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The structure of the shell of *Patella crenata* connected with suggestions to the classification and evolution of the Archaeogastropoda.

by Klaus Bandel and
Werner Geldmacher †

with 15 Plates and 9 Figures

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Address: Prof. Klaus Bandel, Geologisch-Paläontologisches Institut, Universität Hamburg, Bundesstraße 55, 20146 Hamburg.

Abstract

Aragonitic crossed lamellar structure is found only in molluscan shells and not among other invertebrates. The docoglossan archaeogastropod *Patella* in addition has a unique crossed lamellar structure the Docoglossa from other Archaeogastropoda. Both types of crossed lamellar structure in the same shell of *Patella crenata* are described in detail. In the diagenetically altered fossil shells both structural types are difficult to distinguish from each other. The shell structure of modern and fossil archaeogastropods is discussed and connected with the morphology of the shell. An inner nacreous layer is commonly found connected to an outer complex crossed lamellar layer that resembles the crossed composed of calcite. It distinguishes, but is not identical with it. After diagenesis this outer layer can resemble a true crossed lamellar layer. A coherent place in the taxonomic system is presented for the Archaeogastropoda which is based mainly on features of the ontogeny of the shell and can also be detected on a fossil. Archaeogastropod evolution began latest during the Ordovician. From that time onward their development occurred indepedently from the members of the other still existing subclasses Neritimorpha, Caenogastropoda and Heterostropha. Due to the absence of a larval shell in the archaeogastropod shells provide less information than in the other three subclasses of the Gastropoda, and tracing of lineages within the subclass is difficult. Here shell structure data are helpful. Nacre and calcitic crossed lamellar structure are only found in some archaeogastropods among the Gastropoda. The classification available from the text books is not satifactory especially in regard to the numerous fossils. Thus morphogroups are introduced and characterized which are thought to be more helpfull in tracing the course of evolution than traditional taxa which often obscure relations more than reveal them.

Introduction

The shell of *Patella* is very special among gastropods in having similar biostructures of the shell in calcitic and aragonitic modification of the calcium-carbonate. Not many gastropods have both modifications in their shell, and those having calcite in the outer layer and aragonite in the inner layer usually demonstrate rather different structures in both layer. The calcitic outer layer is also found in many Neritimorpha, but it differs in structure from that of the Docoglossa and from that of the inner crossed lamellar aragonitic layer. Among the Vetigastropoda calcite may form a prismatic or spherulitic prismatic layer underlain by aragonitic nacre, as for example in *Cittarium pica* (ERBEN, 1971). The presence of a calcitic crossed lamellar structure in *Patella* is also reason to discuss the occurrence of crossed lamellar structure and nacreous structure found within a single shell. BANDEL (1990) noted that crossed lamellar structure and nacreous structure are not to be found together within a single shell of a living gastropod, which was confirmed by HEDEGAARD (1990) who also studied numerous shells of modern Archaeogastropoda and Neritimorpha. In contrast *Bembexia* from the Devonian of New York seems to have both structural types within one and the same shell CARTER & HALL (1991).

The taxon Archaeogastropoda THIELE, 1925 orignally included the subgroups Docoglossa, Cocculiniformia, Trochoidea, and Zeugobranchia (= Vetigastropoda), and Neritimorpha. HICKMAN (1988) restricted this taxon to basically the Trochoidea and Zeugobranchia and, thus, the Vetigastropoda excluding not only the Neritimorpha, but also the Seguenzioidea, Cocculiniformia and Docoglossa (=Patellogastropoda). HASZPRUNAR (1993) in contrast includes in addition to the groups of THIELE, 1925 the Architaenioglossa (Cyclophoroidea and Ampullarioidea) in the Archaeogastropoda. LEHMANN (1992) suggested that Ampullariidae have reached the caenogastropod level concerning shell formation during the embryological development. BANDEL (1982) demonstrated that the neritimorph condition especially regarding the formation of the early ontogenetic shell is unique among Gastropoda. According to HASZPRUNAR (1988, 1993) and SALVINI-PLAWEN & HASZPRUNAR (1987) the only diagnostic character to the Archaeogastropoda including Neritimorpha and Architaenioglossa is a streptoneurous and hypoarthroid nervous system present at least on the left side. All other characters that can be assembled are only present in some but not all of the Archaeogastropoda. In this scenario the ontogeny of the Archaeogastropoda as presented by BANDEL (1982) can provide a more coherent classification that can also be adapted to include fossil species. As stated by HICKMAN (1988) the actual course of gastropod evolution is resolvable only through the fossil record, which requires effords to develop additional shell characters. Such characters will be presented in this study.

1. Outer shell morphology of *Patella crenata*

The shell of *Patella crenata* appears flatly convex in frontal and lateral view. Where both flanks meet, the apex is usually corroded. Such individuals living on the rocky shore with strong surf have more highly shaped shells than those living in more quiet environment which have a lower shell. Radially arranged ribs form the ornament. Usually a prominent rib is accompanied by two less prominent ones, and the shell margin reflects this in its undulating outline of stronger and weaker folds. An average of 26 prominent and 42 lesser ribs may be found with strong variations in either direction with 17 to 32 strong ribs and 15 to 64 weaker ones. When the number of less prominent ribs is divided by the number of prominent ribs the result should theoretically be 2, but actually is near 1.5. This difference reflects the lower number of lesser ribs near the head portion of the shell. The secondary maximum of 2.5 in figure 3 reflects those shells that have two pairs of minor ribs that accompany each prominent rib. Usually the measured shells from Fuerteventura from calmer living environment have more main and minor ribs and thus a denser ornament than those that have grown in more turbulent water. Here ribs are fewer, but their size is more prominent. *Patella crenata* from Fuerteventura has a different average ornament than *Patella crenata* from Teneriffa (Puerto de la Cruz) and Lanzarote (Arrecife) where ribbing is finer and ribs lie closer to each other. In contrast individuals of this species from Islas Desertas (Madeira) have fewer and coarser ribs.

Minor ribs may be produced into short gutter like processes forming spines. The shell margin is wavy reflecting the end of main and minor ribs on the apertural lip. The outside near the margin is the only place where a thin brown periostracum is preserved, while further back is usually corroded and worn off. The shell outside has been settled with different of calcareous and boring algae and cyanobacteria (Pl.15, figs.1-7). Common are overgrowths by balanids, especially on those individuals that live in the surf zone. More strongly ornamented shells of *Patella aspera* are covered predominantly by algae while more smooth forms like *Patella baudonii* and *P. crenata* usually carry balanids.

2. The inner shell surface of *Patella crenata.*

On the inner surface several layers are differentiated from each other by their luster, color and shape. The layer closest to the margin is composed of the outer calcitic crossed lamellar structure and represents the largest portion of the shell. It has shiny luster and light to dark bluish iridescent coloration. The concentric lamellae of the first order are visible, and this layer is continuous into the outer edge of the shell margin beginning right below the thin periostracum that is present only here (Fig. 1).

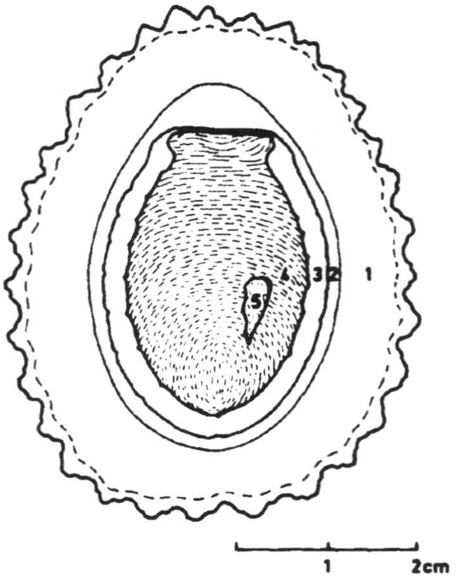


Figure 1: Sketch of the shell interior of *Patella crenata* with the different growth zones indicated and the head portion above. 1: Outer calcitic crossed lamellar layer, 2: Spherulitic myostracum. 3: Crossed lamellar myostracum. 4: Aragonitic hypostracum. 5: Calcitic hypstracum.

Toward the centre of the inner shell surface a dark, grayish-blue band follows which represents the prismatic myostracum. Only here the soft body of the limpet was attached to its shell forming a horse-shoe-shaped scar that is thickened at both ends representing the area above the head. Frontal to the open end of the horse-shoe-scar with up to 4 mm width the frontal lobe is thin and has less than 1 mm width. The prismatic layer of the myostracum forms no continuous band, but is featured into a row of scars with variable number. When this number is counted among different individuals a maximum of 14 is found. Thus, the ring muscle connecting shell and animal with each other was organized into about 7 bundles of muscle fibres in mirror immage arrangement on each side. A number of individuals had 16 and 18 muscle scars above the head-foot, thus, more muscle bundles on each side, that is 8 or 9 respectively. The prismatic myostracum (layer 3, Fig.2) is surrounded by a light grey ring that becomes wider in the frontal area and represents the sphaerolithic myostracum. The muscle "scar" of the prismatic myostracum actually is higher than surrounding outer layer and sphaerolithic myostracum. The central portion of the inner shell of *Patella* is covered by a porcellaneous grey to yellow shiny layer, the so called hypostracum or callus and spatula. In the posterior shell portion the hypostracal layer lies about parallel to the outer shell margin. In the frontal region above the head it forms two sinusses. Within the aragonitic hypostracal layers fully grown shells have more or less extensive zones with a vitreous luster and yellow to brown coloration (Figs. 1,2). These are not organized according to the symmetry of the shell and consist of calcite (calcitic hypostracum).

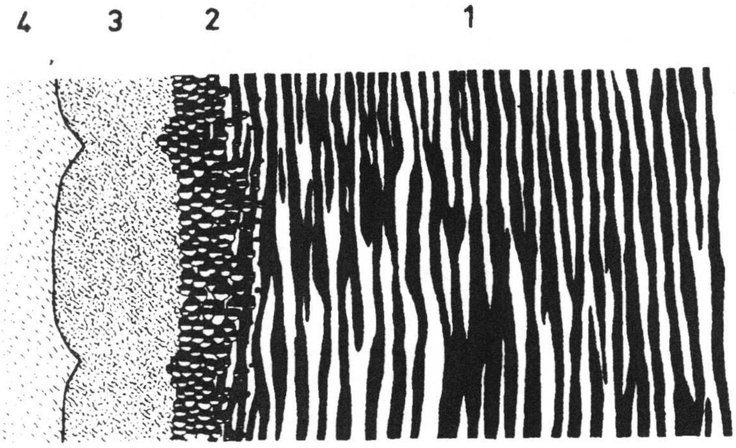


Figure 2: Sketch of the inner surface of a *Patella crenata* shell with the calcitic crossed lamellar layer (1) myostracal layers (1,2) and hypostracum (4) seen with light coming from the right.

