paries geniculatus and marginal spines (reconstruction from serial sections). Type B.

new terms will be introduced: ***paries geniculatus,*** for the vertical shell wall which is formed as a result of geniculation; ***concha alta,*** for the post-brephic geniculated shell; and ***concha plana*** for the brephic non-geniculated shell, as well as for that part of the concha alta which once formed the concha plana [18].

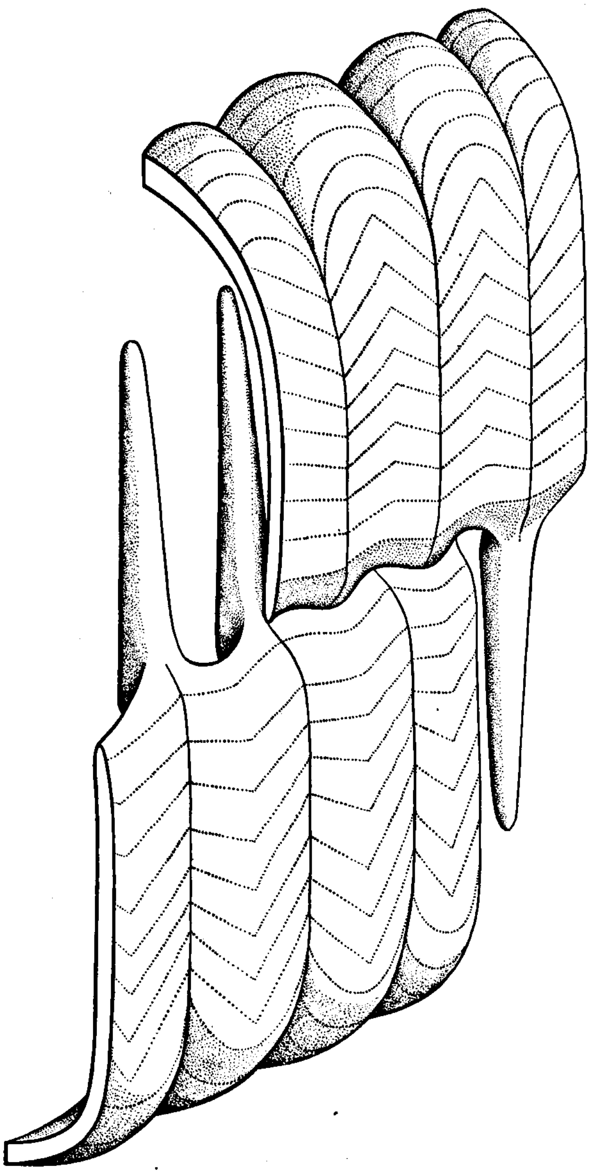

Fig. 45. *Uncinulus pila* and *U. orbignyanus.* Part of the paries geniculatus and marginal spines (reconstruction from serial sections). Type C.

Later a detailed description will be given of the marginal spines in all the species investigated. Here, however, it is sufficient to state that a great variation exists in the length of the marginal spines and in the relative amplitude of the concomitant zigzag deflections in the concha alta. Roughly speaking four types of spined commissures can be distinguished; the division, however

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18. In 1937 Herta Schmidt, who was much (and very rightly) intrigued by the great differences in length of the conchae altae within one species, put forward a remarkable hypothesis to explain this phenomenon. According to this, shells of the Uncinulidae passed through a process of "Mehrzyklisches Wachstum" during which they shed the paries geniculatus; this enabled them to grow in length again for a limited period, after which a new paries geniculatus was formed. This process could be repeated several times. Schumann, 1965, has already given a number of arguments against this hypothesis, and a new one can be added here. In a small number of Uncinulidae *(G. (G.) latus,* and *U. orbignyanus,* inter alia) a series of sections through the articulatory device of the conchae altae has been analysed. The sections were parallel to the plane of symmetry, and thus perpendicular to the hinge axis. In such sections the actual process of articulation can be reconstructed. The shell proved to be capable of opening 20—30°. However, the articulatory device was such that the shell could not be closed if the paries geniculati had been removed. The protection of the shell would therefore have been very greatly reduced. Indeed, great parts of the shell would have had to be dissolved in order to enable the shell to perform its normal protective function. The changes required in the soft parts would have been even much more drastic.

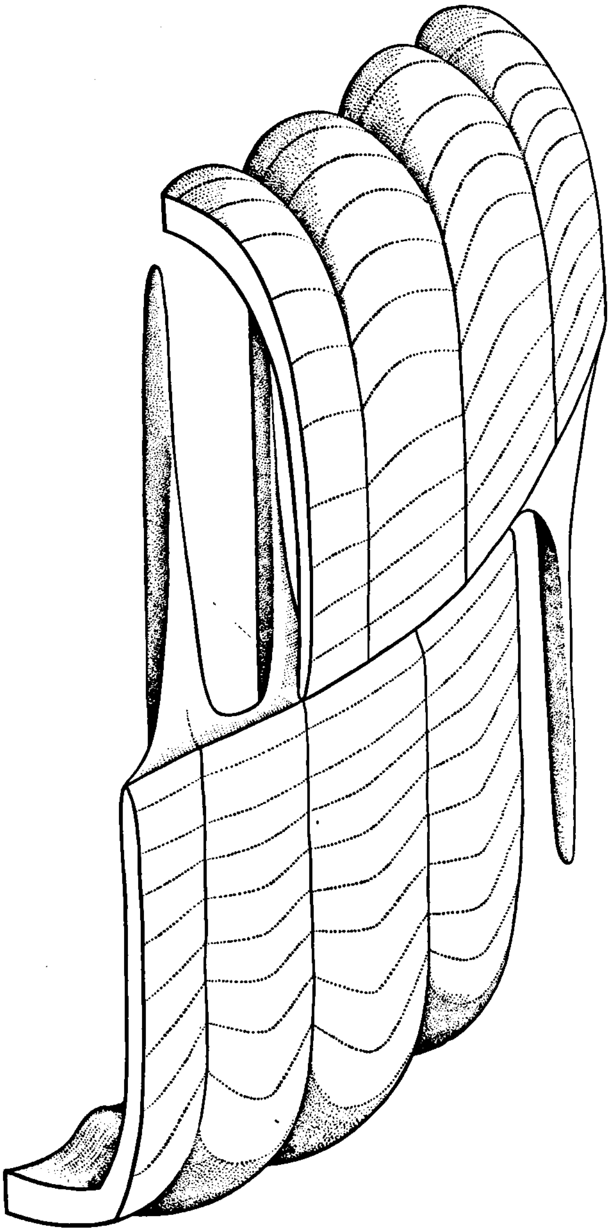

Fig. 46. *Kransia parallelepipeda*. Part of paries geniculatus and marginal spines (reconstruction from serial sections). Type D. On the right side: lateral part of tongue.

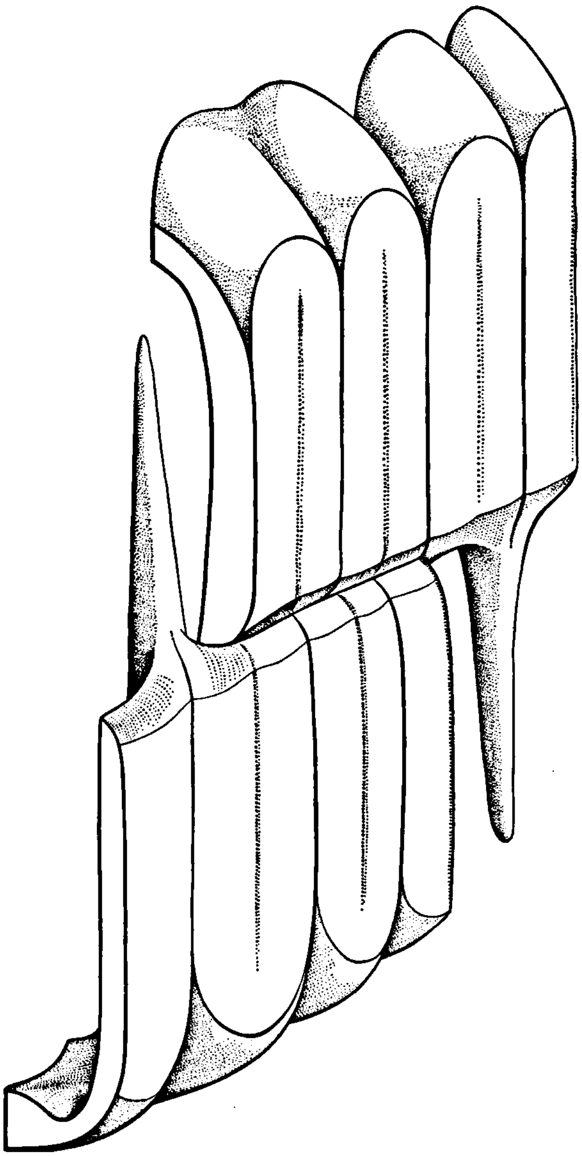

Fig. 47. *Kransia primipilaris*. Part of the paries geniculatus and marginal spines (reconstruction from serial sections).

useful for our purposes, is rather arbitrary since transitional forms occasionally occur.

Type A: well developed serial zigzag deflections in combination with very short marginal spines. The intervals between the spines are very variable. This configuration occurs frequently. Examples: *Spaerirhynchia wilsoni* (fig. 43, Pl. X, fig. 1), *Eoglossinotoechia mystica* (Pl. XI, fig. 1) and *Eucharitina eucharis*.

Type B: poorly to moderately developed serial zigzag deflections in combination with short to rather long marginal spines. The spines are often broad and flattened at their base. Valve-edges and spines of this type occur in glossinulid species, e.g. *G. (G.) latus* (fig. 44; Pl. XI, fig. 3). (Generally the spines assigned to type B are shorter than in *G. (G.) latus.)* The intervals between the spines are moderate to small. *Markitoechia marki* (Pl. XII, fig. 5, 6, 7) and *Obturamentella lebanza* (Pl. XII, fig. 8.) are somewhat different, among other things because of their marked zigzag deflections but nevertheless can best be allocated to this type.

Type C: zigzag deflections nearly absent; marginal spines very long. Example: *Uncinulus orbignyanus*. The intervals between the spines are generally very small (fig. 45; Pl. XII, fig. 9, 10, 11).

Type D: commissure completely straight; no zigzags occur. Spines are very long, sometimes broad and flattened at their base. The intervals between the spines are moderate to small. This occurs in the genus *Kransia.* Examples: *Kransia parallelepipeda* (fig. 46, Pl. X, fig. 3) and *K. primipilaris* (fig. 47, Pl. X, fig. 2). Apparently a simple morphological range can be drawn up corresponding more or less with types A-D in which the length of the spines increases, and at the same time the relative amplitude of the zigzag decreases. All the Uncinulidae investigated fit in with this range.

3. AN ATTEMPTED FUNCTIONAL INTERPRETATION OF THE MARGINAL SPINES

At this point in the argument it is necessary first to take a step back and to survey the function of the valve edges and of all the other elements concerned from a more general point of view. The shell itself obviously performs the function of protection of the animal. This function is best fulfilled when the shell is completely closed. The protection will decrease as the opening increases. On the other hand the animal is unable to communicate with its environment when the shell is tightly closed so that vital processes such as respiration and metabolism are impeded and ultimately obstructed. Only in circumstances of acute danger will the animal resort to complete closure. According to Rudwick (1965a) the brachiopod can survive for periods of at most several hours with the shell tightly closed. The opening of the shell is therefore of vital importance for the animal. Broadly speaking one may say that a minimum opening is necessary to keep the animal alive.

As a result of their location the valve margins can be considered to have two functions: 1. they surround the opening between the valves and thus help to regulate the circulation of seawater through the mantle cavity, and 2. they form the margins of the main protective device: the shell.

The fulfilment of these two functions tends to make different demands on the animal and thus on the valve edges. In my opinion Rudwick has not sufficiently distinguished between these two factors in his analysis

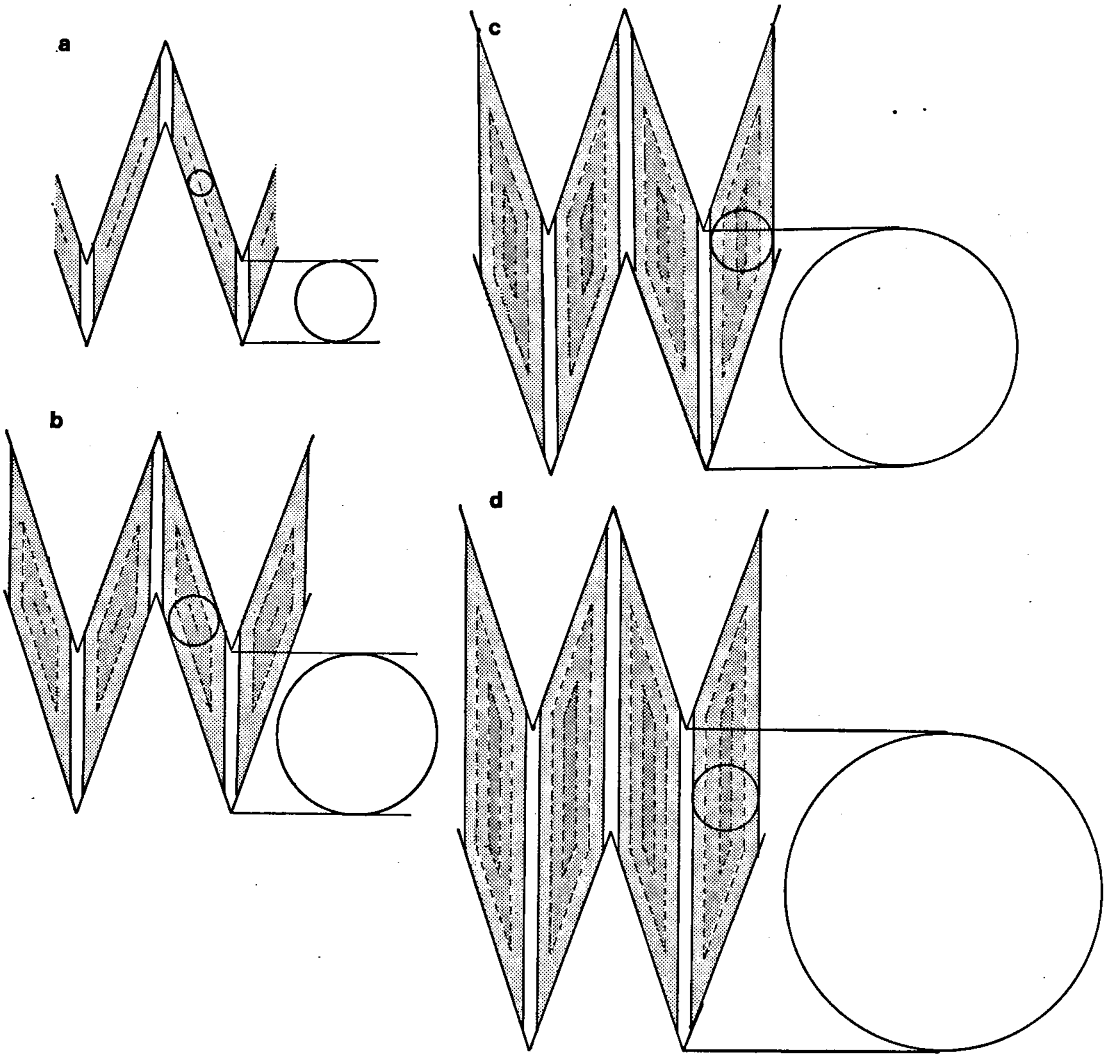

Fig. 48. Control diagrams of hypothetical slit: the zigzag and the degrees of opening are the same as in fig. 41, but elongated slender marginal spines occur.

of the function of zigzag deflections. This however has hardly damaged his argument since the paradigmatic demands involved in the function of protection conflict only to a small extent with those of the water-circulation in so far as the zigzag deflections are concerned: the surface of the opening between the valves is not affected, so that the increase in length of the valve-edges only causes more friction with the water. In a functional interpretation of the marginal spines, however, the factor of the water-circulation must be very clearly and explicitly considered. As a matter of fact a grille of marginal spines in the opening between the valves must have a drastic influence on the water flow. As a result of this both functions will first be analysed separately according to the method introduced by Rudwick. Afterwards an attempt will be made to formulate a paradigmatic specification for a combination of both functions, and to compare the demands involved with the actual fossil structures concerned.

A. *Marginal spines and the function of protection*

In order to gain an insight into the different possibilities of slit control provided by the marginal spines the first aim will be to analyse the control diagrams of the different types of spinal development described above. The control diagrams will be considered in reversed order, thus from type D to A. It is however useful to preface these examinations by the discussion of a hypothetical case: the slit produced by the same zigzag deflected commissure as in fig. 41, at the same four degrees of opening, but now provided with long and slender marginal spines (fig. 48). When the gape is small (fig. 48a) the slit is predominantly controlled by the flanks of the zigzags and the function of the spines is best described by the term "crestal protection" (Rudwick, 1964, p. 153). But with increasing gape the reach of the spines in the slit increases and the reach of the zigzag decreases. The spines then form a grille which partly obstructs the opening. The overall degree of protection does not exceed a certain maximum value which is determined by the distance between the spines. Consequently, the degree of protection [19] increases in direct proportion to the gape, in sharp contrast with the situation in the unspined zigzag. With increasing gape, the control diagram approaches a spined rectimarginate shell.

The control diagrams of the species belonging to types C and D are very similar to each other and will be discussed together (fig. 49. Pl. XII, fig. 2, 3, 4, 9). The spines are here long and rather stout at their bases; distally, they taper gradually. They are generally adjacent when the shell is closed. When it opens, a set of very narrow slits arises and the overall degree of control is extremely high. With increasing gape the overall degree of control decreases very slowly. Consequently, these factors are very independent of each other. Here again, the degree of protection practically increases in direct proportion to the gape. The main difference with the preceding theoretical case is in the fact that the openings are much smaller and that the overall degree of control is much higher.

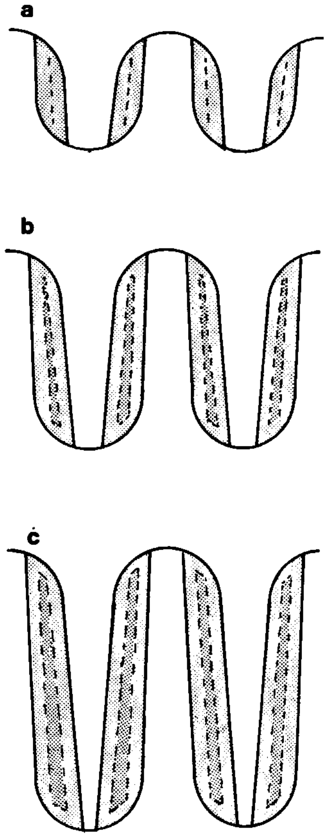

Fig. 49. Control diagrams of slit in spines of type C and D.

Control diagrams of *G. Glossinotoechia latus* (type B) are given in figure 50. Here, too, the openings are extremely reduced when the gape is small. Control is provided mainly by the broad bases of the spines. With increasing gape the slender parts of the spines dominate the picture more and more, but even then the degree of control remains very high. As the spines are often much shorter in one valve than in the other, it can be expected that the short ones do not cross the entire slit when the gape is very large. In such cases local anomalies may occur in the control pattern. This may also occur in the valve-edges of type C and D. On the whole the situation is rather similar to the above cases. Only the decrease of the control is somewhat more pronounced with increasing gape, especially when the spines are relatively short.

Finally, control diagrams of *Sphaerirhynchia wilsoni* and similar forms (type A, fig. 51) show a great resemblane with those of fig. 48 when the gape is small. The function may be described then as "crestal protection". When the spines are not too short there will be a stage in which they predominantly regulate the control, but with large gapes crestal anomalies will arise which are large when compared with those of fig.

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[19] It is recalled here that the term "degree of protection" is introduced by Rudwick (1964). The definition of this term has been given on p. 37.

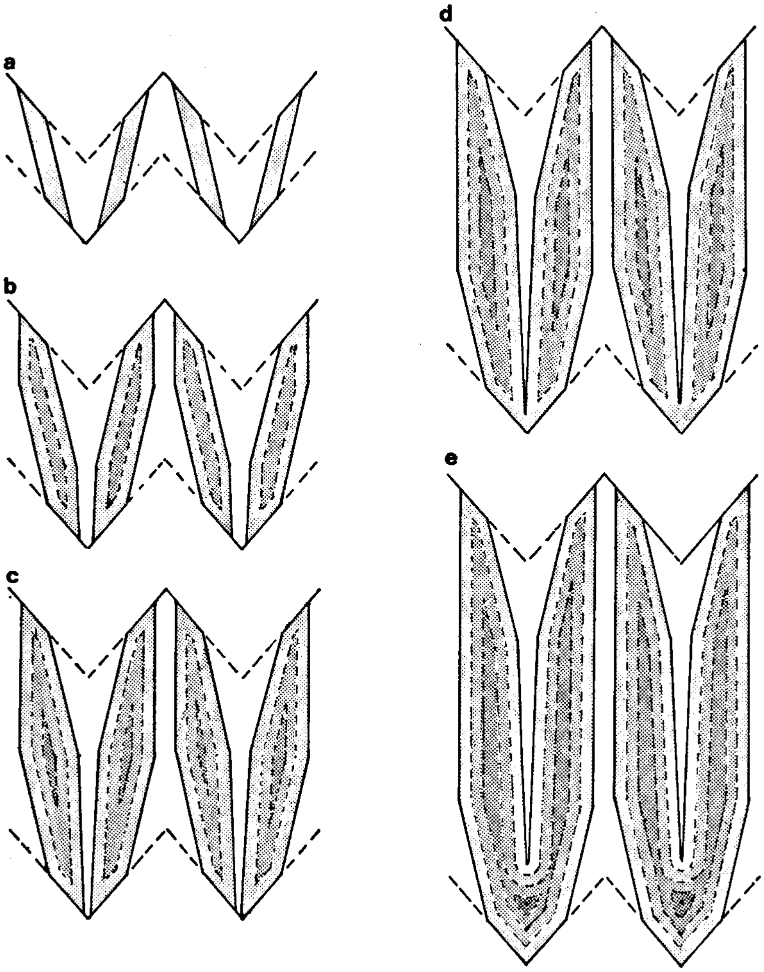

Fig. 50. Control diagrams of slit with spines of type B, with broad bases.

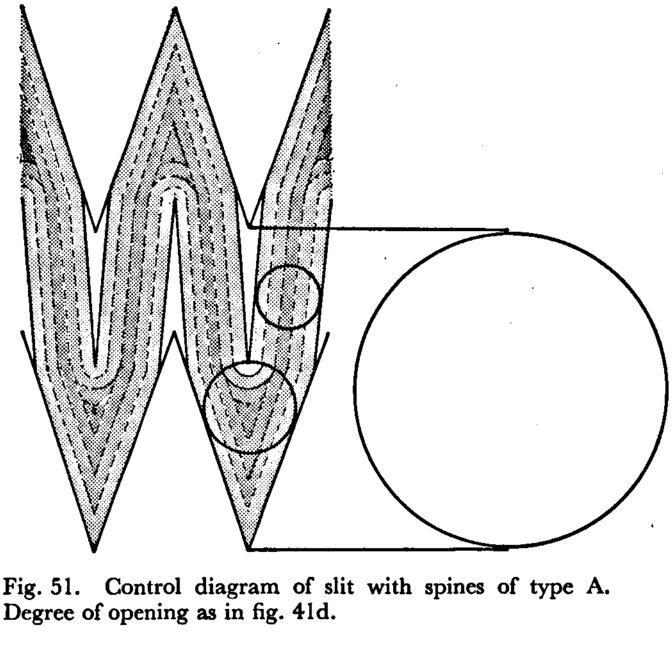

Fig. 51. Control diagram of slit with spines of type A. Degree of opening as in fig. 41d.

50 *(G. (G.) latus)*, but very small in comparison with those of the unspined zigzag-deflected commissure (fig. 41).

In trying to formulate a paradigmatic specification of the marginal spines for the function of protection the following statements can be made:

1. The intervals between the marginal spines should all be equal along the commissure. Aberrations from this rule would involve local imperfections in the overall degree of control.
2. The best protection is achieved by marginal spines which are situated at short intervals. Rudwick's original argumentation in favour of a low crestal number in the mere zigzag deflection has little significance here, since the crestal anomalies are eliminated in most cases.
3. The spines should be elongated.
4. As a result of the decrease in gape towards the hinge the spines should be long anteriorly and decrease in length towards the posterior. In other words the spines should be graded in length.
5. Broad bases as present in species of types B and D are certainly advantageous for the protection.

6. It has been seen that when the spines are short the zigzag deflection plays a significant role in the control diagram. These zigzag deflections should be well developed and graded.
7. When the spines are long the influence of the zigzag deflection on the control diagrams is reduced, especially when the spines are situated at small intervals.

When the different types of marginal spines which were found in the species studied are compared with these paradigmatic requirements involved in the function of protection it may be possible to evaluate the degree of adaptation [20] of the spines in question to this function.

These considerations link up directly with the analyses of the control diagrams given above. Occasionally it will be necessary to anticipate the systematic descriptions of the spines.

Sub 1: In all the species studied the intervals between the marginal spines were found to be almost equal all along the commissure. The animals evidently fulfil this demand very well.

Sub 2: In the different species studied the intervals between the marginal spines are very variable — although much the same within one species.

In the species belonging to type A a great variation exists, ranging from large to small intervals. In the species of type B the intervals are considerable to moderate. Type C: small to very small. Type D: moderate. Generally speaking the morphological range from A to D tends to correspond with a range of gradually diminishing intervals between the spines.

Sub 3: The marginal spines should be long. A great interspecific variation has been found in this respect; the morphological range is based essentially on this character.

Sub 4: The length of the spines should be graded. The spines of all the species investigated are perfectly graded in length towards the hinge, provided that their length exceeds a certain minimum.

Sub 5: Broad, flattened bases of the spines occur in a small number of species which have in common considerable intervals between the spines (this does not mean that all species with large intervals have broad bases).

Sub 6: In species with short spines (and thus belonging to type A or B) the zigzag deflection is generally well developed. The zigzags commonly display a moderate to good grading.