3. Structure of the shell

3.1 Outer calcitic crossed lamellar layer

The layer between periostracum on the outside and myostracum formed at the tissue shell attachment zone consists only of calcite as was verified by Xray diffraction analysis. Even shell repair in this region is purely calcitic. The content of cation admixtures is shown in chapter 4. The structure in radial section vertical to shell surface consists of piles of thin leaves more or less parallel to each other become visible (Pl.1, Fig.2). These piles are oriented concentrically and according to the terminology introduced by BOGGILD (1930) are called the lamellae of the first order. Within these lamellae of the first order thin sheets are seen the lamellae of the second order (Pl.1, Figs.3-6).

Orientation of the lamellae of the first order is such that they form an angle of about 150° with the interior of the shell. Lamellae of the second order in contrast form an angle of about 15° with the inner shell surface. The heigth of the lamella of the first order represents shell thickness and reaches up to 3 mm. Its width, which is also the width of the lamellae of the second order is about 35 micron while its length comes to several mm when measured in the inner side of the shell. Near the outside of the shell lamellae of the first order are commonly bifurcate (Pl.1, Fig.2). But such splitting of lamellae is also found within the shell (Pl.1, Fig.4,5). With magnification of 8000 times it becomes evident that lamellae of the second order are also parallel to each other forming narrow and elongated crystallites (Pl.2, Figs.2-6) which will be termed lamellae of the third order.

Elements of the third order are about 0.6 micron wide, about 0.2 micron high and as long as the lamellae of the second order to which they belong. They usually lie side by side in a simple arrangement. But they may also be arranged like tiles in a corrugated roof pattern (Pl.2, Figs.3-6). This structure is transected by fine growth increments (Pl.2, Fig.6). Lamellae of the third order in their outcrop on the inner shell surface form a radially oriented zig-zag pattern with an angle of 119° in the corners. All variations of smooth and corrugated lamellae of the second order can appear within the same shell.

Lamellae of the second order within neighbouring lamellae of the first order form an angle of about 150° with each other. This arrangement is seen on the shell interior and the larger part of the shell proper, but not just below shell surface and at the marginal shell edge. Here the lamellae of the second order without interuption twist into direction parallel to the outer surface (Fig.3, Pl.1, Fig. 2). MAC CLINTOCK (1967) considered this outermost layer to represent an independent layer which he termed radial crossed foliated. Thin sections oriented in inclined position to shell surface demonstrate the curving lamellae of the second order and, thus, the decrease of the angle between lamellae of the first order until there is no difference in orientation and single lamellae merge with each other and lose their distinction.

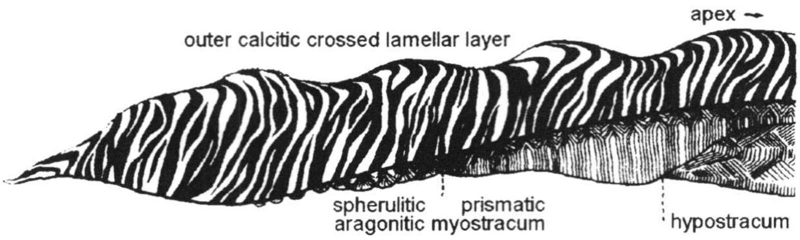


Figure 3: Sketch of a longitudinal section through the shell of *Patella crenata* with the outer calcitic crossed lamellar layer at the left and the layers of the myostracum and hyostracum at the lower left.

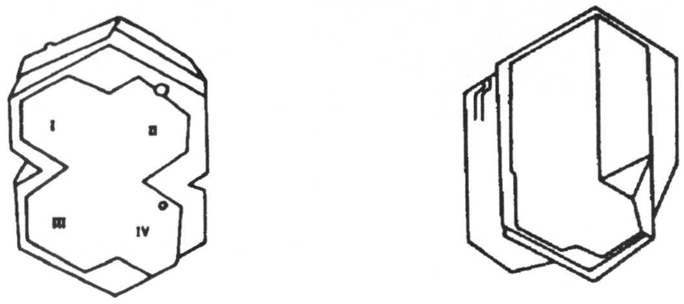
On the surface of the shell collabral growth lines are visible which bear rod-like elements forming a fish-bone pattern (Pl.1, Fig.3). Width of growth lines agrees with width of the lamellae of the first order and rod length agrees with width of the lamellae of the second order (Pl.1, Figs.3,5).

Thus, concentric growth lines represent lamellae of the first order, and the sculpture of the growth lines consists of the heads of the lamellae of the second order. These dip into the shell interior in the same direction which from apex seen toward the shell margin is to the left. Where the outermost layer with the fish-bone pattern is corroded concentric growth lines are also not visible, but lamellae of the second order that appear oriented parallel to the outer surface. Thus, the surface dip twist into surface parallel orientation before becoming arranged into the sheets with lamellae of the second order inclined to each other by 150°.

Orientation of the lamellae of the first order depends on the shape of the shell edge. Thus, also the direction of the endpoints of lamellae of the second order (Pl. 1, Fig.3) rely on the relief of the shell edge. Where morphology is strong, the heads of the lamellae of the second order form more acute angle with the concentric growth lines than where morphology of the shell edge is relatively smooth.

After secretion of the first mineral layer within and below the organic layer of the periostracum shell is thickened further away from the margin. In the growing calcitic crossed lamellar layer particles like grains of sand may become cemented. This agglutination and inclusion creates only minute confusion of the structural pattern. Lamellae of the second order coat single or groups of grains bending around them (Pl.3, Figs. 3,5, Pl.4, Fig.1). Lumina present between inclusion and crystallites of the shell are secondarily closed by prismatic crystallites of needle or columnar shape with pseudohexagonal outline (Pl.4, Figs.3,4). Usually crystallites are twinned (Figs.4,5). The longitudinal axis of the crystallites is arranged vertically on the walls of the small cavity forming cement coats rather like those seen on the inclosed grain as well (Pl.3, Figs.4,6; Pl.4, Figs.1,2). In contrast to the shell-layer these larger crystallites (about 40 micron in maximum diameter) consist of aragonite. Inclusions are common in those parts of the shell that have formed in the area of the free mantle. Within the muscle attachment area inclusions are rare, and behind this zone they are exceptionally present (Pl.3, Fig.2, Pl.4, Fig. 5). This is quite logical since grains entered the room behind tissue shell attachment only very rarely.

The aragonitic crystallites found within the small cavities of the *Patella* shell have grown on calcitic surfaces as well as on aragonitic ones. For example the calcitic spine of a sea urchin (Pl.3, Figs.5,6) is coated as well as the calcitic roofs of the cavity (Pl.4, Figs.1,2). Similar growths have been noted to occur in cavities within the shell, as for example apical cavities in a gastropod shell, hollow spines, hollow keels in ammonites, blisters in the bivalve shell, where rapid deposition of carbonate shell had lost contact to the epithelium of the mantle (BANDEL & HEMLEBEN 1975). In such portions of the pallial liquid that had lost contact to the actual animal biocrystallite formation is no longer controlled and growth is more of an anorganic type, here like a fully marine argagonitic crystal coat as forms in cement crusts during diagenesis. In contrast to the later though, the type of material on which aragonite crystals grow are of no influence, probably due to the mucus that must have been present and coated surfaces.



Figures 4 & 5: Aragonitic crystallite of the inner shell cement with pseudohexagonal shape of twinned crystals.

3.2 Growth of the outer calcitic crossed lamellar layer

At shell edge lamellae of the first and second order form that bend during further shell growth in such a way that they are arranged vertically to the surface and oriented in concentric mode (Fig.3). The number of lamellae of the first order decreases from shell surface to shell interior, reflecting shell curvature ending in the apex. Width of lamellae of the first and the second order differs with ontogeny. Lamellae of the second order in juvenile shells lies near 22 micron, while fully grown individuals have 35 micron thick ones. MAC CLINTOCK (1967) found in the very large *Patella mexicana* 500 to 980 micron wide lamellae. The smallest componente of the structure, the elements of the third order, are always of the same size, measuring 0.6 micron in width and 0.12 to 0.15 micron in height in the case of *Patella crenata*. Increase in width of lamellae of the first and second order is accomplished by more an more elements of the third order added to them. Lamellae of the second order with corrugated pattern show this very well. Here are along the undulations more or less elements added to the structure, making it thinner or thicker (Pl.2, Figs.4,6). Growing lamellae of the second order seen on the inner side of the shell are not homogeneous. Here every element of the third order has a rhombic rod end and grows by rythmic additions (Pl.2, Figs.3,4).

3. 3 Muscle scar deposits

A circular band suceeds the outer calcitic crossed lamellar layer in inward direction seen on the inner shell side. Here the mantle is attached to the shell just below the onset of the ring-shaped ribbon of the retractor muscle (Figs.1,2,3). This so called myostracum consists exclusively of aragonite as was checked by X-ray diffrectometer analysis. Contents of trace elements in this thin layer was not determined, but the composition of the proteins have been analysed as is stated later on in the text.

Within a shell the vertical thickness of the myostracum is variable. Fully grown individuals have a 90 to 230 micron thick layer, in juvenile shells this layer may only be as thin as 4 micron and even less. Large shells with 7 cm length in radial section revealed up to three concentrically oriented zones of larger thickness of the myostracal layer. Most probably these zones reflect stunting in growth and reaction on changes of feeding and weather conditions during the course of a year. The thicker portions of the myostracal layer represent shell growth during winter time.

The myostracal layers of the fully grown shell can be subdivided in two structurally differentiated portions. The first is that layer that succeeds the calcitic crossed lamellar layer on the outside and consists of spherulite sectors, and the second develops from it and is composed of a prismatic structure (Pl.5, Figs.2,3). The layer of spherulite sectors consists of fine needles arranged in inclined fassion around a joint axis. Needle-like biocrystallites with the same angle of inclination are united within cones with circular or elliptical base (Pl.6, Figs.1,3). The common axis of these spherulite sectors is oriented vertically to the shell surface, and their open base points to the inner shell surface. In thin section appears a Brewster cross when Nicols are crossed (Pl.3, Fig.2, Pl.5, Figs,5,6). Fully grown spherulite sectors are about 20 micron high, and the angle of the cone opening is about 108°. The apex of a spherulite sector appears to be ancored on the outer shell layer (Pl.5, Fig.2). But this is not the case. The begin of a spherulite sector rests immediately on the crystallite heads of the lamellae of the second order of the calcits crossed lamellar layer. They consist of round and flattened discs rich with organic material (Pl.7, Figs.1-4). With growth the disc-like shape changes to aggregates of discs with pseuohexagonal shape (Pl.7, Fig.3). Similar crystallites were described by ERBEN (1972, Pl.3, Fig.4) in a transgressing shell layer of the bivalve *Isognomon epihippum*. Later discs and aggregates unite to form a continuous layer, which in the case of *Isognomon* is a nacreous layer, while it is a spherulite sector layer in *Patella*.

On top of the spherulite sector layer a prismatic layer is found. It appears by a change of growth of the inclined needle-like crystallites of the spherulitic layer into vertical growth without an interuption in growth (Pl.5, Fig.3). Needles near to the spherulite sectors have about the same diameter as the needles of the later (Pl. 5, Figs.3,4, Pl.7, Fig.5). With growth these prisms increase their diameter, and their acute triangular shape changes into more massive columnar, rectangular to almost quadrate shape (Pl.6, Figs.5,6). Etched sections vertical to the long axis of the prisms indicate that the transition from spherulitic to prismatic growth is gradational (Pl.6, Figs.4,5). Prisms at first form bundles with the same diameter as the sectors of the spherulite sector layer and only later the radial arrangement disappears. Prisms then consist of hypidiomorph to xenomorph single crystals.

In the juvenile shell the myostracal layer differs from that found in the adult *Patella crenata*. The attachment of tissue to shell is here characterized by a thin layer of concentrically oriented aragonitc crossed lamellar structure (Pl.8, Figs.1,2,5,6). This layer is between 18 and 190 micron thick, with an average of 65 micron. Lamellae of the first order bifurcate commonly with branches pointing towards the outer shell surface (Pl.8, Fig.3). Number of lamellae of the first order decrease toward the shell interior. Lamellae of the first order are composed of sheet-like lamellae of the second order which are oriented in alternate directions in neigboring lamellae (Pl.8, Fig.3). Lamellae of the third order consist of fibre-like biocrystallites that are oriented parallel to the margins of lamellae of the second order. The angle formed by lamellae of the second order in neigbouring lamellae of the first order is about 143°. Width of lamellae of the first order is variable and changes between 1.6 and 21 micron.

The juvenile myostracal layer is transected by fibrillous organic material which in the etched section is clearly seen. These layers follow growth increments and are continuous from the calcitic outer crossed lamellar layer into this myostracal aragonitic crossed lamellar layer (Pl.8, Fig.4). Organic fibres prefer vertical orientation to the borderlines of lamellae of the first order (Pl.14, Figs.3,4). When shells have reached a size of about 1 cm growth of a prismatic aragonitic layer is initiated within the myostracal area. The aragonitic crossed lamellar layer here slowly disappears in direction of the shell edge (Pl.8, Fig.1) and its place is taken by the spherulite sector layer. The prismatic layer covering the crossed lamellar myostracal layer increases in length in this transition (Pl.7, Fig.5; Pl.8, Figs.5,6). This transition is well developed in a 450 micron long radial section through the shell of *Patella guttata* (Fig. 1).

Transitions from crossed lamellar into spherulite sector structure connected to intercalated prismatic layers have also been noted in the shell of the gastropod *Buccinum* (BANDEL 1975). Here acicular structural units of the third order radiate toward the depositional surface from a longitudinal column axis. Spherulite sectors also grade into other structural types like nacre (BANDEL 1977a) or helical structure (BANDEL 1977b). In the transition from crossed lamellar stucture to spherulitic prismatic structure the first order lamellae first pass into composite prisms and the latter then become arranged into concentrically constructed spherulitic prisms (BANDEL 1979a, 1990).

3.4 The inner aragonitic crossed lamellar structure

The apex of the limpet-shell interior of the attachment between tissue and shell is covered by a predominantly aragonitic hypostracum or callus. Calcitic deposits may also be found here in places (Fig.6). Admixtures of other elements have been measured as well as proteins contained within the shell here. Viewed with the binocular microscope fine lines are visible that feature the hypostracal layers. These lines in the area of the head are oriented almost radially to vertical to the plane of symmetry of the shell, and in the posterior part of the shell they orient themselves in concentric directions (Figs.1,2,3). Section and fracture vertical to shell surface reveal that the fine lines represent lamellae of the first order (Pl.9, Figs.1-4). Lamellae of the second order show two features of which one runs parallél to the margins and represents the lamellae of the third order with 0.24 micron width (Pl.9 Figs.4,5), and the other represent dark perpendicular stripes oriented parallel to the inner shell surface and representing growth increments (Pl.9, Figs.4,5). The later are caused by an increased amount ot organic material contained within the mineral shell, and they have a distance of about 0.9 to 2.8 micron from each other. Lamellae of the third order in neigbouring lamellae of the first order form an angle of about 109° with each other (Fig.7). Thus, they form an angle of about 35° with the surface of the shell interior (Pl.10, Figs.1,3,4).

A comparison of the aragonitic with the calcitic crossed lamellar structure demonstrates two major differences besides crystallographic modifications of the calcium-carbonate. The angle formed between neigbouring lamellae of the second order is about 109° and, thus, about rectangular, that of the calcitic crossed lamellar layer follows rhomboidal pattern and is about 149°. In addition lamellae of the first order in the aragonitic crossed lamellar structure are split and bifurcating much more commonly than in the calcitic crossed lamellar structure (Pl.10, Fig.5; Pl.1, Figs.4,5). In *Patella* the aragonitic crossed lamellar layers often contain prismatic intercalations with a high content of organic material. This had also been noted by MAC CLINTOCK (1967, p.49, Fig.61) and also its absense in the calcitic crossed lamellar structure. The diameter of the prisms is usually around 0.27 micron. Length of prisms and, thus, thickness of a prismatic layer varies. In juvenile individuals an average of 2.2 micron was measured while fully grown individuals have about 6 micron thick interlayers.

Transition from the aragonitic crossed lamellar stucture into the prismatic structure is without break, and elements of the third order are continuous into the needles of the prismatic layer forming an angle of 129° with each other (Pl.10, Fig.5). In contrast to the organic components of the prismatic layer of the mystracal deposits those of the prismatic layers in the aragonitic crossed lamellar structure dissove with dissolution of the mineral part. This is an indication for a higher content of organic material and a different composition of the material in the prismatic layer of the myostracal deposits. Here the fibres of the mantle attachment to the shell have become intergrown with aragonitic crystallites. The number of organic layers in the callus of the hypostral deposits in older individuals is higher than in younger ones. Fully grown individuals had more than 30 prismatic intercalations of the hypostracal deposits. Thus, it is likely that the layers rich in organic material are periodically deposited as was also noted in the myostracal layers.

3.5 The calcitic hypostracal layers.

The shell of the adult animal commonly has calcitic layers deposited in the hypostracal area of callus deposits (Figs.1,6). Calcitic areas have commonly irregular outline and may cover an area of 2x3 cm with a 0.5 cm thick deposit. Sections vertical to the inner surface of the shell show dark, densely striped bodies that are of rotation symmetrical or mirror symmetrical outline (Pl.11, Figs.1,2). As in the aragonitic crossed lamellar deposits right next to them these calcitic layer contain prismatic intercalations (Pl.11, Figs.1,2,5,6). MAC CLINTOCK (1967.p.35) considered such an intercalation with irregular outline as lamellae of the first order which would than be oriented almost parallel to the surface of the shell interior. In it lamellae of the second order are almost parallel to inner shell surface and are either flat (Pl.11, Figs.2,3) or of undulating surface (Pl.11, Fig.4). Plane lamellae of the second order are the more common ones, and undulation is caused by alternating inclination of elements of the third order. Elements of the second and third order resemble closely those of the outer calcitic crossed lamellar layer. The width of elements of the third order has an average of 0.64 micron also resembling those of the outer shell layer that have an average of 0.61 micron (Pl.11, Fig.4). THIEM (1917) has noted the mixture or aragonitic and calcitic shell deposits in the hypostracum of *Scurria* as well.

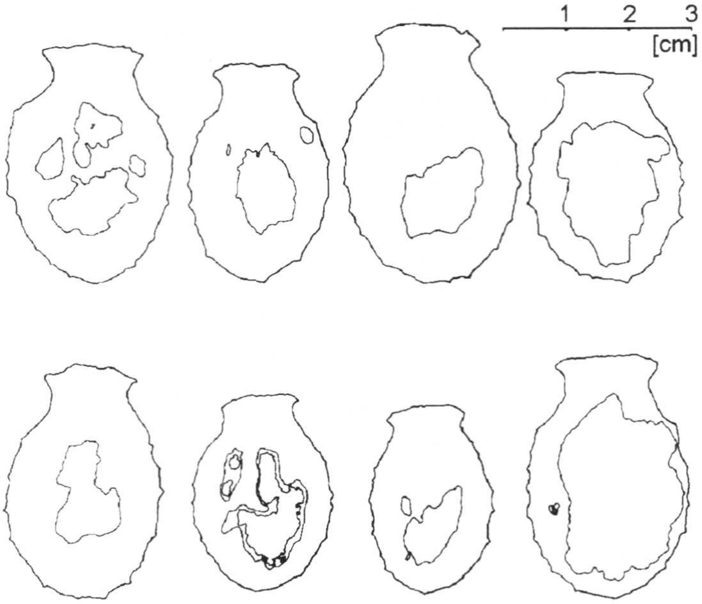


Figure 6: The hyostracal plane of the shell interior of different individuals of *Patella crenata* with extent of calcitic hypostracum indicated.

The calcitic portions of the interior callus are not homogeneous in construction, but show spindle shaped or plait-like inclusions (Pl.12, Figs.1,2). The organic matrix of growth increments continues across the borders between prismatic layers and these inclusions without interruption. Etched sections reveal this layering of organic matter vertical to the plait or spindle-cones and, thus, parallel to growth surface as light and dark layering (Pl.12, Figs.1,2). These inclusions are composed of fine needle-like biocrystallites in spherulite sector arrangement (Pl.12, Fig.2). In sections vertical to the spherulite sectors viewed with light microscopy crossed Nicols bring out Brewster's crosses (Pl.12, Fig.3) which confirm the spherulitic construction of these bodies. Their morphology shows up in fracture of the shell as well (Pl.12, Figs.4,5, Pl.13, Figs.1,5). Apical angle of the spherulite cone is 70° to 105°. The dark horizontal layering within cones reflects periodical increase in organic content during the growth of these structures (Pl.13, Fig. 6). In the REM picture of etched surfaces the layers with more organic material appear lighter than those layers having more mineral material (Pl.12, Fig. 2). Organic sheets are not seen when the shell is etched, but the organic material is distributed without forming concrete layers within the mineral shell.

MAC CLINTOCK (1967, p.32,33) called these structures "complex crossed structures". Accordingly the columnar or plait-like inclusions should be lamellae of the first order. A single cone-like sheet (Pl.12, Fig.4,5) would, thus, represent a lamellae of the second order which is composed of elements of the third order forming a radial umbrella-like structure (Pl.12, Fig.2, Pl.13, Fig.6). The columnar inclusions could well represent aragonitic structures as was indicated by X-ray analysis. This is also indicated by the size of the elements of the third order (0.2-0.4 micron) which are close to that of the aragonitic crossed lamellar structure of the callus. Here lamellae of the third order are 0.22 to 0.29

micron wide while the calcitic lamellae of the third order measure from 0.25 to 1.4 micron. In contrast to the calcitic callus deposits the spherulitic inclusions have dark layering and no undulations in lamellae of the second order.