Sub 7: When the spines are long the zigzag deflections are strongly reduced, conformable to the expectations.

It may be concluded that:

1. so far as the demands no. 1, 4, 6 and 7 are concerned the marginal spines are well adapted to the function of protection.
2. the demands no. 2 and especially no. 3 are indicative of a gradual augmentation of the protection within the morphological range. The analysis of the various control diagrams has already produced adequate proof of this. In valve-edges of type A the spines are hardly more than a device for crestal protection, whereas the spines of types B, C, and D increasingly dominate the picture and cause the overall degree of control to be very independent of the gape.

B. *The marginal spines and the water circulation*

The formulation of a paradigm of the marginal spines for the function of sea-water circulation is rather a complicated matter as there are several conflicting factors involved here. Moreover some of these factors are difficult — if not impossible — to evaluate.

The following factors are involved:

a. Marginal spines constitute a more or less developed grille in the opening between the valves and thus reduce its area. They therefore impede the water current. This contrasts with the mere zigzag deflections, which do not reduce the area of the slit at all. In this respect the development of the marginal spines from the mere zigzag deflections constitutes a deterioration. In view of this factor the following further paradigmatic demands can be formulated; it would be better if no marginal spines were developed at all but when they are developed they must be:

8. situated at large intervals from each other,
9. short,
10. slender (thus no broad bases).

b. The friction with the water current is strongly increased by the presence of marginal spines. This factor is also at play in respect of the zigzag deflection, but generally to a lesser degree. The paradigmatic demands involved are these; it would be better if no marginal spines were developed at all but when they are developed they must be:

11. few (i.e. situated at large intervals),
12. short,
13. streamlined in cross section (thus no broad bases).

Two other factors which may play a role in the circulation of the water and which contrast greatly with (a) and (b) are:

c. The inner epithelium which lines the mantle cavity is provided with cilia which induce the water current. It will be seen that this inner epithelium very probably also used to surround the marginal spines. Thus cilia will have been situated all along the marginal spines. In consequence of their location in the slit these cilia must have been pre-eminently capable of effecting the water flow. The spines of the animal which would use this watercurrent-inducing potential of the cilia to the best advantage would most probably conform to the following structural requirements:

14. they would be long,
15. serried,
16. thin,
17. with large lateral sides and probably reduced anterior and posterior sides (this corresponds more or less with the demand of streamlined shape postulated above).

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[20] The term "adaptation" is used here in the sense proposed e.g. by Rudwick, 1964a: "i.e. the demonstrable relations between the structures of organisms and their functions".

d. Since in species with well developed marginal spines the overall degree of control is highly independent of the gape, the animal can under normal circumstances open the shell widely and increase the area of the slit without a significant decrease in the control, although it will take a little longer to shut the shell in moments of acute danger. The demands involved correspond with those of good protection with a large opening, i.e.:
18 = 1
19 = 2
20 = 3

When it is desired to erect a conclusive paradigmatic specification of the marginal spines for the function of water circulation the demands 8—20 which have just been postulated for the different factors at play must be incorporated. In some instances the demands involved are all in agreement, so that in these cases definite statements on the paradigm involved can be made. When however the demands contradict each other, their relative importance must be evaluated. In so far as the factors a, b, and c are concerned, such an evaluation seems impossible at the present stage of our knowledge. I am inclined to consider that factor d (and thus demands 18—20) is of relatively little importance since it has no influence on the water current at any degree of opening of the shell.

In table I the demands are combined so that deductions can be made as to the final demands.

Table I

	demand +	demand —	final demand
I	intervals equal 18	intervals unequal —	*intervals equal*
II	intervals large 8, 11	intervals small 15, 19	?
III	spines long 14, 20	spines short 9, 12	?
IV	broad bases —	no broad bases 10, 16	*no broad bases*
V	streamlined 13, 17	not streamlined —	*streamlined*

Conclusion. The final paradigmatic demands of the marginal spines for the function of water circulation are the following:
α the spines should be situated at equal intervals,
β broad bases should not be developed,
γ the spines should be streamlined in cross section.

In regard to the magnitude of the intervals and the length of the spines no demand can be positively formulated.
A comparison between these demands and the actual marginal spines encountered in the fossil record will now be attempted.
sub α) it has already been seen that the intervals between the marginal spines are almost equal all along the commissure.
sub β) broad, flattened bases are, as has been seen, incidentally developed.
sub γ) the spines are invariable beautifully stream-lined in cross section, except at places where a broad base is developed, or where the radially facing surfaces of the spines are somewhat flattened, e.g. in *Kransia parallelepipeda.*
The conclusion reached is that the marginal spines of the species studied comply very well with the paradigmatic requirements sub α and γ but not always with those of β. Thus, in so far as judgement permits, the marginal spines can be considered to be moderately to well adapted to the function of water circulation. The data in support of this conclusion are however rather meagre.

C. *The marginal spines and the combined functions of protection and water circulation*

Finally an attempt will be made to erect a paradigmatic specification for a combination of the functions of protection and of water circulation. This will again be carried out in a tabular summary, following the same method used for the function of water circulation.

Table II

	demand +	demand —	final demand
I	intervals equal 1, 18	intervals unequal —	*intervals equal*
II	intervals large 8, 11	intervals small 2, 15, 19	?
III	spines long 3, 14, 20	spines short 9, 12	?
IV	spines graded in length 4	spines not graded in length —	*spines graded in length*
V	broad bases 5	no broad bases 10, 16	?
VI	streamlined 13, 17	not streamlined —	*streamlined*
VII	when the spines are short the zigzag deflections should be well developed and graded 6	short spines: zigzag deflections reduced —	*short spines: well developed graded zigzag deflections*
VIII	when spines are long: zigzag deflections reduced 7	when spines are long: zigzag deflections not reduced —	*long spines: zigzag deflections reduced*

Thus, the paradigmatic requirements for the combination of these two functions are:

A. the intervals between the marginal spines should be equal all along the commissure,
B. the length of the spines should gradually decrease towards the hinge,
C. the marginal spines should be streamlined in cross section,
D. when the spines are short the zigzag deflections should be well developed and graded,
E. when the spines are long the zigzag deflection has only little or no function and may be reduced.

No definite statement can be made about some other factors, viz. the magnitude of the intervals between the spines, the length of the spines, and the development of broad bases, with reference to this paradigm.

Comparison between the actual fossil structures and this paradigm, and some conclusive remarks. — In the foregoing argument it has already been shown that the spines of the species investigated correspond perfectly with all the paradigmatic requirements formulated under A to E. The first conclusion therefore is that there are strong indications that the marginal spines studied are all very well adapted to the combination of the postulated functions of protection and water circulation. In respect of the remaining three factors about which no statements could be included in the paradigm the marginal spines display a great variation. It is exactly in respect of these three factors, and especially of the first two, i.e. the magnitude of the intervals between the spines and the length of the spines that the morphological range could be erected. It has already been seen that this range corresponds with an important increase in protection. In spite of this it is impossible to judge if this range corrresponds with an increase in adaption for the combination of both functions: protection and water circulation.

The valve-edges and the marginal spines are somewhat aberrant in two species: *Obturamentella lebanza* and *Markitoechia marki.* In both these species the zigzags are well developed. The spines are fairly short in *O. lebanza,* but in *M. marki* they are rather elongated. In both species they are provided with well developed broad bases. The tips of the spines fit into small cavities of the opposing valve when the shell is closed. In view of the moderate development of the spines the pronounced zigzag deflections are rather aberrant features; on the other hand the poor grading of the zigzags complies very well with the theoretical considerations. It is however possible that the conditions are somewhat different here, so that the paradigmatic demands cannot be positively applied. These species have not yet been sufficiently studied to permit a sound evaluation of the slight deviations involved. Fig. 61; Pl. XII, fig. 5—8.

An important problem which has yet to be treated is the question whether the paradigmatic demands which have just been formulated for the different functions could be identical with the requirements imposed merely by the structural constitution of the animals. When paradigmatic demands and structural imperatives are the same the conformity of the fossil structures to the demands of the paradigm do not necessarily have to be interpreted as an adaption to that demand. Since little is known of the laws which govern the shell growth of brachiopods it is in most cases impossible to determine the extent to which structural demands play a part. I have a strong feeling however that in this analysis this might be the case especially in respect of two paradigmatic demands, viz. 1. the grading in length of the spines, and 2. the interdependence of the length of the spines and the development of the zigzag deflection. Sub 1. The grading in length of the spines may be correlated with the corresponding grading in height of the paries geniculatus. Sub 2. It is not impossible that the zigzag deflections and the spines must be considered as being phenomena closely related structurally in such a way that the spines can only develop at the expense of the zigzag. The association of the development of the spines and the reduction of the zigzags may therefore be only a structural adaptation. For the time being it is impossible to determine the importance of these factors, but they certainly reduce the strength of the argument.

In the paradigmatic analysis the direction of the marginal spines has not been considered. Nevertheless this factor is of great interest. However, since the problems involved are of a rather peculiar character their treatment has been reserved for this place. In view of the function of protection it is evident that a vertical direction of the marginal spines is the most favorable. The spines would then be situated just behind the paries geniculatus of the opposing valve. Harmful particles would then be detected earlier than if the spines were directed posteriorly and pointed backwards into the mantle cavity. In respect of the function of water circulation the following observations can be made:

Factor a: a posterior direction of the spines is favourable since this causes the openings between the spines of the opposite valve to be enlarged.

Factors b and c: in so far as these factors are concerned the direction of the spines is more or less indifferent.

Factor d: the vertical direction is favourable.

It has already been stated that factor d is most probably of sub-ordinate importance. It is therefore practically certain that in respect of the water circulation a posterior direction of the spines is favourable. However, for the combined functions no definite statement can be made.
In nearly all the fossils investigated the marginal spines appeared to be directed vertically. Only in *Uncinulus orbignyanus* and *Uncinulus pila* did a very reduced number of specimens display a posteriorly directed orientation of the spines. This phenomenon has already been described in detail by Schumann

(1965). This observation constitutes the main argument for his hypothesis that the marginal spines cannot have been the result of an adaptive process, but are in fact non-adaptive structures. It must be noted in this context that Schumann proceeds from the assumption that marginal spines from the moment of their inception continue growing indeterminately till they are stopped in their growth by some other object such as the bottom of the opposing valve. In consequence of this he means that posteriorly directed marginal spines necessarily must have pricked into the anterior body wall and thus must have injured the animal. It must however be stated with emphasis that not a single argument exists which corroborates the assertion that the spines have grown indeterminately. On the contrary, in many species they are very short and rarely are they so long that they reach the bottom of the opposing valve. In all probability the growth of these elements, which undoubtedly were enveloped by the mantle, is a process which is governed with much precision, just as this is obviously the case with all the other shell structures, such as the crura. By no means can the growth process of the marginal spines be compared with that of the horns of a cow or the incisors of a rabbit.

It is nonetheless a fact that this phenomenon to which Schumann called attention constitutes an intriguing problem, although a sound explanation is yet beyond the range of possibility. There is indeed a chance that this development has been unfavourable for the animal and cannot be considered as an adaptation. One can also imagine that in these species, in which the occurrence of very elongated spines at very short intervals is genetically determined, the conditions for water circulation became so unfavourable that a mutant form in which the spines were directed posteriorly provided a certain amelioration. Such fancies can be produced *ad libitum, sed non ad majorem Dei gloriam* to use the words of Hall and Clarke, but they certainly should not lead to far-reaching generalizations as have been proposed by Schumann.

Finally it must be observed that the conditions of the soft parts naturally could not be taken into consideration in this analysis. Data concerning an eventual variation in the sensibility of the mantle-edge, the thickness of the mantle enveloping the spines (and thus the magnitude of the real openings) and the striking force of the cilia, to give only some examples, would have been of great value for this functional interpretation. No such data are however available, and it is also for this reason that there are no means to determine whether the whole configuration in one species has been more favourable than in another. Consequently, the aim here has been more restricted: it has only been attempted to determine 1. whether the shell structures concerned are the result of an adaptive process, and 2. to what extent these structures may have provided better conditions for the animal in respect of the two functions postulated.

The ultimate conclusions can be formulated thus: there are strong indications that the marginal spines and the other shell structures to which they are related are well adapted for a combination of the functions of protection and water circulation. [In the next paragraph — in the discussion of the squama and glotta — another strong argument in favour of the adaptive status of the marginal spines is given.] The morphological range corresponds with an amelioration in the conditions of protection from types A to D, but whether this range can be considered as an increase in adaptation for the function of water circulation or for a combination of both functions cannot be determined.

4. SOME MORE CONSIDERATIONS ON THE MORPHOLOGY OF THE MARGINAL SPINES

A. A close scrutiny of some morphological aspects of the marginal spines and related structures of *S. wilsoni* and *U. orbignyanus* reveals that the clear-cut distinction between these two species is even more fundamental than noticed in the preceding paragraph.

It has already been seen that the protective device of *S. wilsoni* is only moderately divergent from an unspined zigzag deflected commissure, and the following observations may strengthen this impression. The growth lines of *S. wilsoni* show that even in adult specimens the geniculation may not have been completed (fig. 52): it sets in frontally, and then gradually extends to the posterior, but it did not reach the hinge axis in any of the specimens observed. Consequently, the marginal spines are best developed anteriorly, and the most posterior zigzags do not display any spines at all. The transition between the spined and unspined parts of the commissure is gradual. The grading of the zigzag deflection is moderate; the actual grading of the protection caused by the zigzag and the spines will be nearly ideal. Posteriorly, where no spines occur, the deflection fades away towards a suppression point. This suppression point, as well as the hinge-axis, shifts towards the anterior during the entire growth.

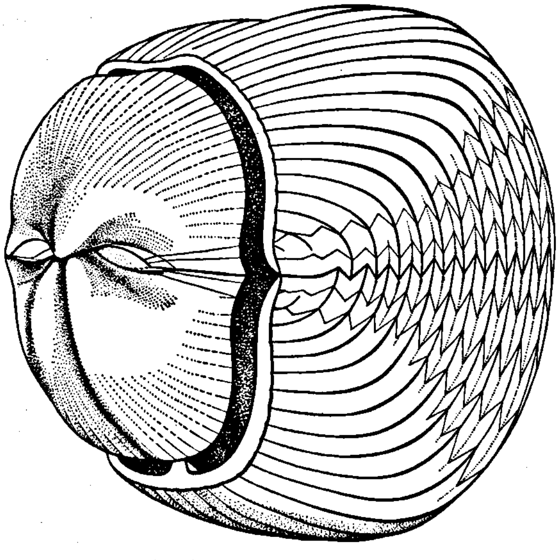

Fig. 52. *Sphaerirhynchia wilsoni.* Shell in posterolateral view. No squama and glotta.

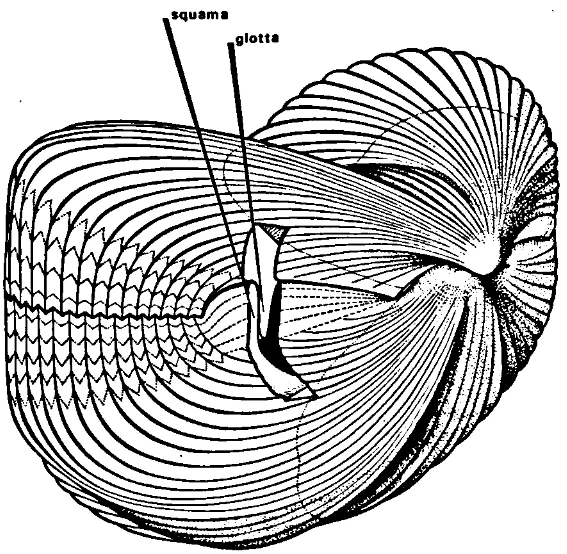

Fig. 53. *Uncinulus orbignyanus*. Shell in posterolateral view. Squama and glotta well developed.

In *Uncinulus orbignyanus* the situation is quite different (fig. 53, Pl. XII, fig. 9, 10, 11). Here, long and slender marginal spines occur, forming an almost perfect grille, and the zigzag deflection is reduced almost to zero. The overall degree of control is the same all along the commissure and highly independent of the gape. The growth lines reveal that the geniculation took place along the whole commissure at one and the same moment. In addition, the hinge axis does not seem to have shifted anteriorly after geniculation.

Near the hinge-axis the paries geniculatus displays an important deviation from the normal pattern. Along two particular rather small arcs, situated symmetrically in the shell and starting from the hinge, exclusively dorsal growth takes place after geniculation. Along the corresponding ventral arcs the outer surface only forms a thickened border. In this way small triangular vertical plates arise which constitute outgrowths of the dorsal valve and cover the posterior parts of the paries geniculatus over their entire height. Anteriorly, the edges of these plates bend sharply and dorsally; halfway along the paries geniculatus they merge into the normal commissure. These little plates will be referred to as *squamae* (sing. *squama*).

In cross sections outgrowths with vertically disposed outward facing surfaces are found in the ventral valve; they are counterparts of the squamae, are situated just behind them and also extend along the entire height of the paries geniculatus. These ventral counterparts of the squamae, which will be called *glottae* (sing. *glotta*), are however essentially different since they are not covered with primary layer and thus belong to the inner structures of the shell. A squama and glotta lie closely against each other. However, the dorsal and ventral mantles must have been situated in between. The costae of the concha plana which have been formed by the same arc as a squama and the corresponding ventral thickening die out at the paries geniculatus.

Undoubtedly, the squamae and the glottae have constituted a nearly complete closure of the corresponding parts of the commissure, even when the shell was widely opened. It is therefore rather surprising to find this construction in shells where the slit is already greatly obturated by a dense grille of rather stout marginal spines. The parts of the mantle which lined the outer surface of the glottae must have been situated at the outer surface of the shell when it was opened. They were most probably provided with numerous nerve endings and thus have formed part of the warning system of the shell.

It is logically possible that the occurrence of the squamae and glottae is the direct consequence of the almost perfect development of the marginal spines and the nearly complete reduction of the zigzag deflection in *Uncinulus orbignyanus*. It is known that this constitution provided a very high and almost constant degree of overall controll all along the commissure and irrespective of the gape. It is very probable that the most posterior zigzag deflections of the concha plana were too weak and too short of space after geniculation to develop a set of marginal spines which would come

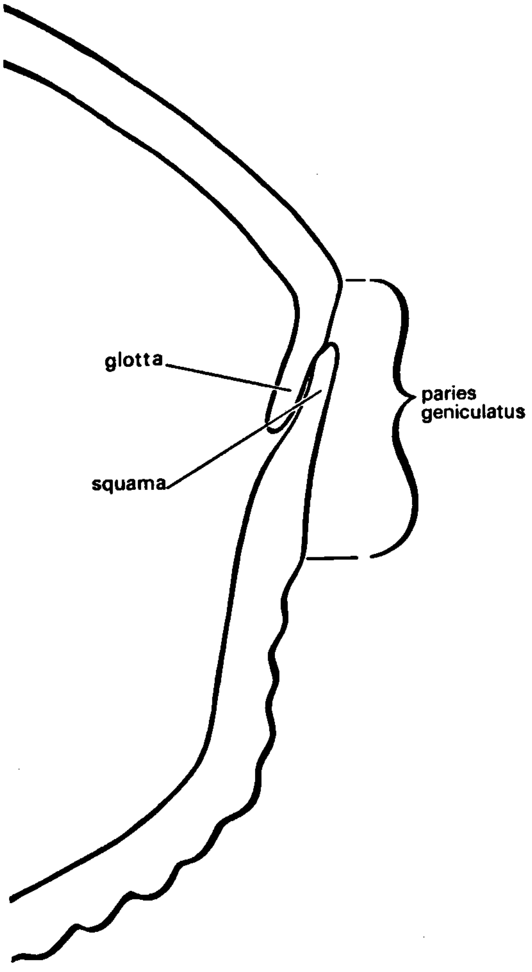

Fig. 54. *Eoglossinotoechia sylphidea*. Lateral part of transverse section through shell. Squama and glotta moderately developed.

up to this most rigid standard. A gradual transition to a poorly or unspined commissure, eventually provided with a suppression point and an unmodified commissure near the hinge-axis would have meant that the control was highly dependent of the gape posteriorly, and independent of it frontally. The great advantage of the advanced development of the spines would have been seriously reduced. One might consider the squama-glotta complex as being a drastic solution of this problem. In *Sphaerirhynchia wilsoni,* where the marginal spines only play a small role, a gradual transition to an unmodified commissure near the hinge-axis is quite a matter of course.

A circumstance in support of this hypothesis is the fact that the morphological range from a sharp serial zigzag deflection with very short marginal spines to long marginal spines and a rectimarginate commissure, of which *S. wilsoni* and *U. orbignyanus* are rather extreme representatives, clearly displays an increasing development of the squama and glotta complex. Transitional forms, such as *Eoglossinotoechia sylphidea* show only a slight overlapping (fig. 54, Pl. XI, fig. 4b). In the somewhat deviating species *O. lebanza* and *M. marki,* where moderately developed spines are combined with a pronounced zigzag deflection, the squamae and glotteae are very well developed (Pl. XII, fig. 5, 8).

In some species, such as *Eucharitina eucharis,* nearly the whole posterior part of the paries geniculatus is occupied by outgrowths of the dorsal valve, but ventral counterparts are not or hardly developed. This may give rise to some nomenclatural confusion. Nevertheless such dorsal outgrowths, in spite of their sometimes little spectacular appearance, will be referred to as squamae. In the genus *Kransia* (fig. 55, Pl. XIV, fig. 3), the squama and glotta differ slightly from those in *Uncinulus orbignyanus* in that the inner surface of the squama and the outer surface of the glotta, instead of being vertical, are slanting, so that a very narrow slit arises when the shell is opened. This slit increases in size with the increasing opening of the shell but nevertheless will most probably remain always narrower than the opening provided by the marginal spines, so that the degree of overall control is not locally reduced.

It has been seen that the formation of squamae and glottae can be understood as being a consequence of the highly protective function of well developed marginal spines. Accordingly they can be considered as adaptations for this particular function.

B. In nearly all the species in which the presence of marginal spines has been demonstrated the costae of the concha plana are fashioned in a most remarkable pattern which will be termed here *crenulation:* the costae are rounded and the grooves are sharp. See e.g. pl. XI, fig. 5, 6. On first sight this crenulate costation constitutes an intriguing little problem: the valve margins involved appear incapable of fitting together (fig. 56). Close scrutiny of the actual commissures in conchae planae, however, show that the crenulation is related with a very special type of composite deflections which can be resolved into a vertical and a radial component. As far as the vertical component is concerned the deflections display a normal zigzag with sharp crests and straight flanks (pl. XI, fig. 6). The radial components of the deflections however show sharp negative anomalies which correspond with the crests of the vertical zigzag, whereas the parts connected with the flanks of the zigzag are rounded and positive (pl. XI, fig. 5). The principle of crenulate costation is now explained by fig. 57 and by our previous general discussion of deformations in the Introduction (p. 7).

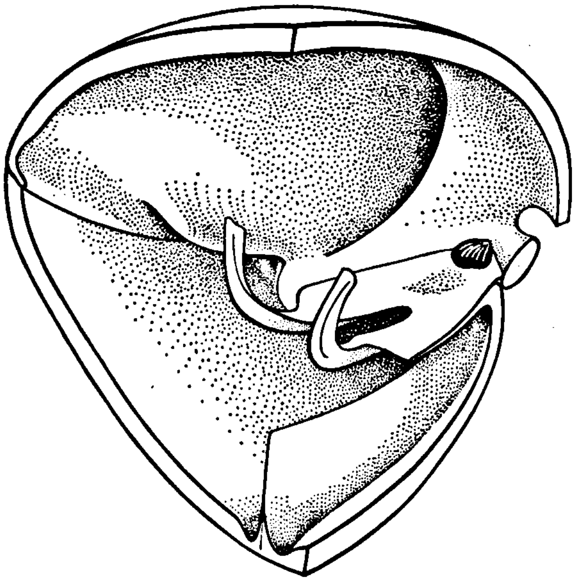

Fig. 55. *Kransia parallelepipeda.* Apical interior of shell. This reconstruction has been made by means of stereo-photographs represented in Pl. IX, fig. 6 a and b.

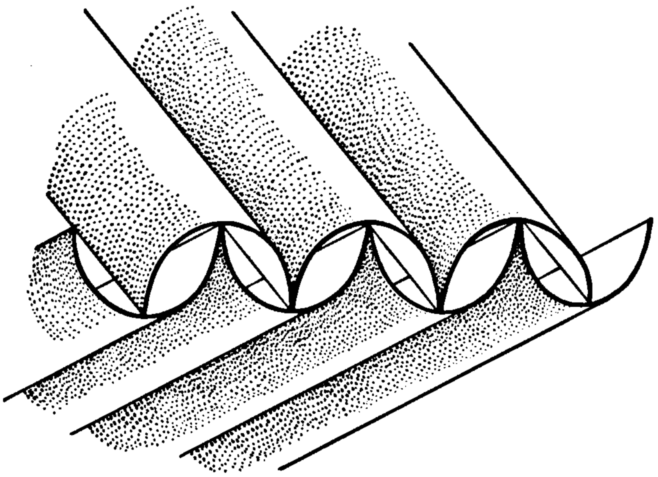

Fig. 56. On first sight the margins of valves which are provided with crenulate costae appear incapable of fitting together.

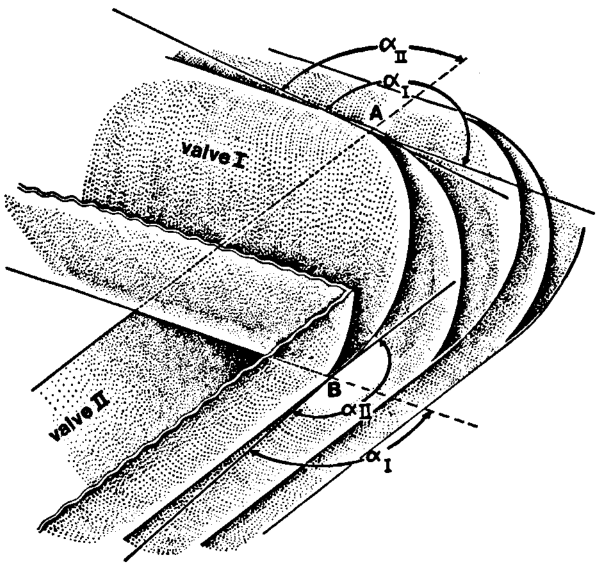

Fig. 57. Crenulate costae are related with a very special type of composite deflections.

The valves make different angles with the curved surface of the deflection. In A the angle α between valve I and the deflection is near to 180°, so that the deformation is minimal; indeed, the corresponding crest of the costa is strongly flattened. However, α is nearly 90° in A in respect of valve II, so that here the deformation is maximal and a very sharp groove arises. In B the situation is reversed: valve II has a rounded costa, and valve I a sharp groove. Along the flanks of the deflection the resulting deformations are transitional.

After geniculation these serial composite zigzag deflections develop into a combination of a set of zigzag deflections and one of marginal spines [21]. The original composite character can still be recognized as here also the crests clearly display negative radial components. The crests which correspond with the grooves in the concha plana also cause slight grooves on the paries geniculatus (the primary grooves) and project moreover into the mantle cavity as the marginal spines. The crests which are connected with the costae, leave only faint grooves on the paries geniculatus — the secondary grooves (fig. 43 and 44, e.g.). For the rest, the ribs are almost completely flattened. This may provide a better starting-point for a morphogenetical explanation of the spines and related structures than the subtle arguments of Herta Schmidt (1954) and the hypothesis of Schumann (1965).

A functional explanation can also be given of the secondary grooves. The primary grooves often continue for some distance along the bases of the marginal spines. If the valves are then to fit closely together — and this is essential for adequate protection — the corresponding part of the deflection of the other valve must also make a backward bend. Additional growth causes this bend to form the secondary groove on the outer shell surface. On the other hand, when the primary grooves do not extend along the bases of the marginal spines, as in *Kransia parallelepipeda* (fig. 46), neither are the secondary grooves developed. This incidental absence of secondary grooves can not be understood in the light of the crenulate costation and the related composite deflections.

C. The question is now how the mantle was situated relative to the marginal spines. In this respect the classical figure by Williams (fig. 9) provides once more an invaluable starting-point. Starting from this figure three conclusions can be drawn: 1. parts of the shell surface which consist of secondary shell material have been lined with outer epithelium; they belong to the inner shell surface; 2. parts of the shell surface which consist of primary shell material have not been lined with epithelium; these parts belong to the outer shell surface; 3. the loci where the boundary between the primary and the secondary layer outcrop are situated very closely to the mantle-edge.

Fig. 58a represents an example of the location of the primary and secondary shell layers in part of a valve-edge with a marginal spine. Nearly all the species studied show an approach to this principle. The inferred position of the mantle has been indicated in fig. 58c. In so far as the shell wall is concerned the situation is quite normal: the primary layer constitutes the outer shell surface and the secondary layer the inner one. At the edge of the valve the boundary between these layers comes to the surface, and it is here indeed that the mantle-edge must have been situated.

Nearly the whole surface of the spine is made up by secondary shell material; only along the radially facing surface is a very narrow strip of primary layer found, extending from the outer shell surface vertically for some distance along the spine. In some species this strip has only been found at the very base of the spine, and in others it runs to the tip. Transitional conditions frequently occur. Both configurations can be found in one and the same genus, so that this character is highly variable. Transverse sections show that the primary layer forms a closed infold into the shell at the grooves; it is this infold which continues along the spines, gradually loses depth, and finally vanishes distally (pl. XIII, figs. 4, 5, 6). The primary layer

[21] This is a very radical conversion for the reason, if for no other, that the jutting crests of the deflection in both valves are no longer in touch with the other valve margin and project freely in the mantle cavity. This has inveigled Schumann in assuming that the spines, as they were no longer limited in their growth by the opposite valve, had indeterminately continued their growth and actually would not have stopped growing till they pricked into the mantle of the opposite shell bottom, and thus might even have harmed the animal. The spines would thus be nothing but accidental outgrowths of the valve edges caused by the fact that geniculation took place so rapidly that the animal lost control of the crests of the deflections, which, as if by mistake, darted behind the other valve.

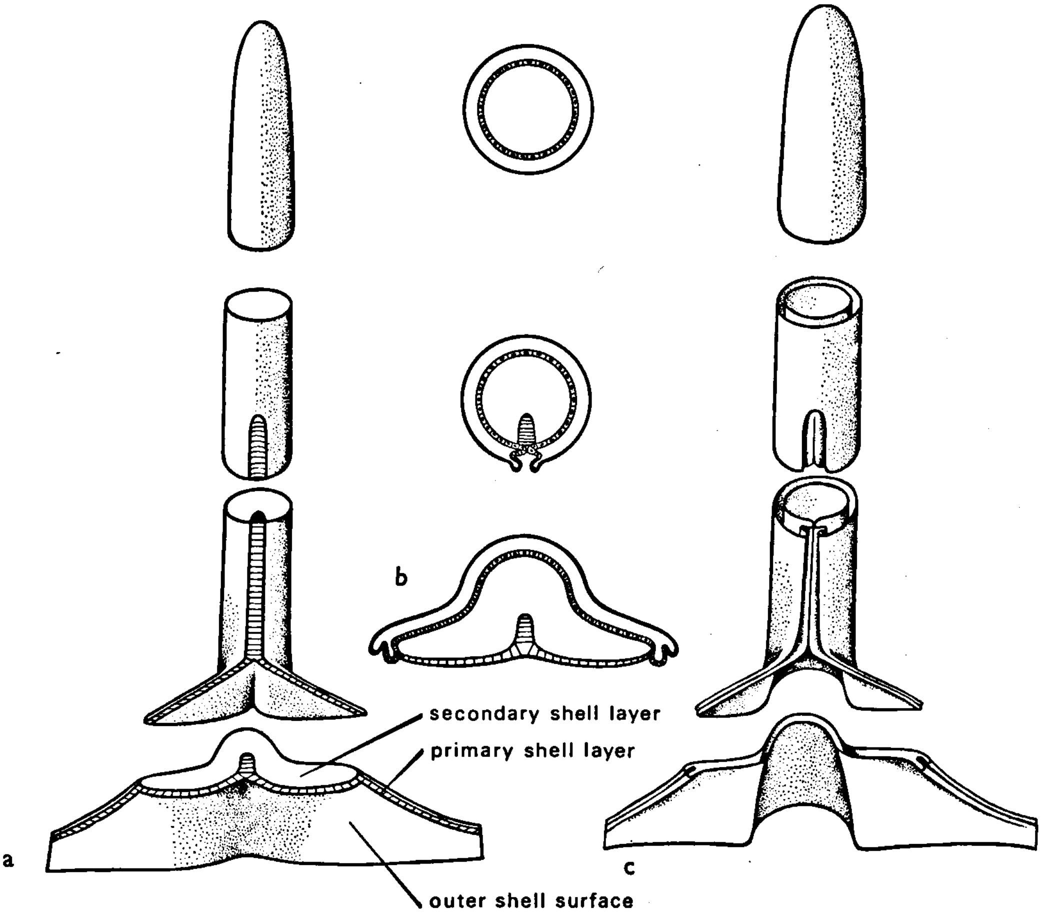

Fig. 58. Situation of the mantle around the marginal spines and the position of the matle border as inferred from the position of the primary and the secondary layers.

of the spines can best be traced in longitudinal sections parallel to the outer surface of the paries geniculatus; its granular structure then contrasts very clearly with the fibrous structure of the secondary layer. See e.g. pl. XIII, fig. 6. Starting from this structural pattern it may be inferred that the mantle enveloped the whole spine and that its edge formed a closed fold situated along the radial surface of the spine. This fold formed a continuation of the parts of the mantle-edge lying along the valve-edges.

It can be concluded that the mantle border makes a compound deflection after geniculation. An alternation of two parts can be distinguished: the commissural parts, following the zigzag deflection of the commissure, and the spinal parts, constituting closed folds which lie along the spines. This compound serial deflection of the mantle border must be considered as a post-brephic modification of the composite mantle-edge deflection of the concha plana, described above.

The spinal part of the primary layer is often very difficult to trace, even in longitudinal sections parallel to the paries geniculatus. It rapidly narrows distally till it can hardly be distinguished or it vanishes completely. The results of the examinations of the spinal parts of the mantle-edge deflections in the species investigated which will be given in the following section are therefore not always very reliable.

It is not clear whether the homologous relation is best formulated thus: "the brephic composite zigzag deflection of the valve-edges is homologous with a post-brephic reduced zigzag deflection of the valve-edges and marginal spines", or as follows: "the brephic composite zigzag deflection of the mantle-edges is homologous with a post-brephic compound deflection consisting of an alternation of reduced commissural parts and spinal parts".

Why do the spinal parts of the mantle-edge make a closed fold? From the fact that when growth proceeds the primary shell material which is secreted by the spinal parts of the compound deflections is incorporated in the shell and does not outcrop in the outer shell surface, it is inferred that the spinal parts are situated inside the (future) shell surface. If the plicae were not closed but open, then corresponding pieces of outer shell surface would be formed in between, and they would be situated inside the overall outer surface of the shell. In other words: the mantle-edge can only project into the shell cavity when it forms a closed fold.

It remains an open question why the parts of the mantle-edge which correspond with the jutting crests of the composite brephic zigzag deflection project into the shell cavity after geniculation. It is most improbable that this fundamental modification of the pattern of deflection was derived from geniculation in a so direct and simple way as Schmidt and Schumann suggest, although both processes are obviously closely related. I believe them to be conditioned by the much more complicated and hitherto obscure factors which rule the entire growth of the animal, rather than by simple mechanical laws.

On the other hand, as fig. 59 may reveal, a closed fold of the mantle border causes the mantle to become so shaped locally that a spine-shaped structure arises automatically. It would appear therefore that some comprehensible correlation exists between the closed folds and the spines. In principle, however, it is possible to conceive marginal spines which consist entirely of secondary shell material.

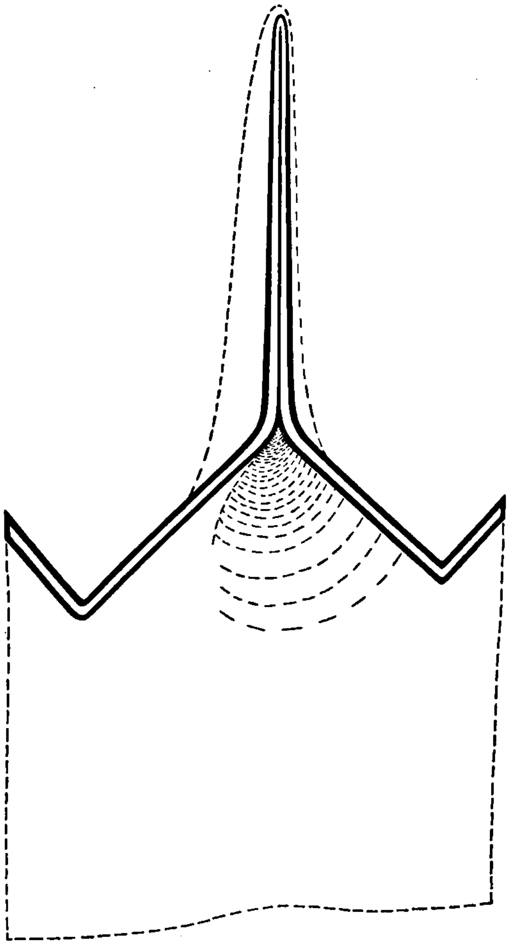

Fig. 59. A closed fold of the mantle border causes the mantle to become so shaped locally that a spine-shaped structure automatically arises.

5. DESCRIPTION OF THE MARGINAL SPINES AND SOME RELATED STRUCTURES IN THE UNCINULID SPECIES INVESTIGATED[22]

1. *Estonirhynchia estonica.* Fine crenulate costae starting at the beak or at some distance from it. Zigzag deflection well developed, moderately graded. Wavelengths of zigzag small, slightly decreasing towards the posterior. No true geniculation and no marginal spines.

2. *Sphaerirhynchia wilsoni.* Fig. 43, 52, 60 a and b, Pl. X, fig. 1. Type A. Zigzag deflection in concha alta pronounced, moderately to well graded. Wavelengths small, equal along the whole commissure. Suppression-point shifting anteriorly during ontogeny. Geniculation starts anteriorly, and then proceeds progressively towards the posterior, generally without reaching the hinge-axis. Paries geniculatus can become very high.
Marginal spines short, not longer than half the amplitude of the zigzag deflection, very short in comparison with the paries geniculatus. In the posterior part of the shell where geniculation has not yet occurred, no marginal spines are developed. No conspicuous broad bases. Spines are well streamlined in cross section. Primary layer extending up to the tip of the spines. Squama and glotta not developed.

3. *Hebetoechia hebe.* Type A. Zigzag deflection on paries geniculatus well developed, medially somewhat reduced; moderate grading. Wavelengths moderate. Geniculation nearly simultaneous along the entire commissure. At the moment of geniculation the suppression-point shifts towards the anterior over a considerable distance. Paries geniculatus very low. Marginal spines very short; anterior surface flattened at base. Primary layer extends along marginal spines, but to what extent could not be ascertained. Squama and glotta not developed.

4. *Eoglossinotoechia cacuminata.* Type A-B. Pl. XI, fig. 2. Zigzag deflection on paries geniculatus well developed, with moderate to good grading. Wavelength small to moderate. Geniculation simultaneous along entire commissure. Paries geniculatus of moderate height. Marginal spines of moderate length, with somewhat flattened radially facing surface. Squama and glotta are present, but not very conspicuous.

5. *Eoglossinotoechia mystica.* Type A. Pl. XI, fig. 1. zigzag deflection on paries geniculatus pronounced, well graded. Wavelengths small to moderate. Geniculation occurs nearly simultaneously along the commissure. Paries geniculatus may reach considerable height. Marginal spines very short well developed broad bases and streamlined at the top. Spinal parts of the primary layer extend to the tips of the spines. No squama and glotta.

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[22] The species are arranged according to their stratigraphic age.

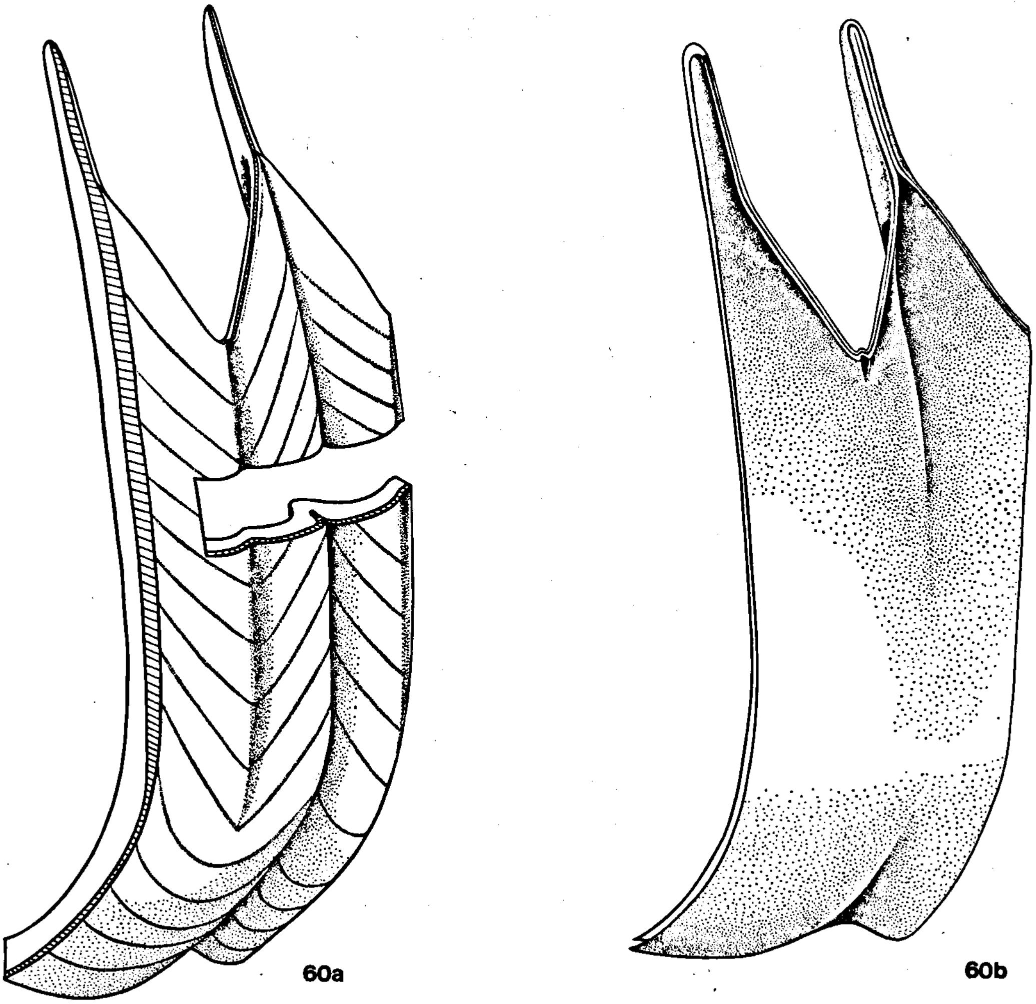


Fig. 60. *Sphaerirhynchia wilsoni.* (a) Position of primary and secondary layers; (b) inferred position of mantle.

6. *Lanceomyonia tarda.* Type A. Zigzag deflection on paries geniculatus pronounced, well graded. Wavelengths large. Geniculation occurs nearly simultaneously along the commissure. Paries geniculatus rather low. Marginal spines very short. Primary layer has not been observed. No squama and glotta.

7. *Plethorhyncha altera* and *P. diana.* Type A. Zigzag deflections on paries geniculatus pronounced, moderately grading. Wavelengths moderate. Suppression-point shifts rapidly in anterior direction during ontogeny (see p. 67). Geniculation occurs in late stage of ontogeny. Paries geniculatus generally very low or not present at all. Marginal spines very short, streamlined. Primary layer indistinct.

8. *Uncinulus subwilsoni.* Type C. Zigzag deflection on paries geniculatus very reduced; no grading; wavelengths small. Geniculation occurs simultaneously along the whole commissure. Paries geniculatus reaches considerable height. Marginal spines long and slender, gradually tapering. Spinal parts of primary layer not very clearly observed; they very probably extend along the spines over a considerable distance, but do not reach the tips. Squama and glotta very well developed.

9. *Obturamentella lebanza.* (Fig. 61 a and b, Pl. XII, fig. 8). Cf. type B. Zigzag deflection on paries geniculatus well developed; grading moderate; wavelengths considerable.
Marginal spines short with small broad bases. Spines fit into appropriate grooves on inner surface of opposite valve. Geniculation occurs simultaneously along the commissure. Paries geniculatus rather low. Squama and glotta well developed.

10. *Eoglossinotoechia sylphidea.* Type B. (Pl. XI, fig. 4, 5). Zigzag deflection on paries geniculatus poorly developed; no grading; wavelength small. Geniculation nearly simultaneous along the whole commissure. Paries geniculatus may become high. Marginal spines rather short, hardly longer than in *S. wilsoni.* Broad

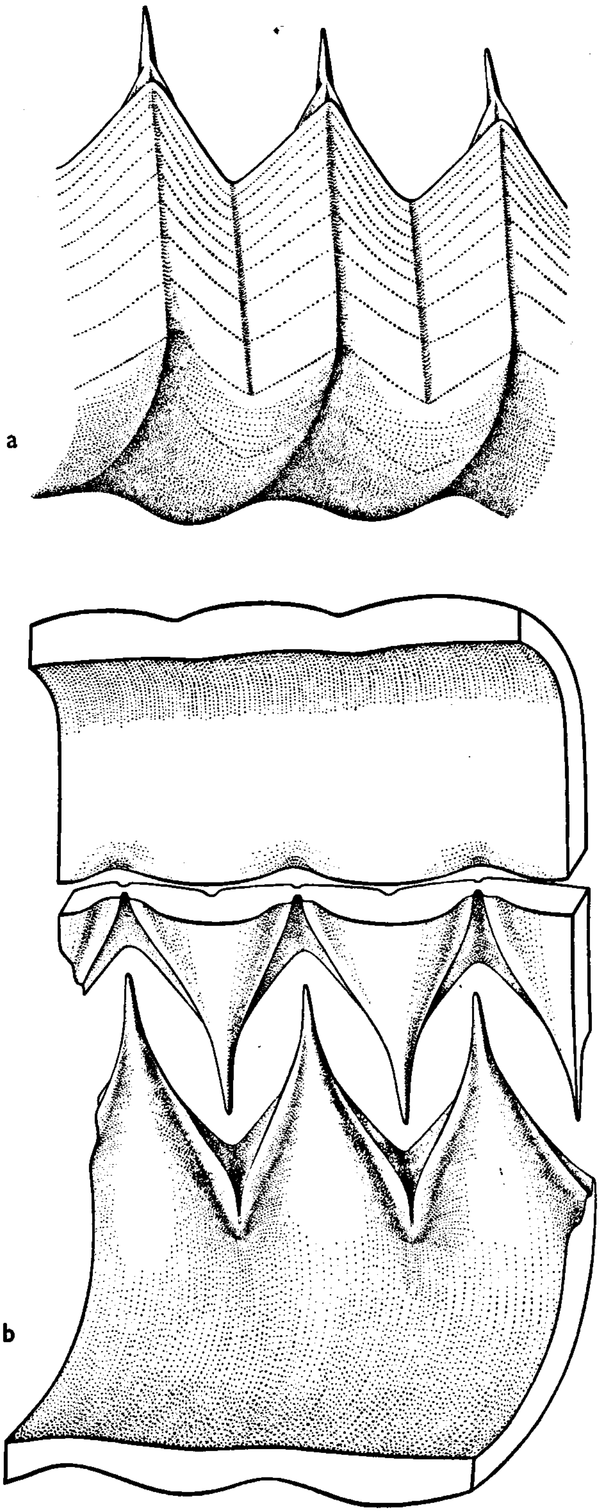


Fig. 61 *Obturamentella lebanza*, marginal spines. (a) exterior; (b) interior.

bases very poorly developed. Spinal parts of primary layer extend to the tips of the spines. Squama moderately developed; glotta very poorly. Overlapping only very slight (fig. 54).

11. *Glossinulus (Glossinotoechia) princeps*. Type B. Zigzag deflection on paries geniculatus varying from moderately developed in relatively young to very much reduced in old specimens. Grading slight to absent, wavelength small. Geniculation nearly simultaneous along the whole commissure. Paries geniculatus may become very high. Marginal spines of moderate

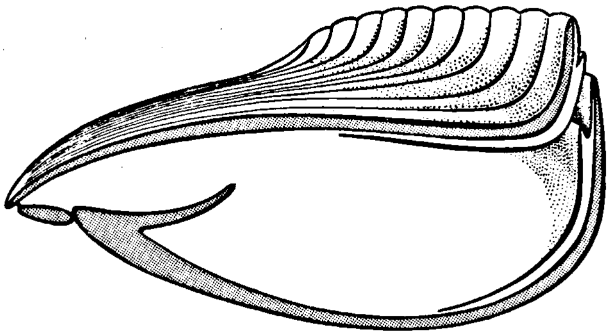


Fig. 62. Probable position of mantle during stage of inversed geniculation in *Glossinulus (Glossinotoechia) henrici*.

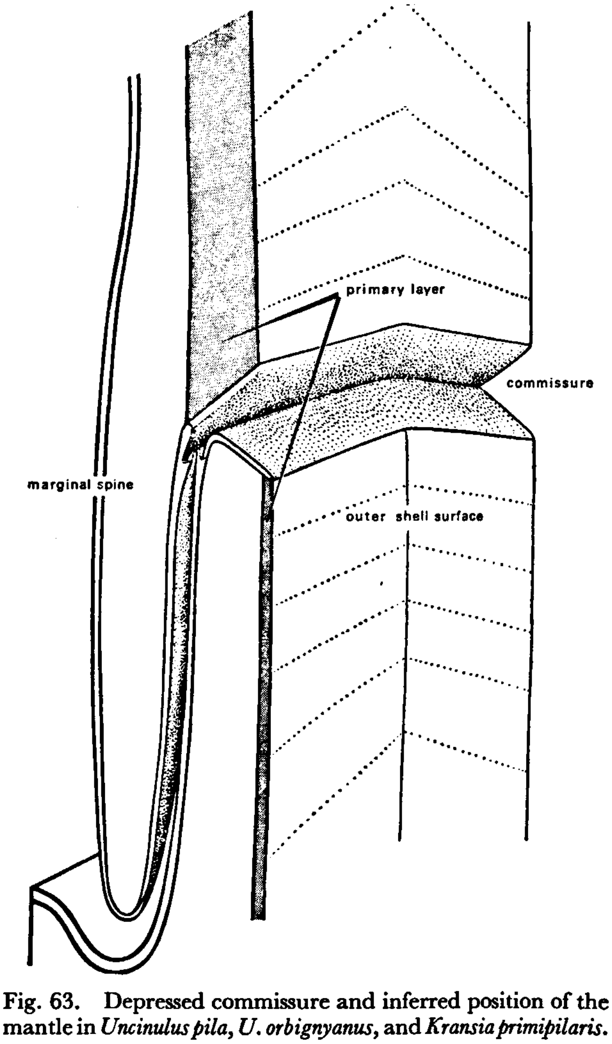


Fig. 63. Depressed commissure and inferred position of the mantle in *Uncinulus pila*, *U. orbignyanus*, and *Kransia primipilaris*.

length. Spinal parts of primary layer appear to extend to the tips of the spines. Squama and glotta moderately developed.