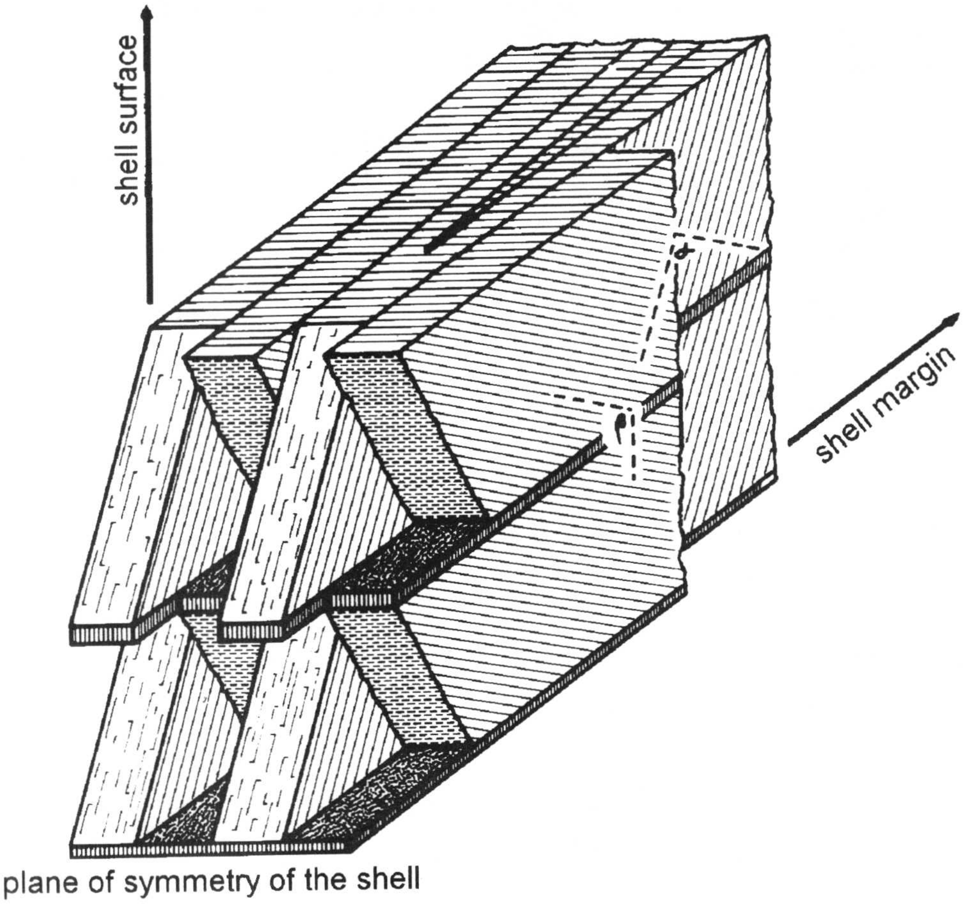


Figure 7: Sketch of the aragonitic crossed lamellar layer within the hypostracum of *Patella crenata* with two prismatic intercalations parallel to the plane of growth.

The callus or hypostracal deposits of *Patella crenata* has four characteristics:

1. The bulk is formed by aragonitic crossed lamellar structure with prismatic aragonitic intercalations.

2. Within the aragonitic callus older individuals may deposit flat sheets of calcitic lamellae of the second order.

3. Within the plane calcitic lamellae aragonitic spherulite sectors can be included which basically are composed in the structural type of the crossed lamellar layer.

4. Calcitic and aragonitic deposits were produced at the same time side by side including the spherulite-sectors within the calcitic layer.

The mixture of calcitic and aragonitic structures within the callus deposits is not caused by pollution or the like, since it is also found in older shells that have grown at least 50 years ago and in even older ones of ancient kitchen mittens. The callus deposits of the interior shell reflect some kind of sloppy deposition which has no ill effect to the producer since outer forces do not act on it. It show the ease in which the mantle of *Patella crenata* and its relation produce complex structures of calcite and aragonite side by side and at the same time next to each other.

4. Other elements than Calcium in the shell

Atomic absorption spectro-analysis and quantometer analysis was carried out to determine the chemical composition of the calcitic outer layer and the aragonitic inner callus. The purity of the samples was checked by Xray analysis to excluse such portions of the shell where many exotic grains had been cemented. The poudered substance was analyzed in wet state in the atomic absorption and in dry state in the quantometer. In order to produce the wet state material was dissolved in HNO3. The dry state powder was affected by the high temperature of carbon-sparks, and the emitted energy was spectrally analysed in a quantitative way.

The calcite crystals may include elements of a different diameter of their ionic state than the aragonite crystals. The crystallographic construction of the calcite crystal prefers elements like Mg, Fe, Zn, Mn, Co, Cd, while aragonite select preferably elements like Sr, Ba, Pb. The inclusions of these elements with the structure of the crystal depends on a number of factors as there are pressure, temperature, pH, salinity and concentration of elements available. An important factor in biocrystals is the composition of the organic substance involved in their growth.

The calcite of the outer crossed lamellar layer of *Patella crenata*.

No. is the number of samples analysed.

Elements	AAS	No.	Quantometer	No
Mg	6050-6670	5	5610-6333	5
Sr	392-556	5	2030-2740	5
Pb	--		5-28	5
Co	13,8-17	5	2-12	5
Cu	5,9-10,9	5	< 2,0	5
Zn	2,5-4,8	5	< 5,0	5

Other elements only traced with the Quantameter are Sodium with 334-482 ppm and Bor with 35-140 ppm. Both reflect the composition of the sea water in which the shells were formed. Some elements were found only in a part of the samples while others were present in concentrations below the sensitivity of the analysis, as there are Ga (<2 ppm), Ti (< 10 ppm), Cr (<5 ppm) and Ni (<2 ppm). The rare occurrence of Ti and Cr as well as the presence of Fe (11,1- 97,0 ppm; AAS) indicates the presence of cemented sand grains in the shell. They in part represent heavy minerals like Magnetit, Ilmenit, Rutil, Chromit or other basaltic minerals of volcanic Lanzarote Island.

The predominating element of the calcite in the shell of *Patella crenata* is the Mg with an average of 6250 ppm. WASKOWIAK (1962) found in *Patella scutellaris* with 100% calcite 14000 ppm Mg, while six further patellids with calcite content of 54 to 80% had 7500 to 24000 ppm Mg in their shell. Lower values have been reported by PILKEY & GOODELL (1964) Mg (3144 ppm) of the bivalve *Anomia simplex* that has 83% calcitic shell.

Next to Magnesium Strontium is the most important element present within the calcite. *Patella scutellaris* with 100% calcite contains 750 ppm Sr, while the other patellids have values ranging from 1200 to 2200 ppm Sr according to WASKOWIAK (1962). The values determined by PILKEY & GOODELL (1964) in the shell of *Anomia* agree in dimension with those determined by quantometer in the shell of *Patella crenata*. Regarding the other elements comparison makes no sense and is not possible.

The aragonite of the callus in the inner shell of *Patella crenata*.

Analysis was carried out with the atomic absorption spectrometer (AAS) and the quantometer (No. represents the number of analysis).

Elements	AAS	No.	Quantometer	No.
Mg	145-165	3	180- 360	3
Sr	580-1000	5	3280-3400	3
Pb	1.6- 1.7	5	15-26	3
Co	14.8-26.2	5	4-9	3
Cu	7.3-13.8	5	<2	3
Zn	1.8-5.2	5	<5	3

With the quantometer Sodium with 334- 408 ppm, Bor with 60 to 80 ppm, Titan with 80-94 ppm, and Chromium with 8-26 ppm were determined. With AAS 9,8 -19 ppm Fe was found. Iron and Chromium of about 14 ppm indicates the presence of a minute amount of chromite in the shell. Titanium is found in the sand of Fuerteventura in the form of Rutil (MÜLLER 1969) with 90 ppm is much more concentrated.

In the aragonite of the shell Strontium is the most abundant further element, and its values in *Patella crenata* resemble those that have been determined from other marine molluscan shells (PILKEY & GOODELL 1964). Magnesium is the second common element again as in other marine molluscs. There is a characteristic difference seen in element admixture in calcit and aragonite of *Patella crenata*. Mg is present with about 6250 ppm in the calcite while there are only 218 ppm in the aragonite. Sr is represented in the calcite with 490/2544 ppm, in the aragonite with 680/3320 ppm. The most significant differences are between calcite and aragonite in regard to the content of Mg ions. Calcite in the shell of *Patella* holds more than 30 times as much Mg as is present in the aragonite of the same shell. This result agrees with what can be expected when the theory of the crystallographic frame of aragonite and calcite are taken into account, but it was not compatible with the data of WASKOWIAK (1962) in regard to *Patella*. A better fit exists with data presented by PILKEY & GOODELL (1964) from the shells of other molluscs.

The difference in Strontium content is less pronounced. Sr-concentration according to AAS from calcite to aragonite is a 40% difference, with quantometer analysis 30%. Again the values of WASKOWIAK (1962) differ from calcite with 750 ppm Sr to aragonite with 2200 ppm Sr representing an almost threefold increase. In contrast PILKEY & GOODELL (1964) noted an increase of Sr between 10 and 35 % from calcite to aragonite within the shells of various molluscs. This later result can be confirmed also with the here presented from *Patella crenata*. The other elements including the iron can show no significant difference between calcite and aragonite.

5. Growth of the shell of *Patella crenata*.

The interior of the shell can be thickened and enlarged at all portions which are in contact to the tissue of the mantle. Between shell margin and the margin of the myostracal layer the calcitic crossed lamellar structure is deposited. Where tissue is attached, the prismatic layer of the myostracum is deposited. They are differentiated in an outer zone of spherulite sector growth and an inner zone of prismatic growth. Inward from the tissue attchment zone aragonitic crossed lamellar structure is usually deposited. Here in regular intervals prismatic layers grow. During ontogeny the myostracal layer covers the calcitic crossed lamellar layer, and its earlier deposits in turn are covered by the callus of the aragonitic hypostracum. Thus, in *Patella* different zones of the mantle, the free portion, the attached portion and the portion behind the attachment excrete different shell structures. Interuptions of growth due to grains intruding between shell and mantle are cemented and coated by shell without major difficulties and impact on the structure. Fully grown and probably senile individuals produce in the callus layer a mixture of calcitic and aragonitic shell that shows rather good organization.

6. Corrosion of shell

As soon as there is a shell, this shell becomes settled from the outside by encrusting and corroding organisms (Pl.15, Figs.1-7). This is easy to do because there is no periostracum to speak of. Chemical dissolution dissolves the aragonitic protoconch and boring algae, fungi, and cyanobacteria drill narrow holes into the shell (Pl.15, Figs.1-5). Thus, adult shells have the apex usually so throughly destroyed that no calcitic outer layer is found here, and the aragonitic crossed lamellar layer excludes intruders. Corrosion is strongest in the apical region. After death organic layers in the shell (Pl.14, Figs.1-5) decompose which is indicated by the disappearance of the shell luster and the disintegration of calcitic lamellae of the outer layer as well as the contacts between the calcitic layer and the myostracal layer.

7. Docoglossa compared with other Archaeogastropoda

TROSCHEL (1856) coined the term Docoglossa to encompass those archaeogastropods that are united by the docoglossan radula. LINDBERG (1988) suggested to replace the name Docoglossa by the term Patellogastropoda since it describes a type of radular morphology, musculature, and function that is not unique to the Patellogastropoda and, thus not only included *Patella* and relation but also the monoplacophores and the polyplacophores. But actually TROSCHEL (1856) had not included the Polyplacophora in his Docoglossa and he knew no monoplacophoran radula therefore could not include it in his Docoglossa. Living monoplacophores that could provide a radula were discovered almost a century later. Thus, Docoglossa are a useful and valid name for the taxon, and it does not need to be replaced by the term Patellogastropoda. TROSCHEL (1956) erected the Docoglossa to include the Patellidae RAFINESQUE, 1815, Acmaeidae FORBES, 1850 and Lepetidae DALL, 1869.

BANDEL (1982) based the definition of the subclass Archaeogastropoda on the mode of shell formation that occurs in the embryonic and larval stages. Only among the Docoglossa larvae can swim in the sea with cilia arranged in rings on the spherical embryo, and the shell grows later (DODD 1955, NIELSEN 1987, SCHARENBERG in prep.). The embryonic shell of the Docoglossa is attached to the teleoconch in asymmetric way, indicating an originally spiral coiling mode (MORSE 1910, THOMPSON 1912, SMITH 1935, LINDBERG 1981, BANDEL 1981,1982). The larva secretes its shell in the same way as do other archaeogastropods, and it also forms an operculum (THORSON 1945, DODD 1955, own observations) which it discarts after becoming a limpet. The limpet form would have developed as secondary feature as it has evolved in many gastropod groups quite independent from each other.

YOCHELSON (1994) suggested that the middle Ordovician *Macroscenella* WILSON, 1951 represents a member of the Docoglossa. This simple conical shell with the apex in almost central position and aperture in one plane with 6 cm long and 5 cm wide oval elliptical aperture was placed here on account of the muscle scars which resemble that found in modern patelloids. The shell is described as very thin, but it is not preserved, and the protoconch is unknown. This fossil is thus rather problematic since it shows neither structure of the shell nor the shape of the protoconch. It could represent an untorted limpet or one of the many limpets found in different systematic positions within the Gastropoda.. Safe Docoglossa are known only from the Triassic (ZARDINI 1978, 1980, BANDEL 1991, 1994), and they can be placed into the Patellidae according to their shell structure, which is well preserved (own observations). If older representatives of the Docoglossa that should have lived in the Paleozoic had trochospirally coiled shells, their shell structure should distinguish them from other Archaeogastropoda while their protoconch should differentiate them from the Neritimorpha with calcitic outer shell layer and aragonitic inner crossed lamellar layer (BANDEL 1990).

The calcitic outer shell layer composed of lamellar sheet calcite distinguishes the Docoglossa (Patellogastropoda) from all other Archaeogastropoda. Docoglossa also have the smallest number of chromsomes among archaeogastropods and the simplest shape of the spermatozoa, as well as a simple osphradium that may be present in single or double number (THIEM 1917, HASZPRUNAR 1985). The limpet- like shell begins right after the embryonic shell without an intermediate stage as is present in the Fissurelloidea among the Vetigastropoda (BANDEL 1982). The embryonic *Patella* swims in the Plankton and lives from it. The shell is formed while doing so and is transformed into usually dextral spiral shape as in the other archaeogastropods. The operculum is present during pelagic life and later it is discarted. In cases where embryos are brooded both embryonic muscle bundles may be retained into the adult stage, contrasting to the usual case among archaeogastropods, where only one of these muscle bundles remains after shell deformation and spiralization has occurred. Also minalization of the embryonic shell may be retarded and the earliest mineralized shell is than of limpet shape (BANDEL 1982).

There are three families to be distinguished, the Acmaeidae, Patellidae and Lepetidae. Acmaeidae have a single ctenidium, Patellidae have no ctenidium but a circle of gills on the mantle margin and the tiny Lepetidae utilize their mantle tissue for gas exchange. The ctenidium of the Acmaeidae can be extended in some species even beyond the shell margin by body liquid pumped into its hollow interior and it can be pulled back by muscles within its tissue pushing the blood into the mantle besides it. The gills of the Patellidae consist of mobile lamellae of the mantle margin and are connected to each other by blood vessels connected to the hollow mantle tentacles which are able to contract due to muscular action, thus pumping the body liquid. The tree families of the Docoglossa can also be differentiated by the morphology of their radula as was worked out by TROSCHEL (1856-63) and as has since been confirmed by several authors (see LINDBERG 1988). The teeth of the radula can only become erected during biting and not spread out as is the case among the other achaeogastropods with a rhipidoglossan radula.. While the Patellidae and Lepetidae have central teeth in their radulae they are absent in the Acmaeidae. Lepetidae and Acmaeidae have the tendency to decrease the number óf teeth in each row. The docoglossate radula may have an independant origin from that of the other Archaeogastropoda; suggesting that among this subclass Docoglassa and Vetigastropoda had a very far back-ranging independant evolutionary history.

In the middle Triassic Docoglossa of the structural type of modern *Patella*, especially similar to that of modern *Scutellastra* from the southern Africa lived in the tropical shallow sea of the Tethys in the area that is now the southern Alps. It had an outer calcitic crossed lamellar layer and not two foliated shell layers overlying the inner crossed lamellar layers as was suggested to represent the primitive condition see in the Patellidae by LINDBERG (1988). The structure of this so far oldest known docoglossan limpet could thus represent a character to the group which should help us to elucidate the ancesters, which may have been a spirally coiled late Paleozoic archaeogastropod with outer calcitic and inner aragonitic layers, both with crossed lamellar fabric. Up to now such a form is not known.

8. The shell of Neritimorpha GOLIKOV & STAROBOGATOV, 1975

The land species belonging to the Helicinidae LATREILLE, 1825 and the Hydrocenidae TROSCHEL, 1856 are composed of aragonitic crossed lamellar structure and their derivatives. The aquatic species of the Neritidae RAFINESQUE, 1815 have an outer calcitic layer with a homogeneous or non distinct structure and an inner aragonitic crossed lamellar structure (BOGGILD 1930, BANDEL 1981, 1990). A similar structure is present in the Neritopsidae GRAY, 1847 and the Platyceratidae HALL, 1859, where the calcitic layer has become especially thick (BANDEL 1992). The Neritininae have a rather thin calcitic layer on a thick aragonitic crossed lamellar layer, similar to the Phenacolepadidae THIELE, 1929 where this outer layer is extremely thin.

Neritimorpha are considered to represent comparatively primitive Archaeogastropoda by HASZPRUNAR (1988, 1993), while KNIGHT et al.. (1960) consider them as highly advanced Archaeogastropoda. BANDEL (1992) demonstrated that their ancient history connected to an ontogeny that differs from all other gastropoda distinguishes the Neritimorpha to such an extend that they represent an independent subclass of the gastropoda that is of equal rank with the Archaeogastropoda. NAEF (1911) and YONGE (1947) had already suggested that neritioidean gastropods should have the same taxonomic level as the archaeogastropods based on anatomical differences. The shell structure of the Neritimorpha presents no argument against this classification. A cladogram placing the Neritimorpha between the Docoglossa and the Vetigastropoda in a reconstruction of evolution within the Archaeogastropoda as proposed by HEDEGAARD (1990) -

that followed HASZPRUNAR's (1988) suggestion - is no solution since Docoglossa and Vetigastropoda have great similarities in regard to their ontogenetic development. In contrast the Neritimorpha follow a different ontogeny that includes a separate phase with planktotrophic larva (BANDEL 1982, 1992).

9. Shell structure and the classification of the Archaeogastropoda.

There exists disagreement in the interpretation of first appearance of biocrystallite structures in the Mollusca. A common view is that nacre is the more ancient of the two complex structures of aragonitic composition found among the molluscs. Thus, HASZPRUNAR (1993) suggested that the presence of nacre is restricted to the archaeogastropod grade among the gastropoda, although many groups have lost and replaced it secondarily. HEDEGAARD (1990) in contrast considers the crossed lamellar structure to represent the original one, and nacre to appear later in the evolution of the archaeogastropoda. BANDEL (1981) demonstrated with a tree-like graph that structural types are unevenly distributed among molluscs. Thus, the Placophora have crossed lamellar structure (HAAS 1972), while the Monoplacophora have nacre (ERBEN et al. 1969). Within the large classes of the gastropods and the bivalves both nacre and crossed lamellar structures are present. The cephalopods in contrast have only nacre (BANDEL & BOLETZKY 1979, BANDEL 1990b) and scaphopods utilize only crossed lamellar structure (HAAS 1972). Within the gastropods extant species either have nacre or crossed lamellar structure (BANDEL 1990a), while within the bivalves rare cases are known, where both structural types occur together in the shell (CARTER 1985, 1990).

According to LINDBERG (1988) the primitive condition seen in the Patellidae appears to be two foliated shell layers overlying two crossed lamellar layers that are separated from one another by the myostracum. It seems that calcitic foliated structure is separated by the myostracal layers from aragonitic crossed lamellar structure, as is the case in *Patella crenata*. According to LINDBERG (1988) in the Nacellidae THIELE, 1891 the crossed lamellar layer was lost, and the Lottiidae GRAY, 1840 abolished the foliated structure. HEDEGAARD (1990) collected data to the mineralogy of a number of Docoglossa like *Acmaea* ESCHSCHOLTZ, 1833, *Lottia* GRAY, 1833, *Scurria* GRAY, 1847 and *Pectinodonta* DALL, 1882, and noted that in general the outer layer of the shell is composed of calcite, and the muscle scar consist of aragonite. The same holds true for the Nacellidae and Lepetidae (HEDEGAARD 1990). This confirms the results of THIEM (1917) who had noted calcite in the outer layer of *Scurria*, aragonite in the myostracal layer and a micture of calcite and aragonite in the inner layer.

The puzzle of crossed lamellar aragonitic structure being present within the different lineages of the Archaeogastropoda like Docoglossa on one side and the Fissurelloidea /Scissurelloidea and Phasianellidae among the Vetigastropoda on the other remains.

In the Fissurelloidea FLEMING, 1822 the aragonitic crossed lamellar structure composed most of the shell (BATTEN 1975; MCLEAN 1984; BANDEL 1990a), and only a few species of the Pacific coast of South America have an outer homogeneous calcitic layer (BOGGILD 1930; LINDBERG 1979; HEDEGAARD 1990). Scissurelloidea are similar, but have a very thin crossed lamellar layer (BATTEN 1975, BANDEL 1982). In the slit bearing forms with nacreous inner layer, most species have an outer layer of different structure, but aragonitic composition. In some species of *Haliotis* BOGGILD (1930) noted some calcite in the outer layer while in most species of this genus the whole shell is aragonitic. The same is the case in the modern Pleurotomariidae (ERBEN & KRAMPITZ, 1972, HEDEGAARD 1990).

Fossil representatives of the Pleurotomarioidea commonly have in general a similar structure of aragonitic outer layer with prismatic layers and a nacreous inner layer. In the Triassic St. Cassian formation several rpresentatives of pleurotomarioidean lineages (Selenimorpha) show similar structure even though the outer layer has a variety of substructures (BANDEL 1991b). Members of the genera *Temnotropis*, *Wortheniella*, *Bandelium*, *Stuorella*, *Raphistomella*, *Kokenella*, *Schizogonium*, and *Laubella* from the St. Cassian were analysed by thin section and peel methods, and showed a main layer consisting of columellar nacre and complex crossed lamellar layers according to the terminology of CARTER (1990) right below the periostracum and it commonly covers the nacre in older portions of the shell interior.