12. *Glossinulus (Glossinotoechia) henrici.* Type B. (Fig. 62, Pl. XI, fig. 7, 8, 9, 10). In this species a very special type of shell growth occurs. The process of growth can be divided into three different stages.

a. In young specimens the shell is extremely flat; both valves are slightly convex and a sulcus and saddle are not developed. The costae are crenulate and the commissure displays a composite deflection as depicted in p. 52.

b. At a certain stage a sudden change occurs in the direction of growth along the anterior and antero-lateral parts of the commissure, comparable with the geniculation of some leptaenids. The radial component of the growth is reduced to zero and both valves grow ventrally for some distance, so that the shell becomes broadly convexo-concave and a sharp ridge (up to 3 mm in height) arises along the commissure. The inner valve surfaces are consequently nearly contiguous in this area (fig. 62). This reversal in growth obviously has had important consequences for the size and the control of the slit. When the angle of opening was not too great the slit will have been very reduced, the control very high and largely independent of the gape. When the shell was opened, a corresponding strip of the ventral mantle border must have projected beyond the shell, possibly giving rise to an "early warning" device (cf. Rudwick, 1965). Moreover, the cilia on this part of the mantle would most probably have been very favourably situated in order to induce a water current, so that the drawback of the slit-reduction is compensated to some extent. It should be noticed in this context that the animal is very likely to have lain on its dorsal valve during its lifetime, in view of the clearly developed mesothyrid foramen. The phenomenon has however not been sufficiently

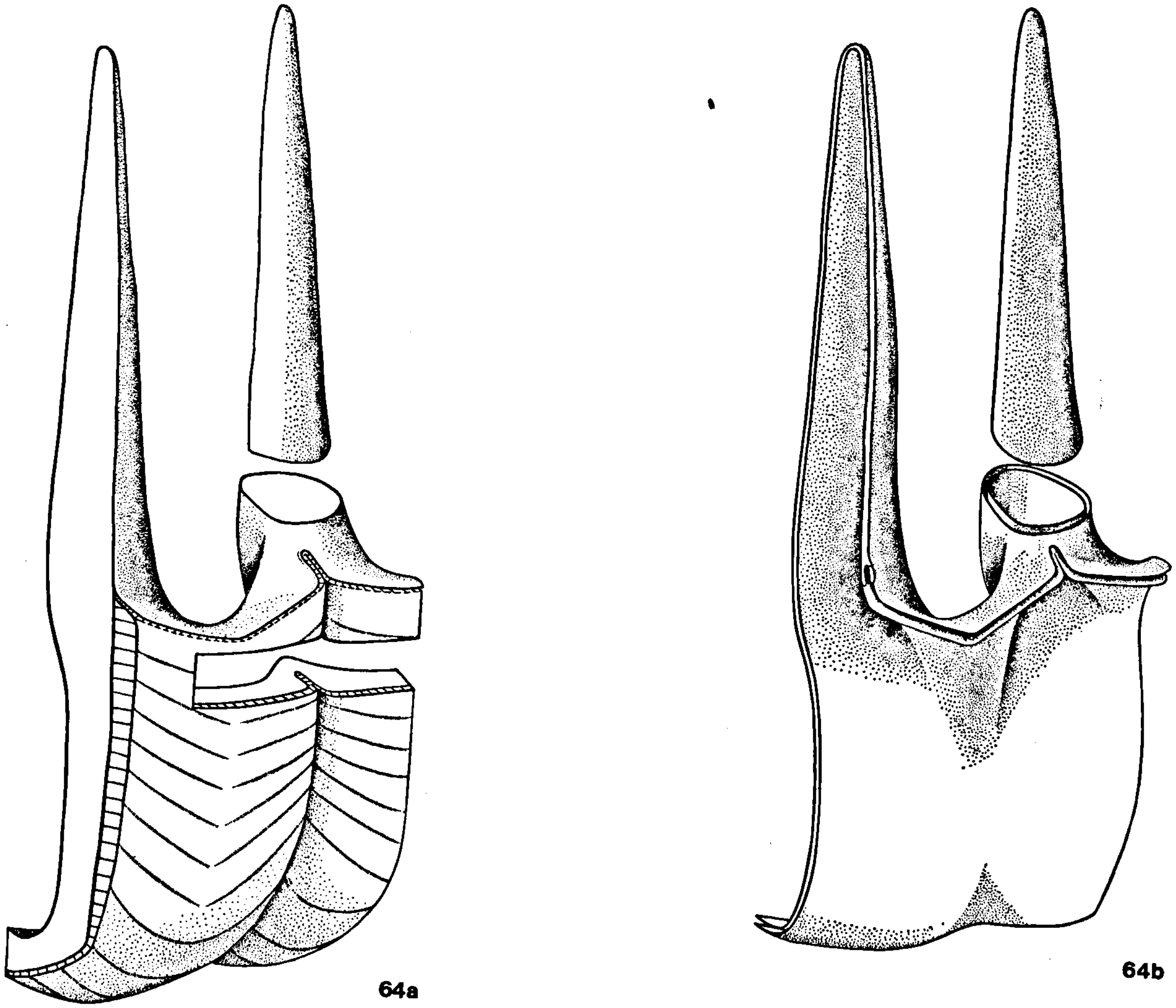


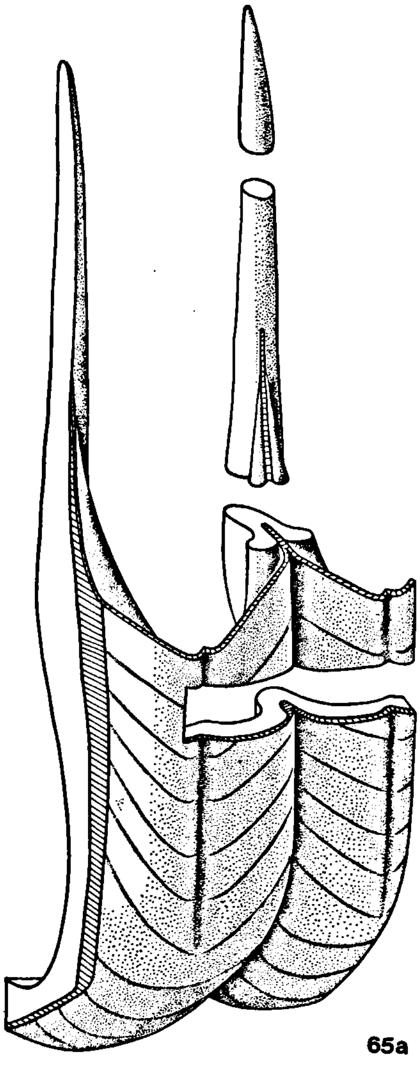
Fig. 64. *Uncinulus pila* and *U. orbignyanus.*
a = position of primary and secondary layers in marginal spines
b = inferred position of the mantle

studied to permit a detailed functional interpretation. The above remarks should therefore not be considered as more than suggestions.

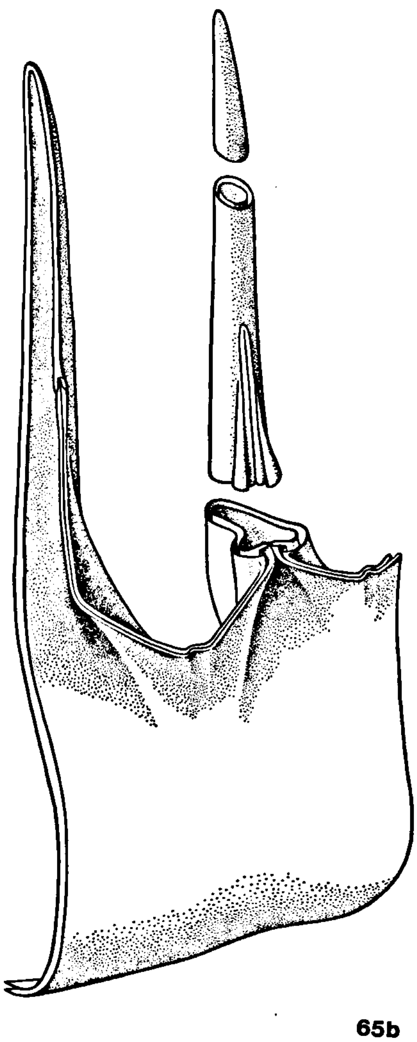
c. A second drastic change in the shell growth involves the formation of a normal paries geniculatus with marginal spines. The ventral valve suddenly started to grow in dorsal direction and the dorsal valve continued its ventrally directed growth. Only a sharp ridge along the border of the ventral concha plana indicates the previous stage of "reversed geniculation". The zigzag deflection on the paries geniculatus was originally very sharp, but the commissure may become nearly rectimarginate in old specimens. The wavelenghts of the deflection are small. The marginal spines are rather short, although somewhat longer than e.g. in *E. sylphidea*. Broad bases are only poorly developed. The spinal parts of the primary layer extend to the tips of the spines. On the paries geniculatus a pronounced and sharply defined tongue arises rapidly, whereas no sulcus and saddle were present in the brephic shell. Squama and glotta are poorly developed.

The conversion from stage b. to c. is especially striking because it abruptly interrupts the development of the "inversed geniculation", to all appearances cancelling the effect of this very remarkable constitution of the valve-edges involved. It would appear that an important specialization achieved at the end of the brephic stage was suddenly done away with and replaced by another one. The significance of this intriguing problem is far from being understood.

13. *Eucharitina eucharis*. Type A. Pl. XI, fig. 6. Zigzag deflection on paries geniculatus well developed, moderately graded. Wavelengths very large. Geniculation takes place simultaneously along the whole commissure. Paries geniculatus low. Marginal spines



65a



65b

Fig. 65. *Glossinulus* (*G.*) *latus*.
a= position of primary and secondary layers in marginal spines. b= inferred position of mantle.

very short, with well developed broad bases. The spines do not fit into corresponding holes as in *O. lebanza* and *Markitoechia marki.* No observations on spinal parts of primary layer.
Squama rather well developed, glotta only very poorly or not at all.

14. *Hebetoechia nitidula.* Type B. Pl. XI, fig. 11, 12. Zigzag deflection on paries geniculatus poorly developed. Wavelengths moderate. Geniculation nearly simultaneous along the whole commissure. Paries geniculatus rather low. Marginal spines rather long, stout at their base and tapering gradually. Proximally the radially facing surfaces of the spines are flattened. The spinal parts of the primary layer extend to the tip of the spines. Squama and glotta incipient.

15. *Uncinulus pila.* Fig. 45, 63, 64 a and b. Type C. Zigzag deflection on paries geniculatus very poorly developed or nearly completely reduced. No grading. Wavelengths extremely small. Geniculation takes place simultaneously along the whole commissure. Paries geniculatus may reach considerable height.
Marginal spines very long, stout at their base, and gradually tapering. Spinal parts of the primary layer only extending to the very base of the spines. Squama and glotta very well developed.
In a very small number of specimens the paries geniculatus is not truly vertical, but the valves make angles of often much more than 180°. In such specimens the marginal spines project into the mantle cavity with a strong posterior component. The subject has been treated at length by Schumann. Another interesting feature in this species is the fact that the actual commissure of the concha alta is depressed: it lies in a more or less pronounced marginal groove and is not flush with the paries geniculatus (fig. 63). The primary layer only extends to the margin of the depression except in the primary grooves where it locally continues to the bottom. Consequently, the walls of the depression

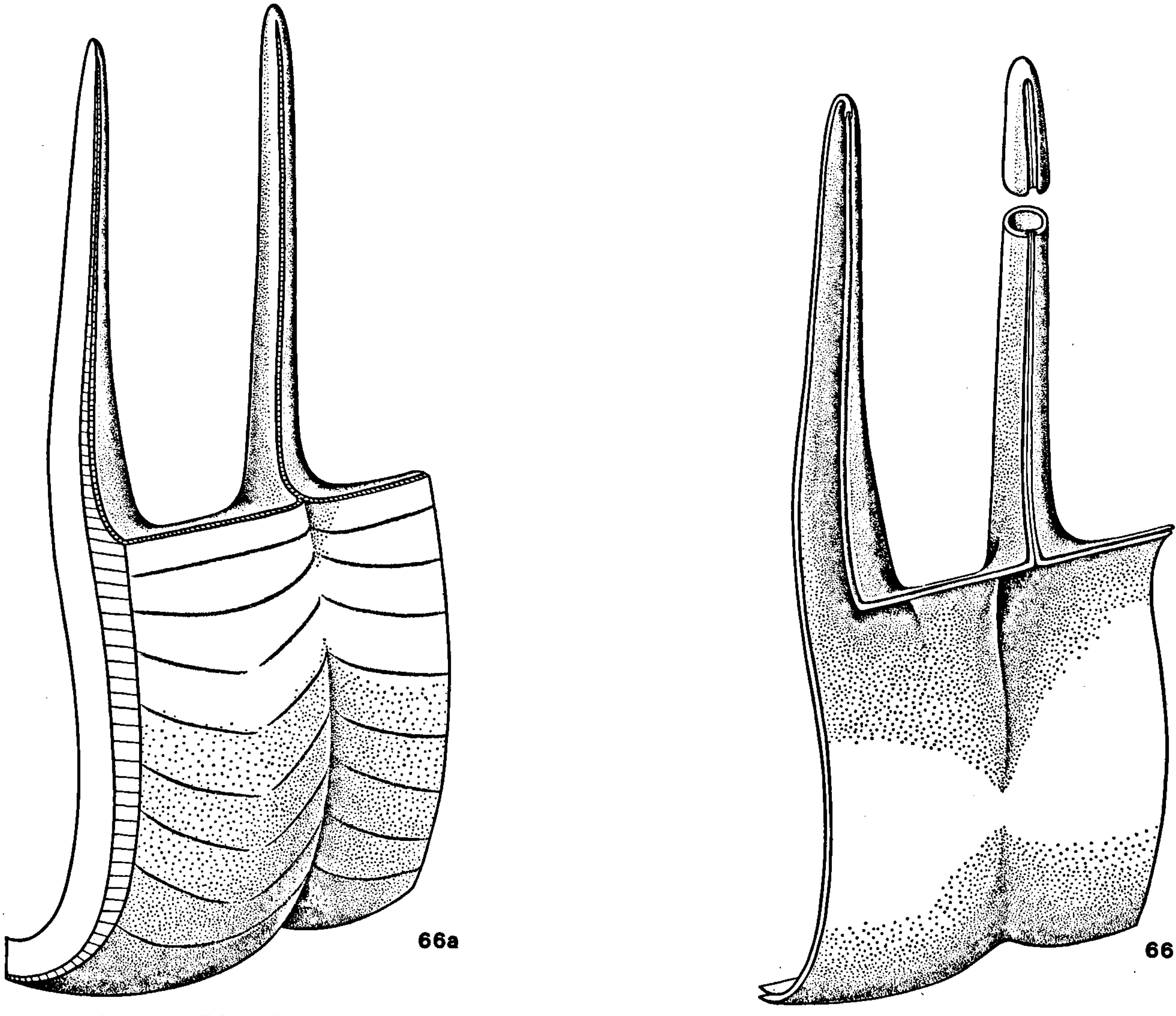


Fig. 66. *Kransia parallelepipeda.*
a = position of primary and secondary layers in marginal spines. b = inferred position of mantle.

must have been lined by the mantle which accordingly protruded from the shell for a very short distance. One might infer that the warning device of these animals was even active when closure of the shell was complete. The protruding parts of the mantle-edges were very probably protected by a cover of periostracum. The situation is also characteristically developed in the closely related *Uncinulus maledictus maledictus* and *Uncinulus orbignyanus,* and independently in the much more remote *Kransia primipilaris.* The constitution of the marginal spines and related structures is identical in *U. pila* and *U. orbignyanus.*

16. *Uncinulus maledictus maledictus.* Type C. Pl. XII, fig. 1, 2, 3, 4. Zigzag deflection on paries geniculatus very reduced. No grading. Wavelengths very small. Commissure depressed on concha alta (see discussion *U. pila).* Geniculation simultaneous along commissure. Paries geniculatus of considerable height. Marginal spines rather long. No broad bases developed. No data available concerning spinal parts of primary layer. Squama and glotta very well developed. The spines seem to be somewhat shorter here than in *Uncinulus pila.* All the other related elements are very similar in both species.

17. *Markitoechia marki.* Cf. type B. Pl. XII, fig. 5, 6, 7. Zigzag deflection on paries geniculatus well developed. Grading rather inconspicuous. Wavelengths considerable. Marginal spines of moderate length with well developed broad bases. Spines fit into appropriate

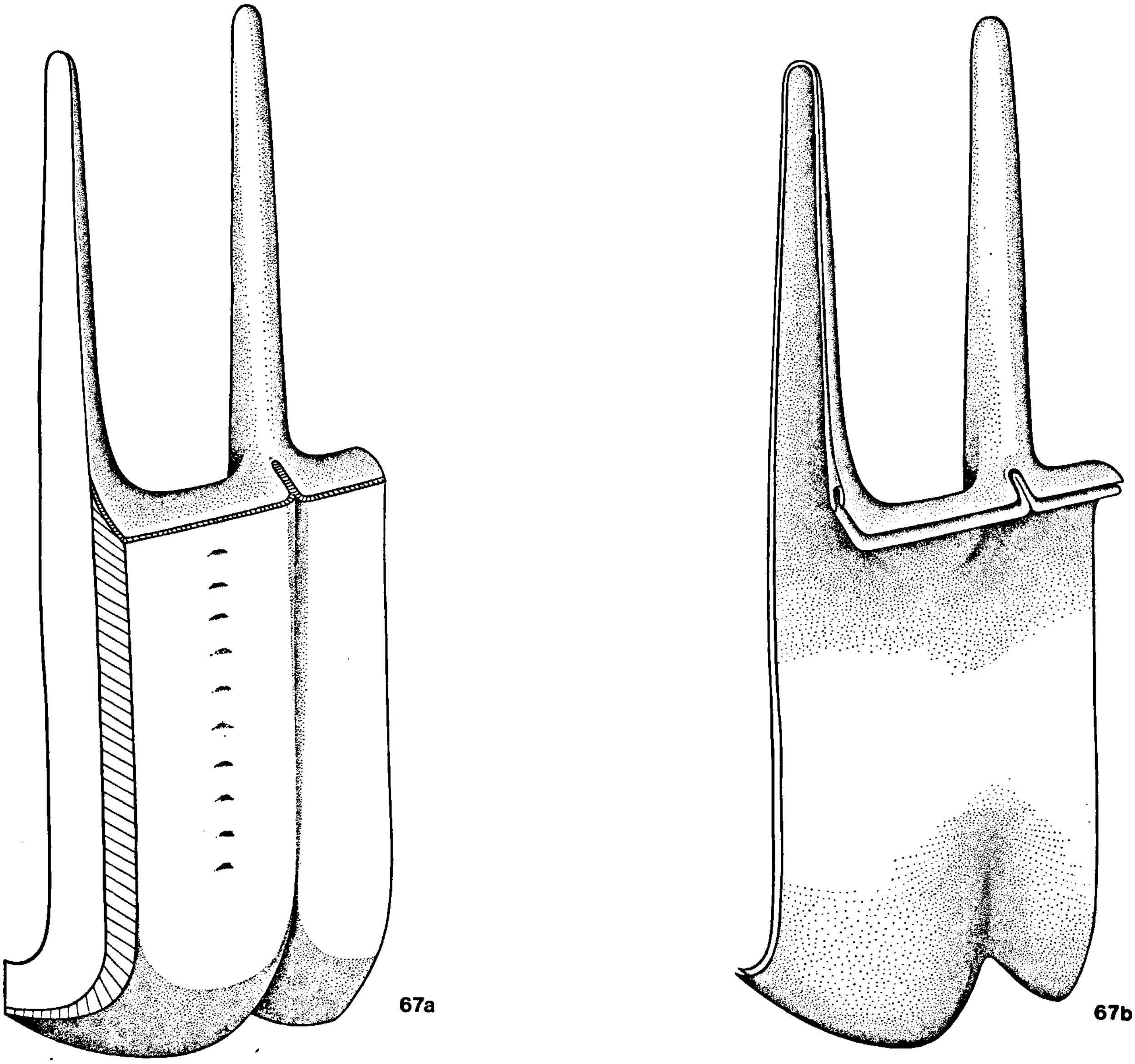


Fig. 67. *Kransia primipilaris.*
a= position of primary and secondary layers in marginal spines. b= inferred position of mantle.

grooves on inner surface of opposite valve. No observations on spinal parts of primary layer. Geniculation occurs simultaneously along the entire commissure. Paries geniculatus rather low. Squama and glotta well developed. Striking similarities exist between the constitution of the spines and related structures in *M. marki* and in *O. lebanza.*

18. *Glossinulus (Glossinotoechia) latus.* (Fig. 44, 65 a and b; Pl. XI, fig. 3; Pl. XIII, fig. 4, 5, 6). Type B. Zigzag deflection on paries geniculatus poorly developed. No grading, wavelengths small. Geniculation nearly simultaneous along the whole commissure. Paries geniculatus may reach considerable height. Marginal spines long. Well developed broad bases. Spinal parts of primary layer extend to near the tips of the spines. Squama and glotta well developed.

19. *Kransia parallelepipeda.* Type D. (Fig. 46, 66 a and b, Pl. X, fig. 3). Zigzag deflection on paries geniculatus completely absent in adult specimens. Wavelengths considerable. Geniculation simultaneous along the commissure. Paries geniculatus of moderate height. Marginal spines long, rather stout at their base and tapering gradually. Proximally the radially facing surfaces of the spines are flattened. The spinal parts of the primary layer extend to the tip of the spines. Squama and glotta very well developed. See section 4 A.

20. *Uncinulus orbignyanus.* Type C. (fig. 45, 63, 64 a and b, Pl. XII, fig. 9, 10, 11). Very similar to *U. pila.*

21. *Uncinulus knjaspensis.* Type C. Zigzag deflection on paries geniculatus moderately developed. Grading inconspicuous. Wavelengths very small. Costae on concha plana are characteristically sharp and rather angular, so that the crenulation is not clearly displayed. On the paries geniculatus the primary and secondary grooves are well developed. Geniculation has taken place simultaneously along the whole commissure. Paries geniculatus may become high. Marginal spines long, rather stout at their base and gradually tapering. Spinal parts of primary layer could not well be traced; they are likely to extend for some distance along the spines. No specimen was preserved well enough to permit observation of the squama and glotta.

22. *Kransia primipilaris.* Type D (fig. 47, 67 a and b, Pl. X, fig. 2). Zigzag deflection on paries geniculatus completely absent in adult specimens. Wavelengths smaller than in *K. parallelepipeda.* Commissure depressed (see discussion *Uncinulus pila).* Costation on concha plana very characteristic (see Biernat, 1966) Geniculation has taken place simultaneously along the commissure. Paries geniculatus of moderate height. Marginal spines elongated, rather stout at their base and tapering gradually, moderately to well streamlined. Spinal parts of primary layer only extending on the very base of the spines. Squama and glotta very well developed (see section 4 A).

23. *Kransia goldfussii.* Type D. (Pl. XIV, fig. 3 a). Zigzag deflection on paries geniculatus completely absent or very much reduced. Wavelengths moderate, larger than in *K. parallelepipeda.* Geniculation has taken place simultaneously along the whole commissure. Paries geniculatus of moderate height. Marginal spines elongated, provided with broad bases. Spinal parts of primary layer extend to halfway the spines. Squama and glotta very well developed (see section 4 A).

24. *Kransia minor minor.* Type D. Zigzag deflection on paries geniculatus completely absent or very much reduced. Wavelengths relatively small. Geniculation has taken place simultaneously along the whole commissure. Paries geniculatus low. Marginal spines short, flattened radially. Squama and glotta very well developed (see section 4 A).

6. MARGINAL SPINES IN SOME OTHER SPECIES

In the Introduction (p. 11) it has already been noticed that the systematic position of *Hypothyridina, Decoropugnax* and *Corvinopugnax* relative to the Uncinulidae is very problematical. The marginal spines of the type species of these genera will now be discussed. Unfortunately, only the exterior features of *Corvinopugnax corvinus* could be studied, but nevertheless some careful inferences can be made regarding the spines of this species.

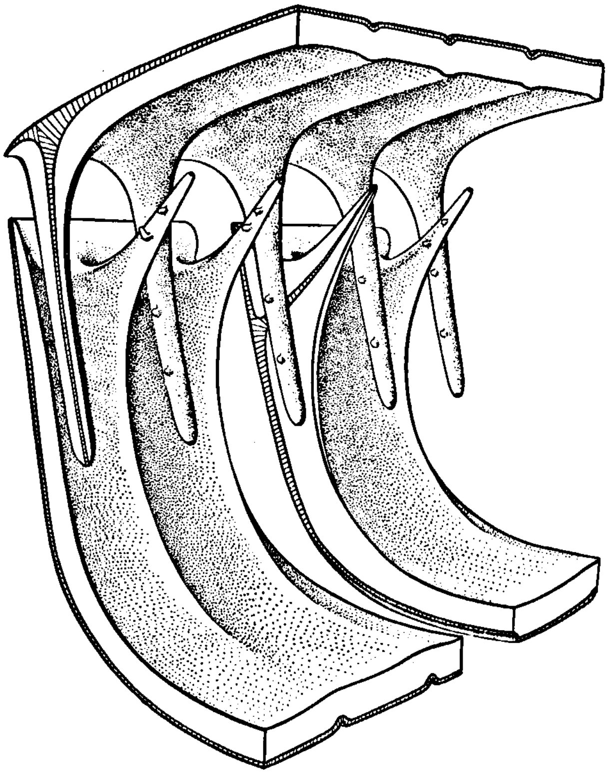


Fig. 68. *Hypothyridina cuboides.* Marginal spines and partitions; position of primary and secondary layers. The position of the small protuberances is supposed.