The Seguenziidae KEEN, 1971 are aragonitic with similar inner and outer layer, consisting of needles enclosing the central nacre as in the pleurotomariids. BANDEL (1979) called these structures acicular prismatic, dendritic and disected, crossed acicular depending on the orientation of the needles, composing them and the degree in which they interact with each other. Fractured sections of these layers seen with the scanning electron microscope demonstrate quite clearly that these complex crossed lamellar structures (CARTER 1990) or spherulitic prismatic, scaly and disected crossed lamellar structures (BANDEL 1990) differ from the crossed lamellar structure. These complex crossed lamellar structures may grade directly into the nacreous structure and into the crossed lamellar structure. In sections of shells from which peels have been prepared or which have been thin sectioned it is not easy to distinguish complex crossed lamellar structure from crossed lamellar structure. In recrystallized shells peels often reveal the original shell structure even though shells are now preserved as calcite. Here the distinction of crossed lamellar structural types is even more complex since it is difficult to asses what has been the original modification, aragonite or calcite. No gastropod is presently known in which nacreous and crossed lamellar structures occur within the same shell. This can be extended to all the shells with originally mineralogy analysed from the St. Cassian Formation. CARTER (pers. communication) noticed a thick crossed lamellar layer overlying the nacre in Devonian *Bembexia sulcomarginta* (CONRAD, 1842) from New York in a diagenetically totally calcitic shell. Other selenimorphs from the Carboniferous, like *Shansiella* YIN, 1932, *Trepospira*, *Glabrocingulum*, *Worthenia*, and *Phymatopleura* GIRTY, 1939 seem to have the same structure as seen in modern and Triassic Selenimorpha with nacre (BATTEN 1972, own peels and thin sections).

Similar shell structures in species with nacreous shell are seen in a number of Trochoidea. Here *Cittarium pica* represents an exception by having an outer layer of calcitic composition (WISE & HAY, 1968, ERBEN 1971). Genera like *Umbonium* and *Tegula* can be included (KOBAYASHI 1983; WISE 1970). HEDEGAARD (1990) analysed quite an additional number of genera like *Astraea*, *Liotina*, *Liotia*, *Turbo*, *Angaria*, *Calliostoma*, *Gibbula*, *Euchelus*, *Granata*, *Margarites*, *Cantharidus*, *Diloma*, *Monodonta*, *Bathybembix*, *Thalotia*, *Jujubinus*, *Bankivia*, *Solariella*, *Clanculus*, *Tectus*, *Trochus*, and *Monilea*. Here the outer layer is spherulitic prismatic of simple prismatic or composite prismatic aragonitic, and the inner layer consists of nacre, and a callus covering it in older whorls. Triassic genera like *Woehrmannia*, *Zardinihelix*, *Rolandomphalus*, *Eunemopsis*, *Pseudoclanculus*, *Cassianastraea*, *Ampezzalina*, *Anomphalus*, *Eunema*, *Ampezzotrochus*, *Coelocentrus*, and *Eucycloscala* consist of the outer aragonitic layer composed of needles in more or less complex crossed lamellar or spherulitic or prismatic arrangement, the central columellar nacre, and the inner, commonly disected acicular or disected platy layer (BANDEL 1993, own data on thin sections and peels).

Homalopoma and *Leptothyra rubicincta* has no nacreous structure, but there is no crossed lamellar structure replacing this missing layer, but the outer layer seems to be overlain by the inner callus layer directly (HEDEGAARD 1990). Another species of *Leptogyra*, *L. verruca*, studied by HEDEGAARD has normal columnar nacre like other Trochoidea and Turbinidae. Thus, they do not resemble the Tricoliidae and Phasianellidae which have an outer layer of spherulitic prismatic structure and an inner layer of crossed lamellar structure, totally in aragonitic composition. Skeneidae also deviate from the normal structure being close to the Phasianellidae (HEDEGAARD 1990) or resembling the nacre less members of the Turbinidae, Homalopominae with reduced or absent nacre layer. Among the late Triassic genera *Triadoskenea* has a crossed lamellar structure (BANDEL 1993).

The Phasianellidae among the trochomorph archaeogastropods have shell structures very different from the other Trochoidea (BOGGILD 1930; HEDEGAARD 1990; HICKMAN & MCLEAN 1990). Intersected crossed platy structure may be derived from the nacre as well as from the crossed lamellar structure and can be found in small species as different as *Scissurella*, many Cocculinimorphia, Skeneidae among the Archaeogastropoda, but also the thin shelled Heteropoda and others among the Caenogastropoda. In order to study the evolution of shell structures the gradual transitions between layers with different structure may help in understanding (BANDEL 1977, 1979, 1990a,b). It was found that there is a close relationship between cossed lamellar structure and spherulitic and spherulitic prismatic structure, and a close relationship exists between nacre and spherulitic prismatic structure, with crossed platy and disected prismatic structures intermediating.

BANDEL et al. (in prep) analysed a small turbinimorph archaeogastropod from the Buckhorn asphalt of younger Carboniferous age that has a non-nacreous shell composed of aragonitic crossed lamellar structure, which represents an unusual feature among trochomorph gastropods (BOGGILD 1930, BANDEL 1993). The Carboniferous gastropod with crossed lamellar shell structure may represent a precurser or relative of a precurser of the Scissurelloidea/Fissurelloidea as well as the oldest known representative of the Phasianellidae/Tricoliidae.

10. The subclass Archaeogastropoda

In his original concept THIELE (1929) included in the Archaeogastropoda THIELE, 1925 five subgroups consisting of the slit bearing Zeugobranchia with two gills, the Docoglossa, the Trochoidea, the Neritoidea (now Neritimorpha) and the Cocculinoidea (now Cocculiniformia). WENZ (1939) utilized THIELE's concept and in addition included some fossil groups like the Tryblidoidea (later to become an own class of the Mollusca, the Monoplacophora), the Bellerophontoidea (still disputed bilaterally symmetrical molluscs). According to HASZPRUNAR (1993) the only diagnostic character to the Archaeogastropoda is the presence of a streptoneurous and hypoathroid nervous system present at least at the left side. All other characters of shell and anatomy are present in other groups as well.

BANDEL (1982) defined the subclass Archaeogastropoda according to the formation of the early ontogenetic shell. They than hold the Docoglossa, Cocculiniformia and Vetigastropoda, but not Neritimorpha and also not the Architaenioglossa (Cyclophoroidea and Ampullaroidea) that were suggested by HASZPRUNAR (1988, 1993) to represent Archaeogastropoda. While the latter were regarded as members of the Caenogastropoda (BANDEL 1993b), the Neritimorpha are considered to represent an own independent subclass of the gastropoda (BANDEL 1992).

In a classification of the Gastropoda as indicated above the archaeogastropod shells can be recognized in the fossil record and can be differentiated from those of the other subclasses of the Gastropoda (BANDEL 1992). Even when the features of the protoconch features are interpreted as suggested by BANDEL (1982) and the Neritimorpha and Architaenioglossa of HASZPRUNAR's (1988, 1993) are excluded from the Archaeogastropoda, the subclass Archaeogastropoda may represent a paraphyletic taxon and not a clade, because they may hold the stem groups of some of the other subclasses of the Gastropoda, such as the Neritimorpha and Caenogastropoda. But the case will be very difficult to prove since the stem group species for Neritimorpha, Caenogastropoda, and probably also the Heterostropha have lived in the Ordovician and must be detected among fossils from that time.

It still remains mysterious how Caenogastropoda with their right coiled shell and Heterostropha (=Heterobranchia) with the left coiled protoconch and right coiled teleoconch are related to each other. They certainly are different taxa by Devonian time and probably exist side by side even earlier (BANDEL 1995a,b,c). The common ancestors to the Neritimorpha, Caenongastropoda/ Heterostropha and the Archaeogastropoda have lived in late Cambrian or early Ordovician times (BANDEL 1992, 1993b).

HICKMAN (1988) defined Archaeogastropoda in a different way only including the superfamilies Pleurotomarioidea, Fissurelloidea and Trochoidea. Thus, they would be close to what SALVINI PLAWEN & HASZPRUNAR (1987) considered to represent the Vetigastropoda. HICKMAN (1988) also suggested that archaeogastropod taxonomic diversity and morphological diversity are centred in the Paleozoic era. According to their interpretation most of the nearly 600 million years of gastropod fossil record is a strictly archaeogastropod fossil record as laid down by KNIGHT et al. (1960). But many of the superfamilies presented by KNIGHT et al. (1960) actually do not represent Archaeogastropoda if these are defined by the modern and fossil Docoglossa, Cocculinimorpha and Vetigastropoda as originally suggested by THIELE (1925) (but including the Neritimorpha). Many

Paleozoic gastropods have since been shown to represent members of the Caenogastropoda, Neritimorpha, and Heterostropha (BANDEL 1993, 1994, 1995a,b,c).

Thus, it is not very senseable to infer that shells of different morphology belong into one and the same interrelated evolutionary group, just because they have lived in the Ordovician, if the initial shell portions and shell structure of the analysed species are unknown. Such a scheme has recently been presented by WAGNER (1995) who considered the lophospirids appearing with the early Ordovician (middle Arenig) to represent a taxon that encompasses a wide range of morphologies. WAGNER included within this group species with selenizone belonging to the genera *Trochonemella* and *Ruedemannia*, with only an apertural sinus as in the genus *Lophospira*, without a slit as in the genus *Trochonema*, and such with murchisoniid, high spired shape belonging to the genus *Donaldiella*. He suggested that they had all developed from each other during Ordovician time. He neither knew or cared to know what the shell structure is like nor what the morphology of the early whorls may be. But even without this knowledge WAGNER presented his cladogram interpreted as stratigraphic test on how evolution may proceed. If we take into consideration that during that same time of the Ordovician all major groups of gastropods have differentiated WAGNER (1995), could with the same meagre data - but aided by elaborate computer models - come to the conclusion that lophospirids represent the ancestors to all subclasses of the Gastropoda. Perhaps it is better to proceed more slowly and to assemble at least a few more data. To begin with that task some morphogroups are here assembled.