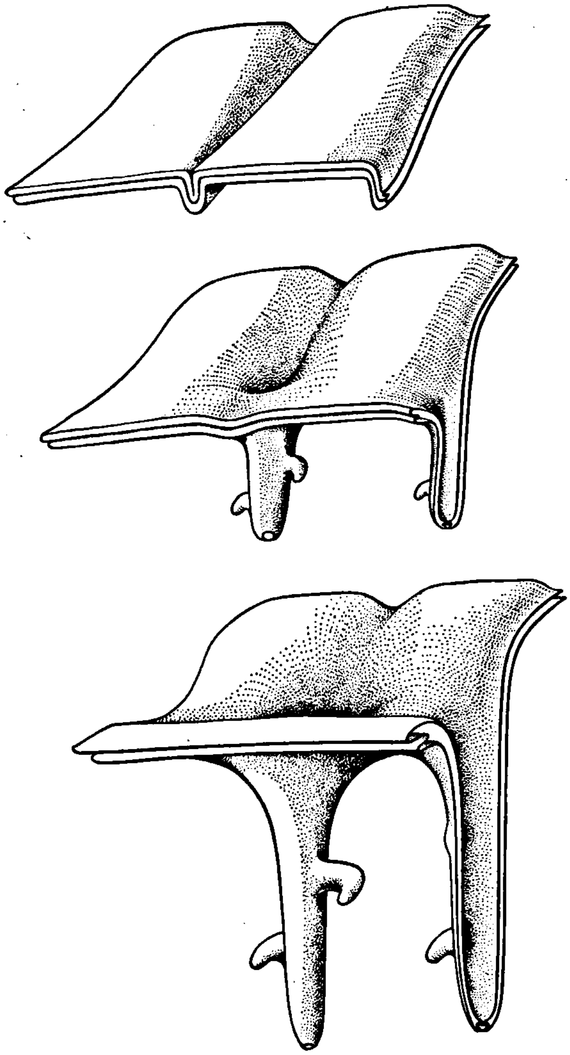


Fig. 69. *Hypothyridina cuboides.* Inferred growth of the mantle involved in the formation of a marginal spine.

Decoropugnax berenice. Well developed paries geniculatus. Geniculation is likely to have taken place simultaneously along the whole commissure. Costation fine; on paries geniculatus primary and secondary grooves are well developed. Well developed zigzag deflection on the paries geniculatus. Wavelengths very small. In some specimens the posterior 3 or 4 zigzags have a relatively large wavelength and display a good grading towards a suppression-point. Here, no secondary grooves occur so that these zigzags probably have not borne marginal spines. Spines short, reaching about 3/4 of the amplitude of the deflections. Well streamlined. Reminiscent of the spines of *S. wilsoni.* No observations on spinal parts of the primary layer. No squama and glotta.

Corvinopugnax corvinus. Geniculation occurs only in old specimens. Zigzag deflection on paries geniculatus very sharp and well graded. Wavelengths rather large. Primary and secondary grooves well developed. No direct observations on marginal spines. The presence of a paries geniculatus with secondary grooves in old specimens, however, suggests that they are present. Most probably they will be very short in view of the pronounced zigzag deflection.

Hypothyridina cuboides (fig. 68, 69; Pl. XIII, fig. 1, 2, 3; Pl. XIV, fig. 1). The marginal spines in this species were described for the first time by Schmidt (1937). Paries geniculatus very high in adult specimens. Commissure is located along its margin. Consequently the paries geniculatus is medially entirely constituted by the ventral valve and laterally by the dorsal valve. Thus, in each of these three sectors one valve grows in vertical direction after geniculation and the other continues growing radially. Vertically directed spines arise from the bottom of the non-geniculated valve. They are arranged in a long row just behind the paries geniculatus, and alternate with radially and vertically arranged partitions which project from the opposing valve into the mantle cavity. Partitions and spines are evidently homonomous structures since both arise from the grooves of the outer shell surface and are similar in structure. The spines and the partitions both consist of a rod-like extension of the primary layer in the core, surrounded by fibrous secondary shell material. Consequently, the mantle which surrounds the spines must have been situated as indicated in fig. 69. The position of the mantle of the partitions is similar. Buds of the mantle-edge must have been situated at the tips of all these structures.

The outer shell surface is provided with fine crenulate costae. At the moment of geniculation the primary layer at the bottom of the grooves buds off and projects into the mantle cavity, surrounded by secondary shell material, to form the spines and partitions. Afterwards, when the budding is completed, the zigzag deflections have nearly vanished, and only very shallow costae are left in the corresponding marginal parts of the valves. Secondary grooves do not occur.

From the partitions as well as from the spines nodular protuberances arise which project laterally at their base and are often bent radially at their tips. These protuberances have been found in all specimens investigated — and these are rather numerous — and can therefore not be interpreted as pathological formations.

It is beyond the scope of this publication to give an extensive functional analysis of these structures. It is however not impossible that this construction could be a very specialized warning device, and thus could be compared with the grill of marginal spines of the genuine Uncinulidae. Indeed, the spines and the partitions are located at equal and small intervals along the whole commissure, and they are graded in length. The fact that they partially and sometimes wholly replace the zigzag deflection of the commissure further corroborates this hypothesis. The function of the protuberances which occur on the spines and partitions remains rather obscure. Their exact positions should be considered more closely before further inferences can be made on this point. Since the spines are all situated inside the mantle cavity and somewhat behind the actual opening of the shell they are likely to have functioned somewhat later and thus less effectively than the real marginal spines of the Uncinulidae. On the analogy of the characterization by Rudwick (1965) of the spines in *Acantothyris* as early warning devices the spines and partitions in *Hypothyridina cuboides* might be typified rather paradoxically as a delayed warning device. Of course these observations are merely speculations and should not be taken very seriously.

Are these spines and partitions to be considered as homologous with the marginal spines in the Uncinulidae, or are they the result of a homoplastic (e.g. convergent) development? The same question applies to the spines of *Decoropugnax berenice.* The spines of the latter species have shown no important differences in structure with those of the genuine Uncinulidae. In *H. cuboides* the primary layer of the outer shell surface buds off into the spines and partitions which are being formed, while the outer shell surface continues its growth in the original direction. This does not occur in the Uncinulidae and in *D. berenice* and thus forms the main difference between *H. cuboides* and them. It is however possible, although no evidence in the fossil record has been encountered, that the construction in *H. cuboides* is derived from the spines of the uncinulid type. With some imagination one could conceive a morphological series which would link the spines of the Uncinulidae with those of *Hypothyridina.*

Rhynchopora nikitini. Rudwick (1964) has already demonstrated the presence of marginal spines in this very remote species. The specimens which were studied for this account originate from the Namurian of Latores, Cantabrian Mountains, Spain. The zigzag deflection on the paries geniculatus is well developed. The grading of the zigzags is good and their wavelength is large. Well developed paries geniculatus. The spines are of moderate length and are provided with longitudinal ridges along their radially facing surface. When the shell is closed the spines fit into appropriate grooves in the inner surface of the opposite valve. Accordingly, these grooves are situated just behind the secondary grooves on the outer shell surface; they too are provided with longitudinal ridges. The presence and constitution of the spines in this species present an interesting case of homoplasy.

7. CONCLUSIONS AND ULTIMATE REMARKS

A. *The phylogenetical development of the marginal spines in the Uncinulidae.* — The morphological habit of the marginal spines in the uncinulid species studied is very schematically represented in enclosure I. The species are arranged according to their chronostratigraphical position. The morphological range which was drawn up earlier in this chapter is very obviously more or less parallel with the stratigraphical succession. Species with spines of type A occurred during the time interval ranging from Wenlockian to Siegenian, whereas the origin of these species in time ranges from Wenlockian to lower Gedinnian. Exceptions are *Eucharitina eucharis* and *Corvinopugnax corvinus;* the systematic position of these two species however is uncertain. Spines of type B have been found in species which occurred from middle Siegenian to lower Eifelian. Type C: middle Siegenian to upper Eifelian. Type D: upper Emsian to upper Givetian. *Hypothyridina:* Givetian to Frasnian.

Some careful conclusions may be drawn from these data in respect of the phylogeny of the group. The spines of types B, C, and D seem to have been derived phylogenetically from spines of type A. It appears that spines of the types B and C were developed in the Siegenian. Type D will have been developed from C or B. In chapter V, where more data come into consideration an attempt will be made to give more detailed inferences on the phylogenetical relations in the Uncinulidae. It should however be kept in mind that only a small part of all the uncinulid species (and even genera) known have been studied, so that all conclusions on the phylogeny in this taxon are rather of a speculative nature.

Broadly speaking one may conclude that the spines of the Uncinulidae have undergone a phylogenetical development from Wenlock to Givetian, during which they gradually increased in length at the expense of the related zigzag deflections of the commissure, whereas squamae and glottae came into being. It has been seen in the functional analysis that this corresponds with a concomitant increase in the protective potential of the shell structure involved, ranging from hardly more than crestal protection of the well developed zigzag deflection in the most primitive species to a beautifully developed protective grille of marginal spines and a complete reduction of the zigzags in the species assigned to *Kransia,* where the overall degree of control is highly independent of the gape. Although strong indications were obtained that in all the species investigated the constitution of the spines and related structures are such that they are adapted to a combination of the two functions which can be postulated for these elements, namely the protection and the circulation of the seawater, no criterion could be found which would make it possible to compare the status of adaptation for the combination of these functions in the different species. Consequently, it is impossible to determine whether the phylogenetical development described which is so obviously correlated with an increase in protection can also be considered as an increase in adaptation relative to the combined function. Unfortunately, it can therefore not (yet) be decided whether this development is to be explained as an orthogenetical trend (in the ideology of e.g. Schindewolff), or as a result of an adaptation-selection mechanism which would have been in accordance with the synthetic theory.

B. In most species investigated the ontogenetical development of the commissure after geniculation could be easily studied as a consequence of the often very pronounced development of growth lines on the paries geniculatus. Invariably, the zigzag deflections turned out to display a more or less strong reduction of their amplitude during this part of the ontogeny. Sometimes this reduction was preceded by a stage in which the amplitude somewhat increased, just after geniculation took place. This complies with the general trend of increase in amplitude of the zigzags in all costate brachiopods. The subsequent reduction must be related with the gradual development of the related spines. This development complies with the phylogenetical trend in which, as we have seen, the spines also develop at the expense of the zigzag deflections.

C. Although the presence of marginal spines has also been demonstrated in very remote species, such as *Rhynchopora nikitini,* one may ask why these structures have not been found to occur much more frequently among brachiopods. This can be explained in two ways: 1. Marginal spines are hidden from external view, and are therefore easily overlooked. It is almost certain that many species will appear to be provided with marginal spines as soon as more detailed morphological investigations have been carried out. 2. The presence of marginal spines is conditioned by two features: geniculation and zigzag deflections. The combination of these two phenomena seems to be rather rare among brachiopods.

IV ARTICULATION

1. EXTERIOR FEATURES OF THE HINGE

In his 1959 paper on the "growth and form of brachiopod shells" Rudwick gave an analysis of the exterior features of the articulatory device. In this account he distinguished between a *strophic* and a *non-strophic* growth pattern of the hinge. The most important points of his argument will be given here in brief. Next, a more detailed explanation and critique will follow. According to Rudwick strophic shells are characterized by the fact that: 1. "the growing edges of the valves are exactly identical in extent" and 2. "some arc of the growing edge of each valve lies exactly in the line of the hinge axis". Such arcs constitute a true *hinge line;* they act as a "pivot" of the articulation. The sectors produced by the growing hinge lines are called *interareas.*

Non-strophic shells are — again following Rudwick's interpretation — characterized by the fact that: 1. "there are certain arcs of one growing edge which have no equivalents on the other growing edge" and 2. no arc of the growing edge lies exactly in the line of the hinge axis. The sectors produced by the posterior arcs — called *cardinal margins* — are termed *palintropes.* "All non-strophic shells conform to a single distinctive pattern. The dorsal umbo is always relatively strongly incurved, is tucked into the delthyrium, and is therefore hidden from external view. Consequently the ventral umbo is relatively conspicuous".

"The growing edges of the valves are not identical. Growth on the dorsal valve is "hemiperipheral": it does not extend as far back as the hinge axis. The most posterior arcs of the ventral growing edge have no equivalents on the dorsal growing edge. The points at which the dorsal growing edge terminates will be termed the *nick points".*

"The growth rate on the dorsal valve at the nick points is greater than zero. The dorsal valve edge between the nick point and the umbo therefore has a roughly logarithmic spiral form, representing the locus of the nick point itself during the growth of the valve. If the two valve edges are to be in close contact with one another between the nick point and the hinge axis, as they are on the rest of the commissure, the ventral growing edge on this arc must be deflected to "fit" the logarithmic spiral in the dorsal valve edge. This is achieved by a localized anomaly in the vertical component growth rate on the ventral growing edge; but unlike a true deflection there is no corresponding anomaly in the dorsal growing edge".

"The non-strophic growth pattern can thus be recognized not only by the lack of a true hinge line, but also by the presence of a dorsally directed deflection the commissure near the hinge axis. On many shells this deflection is conspicuous; it will be termed the *non-strophic deflection".*

"It is difficult to conceive any single morphological series which could link the non-strophic to the strophic hinge pattern, and the distinction between them must be regarded as an important feature of formal morphology".

A close scrutiny of the hinge of the rhynchonellids studied has revealed that these statements made by Rudwick can be improved on in some respects. The problems involved will now be discussed in the light of some examples.

Let us first consider a good example of a strophic shell: *Cyrtospirifer syringothyriformis* (fig. 70). The hinge line, which indeed is in the line of the hinge axis, is very elongated. The dorsal and ventral interareas are well developed, as are the delthyrium and the notothyrium which are bounded by the delthyrial and notothyrial margins respectively. The actual articulation points *(hinge points)* are situated near the intersection of the delthyrial and notothyrial margins and the hinge line. The extremely lateral points of the hinge line will in the following account be shown to be fully homologuous with the nick points of the non-strophic shells and will therefore be referred to with that name. (The term cardinal extremity is also correct — Williams and Rowell, 1965). The growth lines in fig. 70 indicate how the growth of the interareas has taken place (see also Vandercammen 1959, Williams 1956, Williams and Rowell, 1965, Krans 1965). The articulation points appear to have

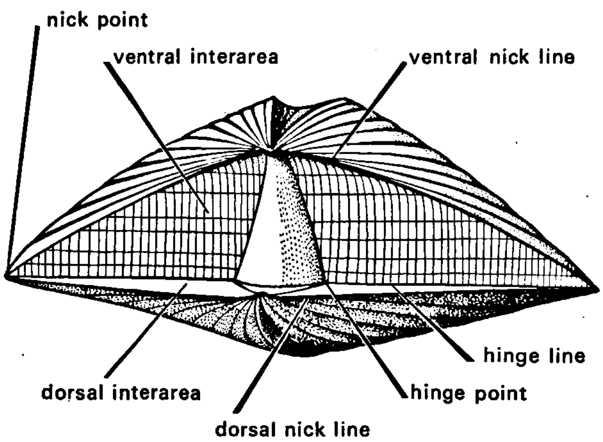


Fig. 70. *Cyrtospirifer syringothyriformis.* Exterior features of the hinge.

shifted in both valves from the beaks along the notothyrial and delthyrial margins towards their actual positions, and the nick points have shifted along the lateral borderlines of the interareas. These borderlines may therefore be called *nick lines.* The interareas of strophic shells may be curved, but the axis of the curvature must be parallel to the hinge line. When this condition is not fulfilled the "hinge line" is not straight and the shell is non-strophic. This is an important and simple criterium for the discrimination between strophic and non-strophic shells in cases where the cardinal margins are not clearly displayed (see e.g. p. 68 *Corvinopugnax corvinus*).

Let us now consider an obvious example of a non-strophic shell: *Kallirhynchia concinna* (fig. 71). The cardinal margin is indeed not in the line of the hinge axis; it is well developed and clearly displays the non-strophic deflection. Posteriorly it gradually merges into both the delthyrial and the notothyrial margin. The (ventral) palintrope is conspicuous and the nick line as well as the nick point are clearly visible. The dorsal umbo is tucked into the delthyrium which for the rest is partly obturated by a well developed deltidium. The notothyrium is of course hidden from external view. Consistent with the statements of Rudwick no dorsal counterpart of the palintrope seems to exist, but transverse serial sections reveal that there is an extremely narrow surface situated nearly perpendicular to the surrounding outer shell surface at the very place were a dorsal palintrope could be expected — along the dorsal shell margin between the nick point and the beak. This small surface is covered with primary shell material and thus belongs to the outer shell surface. These are strong indications that in this non-strophic shell a dorsal palintrope exists, only it is so narrow that it is very easily overlooked: the nick line and the cardinal and notothyrial margins nearly coincide.

In spite of the smallness of the dorsal palintrope the consequences of its observation are of considerable importance for our understanding of the non-strophic hinge growth. In the first place growth of the dorsal valve is not "hemiperipheral" as Rudwick suggests, but it extends as far back as the hinge axis. Of course, growth along the cardinal margin is extremely slow and in some species it might even not take place during the entire ontogeny of the animal. But *in principle* it is possible for a dorsal palintrope to occur. The only difference between strophic and non-strophic shells is whether or not the posterior arc of the growing edge is in the line of the hinge axis. In the second place the

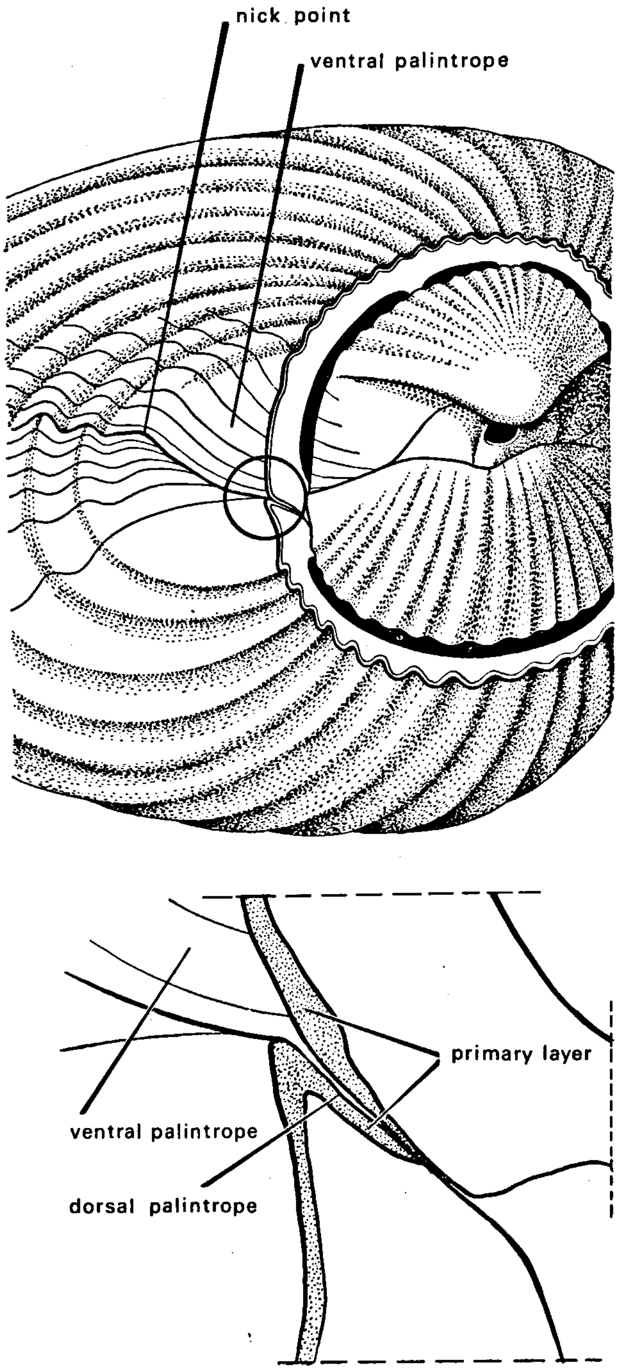


Fig. 71. *Kallirhynchia concinna,* Bathonian, Calvados (France). Exterior features of the hinge.

distinction between the strophic and non-strophic shells is by no means so clear-cut as Rudwick suggests. As a dorsal palintrope appears to exist it is possible to conceive a morphological series which links the non-strophic to the strophic hinge pattern. It is even very difficult in some cases to discriminate between the two types.

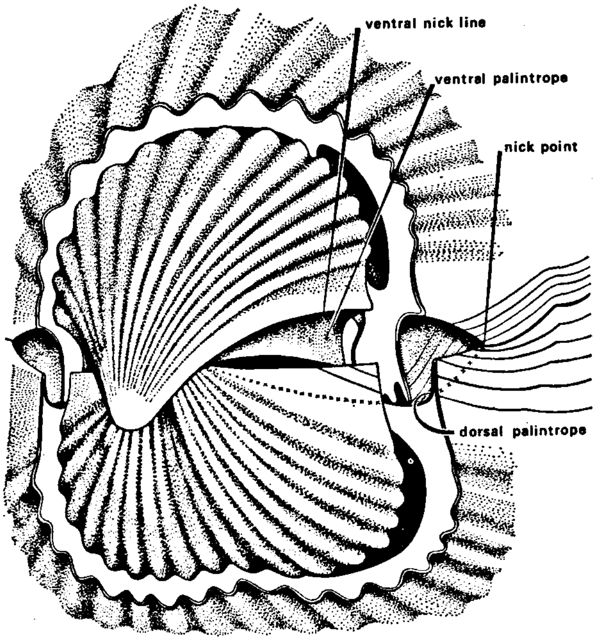


Fig. 72. *"Stegerhynchus" pseudolivonicus*. Koněprusy Limestone, Bohemia. Exterior features of the hinge.

In many representatives of the palaeozoic family Trigonirhynchiidae McLaren the cardinal margin and the dorsal and ventral palintropes have been found to be very characteristically disposed (fig. 72; pl. XIV, fig. 4, 5). The cardinal margin makes a sharp anteromedially directed curve so that its posterior part is directed more or less anteriorly and its anterior part ventrolaterally. As a result, the ventral palintrope is strongly depressed: that part of it adjacent to the nick line is more or less horizontal and the other part, close to the delthyrial margin, is vertical in transverse sections through the shell. In the dorsal palintrope the situation is reversed: the part adjacent to the nick line is vertical and the other part, close to the notothyrial margin, horizontal. The test of the vertical part of the dorsal palintrope is very thin, and consequently this part of the shell is only very rarely preserved in the fossils. The palintropes partially enclose a small cavity which is nearly always filled up with internal mould material and thus can best be studied in sections. The primary layer cover of the dorsal palintrope is very thin and often not easy to detect, but in some instances its presence has been demonstrated.

This type of hinge has been found in e.g. *Iberirhynchia santaluciensis*, *Trigonirhynchia pareti*, *"Stegerhynchus" nympha* and *"S." pseudolivonicus*, *Nymphorhynchia asiatica* and also in three species from the Crémenes Limestone (Frasnian-Famennian boundary, N. Spain), *Cupularostrum cantabricum*, *Ptychomaletoechia cf. gonthieri*, and *"Trigonirhynchia" boloniensis* (see Westbroek, 1964). This character, which doubtless is of great systematic value, will certainly be present in many other species.

The function of this cavity can only be guessed at. One can e.g. imagine that it was filled up with periostracum. Williams has repeatedly described the palintropes and cardinal margins as being covered with a thick

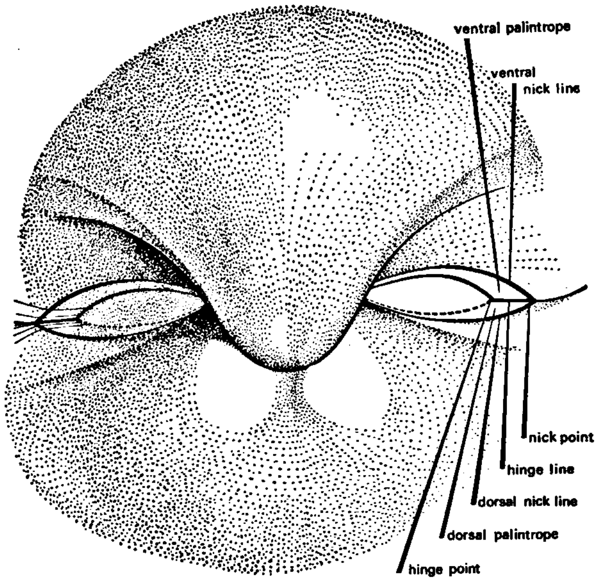


Fig. 73. *Uncinulus subwilsoni*. Exterior features of the hinge.

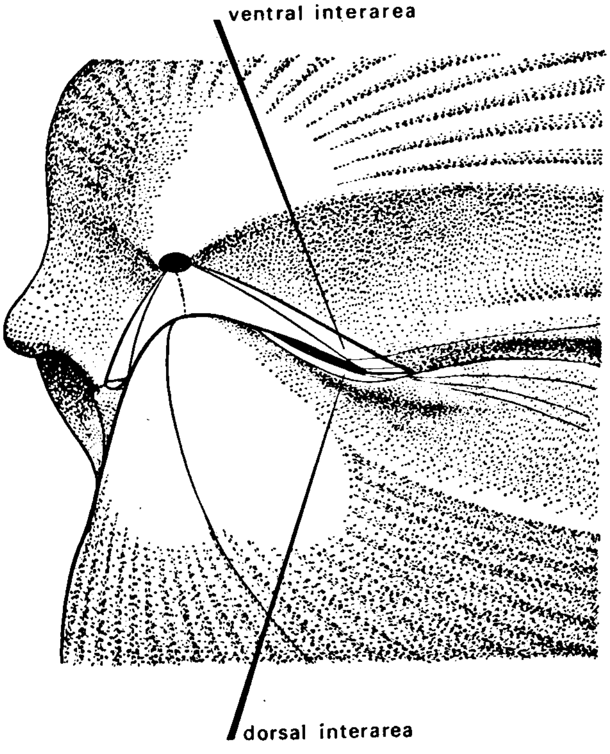


Fig. 74. *Glossinulus (Glossinotoechia) latus*. Exterior features of the hinge.

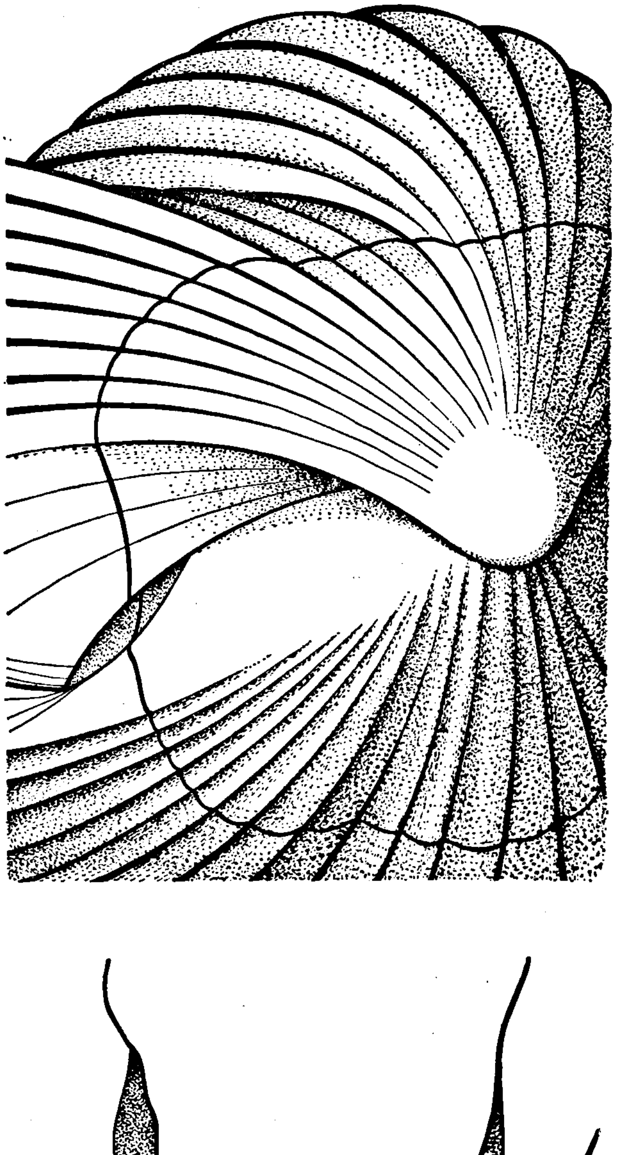
periostracal pad, secreted by the fused mantle lobes which underlie the cardinal margins. Thus when the cavity enclosed by the palintropes had accomodated a thick periostracal pad this might have functioned as the resilium in some pelecypods: as it would have been best developed somewhat anterior to the hinge-axis it might have been operative in opening the shell.

In three uncinulid species the hinge has been found to be perfectly strophic: *Estonirhynchia estonica, Sphaerirhynchia wilsoni* and *Uncinulus subwilsoni* (fig. 73; pl. X, fig. 1). The hinge lines are very short but lie exactly in the line of the hinge axis, and consequently the interareas are narrow and elongated. Some confusion is caused by the fact that the dorsal umbo is tucked into the delthyrium in all three species, so that the interareas form an acute depression anteriorly which commonly is filled up with internal mould materials so that the hinge line is hidden from view. Thus it is seen that also in strophic shells the dorsal umbo may be tucked into the delthyrium; this situation is obviously not the monopoly of non-strophic shells. Again the depression formed by the interareas may have been filled up with periostracum. Such a periostracal pad can however only have been operative as a resilium in the closure of the shell.

In *Glossinulus (Glossinotoechia) latus* the hinge strongly suggests a strophic growth pattern (fig. 74). The hinge lines are extremely short (often less than one mm) so that it is very difficult if not impossible to ascertain whether they are actually situated in the line of the hinge axis. The ventral interarea is nothing more than a flattened horizontally disposed rim flanked by the deltidium; the dorsal interarea is generally concealed by the ventral valve and by outgrowths of the dorsal interior (see fig. 8).

In *Uncinulus orbignyanus, U. pila,* and the studied species belonging to *Kransia* the hinge line is reduced to nearly zero (fig. 75). No dorsal and ventral interareas (or palintropes) seem to be developed and the nick points and hinge points must almost have coincided throughout the ontogeny of these animals. Consequently the question whether this hinge pattern is strophic or non-strophic is senseless. However, this type of hinge could be considered as being phylogenetically derived from a strophic hinge as species which probably are closely akin to their ancestors such as *Sphaerirhynchia wilsoni* and *Uncinulus subwilsoni* are strophic.

Both *Plethorhyncha altera* and *P. diana* display a beautifully developed non-strophic hinge (fig. 76; Pl. XIV, fig. 2). The ventral palintropes are very large. The dorsal ones are rather reduced. They can only be seen in sections through the shell; in these they appear to face medially. These palintropes are somewhat unusual in that the curvature of their nick lines is much weaker than that of the posterolateral costae: during growth the nick points shift quicker towards the anterior than the most posterior zigzags so that the latter are suppressed and the former act as suppression points. In cumulative terms: the posterior costae are cut off by the nick lines [23].



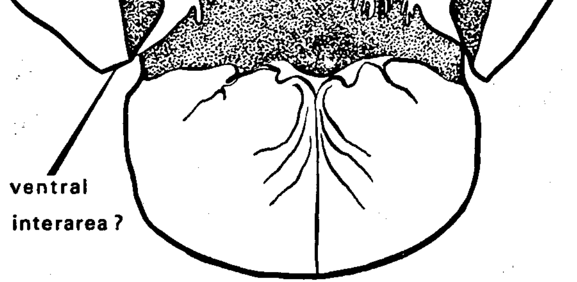


Fig. 75. *Uncinulus orbignyanus.* Exterior features of the hinge.

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[23] In this connection it is interesting to ask which is radially directed: the nick line or the posterior costae? In my opinion no preference can be given on grounds of apriority. The concept of radiality is purely of a heuristic nature.

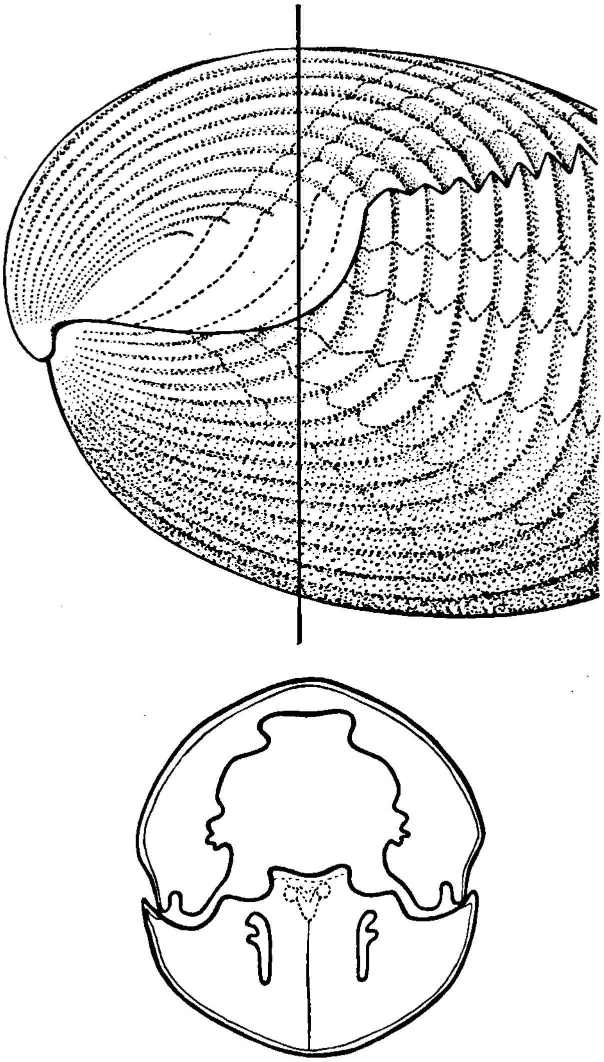

Fig. 76. *Plethorhyncha altera.* Exterior features of the hinge.

Such a state of affairs has been found in no other uncinulid species, and it may therefore be characterized as an important deviation. It becomes even doubtful if these species may be included among the Uncinulidae. Unfortunately, the type species of *Plethorhyncha* — *P. speciosa* (Hall, 1856) — could not be studied so that it could not be ascertained whether *P. altera* and *P. diana* belong to this genus.

The investigation of the exterior characters of the hinge in most Uncinulidae requires an exceptionally good state of preservation: growth lines must be clearly visible and the hinge lines or cardinal margins, which are generally situated at the bottom of a sharp depression, must not be obscured by sediment. Moreover all the structures concerned are very small. It is for that reason that the actual hinge pattern could be studied in detail only in a few species. In other species the inferences are more or less speculative.

Very short characterizations will now be given of the hinge pattern in the uncinulids studied according to their stratigraphical age. Cases of uncertainty are queried.

Estonirhynchia estonica — strophic growth; see description above.

Sphaerirhynchia wilsoni — strophic growth; see description above. Pl. X, fig. 1.

Decoropugnax berenice — the rather poor preservation of the material did not permit a sufficiently clear determination of the hinge pattern.

Hebetoechia hebe — strophic? Hinge seems to be similar to that of *Sphaerirhynchia wilsoni,* but no very clear observations could be made.

Lanceomyonia tarda — strophic? Same difficulty of observation as in *H. hebe.*

Eoglossinotoechia cacuminata — strophic? The hinge is very similar to the one of *G. (G.) latus.*

Eoglossinotoechia mystica — strophic? As *G. (G.) latus.*

Plethorhyncha altera and P. diana — non-strophic. See description above. Pl. XIV, fig. 2.

Uncinulus subwilsoni — strophic. See description above.

Obturamentella lebanza — strophic? Cardinal margins short.

Eoglossinotoechia sylphidea — strophic? As *G. (G.) latus.*

Glossinulus (Gl.) princeps — strophic? As *G. (G.) latus.*

Glossinulus (Gl.) henrici — strophic? As *G. (G.) latus.* Pl. XI, fig. 8.

Eucharitina eucharis — strophic? Similar to *G. (G.) latus.*

Uncinulus pila — hinge line reduced almost to zero. See description above.

Uncinulus maledictus maledictus — hinge line reduced to zero; as *U. orbignyanus.*

Markitoechia marki — strophic? Similar to *G. (G.) latus.*

Glossinulus (Gl.) latus — strophic? See description above.

Corvinopugnax corvinus — non-strophic? No cardinal margin or hinge line was clearly seen, but the ventral palintrope (?) is strongly curved. The axis of the curvature is parallel to the nick line and not to the hinge axis, so that in all probability the hinge is non-strophic (see p. 65).

Uncinulus orbignyanus — hinge line reduced to zero. See description above.

Uncinulus knjaspensis — No sufficiently preserved hinge has been observed.

Kransia parallelepipeda — hinge line reduced to zero. See description above.

Kransia primipilaris — hinge line reduced to zero. See description above.

Kransia goldfussii — hinge line reduced to zero. See description above.

Kransia minor minor — hinge line reduced to zero. See description above.

Hypothyridina cuboides — hinge very similar to the one of *C. corvinus.* However, the interarea is not curved parallel to the nick line but to the hinge axis, so that most probably the hinge is strophic.

2. INTERIOR FEATURES OF THE HINGE

Primarily the articulatory device consists of a pair of ventral teeth, fitting into dorsal sockets, and a set of paired adductor and diductor muscles. The teeth fit precisely into the sockets so that there is only room for a slight rotation which enables the shell to be opened and closed. The teeth and sockets of *Trigonirhynchia pareti* have pronounced transverse ridges so that they grip each other like cog-wheels (fig. 7; pl. VIII). This may illustrate that the actual hinge axis has no fixed place in the shell but shifts slightly to and fro during the articulation process. In no other species have such pronounced transverse ridges been found. In the socket an inner and an outer socket ridge and a socket floor are generally distinguished.

In strophic shells, such as of *Sphaerirhynchia wilsoni*, the hinge line lies more or less in the line of the hinge axis. It acts as a "pivot" or "axle" of the articulation, to use the words of Rudwick. The teeth are separated from the hinge points by more or less pronounced — sometimes locally absent — denticular cavities (Muir Wood, 1934).

In non-strophic shells the teeth are often more or less parallel to the cardinal margin. Here too a denticular cavity is present. The ventral part of the cardinal margin is often called the denticulum and has been observed by some authors (e.g. Muir-Wood, 1934) to be accomodated in an accessory socket which is situated in the outer socket ridge. The cardinal margins of both valves in addition to the function of closure of the corresponding part of the shell during articulation might have had an accessory articulatory function. I have the impression therefore that the entire cardinal margin is operative in the articulatory process, so that no single hinge axis can be designated as suggested by Rudwick.

During the growth of the hinge the entire articulatory device — i.e. the teeth, the functional parts of the sockets and the cardinal margin — shifts in anterior direction. The shifting of the cardinal margins and the resulting growth of the interareas or palintropes has been considered in the previous section. The growth of the socket proceeds anteriorly by enlargement of the surrounding epithelial fold (cf. Krans, 1965, fig. 49) whereas the posterior part of the socket loses its articulatory function. This part of the socket is generally covered with secondary shell material so that a narrow cavity results and this extends towards the dorsal beak as in the continuation of the functional part of the socket.

In all the species studied the dorsal umbo is tucked into the delthyrium. This has an important consequence for the growth of the teeth (fig. 77). The teeth have been seen to be dorsally directed outgrowths of the shell interior which fit into the dorsal sockets and for that reason must protrude beyond the cardinal margin. The outer socket ridge extends from the dorsal umbo — which is situated ventrally in respect of the cardinal margin — towards the cardinal margin. Therefore it must necessarily cut off the tooth posteriorly. One can thus only conceive that the teeth have grown by accretion along their anterior surface and simultaneously have been dissolved posteriorly. In chapter II (p. 30 and 34) two other arguments have been given to corroborate this hypothesis.

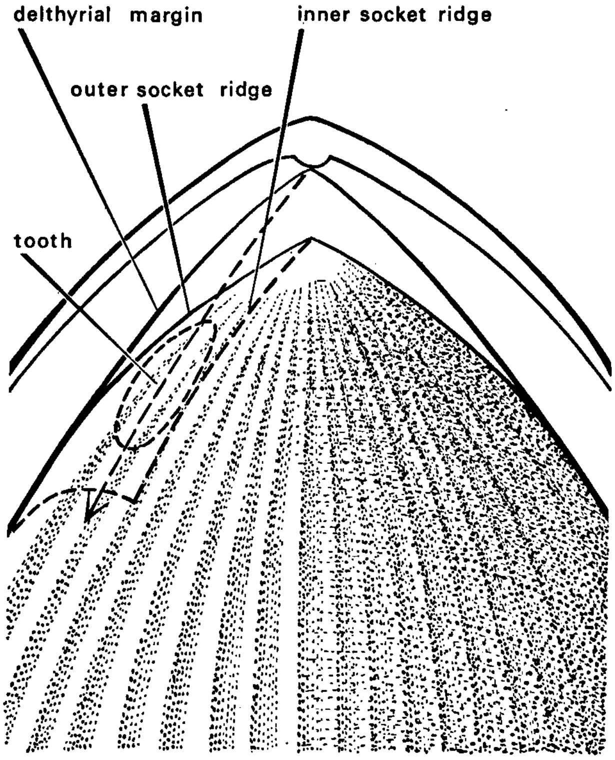

Fig. 77. Very schematic representation of rhynchonellid shell in dorsal view.

In chapter III it has been seen that in the uncinulids which are provided with well developed marginal spines and where geniculation takes place simultaneously all along the commissure the shifting towards the anterior of the articulatory device tends to stop at the moment of geniculation. This is very clearly the case in e.g. *Uncinulus orbignyanus* (fig. 53). When growth proceeds after geniculation the shell only opens gradually and internally the hinge is constantly adapted by changes in the form — not in the position — of the elements concerned.

A problem which must be discussed in this context concerns the closure of the shell in the area of and posterior to the hinge. It is clear, that since the posterior part of the shell protects the most vital parts of the animal, the closure must be permanent here. This is primarily achieved by the posterior part of the body wall which closes the delthyrio-notothyrial opening, as has been seen in the Introduction (p. 3, fig. 3). The corresponding part of the ectodermal epithelium, the pedicle epithelium, secretes a thick protective cuticle. The pedicle, a posterior elongated outgrowth of the body wall, projects through the delthyrium. In addition, a complex of elements of the shell is also operative in the closure of the posterior part of the shell. This is particularly well illustrated

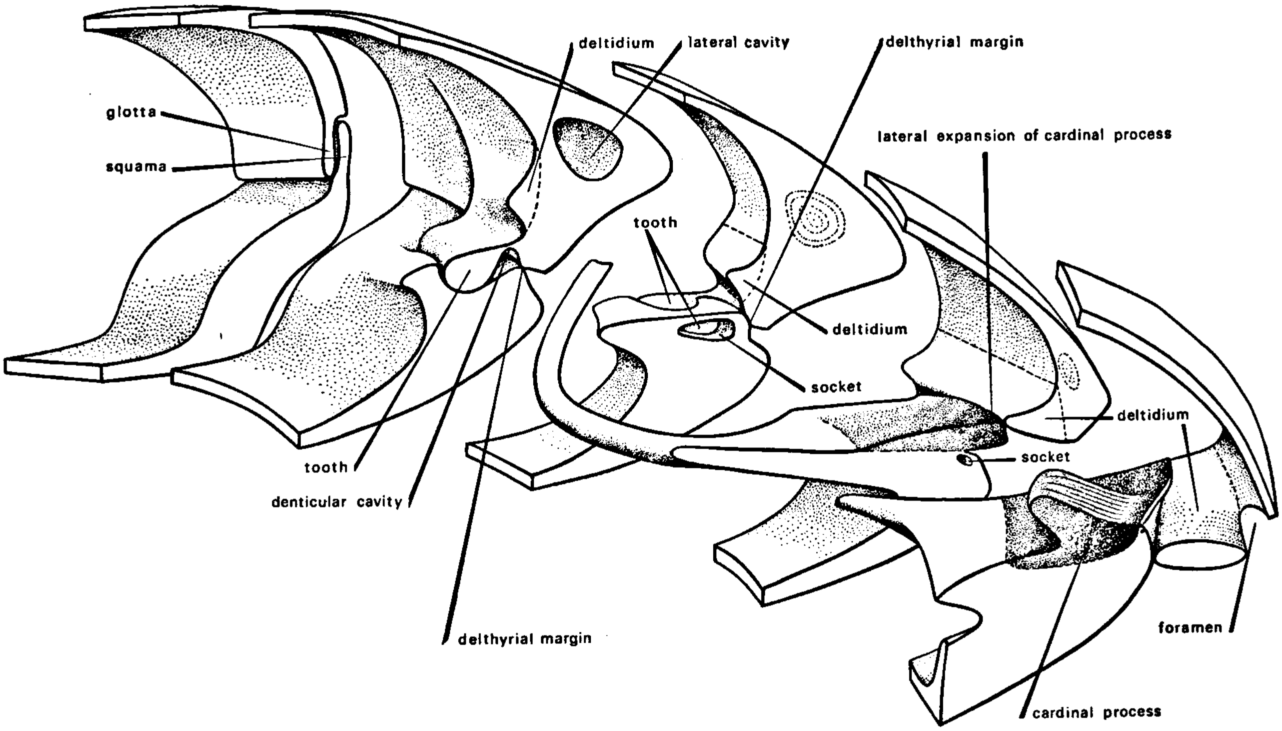

Fig. 78. *Glossinulus (Gl.) latus.* Block diagram of apical interior. Closure of the shell posterior to the hinge axis.

by *Glossinulus (Gl.) latus,* in which an almost perfect closure is achieved. Fig. 78 shows a block diagram through the posterior part of the shell. All the sections are parallel to the plane of symmetry. In the first place the shell is closed by the fact that the dorsal umbo is tucked into the delthyrium. As a result the notothyrium and a large part of the delthyrium are constantly protected at any angle of opening of the shell. Secondly, a large part of the delthyrium is covered by the deltidium. Only at the very beak of the ventral valve is a mesothyrid foramen left. The deltidium extends along the inner surface of the dental plates as an elongate thickening. In the dorsal valve a thick cover of the hinge plate is formed which is coloured black and at one place forms a typical jutting cardinal process. Laterally, this cover forms outgrowths which project beyond the sockets and the dorsal palintrope. These will be referred to as "lateral expansions of the cardinal process". The lateral margins of these outgrowths are vertical flattened surfaces (see fig. 8) which are in close contact with the deltidium.

When the elements of the shell which effectuate its closure at and behind the hinge are considered it can be established, judging from fig. 78, that near the dorsal beak the deltidium is lying against the outer surface of the dorsal valve and that from there on anterolaterally the closure is provided by the following combinations of elements in succession: deltidium against lateral expansion of cardinal process; delthyrial margin and deltidium against outer socket ridge; delthyrial margin against outer socket ridge (this is the case at the hinge; when articulation takes place the outer socket ridge is tucked into the denticular cavity; this cavity is absent at the hinge line and therefore is the result of resorption. The deltidium has here no obvious function in the articulation); glotta against squama. It is interesting to imagine how all these elements glided along each other when articulation took place. In the specimen used for the construction of fig. 78 the closure was obviously perfect at any angle of opening of the shell.

The closure by shell structures behind the hinge is very variable in the different genera under consideration, and constitutes in my opinion a complex of characters of great systematic value. In *Trigonirhynchia pareti,* e.g., the deltidial plates are very poorly developed and a cardinal process with lateral outgrowths comparable with those of *Glossinulus (Gl.) latus* is absent so that between the valves considerable openings exist. On the other hand, the delthyrial margins fit more closely around the dorsal umbo than in *G. (G.) latus.*

Short descriptions will now be given of the system of posterior closure in the uncinulids studied. *Decoropugnax berenice, Hypothyridina cuboides* and *Corvinopugnax corvinus* have not been sufficiently studied in this respect. All three species seem to have a well developed deltidium.

Estonirhynchia estonica. Deltidial plates only very poorly developed. Hinge plate has no cover with lateral expansions and cardinal process, as in *G. (G.) latus,* but well developed outgrowth of inner socket ridge instead. Delthyrial margins fit very closely around the dorsal umbo.

Sphaerirhynchia wilsoni. Very similar to *E. estonica.*

Hebetoechia hebe. Cardinal process present, but no lateral expansions of it have been observed. Instead, the inner socket ridges are well developed and seem to fulfil their function. Ventral umbo rather projecting (but much less than in *Glossinulus*). Well developed deltidium.

Lanceomyonia tarda. No cardinal process. Deltidium present. Inner socket ridge may function in closure mechanism. Ventral umbo rather projecting.

Eoglossinotoechia cacuminata. Ventral umbo strongly jutting. Well developed deltidium. Cardinal process incipient, variable in size. Inner socket ridges as well as lateral expansions of cardinal process may function as dorsal devices for the closure.

Eoglossinotoechia mystica. In principle the situation is here very similar to that in *E. cacuminata.*

Plethorhyncha altera and *diana.* Delthyrial margins fit closely around the dorsal umbo. Deltidium present. Lateral expansions of small cardinal process do not seem to have any function in the closure.

Uncinulus subwilsoni. Delthyrial margins fit closely around dorsal umbo. Deltidium present, but its size could not be established. Cardinal process and lateral expansions well developed.

Obturamentella labanza. Delthyrial margins do not fit closely around the dorsal umbo: ventral umbo rather projecting. Well developed deltidium. Cardinal process and lateral expansions well developed.

Eoglossinotoechia sylphidea. Ventral umbo strongly jutting. Well developed deltidium. Cardinal process and expansions extremely well developed. Closure mechanism very similar to that in *Glossinulus (Gl.) latus.*

Glossinulus (Gl.) princeps. Very similar to *Gl. (Gl.) latus* and *E. sylphidea.*

Glossinulus (Gl.) henrici. Very similar to *Gl. (Gl.) latus* and *E. sylphidea.*

Eucharitina eucharis. Delthyrial margins do not fit closely around the dorsal umbo. Well developed deltidium. Well developed cardinal process and lateral expansions.

Uncinulus pila. Delthyrial margins fit closely around dorsal umbo. Deltidium probably poorly developed (only small deltidial plates?). Well developed cardinal process with lateral expansions.

Uncinulus maledictus maledictus. Delthyrial margins fit closely around dorsal umbo. Deltidium has not been observed. Well developed cardinal process and lateral expansions.

Markitoechia marki. Delthyrial margins do not fit closely around the dorsal umbo. Well developed deltidium. Strongly projecting cardinal process. No good observations on lateral expansions.

Glossinulus (Glossinotoechia) latus. See detailed description above.

Uncinulus orbignyanus. As *U. pila.*

Uncinulus knjaspensis. Delthyrial margins fit closely around dorsal umbo. Deltidium could not be observed due to the poor preservation of the material available. Havlíček (1961) mentions the presence of a low cardinal process with considerable lateral expansions in the normal specimens with a thick test; in a specimen with a thin test he found no cardinal process at all.

Kransia. Since all the species which are assigned to this genus here are very similar in respect of the posterior closure of the shell they are treated together. Delthyrial margins do not fit closely around the dorsal umbo; the ventral umbo projects posteriorly. Well developed deltidium. Well developed cardinal process and lateral expansions extending beyond the edge of the dorsal valve.

3. RECONSTRUCTION OF THE EPITHELIUM IN THE POSTERIOR PART OF THE SHELL OF *SPHAERIRHYNCHIA WILSONI*

At the end of this chapter an attempt will be made to reconstruct the epithelium in the posterior part of the shell of *Sphaerirhynchia wilsoni,* which may serve an example here. I do not think that there is reason to believe that the problems involved will be essentially different in other uncinulids. The considerations given by Williams (1956), and Williams and Rowell (1965) on this topic will be taken as a starting-point. Moreover, sound arguments are provided by Krans (1965).

In fig. 79a the structure of the posterior part of the shell is given in a block diagram. The shell has been transversely cut into a number of slices which have been spaced out. The problems involved in the reconstruction of the epithelium are numerous, and they too will be dissected in the following observations.

In fig. 79b my reconstruction of the epithelium is demonstrated; the slices of epithelium correspond exactly with those of the shell in fig. 79a. The numbers correspond with those in the following text.