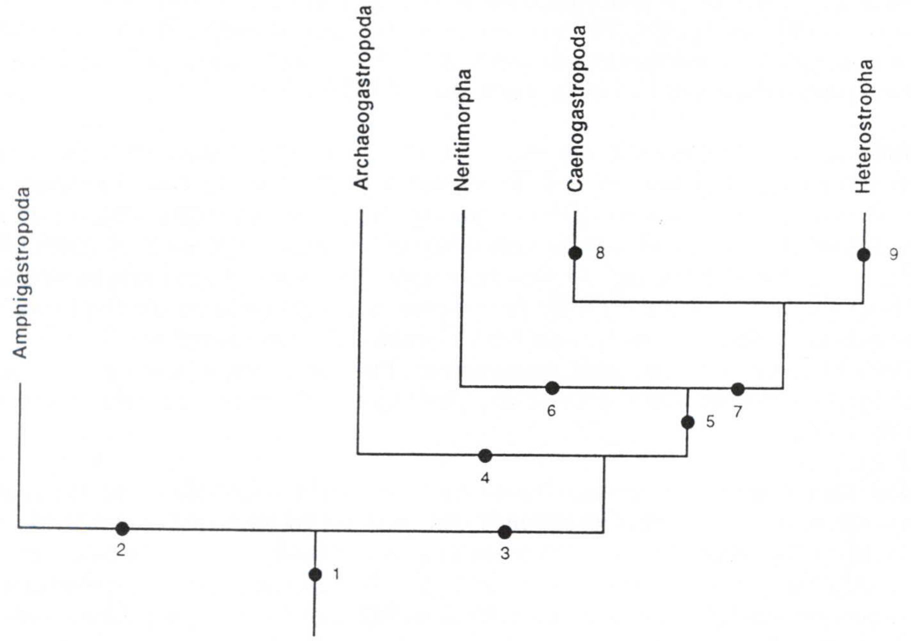


Figure 8: Relation of gastropod subclasses to each other seen as monophylum.

Fig 9

1. Torsion of the soft body. 2. Aragonitic lamellar structure. 3. Torsion of the soft body during embryonic development. 4. Torsion of the soft body after embryonic development. 5. Feeding larval stage. 6. Nacreous aragonitic structure. 7. Limpet shape. 8. Aragonitic lamellar structure. 9. Heterostrophic shell.

11. Trochomorpha

Archaeogastropoda that lived during the last 50 million years can usually be grouped with one or the other of the extant taxa. Older species are often difficult to place. Convergence among modern forms calls for caution. Thus, placement of Paleozoic and Mesozoic genera of slit-less Archaeogastropoda near to a modern group commonly remains engimatic. A more complete evaluation of the fossil record will eventually enable a better understanding of evolution through times, but this rules out groups that have not survived into our time. It therefore makes sense to define fossil taxa and to keep them separate from modern ones (BANDEL 1993).

Trochomorpha NAEF 1911 holds all extant species of the Trochoidea as defined by HICKMAN & McLEAN (1990) and the fossil species of Archaeogastropoda without slit and selenizone. The anatomy of these fossil gastropods will also in the future not be determinable, and they are only excessible by the morphology and structure of the shell. NAEF (1911) created the taxon Trochomorpha that can be utilized to hold the modern Trochoidea Rafinesque, 1815 as well as similar fossil Archaeogastropoda in one group.

This classification relies on the premis that a member of the Archaeogastropoda can be recognized by the morphology of its embryonic shell as was defined and suggested by BANDEL (1982). Placement of a fossil archaeogastropod in one of the groups formed by extant Vetigastropoda without slit to a large extend relies on subjective judgement. This is so because the classification ot modern Trochoidea is based on anatomical features as can be gathered from the most recent classification presented by HICKMAN & McLEAN (1990). Morphology and construction of the shell has shown many convergent features, and shells of different groups may be very similar to each other.

It may be discussed whether modern Vetigastropoda without slit can be grouped according to the suggestions of HICKMAN & McLEAN (1990). Regarding fossil species the situation is not acceptable since WENZ (1939) recognized the Trochoidea only from the Triassic onward. This was accepted to a large extend by HICKMAN & McLEAN (1990) even though these authors discuss the possibility that trochoids began their evolutionary own development as early as the Ordovician. KNIGHT et al.. (1960) include the Trochoidea within the higher taxon (suborder) Trochina COX & KNIGHT, 1960 which had species in the Paleozoic. The taxon Trochina, thus, represents to a large extend a synonym to the Trochomorpha NAEF, 1911. KNIGHT et al.. (1960) recognized five Paleozoic superfamilies of the Trochina, the Pseudophoroidea, Platyceratidea, Microdomatoidea, Anomphaloidea and Palaeotrochoidea. These taxa represent groups into which KNIGHT et al.. (1960) included all those shells that resemble modern Archaeogastropoda and are older than Triassic. Thus, these taxa hold to a large extend those species which were placed in the Trochonematoidea by WENZ (1938).

We therefore have a taxonomic system in which many living Vetigastropoda are not well known, and the classification, thus, incomplete and in which fossil species are interpreted according to the theory that the Permian/Triassic transition had great impact on the taxonomy of the Vetigastropoda. HICKMAN & McLEAN (1990) describe the Trochoidea RAFINESQUE, 1815 in regard to features of the shell as slitless form and conospiral shape with slow increase in shell diameter during growth with or without umbilicus and usually, but not exclusively rounded aperture that may or may not be inclined to the axis of coiling. An operculum is usually present and may be organic as well as calcified. No attention was placed to the characters of the early ontogenetic shell. All other characters and, thus, practically all those that are of good use in systematics in this taxon regard the anatomy including the radula which have never been found preserved in a fossil.

HICKMAN & McLEAN (1990) differentiated three families of the Trochoidea. In regard to shell features presented by these authors they differ very little one from the other. Thus, not pigmented shells only up to 5 mm large shells are usually placed in the Skeneidae CLARK 1851. Pigmented and usually larger shells with a size more than 5 mm are found in the Turbinidae RAFINESQUE, 1815 and Trochidae RAFINESQUE, 1815. Turbinidae differ from Trochidae by the length of the growing edge of the operculum and by shape of the central tooth of the radula. Both these differences are of little help in keeping fossil Trochidae separated from fossil Turbinidae. Since pigmentation is usually lost during diagenesis and all species begin their life with small shells, the Skeneidae can also not be differentiated from the other two taxa once they have been fossilized.

According to HICKMAN & McLEAN (1990) the Turbinidae may be split into nine subfamilies which can be traced only to the Upper Cretaceous with the earliest member of the genus *Turbo* LINNEUS, 1758. But on the other hand these authors think it possible that *Gizhouia* YIN & YOCHELSON from the Chinese Triassic could be related to modern *Astraea* RÖDING 1798. HICKMAN & McLEAN (1990) distinguished 12 subfamilies within the Trochidae , some of which are thought to be related to Mesozoic genera among others for example the genera *Hamusina* and *Cirrus*.

12. An extinct group of Archaeogastropoda

HICKMAN & McLEAN (1990) included the sinistral genera *Hamusina* GEMMELLARO, 1878 and *Cirrus* SOWERBY, 1815 in the Eucylinae KOKEN, 1897. BANDEL (1993) in contrast suggested to contain them in the superfamily Cirroidea COSSMANN, 1916 in the Archaeogastropoda and here most likely the order Vetigastropoda. Cirroidea have a nacreous inner shell layer and the characteristic protoconch of the Archaeogastropoda. It seems that they developed from early Paleozoic slit bearing dextral nacreous ancestors with first recognizable species in the late Silurian (FRYDA, in prep.). In contrast to all other superfamilies their juvenile dextral shell changed coiling direction during the growth of the teleoconch, usually into a sinistral shell, sometimes into planispiral shell. In it the Agnesiinae KNIGHT, 1956 presented genera with a high-trochospiral shell like *Hesperiella* HOLZAPFEL, 1889, a trochiform shell like *Antitrochus* WHIDBORNE, 1891, a low turbiniform shell like *Agnesia* KONINCK, 1883 and the late Triassic *Enantiostoma* KOKEN, 1889. They all have a labial slit low on their outer lip. Planispiral *Porcellia* LÈVEILLÈ, 1835 with rounded whorls and discus-like *Coloniacirrus* BANDEL, 1993 with compessed whorls have a median labial slit and belong to the Porcelliinae BROILI, 1924. The slit-less family Cirridae COSSMANN, 1916 appears in the Triassic with conical trochiform genera like *Hesperocirrus* HAAS, 1953, *Sororcula* HAAS, 1953, *Hamusina* GEMMELLARO, 1878, *Shikamacirrus* KASE, 1984 and *Sensuitrochus* QUINTERO & REVILLA, 1966 and turbiniform *Scaevola* GEMMELLARO, 1879 in the Hesperocirrinae HAAS,1953. The planispirally coiled *Cirrus* and *Discocirrus* AMMON, 1892 are united in the Cirrinae COSSMANN, 1916.

Porcelliidae BROILI, 1924 with labral slit and selenizone and Cirridae without slit are connected to each other by species with small body size that retained the character of juvenile Agnesiinae as found in the small Triassic *Cassianocirrus* BANDEL, 1993 and *Zardinicirrus* BANDEL, 1993 representing the Cassianocirrinae BANDEL, 1993. *Agnesia* and *Hesperiella* usually developed the slit after some whorls of the teleoconch had formed without labral sinus. With begin of the Jurassic small forms gave rise to larger ones as found in the genus *Hamusina* and diversified into groups of different shell shape from high trochospiral to planispiral interconnected by intermediat forms. Low spire species of the Cirridae, and here in the Cirrinae branch, may have given rise to the Discohelicidae SCHRÖDER, 1995 with planispiral apex and inner nacreous shell structure. Discohelicidae with the name giving genus *Discohelix* DUNKER, 1848, the Jurassic *Asterohelix* SZABO, 1984 and *Pentagonodiscus* WENDT, 1968 represent typical archaeogastropods of the Jurassic. They may have had their origin in the Triassic in species as in the genus *Triadodiscus* BANDEL, 1993, and they are still found in the older Cretaceous of Poland (BANDEL 1988,1993, SCHRÖDER 1995). While the discohelicids disappeared during the early Cretaceous, the cirroids have survived to the Campanian before the group became extinct. Cirroidea, thus, represent a totally fossil group of the Archaeogastropoda, probably the Vetigastropoda. They unite species belonging to the Selenimorpha with such belonging to the Trochomorpha. This represents a case as is found in the modern superfamily Seguenzioidea among the Vetigastropoda (QUINN 1983, MARSHALL 1983, 1988), where slit bearing and non-slit species are united in one taxon. Cirroidea also demonstrate that not all groups that evolved within the Archaeogastropoda have survived to modern times and that there may be more such totally extinct larger taxa hidden among the fossil Trochomorpha and Selenimorpha.

13. Groups of the Trochomorpha

13.1 Trochomorph group *Araeonema*

Higher than wide with rounded whorls that are ornamented with spiral lirae and with simple rounded aperture. The inner shell is nacreous and the protoconch of the archaeogastropod type.

Yunnania MANSUY, with Permian genotype lived in the late Triassic and here represents a nacreous archaeogastropod (BANDEL 1993). *Araeonema* KNIGHT, 1933, *Amaurotoma* KNIGHT, 1945 and *Rhabdotocochlis* KNIGHT, 1933 from the Australian early Carboniferous could belong into the same relation (YOO 1988, 1994). Late Carboniferous *Rhabdotocochlis rugata* KNIGHT, 1933 from the North American Pennsylvanian is the type of the genus and a very similar shell from the Buckhorn Asphalt in Oklahoma studied by BANDEL et al. (in prep.) has the protoconch and an inner nacreous layer preserved. The Triassic *Yunnania zardini* BANDEL, 1993 has the same type of ornament and shell stucture, but is higher than *Rhabdotoconchlis*. *Araeonema microspirulata* YOO, 1994 from the Australian early Carboniferous is preserved with the protoconch and resembles *Araeonema virgatum* KNIGHT, 1933 from the Pennsylvanian of Missouri representing the genotype.