1. The inner surfaces of the valves are lined with outer epithelium. This epithelium may show some local differentiations, but this is not taken into consideration, here. It is evident that most problems arise with the attempted reconstruction of the epithelium at the valve edges.
2. Anterior to the hinge the outer epithelium of both valves merges via the mantle lobes into the inner epithelium (cf. fig. 3).
3. In the reconstruction the dorsal and ventral outer epithelia underlying the hinge line are fused; at their

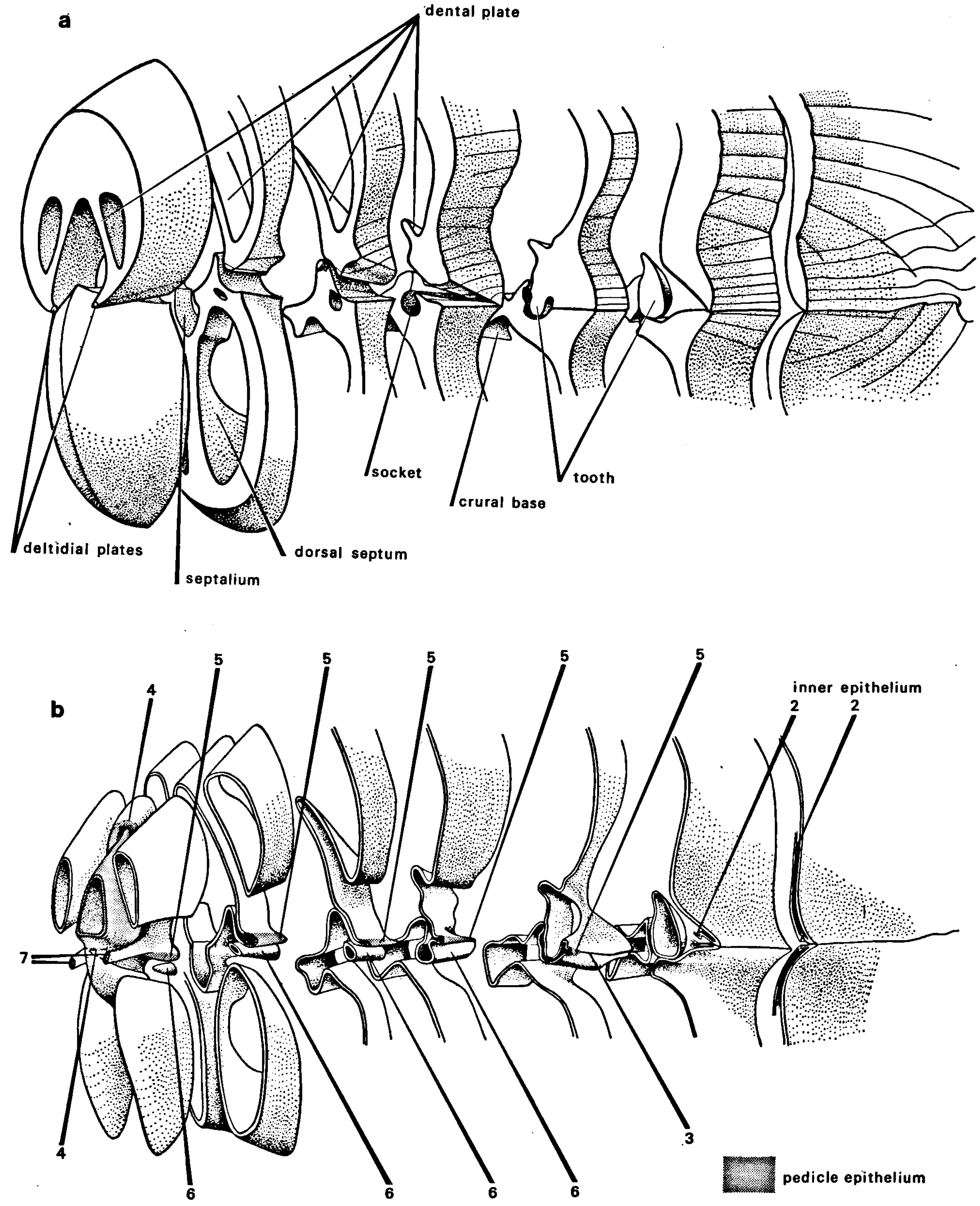

Fig. 79. *Sphaerirhynchia wilsoni.* (a) Block diagram of apical part of shell. (b) Reconstruction of mantle in (a). The numbers are referred to in the text.

fusion a generative zone occurs. This is in accordance with the statements made by Williams.

4. At the notothyrial and delthyrial margins the outer epithelium merges in principle into the pedicle epithelium. However, according to Williams, the pedicle-outer epithelial junction retreats anteriorly during the growth process, leaving behind a semicircular ridge of secondary calcite — *the pedicle collar* — and a very faint ridge — the *antygidium* — in the ventral and dorsal valves respectively. No trace of either of these structures has been found in the species studied (except in *Kallirhynchia concinna),* but since these structures may only be extremely faint ridges which are easily overlooked in sections, a retreat of the junction is not beyond possibility. In any case, in my reconstruction I have drawn a strongly retreated pedicle-outer epithelial junction.
5. A loose flap of pedicle epithelium has been drawn extending from the actual articulatory device posteriorly where it merges gradually into the broad extension of pedicle epithelium subtended between the "pedicle collar" and the "antygidium". This flap links up the dorsal and ventral outer epithelia posteriorly to the hinge axis. It is very narrow at the hinge and gradually broadens posteriorly. I have allowed it this space because it must permit the dorsal and ventral pedicle-outer epithelial junctions to move apart when articulation carries on.
6. As a matter of fact the socket is lined with dorsal outer epithelium. The inactive posterior part of the socket is partially closed and a tubular extension of the epithelium lining the active part of the socket must have covered this cavity internally.
7. Along the delthyrial margin poorly developed deltidial plates are secreted. The situation of the epithelial outgrowths involved in the secretion of these plates is probably similar as in *Laqueus* (see Williams and Rowell, 1965, fig. 89 D). This would mean that the anterior surfaces of these plates were lined with elongated tubular extensions of the epithelium consisting of an outer epithelial part lining the deltidial plates and a free part of pedicle epithelium. Consequently, the pedicle-outer epithelial junction is situated on either side of this epithelial extension.

V SOME INFERENCES ON THE PHYLOGENY AND THE CLASSIFICATION OF THE UNCINULIDAE

1. INTRODUCTION

In the enclosure I short descriptions are given of the 24 uncinulid species which have been examined in this publication. The species are listed according to their chronostratigraphical position. Seventeen different characters have been distinguished and the descriptions are based on them. Most of the information given has been acquired by my personal observation; it has been treated to a large extent in the preceding chapters. Some data concerning characters which have been insufficiently studied in this account are borrowed from other publications.

The aim of this chapter is then an attempt to perceive on the base of these data some of the phylogenetical relationships within this family and to make some suggestions as to the classification. There are however two factors in play which seriously reduce the value of this analysis. 1. It is a generally accepted assumption in taxonomy that a sound classification should be based on a great number of non-correlated characters (see e.g. Mayr, 1965). Numerical pheneticists such as Sokal and Sneath (1963) even claim that at least sixty characters should be taken into consideration. The data at our disposal do not permit any such treatment of the Uncinulidae. Moreover, not all the characters normally used for brachiopod classification can be considered here. The musculature, the mantle canal systems and the shape of the crura, to give only some examples, certainly constitute characters of great systematic importance, but for lack of sufficient knowledge I cannot make use of them. 2. The species which have been investigated in this account constitute rather a small and arbitrary association out of the great number of uncinulid and related species known. This association is to a large extent determined by the travel limitation of the author and by the materials which accidentally have come into his hands. As a result it may not be very representative of this family, and it probably is not very suitable for sound classificatory purposes. On the other hand it should be kept in mind that the species which are described here are rather regularly distributed over the geological time interval in which the Uncinulidae are known to have occurred. Moreover, the percentage of established genera of which representatives have been investigated is considerable. Therefore I think that at the least some suggestions can be given as to the phylogeny and the classification of this family. In this account a quantitative treatment is attempted of the data given in enclosure I. This has the advantage that a large number of data can be surveyed at once. It does not seem worth while to apply the existing numerical and statistical methods which are in use for the establishment of phylogenetical trees. They are very laborious and do not seem very well adapted to the particular problems involved here; they can only fruitfully be applied when many more data can be taken into account than is possible here. The method used is self-made. Although the results of this analysis are not very reliable they are so striking that it nevertheless is useful to publish them.

2. PROCEDURE

The first aim of this analysis is to assess the phylogenetical relationships of the 24 uncinulid species studied. For this purpose the following data are available:

1. In total 17 characters have been taken into consideration. In enclosure I short descriptions are given of all these characters in the species investigated.
2. An attempt has been made to determine the time intervals between the species. This has been done using data given in the literature. To start with, the chronostratigraphical positions of the species were determined as precisely as possible. Next, it was attempted to express the ages in m.y. The publications of Friend and House (1964) and of Strachan (1964) served here as starting-points. The entire development of the Uncinulidae studied must have covered some 60 m.y.

The species were arranged in the enclosure according to their age and then numbered. So the oldest species is no. 1 and the youngest one no. 24. For the purpose of a phylogenetic study the first appearance of a species is considered as the most significant moment in its history. For each species a time index has been determined. This index corresponds with the number of m.y. intervening between the first appearance of this species and the first appearance of the oldest species studied (viz. *S. wilsoni* and *E. estonica*). The time interval between any two species is then the absolute value of the difference of their time indices.

An important question now to be posed is: are any of the considered characters structurally, functionally, genetically, or otherwise correlated? Obviously such correlations are extremely difficult to detect in fossil material. Two clear-cut cases however can be discerned here. 1. An obvious correlation exists between the development of the cardinal process and its lateral expansions (see chapter IV). Only when a well developed process exists can the expansions be formed. When the process is absent its expansions are also absent and the inner socket ridges are often developed in such a way that they fulfill instead the corresponding function of posterior shell closure. 2. The degree to which the ventral umbo juts beyond the dorsal umbo largely determines the development of the deltidium. When the delthyrial margins closely embrace the dorsal umbo (i.e. when the ventral umbo is short) only a very reduced deltidium can come into existence (e.g. in *S. wilsoni*); a strongly protruding ventral umbo on the other hand gives rise to a large deltidium (e.g. in the genus *Glossinulus*). In consequence of this each of these two pairs of characters is considered as one single character. Among the other characters no clear-cut correlations could be detected, although they may very well be present. All these characters are therefore considered as independent ones. Thus, the actual number of characters considered is 15 .

For most of these characters a morphological range has been composed. In all these ranges four successive stages are distinguished; they have been indicated with the numbers 1, 2, 3 and 4, respectively. In table A, enclosure II, the species have been indicated by their consecutive numbers in the left column. In the next column the time indices are given and the fifteen characters studied are entered in the remaining columns. For all the species the constitution of each character is represented by the most appropriate number of the corresponding morphological range. This table constitutes the starting-point for the further considerations.

First all the 15 characters and their morphological ranges must be briefly discussed.

1. Shell mosaic

1 = mosaic elements fine
2 = mosaic elements of medium size
3 = mosaic elements coarse
4 = mosaic elements very coarse

2. The ventral umbo and the deltidium

1 = ventral umbo short, strongly curved, deltidium incipient
2 = ventral umbo short, moderately curved, deltidium small
3 = ventral umbo rather short, nearly straight, deltidium well developed
4 = ventral umbo strongly protruding, nearly straight, deltidium large

3. Costation

It has been attempted to combine some features of the costation which seem to be more or less related: coarseness of the costae, distance of their origin from the beak and the degree of splitting of the costae. Fine costae mostly start at the beak, while coarse ones generally have their origin at some distance of it, or are even restricted to the anterior and lateral parts of the shell. Fine costae split more easily than coarse ones.

1 = costae very fine, starting at the beaks, splitting strongly
2 = costae fine, starting at the beaks, splitting varying from moderate to strong
3 = costae of moderate coarseness, starting near the beaks and not splitting
4 = costae coarse, restricted to anterior and lateral parts of the shell, not splitting

Not all the costation patterns studied fit readily into one of these categories. In such cases the pattern is conveyed to the category to which it shows the greatest similarity.

4. Size of the shell

1 = very small
2 = small
3 = moderate size
4 = large

5. Connectivum

In some of the species studied no connectivum could be detected, in others it was well developed. Intermediate cases as have been described by Havlíček (1961) in e.g. ***Stegerhynchus pseudolivonicus*** have not been found in the species under consideration. In a number of species no septalium was developed: the dorsal septum directly supported the hinge plate, just as e.g. in ***Septalaria.*** It is not clear whether the parts of such hinge plates which lie between the crural bases are homologous with the septalium, with the connectivum, or with both. The location of these parts of the hinge plates and of the connectivum are very similar, so that their function may also have been similar (see p. 10). Consequently the connectivum has been considered to be very probably present in those cases. The following evaluations are given:

1 = connectivum absent
2 = hinge plate continuous and directly supported by the dorsal septum
4 = connectivum present

It must be remarked that, when the posterior part of the shell is strongly thickened, most of the internal apical structures can only be distinguished in sections; they often do not project beyond the inner shell surface and are partly or completely involved in the kallus. In the sections they constitute zones of finely fibrous material, whereas the kallus is much coarser in structure. Schumann (1965) states that such finely fibrous zones are only secreted along very narrow ridges on the inner shell surface and that they can hardly be used for systematic purposes. It must however be pointed out that these finely textured zones are always easily comparable with the structures which occur in species where no such thickening of the shell occurs. Schumann starts from the unproved assumption that the growth of these structures has kept pace with the growth of the surrounding kallus during the entire ontogeny of the shell. Although it is not excluded that Schumann is right in some cases it must be mentioned here that at least some exceptions have been shown to occur. Havlíček (1961) has described a specimen of *Uncinulus knjaspensis* of which the shell was very thin. Its dorsal apical structures were pronounced and well differentiated features which projected freely into the shell cavity. Generally however the dorsal apices of the shells of this species are rather clogged with kallus. This suggests that the excessive development of the kallus has taken place at a relatively late stage of growth. I have found something similar in shells of *Kransia parallelepipeda*. Thus, although the assumption of Schumann is certainly interesting, there is no evidence available at this stage of our knowledge to prove it.

6. The thickening of the posterior part of the shell by kallus

1 = posterior part of the shell thin
2 = posterior part of the shell of moderate thickness
3 = posterior part of the shell thick
4 = posterior part of the shell very thick

7. The development of the cardinal process (and its lateral expansions)

1 = cardinal process absent
2 = cardinal process incipiently to moderately developed
3 = cardinal process well developed
4 = cardinal process elongated, tongue-shaped

8. The structure of the dorsal septum (ch. II, p. 30)

1 = fibres of the septum parallel
2 = fibres slightly diverging
3 = fibres moderately diverging
4 = fibres strongly diverging; a mediotest is developed

9. The length of the hinge line (chapter IV, p. 68)

The hinge line is short in all the species investigated. It can even be so much reduced that it can no longer be distinguished.

1 = hinge line short
2 = hinge line very short
3 = hinge line extremely short
4 = hinge line reduced to almost zero

A difficulty arises with the non-strophic species *P. altera*. Since in non-strophic shells no hinge line occurs its length could not be given for this species. Instead, the length of the (homologous) cardinal margin is considered here. Because of its considerable length this feature is best assigned to the first category. The fact that the shell of this species is non-strophic is expressed by character no. 12.

10. The septalium

In none of the species studied is the septalium very large. When present, it is generally restricted to the very posterior part of the shell. Moreover, its depth is reduced. In this context attention is only given to the depth of this structure and its anterior extension is not considered. Inferences regarding the depth of the septalium can be made from sections, although with due reserve [24].

1 = septalium of moderate size in sections
2 = septalium small
3 = septalium very small
4 = septalium reduced to almost zero and the hinge plate is continuous (see the discussion of the connectivum. The remarks which are made there in regard to the clogging of these structures with kallus also apply to this case).

11. The marginal spines

In chapter III a distinction was made between four types of marginal spines, viz. the types A, B, C and D. It has been shown that in this succession these four types constitute a morphological range. These types are given here the respective numbers 1, 2, 3 and 4.

Only in *E. estonica* are no spines developed. This is also indicated with 1.

The four remaining characters are somewhat different from the preceding ones in that differences are found only incidentally in them. No true morphological ranges could therefore be composed for these characters. The usual situation has here always been indicated by 1 and the incidental divergence by 4. Only in one character (the stratification of the shell) an intermediate figure has been given.

12. Strophic and non-strophic shell. The shell is usually strophic in the Uncinulidae studied (1). Only in *P. altera* is the shell non-strophic (4).

13. The double geniculation in *Glossinulus (G.) henrici.*

14. In *Obturamentella lebanza* and in *Markitoechia marki* the marginal spines have been found to fit properly into corresponding grooves of the opposite valve (4). In the other studied species no such grooves have been found (1).

15. Species with stratified shells are denoted by 4 for this character. Species with a more or less chaotic structure received an intermediate figure (3). Species in which no such phenomena have been observed were denoted by 1.

In principle two evolutionary processes can be distinguished in a phylogenetical development: 1. *cladogenesis,* i.e. the branching of the lineages, and 2. *anagenesis,* i.e. the evolutionary change which occurs in each lineage since the last furcation. It is known that the rate of the anagenesis forms a most variable factor in evolution. When an attempt is made to reconstruct a phylogenetical tree it must be tried to detect both the cladogenetical and the anagenetical

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[24] As the problems involved are too complicated to be treated here they will be considered in another article.

developments which have occurred during the evolution of the group of organisms under consideration.

It has already been shown that the available data in this investigation are of two types: 1. the phenetical distances between the species, and 2. the chronological situation of the species. The phenetical distance between any two species can be found for each character by determining the absolute value of the difference between the corresponding values for that character which are given in table A (enclosure II). It is obvious that the phenetic distances between the species are the result of both cladogenesis and anagenesis. In biology, where only simultaneously living species are examined, it is very difficult, if not impossible to determine these two factors on the ground of phenetic distances alone. But the species which have been examined in this account have not all lived simultaneously, but are scattered about more or less regularly in the whole period the Uncinulidae are known to have existed. This fact forms a most important key for the construction of the phylogenetical tree of this taxon. Nevertheless, it appears impossible to avoid completely every trace of reasoning in a circle. On the contrary, it is necessary in a number of instances to assume the evolution to have proceeded at a certain rate without sufficient evidence being available. Our results are therefore rather speculative.

For the further elaboration of the material the following procedure is followed. For each pair of species the phenetic distance is measured for all the 15 characters in succession. This is done by reference to table A. For each character the value of the oldest species is subtracted from the value of the youngest species. The resulting number may vary from — 3 to + 3. Starting from this measurement of the phenetic distance for that particular character and from the time interval between the two species an evaluation is made of the cladistic affinity of the species. This evaluation is expressed in a number. This process is repeated for all the 15 characters. The 15 resulting evaluation numbers are added and the final correlation factor forms the quantitative expression of the author's opinion on the cladistic affinity. It must be stressed that the cladistic affinity itself cannot be indicated here with such a number. The phylogenetical tree is then constructed on the basis of the correlation factors and on a rough estimation of the phenetic distances between the species.

Two important questions remain: 1. "according to which system is the evaluation for each character expressed in a number?" and 2. "according to which standard are the phenetic distances evaluated?"

With respect to the first question it must be remarked that each evaluation number contains two elements: the strength of the argument and the magnitude of the cladistic affinity. In both elements three possibilities are distinguished:

argument	*suggested cladistic affinity*
1. strong	a. strong
2. moderate	b. moderate
3. poor	c. slight

For each possible combination of argument and affinity a score has been given. When a strong argument exists for a strong affinity (1 — a) the score is of maximum height (= 7); when a strong argument exists for a slight affinity (1 — c) the minimum score is obtained (= 1). The whole evaluation scale is as follows:

1 — a = 7 2 — a = 6 3 — a = 5
1 — b = 4 2 — b = 4 3 — b = 4
1 — c = 1 2 — c = 2 3 — c = 3

When no argument is present in favour of one of the three possibilities of the suggested affinities a 4 is given. It must be noted that especially a score of 4 points can have various meanings, viz. a strong, a moderate and a poor argument for a moderate affinity and no argument at all. This certainly forms one of the imperfections of this method but I do not see an alternative at this moment.

The problem remains how to translate the phenetic distances into sound suggestions for cladistic affinities. With regard to this two preliminary remarks must be made.

a. It is obvious that the magnitude of the time interval between two considered species has a great influence on the evaluation. The greater the time interval, the larger the probability that a difference or a similarity in one character is brought about by an anagenetical development. Consequently, the strength of the argument in the evaluation of the cladistic affinity generally decreases when the time interval increases, so that the evaluation numbers will generally be less extreme. The time intervals are divided into three categories:

1. ⩽ 10 m.y. As the possible deviation from the values obtained is roughly estimated as 10 m.y. species with such intervals are treated as being more or less contemporaneous.
2. > 10 m.y. and ⩽ 25 m.y. These intervals are considered as being of moderate magnitude.
3. > 25 m.y. Large intervals.

This division has been made such that the time span covered by these categories increases together with the time interval: the first category covers 10 m.y., the second one 15 m.y. and the third one about 35 m.y. This has been done intentionally, since in my opinion the significance of phenetic distances and similarities for the evaluation of cladistic affinities decreases progessively with increasing time interval between the species under consideration.

b. Using Kendall's correlation method it has been determined for the characters no. 1—11 to what extend a trend is present in the sequence of values for the 24 species (the characters no. 12—15 have not been considered). This has been carried out with the aid of a computer[25]. The following values are obtained.

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[25] I wish to express my sincere thanks to Dr. J. R. Möckel, Leiden , for the elaboration of both computer programs used in this publication.

Character no.	Kendall's S	Character no.	Kendall's S
1	— 5	7	102
2	— 1	8	146
3	—12	9	165
4	—35	10	165
5	59	11	175
6	95		

On the basis of these values this set of characters is divided into three groups: (1) characters with no "significant" trend, comprising no. 1—5; characters with a moderate trend (no. 6 and 7); and (3) characters in which the trend is very strong (no. 8—11). A fourth group is formed by the characters in which differences occur only incidentally (no. 12—15).

For each of the four groups of characters a standard evaluation table is composed in which the proposed evaluation of the phenetic distances are given (table B, enclosure II).

These tables are naturally the result of the personal judgement of the author. It is impracticable to give here all the arguments which have led to these evaluations. Instead, a few general observations are made.

a. In characters of the first group only the time interval and the absolute value of the phenetic distance are important. The sign of the phenetic distance and thus the sequence of the species in time is immaterial. In characters of the groups 2 and 3 the sequence in time is most important. Whether in two species with a large time interval a great difference for one of these characters is parallel or opposite to the general trend in that character is of great influence on the evaluation. When the difference corresponds with the trend this is considered as being in the line of the expectations and an evaluation of 4 or 5 is given. But when the sequence of the character values is contrary to the trend this is considered as a strong argument for a slight cladistic affinity and a 1 is awarded. When the time interval between the species is small the sequence of the character values has no influence on the evaluation, even for characters of type 2 and 3.

b. In characters of group 1 a difference between two species with a small time interval receives a very low evaluation; the evaluation of a similarity under these circumstances is very high. The probability that a difference or a similarity is brought about by an anagenetical development increases with increasing time interval and the strength of the argument decreases similarly. Consequently the evaluation numbers must be less extreme according as the time intervals increase.

c. When for a character of group 3 the time interval between two species is small a great similarity is normal. In such a case no argument in favour of either a strong, a moderate, or a slight affinity is present and a 4 is awarded. However, when a great difference exists a strong argument exists for a slight relation and the evaluation is 1.

N.B. For a character of group 3 and a large time interval a similarity receives a lower evaluation than a difference when the sequence of the character values corresponds with the trend.

d. The characters of group 4 are evaluated in a somewhat different way. The evaluation scale ranges from —3 (strong argument for slight affinity) to +3 (strong argument for strong affinity). When for each of two species such a character has the number 1 the evaluation number 0 is given (i.e. no argument can be given in respect of the cladistic affinity). When the character values are 4—1 and 1—4 the evaluations are negative. The strength of the argument decreases when the time interval increases. The sequence of the character values is considered to be of some influence on the evaluation. Although it is known that the law of irreversability is highly disputable, especially when single characters are considered (see Simpson, 1955, pp. 310—312) it does not seem very probable for such a character to have disappeared, whereas it is quite certain that it has arisen during evolution. The evaluations of the character values 3 are somewhat lower than when they amount up to 4.

e. The rate of the evolution has been estimated to be rather low. In other words: when the actual rates of evolution have been high in some instances low evaluation numbers are given.

It has already been stated that the further elaboration of the data is as follows: for each pair of species all the characters are evaluated in succession according to the above evaluation tables. The obtained values are then added and the resulting correlation factor forms the quantitative expression of the author's opinion on the cladistic affinity of the species in question. On the basis of the correlation factors and of rough estimations of the phenetic distances between the species the final phylogenetical tree is composed. The determination of the correlation factors is a purely mechanical and laborious proceeding. It has been carried out by means of the computer.

The correlation factors are given in table C (enclosure II). They vary from 25 (for the affinity between the species 5 and 8) to 59 (15—16 and 16—20). High values mean that according to the author the cladistic affinities are strong; low values that these affinities are considered to be slight. Let correlation factors of 50 and more be considered as strong indications for strong cladistic affinities. Then this is the case for the following pairs of species:

1 — 2 (56)
1 — 22 (50)
2 — 22 (50)
3 — 14 (51)
4 — 5 (51)
5 — 10 (50)
8 — 15 (54)
8 — 16 (54)
10 — 11 (54)
10 — 12 (52)
10 — 18 (52)
10 — 22 (50)
11 — 12 (50)
11 — 18 (50)
14 — 19 (52)
14 — 22 (50)
14 — 23 (50)
14 — 24 (53)
15 — 16 (59)
15 — 20 (53)
15 — 21 (50)
16 — 20 (59)
16 — 21 (53)
19 — 22 (50)
19 — 23 (52)
19 — 24 (50)
20 — 21 (53)
22 — 23 (51)

With this selection of data as a starting-point the following groups of more or less closely related species can be distinguished preliminarily:

(a) : 1 — 2 — 3 — 14 — 19 — 22 — 23 — 24
(b) : 4 — 5 — 10 — 11 — 12 — 18
(c) : 8 — 15 — 16 — 20 — 21

Two remarks must be made in this connection:
1. the species 6, 7, 9, 13, and 17 do not occur in one of these groups. No clear indications exist for their cladistic position.
2. Only in one case does the correlation factor amount to 50 or more for two species which belong to different groups, viz. 10 — 22 (50).

In table D a, b and c (enclosure II) the correlation factors of the species within each of the three groups is represented. From these numbers the following conclusions can be drawn.
1. The positions of the species 1, 2, 3, 4, 5 and also 8 in the above groups seems to be rather uncertain. Only rarely are high correlation factors attained for these species.
2. However, since the strength of the arguments is strongly reduced with increasing time-interval, it is evident that in general the correlation factors of closely related species with long time intervals will not be so high as when the time intervals are small. That the correlation factors of 3 — 19, 3 — 22, 3 — 23, 3 — 24, 4 — 10, 4 — 11, 4 — 12, 4 — 18, 5 — 11, 5 — 12, 5 — 18, 8 — 20 and 8 — 21 are rather low and generally decrease when the time interval increases is therefore not astonishing. In any case this is not an argument by which the proposed assignment of the species no. 3, 4, 5, and 8 to the above groups becomes very questionable.
3. For species 1 and 2 the situation is however quite different. They display high correlation factors with 22 and 23, but with the probable ancestors of these species, viz. 3 and especially 14, these numbers are much lower. The situation of species 1 and 2 in stock (a) is therefore most contentious. Probably their suggested affinity with 22 and 23 is the result of a "homoplastic" development. The situation of these species in the phylogenetical tree will be discussed afterwards. The high correlation factor of 10—22 can probably be explained in the same way, since the correlation factor of 3—10 is 40 and that of 10—14 is only 36.
4. The only effect of these considerations on the original grouping of the species is that species 1 and 2 are left out of group (a).

The suggested affinities between the different groups (a), (b) and (c) are represented in table E a, b and c (enclosure II). In respect of these numbers the following conclusions are drawn.
1. The suggested affinities between group (a) and group (b) are rather high, but as a rule they remain considerably lower than they are within the groups themselves. The rather exceptional position of species 22 in this respect has already been explained above as a probable case of "homoplasy". These are strong indications that the two groups in question keep their identity relative to each other; they are clearly separate.
2. It is suggested that the cladistic distances between group (a) and group (c), and between group (b) and group (c) are very large. The identity of these two sets of groups relative to each other appears to be very high.
3. It may finally be concluded that strong indications exist that the three groups of species which have been distinguished above, viz. (a) : 3 — 14 — 19 — 22 — 23 — 24; (b) : 4 — 5 — 10 — 11 — 12 — 18; (c) : 8 — 15 — 16 — 20 — 21, have all a considerable identity and do not seem to be closely related phyogenetically.

3. CONCLUSIONS ON THE PHYLOGENY OF THE UNCINULIDAE

Fig. 80 shows a preliminary phyletic diagram which is entirely based on the correlation factors of table C. Consequently only the cladogenesis is represented, the anagenetical developments are not considered. The

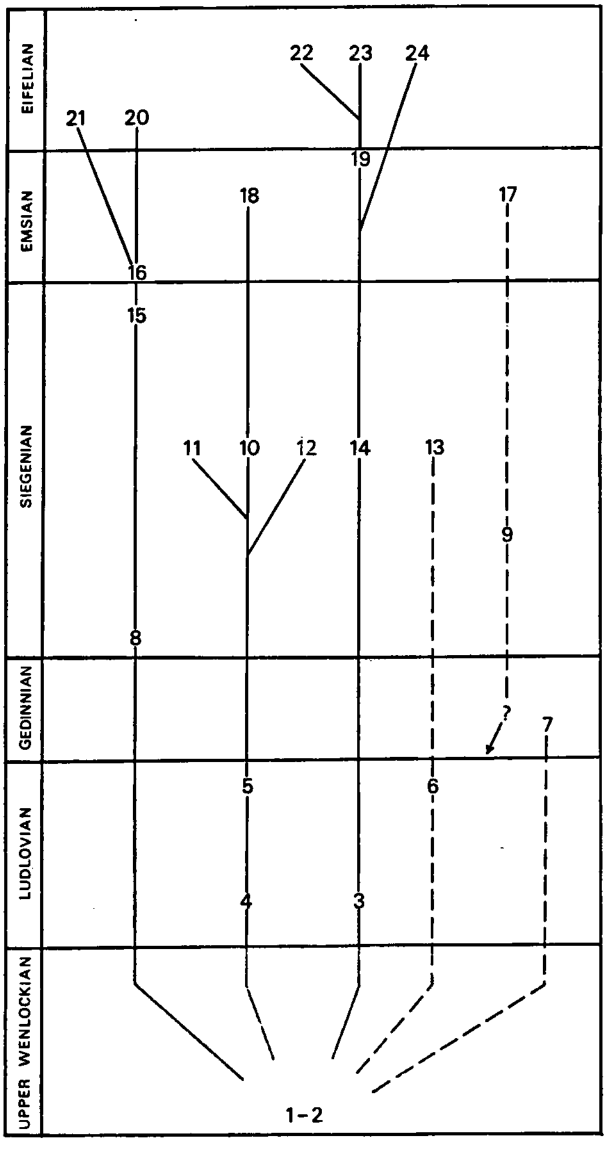

Fig. 80. Phyletic diagram of Uncinulidae.

three different groups of species which have been distinguished above are represented as three independent main lineages. The most probable positions of the species 1, 2, 6, 7, 9, 13 and 17 are also indicated. The three lineages very likely had a common origin somewhere during the Wenlockian stage. It is in fact not improbable that the species 1 and 2 were closely related to the common ancestors; they may even be the ancestors themselves. Afterwards a radiation must have taken place which gave rise inter alia to the three main lineages of the represented tree. It is well known that such a period of radiation is relatively short and may leave only a few traces in the geological record. Moreover the evolutionary change during such a period is very rapid and strong. It is evident that these incipient evolutionary trends can hardly or not be detected by means of the method which has been used in the reconstruction of this phylogenetical tree since the rates of evolution were here presupposed to be moderate to slow. This may explain the fact that the correlation factors for the relations between 1 and 2 on the one hand and the oldest representatives of the three lineages on the other are rather low.

Figure 81 represents the ultimate reconstruction of the phylogenetical tree. In stead of the consecutive numbers the names of the species are given. It appears that the three main lineages represent the following groups of genera: a. — *Hebetoechia* — *Kransia;* b. — *Eoglossinotoechia* — *Glossinulus;* c. — *Uncinulus.* The most interesting point in this conclusion is the fact that *Kransia* and *Uncinulus,* which up to now have always been considered as one single genus very likely belong to entirely different stocks. The very low correlation factors given in table E b form a strong argument in support of this conclusion. The erection of the genus *Kransia* is clearly justified.

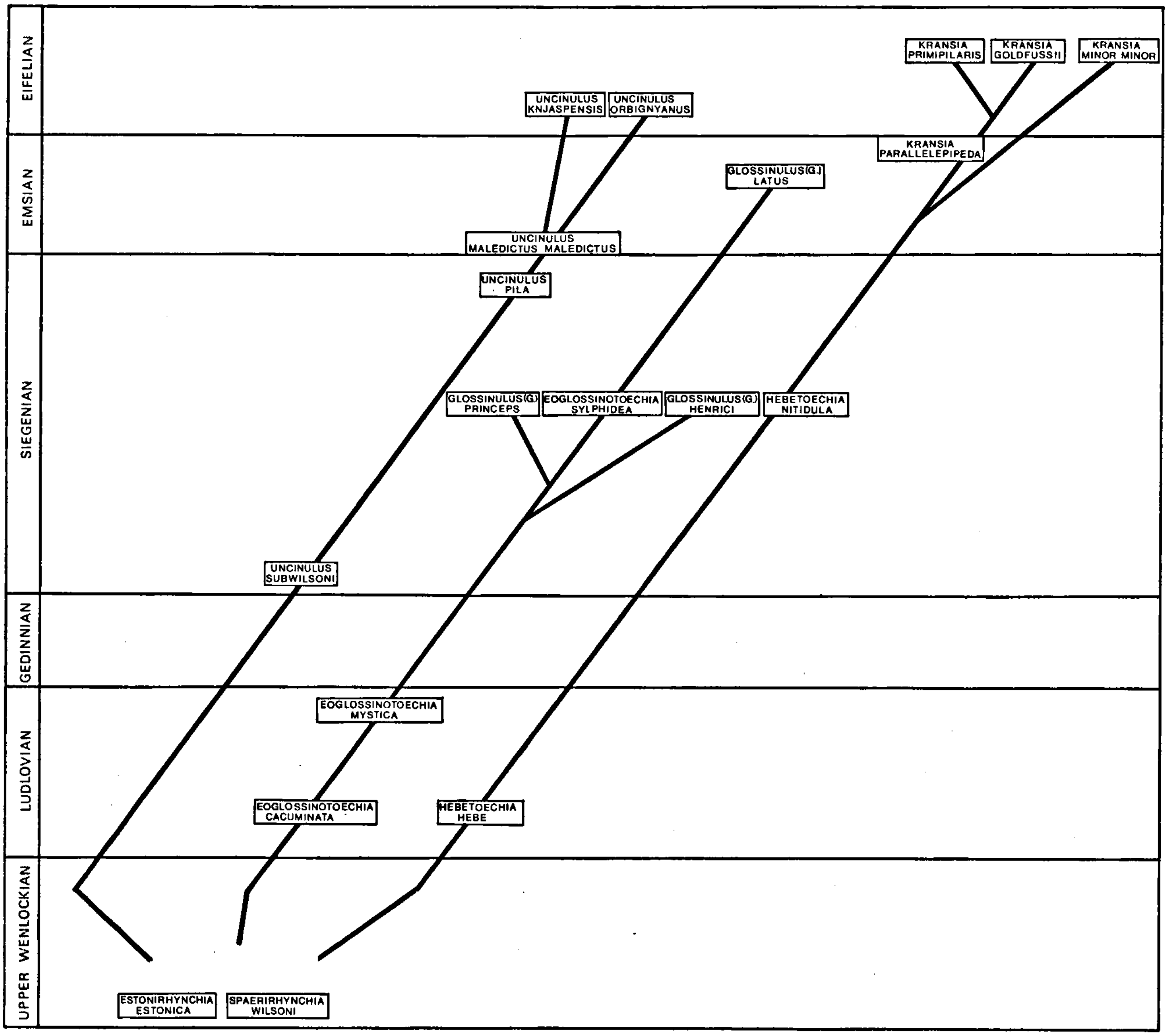

Fig. 81. Phylogenetical tree of Uncinulidae (only the three most important stocks are represented).

In fig. 81 an attempt is also made to express very roughly the anagenetical development in the three stocks. The anagenesis can be derived from the cladogenesis and the phenetic distances between the species. It has been roughly estimated from table F where for the characters no 1 — 11 and 15 the character numbers are given in the three stocks. It appears that for many characters, especially those of group (2) and group (3) a certain parallellism occurs in the three stocks. It is this parallel evolutionary development which has been expressed in fig. 81 [26].

The proposed pattern of evolution of the Uncinulidae bears a great resemblance to the evolution of the Taeniodonta as described by Patterson (1949) and later by Simpson (1955). The interpretation by Simpson of the Taeniodonta can probably also be applied to the Uncinulidae. The initial phase of radiation is then considered as quantum evolution and the subsequent parallel evolution in the three lineages as a trend evolution taking place in different adaptive zones which have undergone a parallel, steady secular change. However, at this state of our knowledge it is impossible to determine whether such an interpretation of the uncinulid phylogeny is in accordance with the facts. We have already seen in chapter III that the evolutionary development of the marginal spines can also be interpreted according to the theory of Schindewolf.

4. IMPLICATIONS FOR THE CLASSIFICATION OF THE UNCINULIDAE

According to the orthodox evolutionary taxonomists a sound classification of any coherent group of organisms should be consistent with the phylogeny of that group. For these taxonomists a dendrogram or a phylogenetical tree (i.e. phyletic diagrams in which the branching of lineages as well as the subsequent divergent evolution of daughter lines is represented) constitutes the main basis of classification. Nevertheless, many different classifications which are consistent with one phylogenetical tree are possible, as has eloquently been demonstrated by Simpson (1961). Classification is a "useful art" and the classifier is to some extent allowed to choose the classification which in his opinion is the most elegant one. This implies that no strict rules can be given for classificatory procedure.

The classifications of the Uncinulidae which have been given up to this time are rather unsatisfactory in that they are not essentially consistent with the phylogeny, but based on only very few characters. Havlíček (1961) distinguishes between two families, the Hebetoechiidae and the Uncinulidae (in this account these families are joined to form one single family Uncinulidae). According to Havlíček the main distinction between his two families consists of the absence or presence of a connectivum. It must be noted in this connection that, in contradistinction to the point of view taken in this publication, Havlíček considers the connectivum to be positively present in species where the septalium is almost completely reduced. With this criterion as a starting-point the Hebetoechiidae comprise most of the old and primitive genera, while the Uncinulidae (sensu Havlíček) generally are the later genera. There are however some unsatisfactory implications. *Glossinulus* is e.g. included in the Hebetoechiidae and *Eoglossinotoechia* and *Glossinotoechia* in the Uncinulidae. In my opinion the presence or absence of the connectivum is an insufficient reason to place such closely related genera into two separate families. Another incongruity is the fact that the very old genus *Tadschikia* is allocated to the Uncinulidae.

The leading principle in the classification of Schmidt and McLaren (1965) of the uncinulids is the development of the cardinal process. We have seen that in this character also an obvious trend-like development occurs during the evolution of the uncinulids. Consequently, here too a distinction is made between primitive forms (subfamily Hebetoechiinae) and more progressive forms (subfamily Uncinulinae). (The subfamilies Hypothyridininae and Hadrorhynchiinae of Schmidt and McLaren, which according to these authors are also included in their family Uncinulidae, are not taken into account here). This classification does not display such important incongruities as the one of Havlíček.

Havlíček as well as Schmidt and McLaren have obviously perceived the gradual change which occurs nearly simultaneously in many characters of the whole family of the Uncinulidae during their evolution, and all have tried to establish a classification in primitive

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[26] Table F shows many interesting aspects of uncinulid development. We only will draw the attention here to the development of the marginal spines (see chapter III). It appears that the evolutionary trend of this character which has been demonstrated to occur in the Uncinulidae as a whole can be traced in each of the three lineages. One can easily imagine that the marginal spines in Uncinulus (type C) have developed from those of *Sphaerirhynchia wilsoni* (type A). It is moreover interesting that neither in the lineage of *Uncinulus,* nor in the one of *Eoglossinotoechia* — *Glossinulus* has it been found that a completely rectimarginate shell was attained (type D). This only occurs in the genus *Kransia.* It must be noticed that the fact that the evolutionary trend in the marginal spines of the Uncinulidae occurs independently along at least three lineages does not influence in the least the ultimate conclusion of the third chapter, namely that no conclusive arguments have been found by which it can be decided whether this development is to be explained as an orthogenetical trend according to the ideology of Schindewolf or as a result of an adaptation-selection mechanism.

In respect of table F it must be remarked that it forms a typical example of reasoning in a circle. One of the starting-points in the composition of the evaluation tables (table B) was that the anagenesis in this group had proceeded rather slowly. By means of these tables an estimation has been made of the cladogenesis and this, in turn, has led to the preparation of table F which again roughly suggests that the anagenesis proceeded rather slowly. It must however be kept in mind that the original assumptions on the evolutionary rate are not merely speculative, especially in so far as the characters of group 2 and group 3 are concerned, since in these characters the presence of a rather slowly proceeding evolutionary trend was already demonstrated before the cladistic evaluations were made.

and progressive forms on the base of one single character. In both classifications the intention is good but the starting-point is unrealistic. Such a division should at least be based on as many characters as possible or, even better, on a phylogenetical tree. Indeed the Uncinulidae, with their striking development, are readily divided in such a way, but nevertheless any such classification has the drawback that the boundary between the subfamilies is rather arbitrary, and that species of one lineage which lie on either side of and close to the boundary line and which therefore are generally closely related, will be assigned to different subfamilies.

The preliminary phylogenetical tree which has been given above suggests that the Uncinulidae may better be classified in another way. The three lineages which were distinguished clearly display a parallel trend for many characters, but the distances which nevertheless exist between them are so obvious that there are no objections to them being considered as three different taxa of approximately the subfamily rank. Very primitive genera, such as *Sphaerirhynchia* and *Estonirhynchia,* and perhaps also *Lanceomyonia,* can then be included in a fourth taxon. The resulting taxa would constitute very homogeneous groups of genera. The obvious drawback of this principle is that often new taxa must be made for all the groups of genera which belong to other lineages than those which have been distinguished here and nevertheless must be conveyed to the Uncinulidae. This is e.g. the case for *Obturamentella* and for *Markitoechia.* Without any doubt many more of these complications will arise as the knowledge of the Uncinulidae increases.

It has been stated that the proposed phylogenetical tree is based to a large extent on speculation and that only relatively few characters and species could be considered. It would therefore be unwise to give at this stage a more official status to the preceding conclusion on the classification by introducing one or two new subfamilies. For the moment the division by Schmidt and McLaren is acceptable in broad outline although it has not been fully applied in this publication, but future developments in the research on the Uncinulidae may bring about a classification which is more consistent with the suggestions given here.

APPENDIX

KRANSIA Westbroek, n. gen.

Type species. — *Terebratula parallelepipeda* Bronn, 1837. Fig. 46, 55, 66; Pl. II, Fig. 3, Pl. III, fig. 5, Pl. IX, fig. 1, 2, 6, Pl. X fig. 3.

Derivatio nominis. — The genus is named for Th. F. Krans, Leiden.

Diagnosis. — Small to medium-sized uncinulid brachiopod. Outline pentagonal. Uniplicate. Sulcus and saddle of variable size, generally originating in the middle of the concha plana. Hinge lines reduced to almost zero. Cardinal areas not developed. Ventral beak suberect, rather short. Well developed deltidium. Foramen submesothyrid. Paries geniculatus of low to medium height. Costae varying from fine to coarse, crenulate to rather angular, originating at the beaks or in the middle of the shell; sometimes even restricted to the anterior and lateral parts of the shell. Commissure of adult specimens completely straight (apart from medium plication), without zigzag deflections. Elongated and stout marginal spines (except in *K. minor minor,* where the paries geniculatus is very low and long marginal spines cannot develop). Squama and glotta very well developed. The inwardly facing surface of the squama and the outwardly facing surface of the glotta are slanting. The elements of the shell mosaic are extremely coarse and square in outline (locally finer mosaics may occur). Thickness of inner apical structures varies from thin to very thick. Well developed septum directly supports the hinge plate; septalium is reduced to almost zero. Crura slightly divergent, rodlike, pointing anteriorly at their base and in ventral direction at their distal ends. They are provided with longitudinal ridges, and are rather flattened distally. In the dorsal septum the fibres are strongly divergent and a mediotest is developed. The fibres appear to be slightly divergent only in *Kransia minor minor.* Cardinal process well developed, provided with numerous longitudinal ridges. Lateral expansions generally occur. Dental plates developed, relatively thin, only leaving very narrow lateral apical cavities. Central apical cavity of the ventral valve is very wide. Scars of diductors in ventral valve very deep and large, delimited posteriorly by thick padlike outgrowths of secondary shell material. Adductor scars in ventral valve very small, situated medially in deep depressions between padlike outgrowths. Left and right scars are divided by myophragms. Adductor scars in dorsal valve very vague.

Discussion. — At first sight *Kransia* appears to be very similar to *Uncinulus.* There are however some significant differences: the mosaic elements in *Kransia* are very coarse and in *Uncinulus* they are very fine; a stratified or chaotic structure of the test has never been found in *Kransia;* the ventral umbo is suberect in *Kransia* and a deltidium is well developed; in *Uncinulus* the ventral umbo is strongly curved and the deltidium is very small or only incipient; the costae are finer in *Uncinulus* than in *Kransia;* the marginal spines of *Uncinulus* are of type C, in Kransia they are of type D; in *Uncinulus* the fibres of the dorsal septum are moderately divergent, in *Kransia* they are generally strongly divergent and a mediotest is developed.

Kransia seems to be closely related to *Hebetoechia.* These two generally differ in the following characters: thickness of the posterior part of the test, cardinal process and lateral expansions, structure of dorsal septum, length of hinge line, septalium, marginal spines, squama and glotta.

The following species are provisionally assigned to *Kransia: Kransia parallelepipeda, K. goldfussii, K. minor, K. primipilaris, K. signatus.*

REFERENCES

Bemmelen, J. F. van, 1882. Over den bouw der schelpen van brachiopoden en chitonen, 111 pp., 1 pl., Leiden.

Biernat, G., 1966. Middle Devonian brachiopods of the Bodzentyn Syncline (Holy Cross Mountains, Poland). Palaeontologia polonica, no. 17, 162 pp., 51 fig., 32 pl.

Binnekamp, J. G., 1965. Lower Devonian brachiopods and stratigraphy of North Palencia (Cantabrian Mountains, Spain). Leidse Geol. Med., vol. 33, 1—62, 29 fig., 11 pl.

—, and Th. F. Krans, 1965. Présence de myotest et de médiotest dans Athyris undata (Defrance, 1828). Leidse Geol. Med., vol. 33, 319—321, 2 fig., 2 pl.

Blochman, F., 1908. Zur Systematik und geographischen Verbreitung der Brachiopoden. Zeitschr. Wiss. Zool., vol. 90, 596—644, 5 pl.

Carpenter, W., 1843. Report on the microscopic structure of shells. Brit. Association Report.

—, 1855. On the intimate structure of the shells of Brachiopoda. Ch. II in T. Davidson, British fossil Brachiopoda. Palaeont. Soc., I, 22—40.

Cloud, P. E., 1942. Terebratuloid Brachiopoda of the Silurian and Devonian. Geol. Soc. Amer., Spec. Paper 38, xi + 182 p., pl. 1—26.

Drot, J., 1964. Rhynchonelloidea et Spiriferoidea siluro-dévoniens du Maroc pré-saharien. Notes et Mém. Serv. géol. Maroc, vol. 178, 286 pp., 92 fig., 1 map, 2 tables, 24 pl.

—, and P. Westbroek, 1966. Iberirhynchia santaluciensis, nouveau. Rhynchonellacea du Dévonien de León (Espagne). Leidse Geol. Med., vol. 38, 165—172, 2 fig., 1 pl.

Friend, P. F. and M. R. House, 1964. The Devonian period. In: The Phanerozoic time-scale, symposium. Quart. Journ. Geol. Soc. London, vol. 120s, 233—236, 1 table, 1 fig.

Havlíček, V., 1961. Rhynchonelloidea des böhmischen älteren Paläozoikums (Brachiopoda). Rozpr. Ústřed. úst. geol., Prague, vol. 27, 207 p., 87 fig., 27 pl.

King, W., 1867. On the histology of the test of the class Palliobranchiata. Trans. Royal Irish Acad., vol. XXIV.

Leidhold, C., 1920 (1921). Beitrag zur genaueren Kenntniss und Systematik einiger Rhynchonelliden des reichslandischen Jura. N.Jb. Min. Geol. Pal., vol. 44, 343—368, 3 tables, 1 fig.

Krans, Th. F., 1965. Études morphologiques de quelques spirifères dévoniens de la Chaîne Cantabrique (Espagne). Leidse Geol. Med., vol. 33, 74—148, 71 fig., 16 pl.

Mayr, E., 1965. Numerical phenetics and taxonomic theory. Systematic Zoology, vol. 14, no. 2, 73—97, 3 fig.

Muir-Wood, H. M., 1934. On the internal structure of some Mesosoic Brachiopoda. Philos. Trans. Royal Soc. London, ser. B., v. 223, 511—567, pl. 62—63.

Rudwick, M. J. S., 1959. The growth and form of brachiopod shells. Geol. Mag., vol. 96, 1—24, 14 fig.

—, 1964. The function of zigzag deflexions in the commissures of fossil brachiopods. Palaeontology, vol. 7, 135—171, 14 fig., 9 pl.

—, 1964a. The inference of function from structure in fossils. Brit. Journ. Phil. Sc., vol. 15, p. 27—41.

—, 1965. Sensory spines in the Jurassic brachiopod *Acanthothiris.* Palaeontology, vol. 8, pt. 4, 604—617, 3 fig., 4 pl.

—, 1965a. Ecology and paleoecology. In: R. C. Moore, Treatise on invertebrate paleontology, H., Brachiopoda, vol. 1, H199—H214.

Schindewolf, 1950. Grundfragen der Paläontologie. Stuttgart, Schweizerbart.

Schmidt, Herta, 1937. Zur Morphogenie der Rhynchonelliden. Senckenbergiana, vol. 19, 22—60, 56 fig.

—, 1954. *Spaerirhynchia (Estonirhynchia) estonica* n. subgen., n. sp. Senckenbergiana lethaea, 35, 235—245.

—, and McLaren, D. J., 1965. Palaeozoic Rhynchonellacea. In: R. C. Moore, Treatise on invertebrate paleontology, H. Brachiopoda, vol. 2, H552—H597.

Schumann, D., 1965. Rhynchonelloidea aus dem Devon des Kantabrischen Gebirges (Nordspanien). N.Jb. Geol. Pal. Abh., vol. 123, part 1, 41—104, 24 fig., 3 pl., 11 tab.

Simpson, G. G., 1955. The major features of evolution. Columbia University Press, New York, 2nd edition, 434 pp.

—, 1961. Principles of animal taxonomy. Columbia University Press, New York; Oxford University Press, London, 247 pp.

Sokal, R. R. and P. H. A. Sneath, 1963. Principles of numerical taxonomy. Freeman & Co., San Francisco and London, 359 pp.

Strachan, I., 1964. The Silurian period. In: The Phanerozoic time-scale, symposium. Quart. Journ. Geol. Soc. London, vol. 120s, 233—236, 1 table, 1 fig.

Vandercammen, A., 1959. Essai d'études statistiques des Cyrtospirifères du Frasnien de la Belgique. Mém. Inst. roy. Sci. nat. Belg., vol. 145.

Westbroek, P., 1964. Systématique et importance stratigraphique des Rhynchonelles du Calcaire de Crémenes (Dévonien supérieur, province de León, Espagne). Leidse Geol. Med., vol. 30, 243—252, 2 pl.

Williams, A., 1956. The calcareous shell of the Brachiopoda and its importance to their classification. Cambridge Philos. Soc., Biol. Reviews, vol. 31, 243—287, 8 fig.

—, 1966. Growth and structure of the shell of living articulate brachiopods. Nature, vol. 211, no. 5054, 1146—1148, 6 fig.

— and A. J. Rowell, 1965. Brachiopod anatomy, and Morphology. In: Treatise on invertebrate paleontology, part H, Brachiopoda, vol. 1, H7—H155.