Remarks: *Araeonema* and *Rhabdotocochlis* were placed among the Gyronematinae KNIGHT, 1956 of the Holopeidae WENZ, 1938. According to WENZ (1938) *Yunnania* represents a trochonematid, while KNIGHT et al. (1960) place it into the Platyceratoidea. The later placement is definitely erroneous since Platyceratoidea are related to the Neritimorpha (BANDEL 1992). The Holopeidae *Holopea* HALL, 1847 as well as members of the genus *Gyronema* ULRICH, 1897 placed here by CARTER & HALL (1991) represent nacreous species which according to these authors are close to the Eotomariidae WENZ, 1938 (Pleurotomarioidea). The species of the trochomorphs *Araeonema* may relate to the modern Margarininae or Solariellinae of the Trochidae/Trochoidea as suggested by BANDEL (1993). Thus, we could take the subfamily Gyronematinae with *Araeonema* and *Yunnania* from the *Platyceras* relation and place them into the Trochoidea. But species of the genus *Yunnania* can also be associated with modern Skeneidae like *Lissotesta* IREDALE, 1915 from New Zealand. HAAS (1953) included a number of small silizified shells from the Triassic of Peru with the Solariellidae, but these are undeterminable (BANDEL 1994). *Semisolarium* COSSMANN, 1915 and *Periaulax* COSSMANN, 1888 of the Cretaceous of Europe and Japan have been included in to the Margaritinae STOLICZKA, 1869 by KASE (1984), while HICKMAN & McLEAN (1990) preferred the Solariellinae POWELL, 1951, since they have a knobbed periphery of the umbilicus.

13.2 Trochomorph group *Microdoma*

The trochiform elongated conical shell has almost plane whorls-flanks, shallow sutures, and roundly flattened base. Its outer lip is straight and gently oblique backwards.

Microdoma MEEK & WORTHEN, 1867 from the North American Carboniferous is closely related with *Eunemopsis* KITTL, 1891 and *Ampezzotrochus* BANDEL, 1993, both representing nacreous Archaeogastropoda with trochid type of shell composition (BANDEL 1993). *Eunemopsis* connects the Paleozoic members of the Microdomatidae with species grouped in the Jurassic Amberleyidae. *Microdoma* from the Carboniferous Buckhorn Asphalt of Oklahoma has nacreous structure (BANDEL et al. in prep) and *M. angulata* YOO, 1994 from Australia shows the protoconch. *Anematina* KNIGHT, 1933 is very similar to *Microdoma* and has species in the Devonian and Carboniferous of Germany and Belgium. It also resembles species of the genera *Dutrochus* BLODGETT, 1992 and *Devonospira* BLODGETT & JOHNSON, 1992 from the mid Devonian of North America. The slender shells of the genus *Eucycloscala* COSSMANN, 1895 belong here (BANDEL 1993), and they have a nacreous inner layer just like the minute *Sabrinella* BANDEL, 1993. The columellar denticle present in the aperture of *Eunemopsis* connects this genus with *Pseudoclanculus* COSSMANN, 1918 that has a similar early ontogenetic shell as found in the *Microdoma* group, but fully grown individuals resembles a modern *Clanculus* MONTFORT, 1810 (BANDEL 1993).

Remarks: KNIGHT et al. (1960) place *Eucycloscala* into the Liotiinae, *Pseudoclanculus* in the Chilodontinae WENZ, 1938, *Eunemopsis* in the Amberleyidae WENZ, 1938, *Microdoma* in the Microdamatidae WENZ, 1938, *Anematina* in the Elasmonematidae KNIGHT, 1956. After selecting out of those representatiyes of the genus *Eucycloscala* from the St. Cassian that belong to the Caenogastropoda BANDEL (1993) placed these turriform gastropods with nacreous shell in the Trochidae. Due to the characteristic ornamental pattern of the juvenile teleoconch they can be connected to the Eucyclinae KOKEN, 1897 into which HICKMAN & McLEAN (1990) suggested to place *Pseudoclanculus* and *Eunemopsis,* but also the sinistral *Cirrus* and *Hamusina*. Thus the morphogroup *Microdoma* brings together very similar shells with comparable shape and shell structure. Still they have been classified in rather different units wide apart from each other due to theoretical assumptions. HICKMAN & McLEAN (1990) group the Chilodontinae WENZ, 1938 within the Eucyclinae which contain the Triassic *Pseudoclanculus* with shell resembling that of modern *Calliotropis* SEGUENZA, 1903 or *Euchelus* PHILIPPI, 1847. Modern *Clanculus* MONTFORT, 1810 (Trochinae) in contrast resembles *Pseudoclanculus* in fully grown shape, but not in regard to the juvenile ornament (BANDEL 1993). Jurassic *Chilodontoidea* HUDDLESTON, 1896 and *Wilsoniconcha* WENZ, 1939 as well as predominantly Cretaceous *Chilodonta* ETALON, 1862 and the exclusively Cretaceous *Calliomphalus* COSSMANN, 1888 and *Planolateralus* SOHL, 1960 represent the larger part of this fossil group of the Chilidontinae as suggested by WENZ (1938) and SOHL (1987) which supposedly became extinct in the transition from the Cretaceous to the Tertiary.

13.3 Trochomorph group *Eucochlis*

The small turbiniform shell has an ornament of fine transverse costae and a straight, oblique outer lip of the aperture. The first whorl is smooth, and ornamentation arises gradually at second whorl.

Eucochlis KNIGHT, 1933 closely resembles the Triassic *Lanascala* BANDEL, 1992 which is also similar to *Eucycloscala* and *Ampezzoscala*, but in contrast to these has crossed lamellar structure in its shell, not nacreous. *Lanascala* resembles the Carboniferous *Eucochlis* as described from the USA by KNIGHT (1933, 1941) and from Australia by YOO (1989, 1994). YOO described a similar species with rounded whorls as *Kyndalynia* YOO, 1989 that may also belong in this morphogroup. For the Paleozoic species shell structure still is unknown, and the embryonic shell of *Lanascala* is not well known, so there remains doubt whether Paleozoic and Mesozoic species are really related, and if so whether they represent archaeogastropods. If they prove to be related, they can be placed in the Lanascalidae BANDEL,1992.

13.4 Trochomorph group *Anomphalus*

Rotelliform to sub-lenticular shells with low spire, a rounded periphery, deeply embracing whorls, shallow sutures and a slightly flattened umbilicate base with umbilicus commonly filled by callus. Whorls are rounded, and ornament consists of growth lines only. The aperture is rounded and the outer lip oblique. The the inner shell layer is nacreous.

Mesozoic and Paleozoic fossils resembling closely the modern *Umbonium* LINK, 1807 are present in Europe and the USA with the Devonian *Antirotella* COSSMANN, 1918 and *Isonema* MEEK & WORTEN, 1866 and in the Carboniferous of Europe and North America with *Anomphalus* MEEK & WORTHEN, 1867, *Tychonia* KONINCK,1881 and *Turbinilopsis* KONINCK, 1881.

Remarks: The modern Umboniinae ADAMS & ADAMS, 1854 can be connected with Paleozoic and Triassic Anomphalidae WENZ, 1938 (BANDEL 1993). HICKMAN & McLEAN (1990) in contrast suggested that *Umbonium* and relation with their special ecology as filter feeders that hide in the sand began their diversification in the early Tertiary. But since shell structure and morphology of the Carboniferous and the Triassic *Anomphalus* is exactly like that of modern *Umbonium* and the fossil species are found in sediments that indicate that they could also have lived in a similar way. Thus, it was suggested that the Umboniidae range back to at least Devonian time (BANDEL 1993). If this later scenario is correct, HICKMAN's (1988) whole hypothesis of trochoidean evolution collapses. She suggested that the Trochoidea arose in the Ordovician from slit bearing forms. According to her theory these Paleozoic trochomorphs by some unexplained and obscure change in calcium-carbonate metabolism changed into the Trochidae during the Triassic. From trochid stock the Umboniidae are interpreted to have arisen during the Cretaceous by departing from hard substrate into the soft sediment.

13.5 Trochomorph group *Platyschisma*

The shell shape closely resembles that of the *Anomphalus*-Group, but the outer lip of the aperture is sinuous, and the umbilicus remains open.

The genus *Platyschisma* McCOY, 1844 has a large shell that is globular with narrow umbilicus, low spire, and notch-like sinus in the upper half of the outer lip (KNIGHT 1941). The genotype is *Ampullaria helicoides* Sowerby, 1826 from Queens County Ireland and *Platyschisma helicomorpha* KONINCK, 1881 with the same age but from Belgium has a sinuous outer lip with a shallow lobe in its centre accompanied by a narrow bay on the apical flank and a wider one near the umbilicus. The Australian *Platyschisma vitrea* YOO, 1994 has a protoconch that could well belong to an archaeogastropod but its border to the teleoconch is not preserved (YOO 1994, Pl.3, Fig.12). Another species from the same locality was placed in the genus *Straparollus* by YOO (1994) is here transferred into the genus *Platyschisma* and called *P. brevis* (YOO, 1994). Here the embryonic shell represents an archaeogastropod-like embryonic shell. The type of the genus *Straparollus* MONTFORT,1810 is *S. dionysii* MONTFORT,1810 from the early Carboniferous of Belgium has a totally different protoconch morphology (own data) and size of both species differ considerably. Species of the genus *Straparella* FISCHER, 1885 with the type *Straparollus fallax* KONINCK, 1843 from the early Carboniferous of Belgium also have a heliciform shell with gently arched whorl profile, sharply rounded periphery and a characteristic ornament of collabral axial lirae that demonstrates a shallow sinus.

Remarks: KNIGHT et al. (1960) used *Platyschisma* to create the Platyschismatinae KNIGHT, 1956, which together with the Turbonellinae KNIGHT, 1956 compose the family Sinuopeidae WENZ, 1938. This later group was founded around the genus *Sinuopea* ULRICH, 1911 based on a late Cambrian shell that has a sinus in the outer lip of the aperture. WENZ (1938) considered this group to represent a questionable unit belonging to the Raphistomatidae KOKEN, 1896, which are placed jointly with the Sinuopeidae in the Pleurotomarioidea by KNIGHT et al. (1960). But just the presence of a sinuous outer lip does not place the genus *Platyschisma* with any selenimorph group, on the other side is the normally coiled archaeogastropod-like protoconch an indication that there is no closer relation to the *Euomphalus*/ *Straparollus* group.

13.6 Trochomorph group *Turbonellina*

Euomphaloid, low trochoidal shell shape is connected to a deep umbilicus and ornament of fine spiral liration. The apex and base are rounded. The aperture is oblique, with angulation at the rounded edge to the base, connected to a change of orientation of the outer lip forming a sinus here but no slit.

In the genus *Turbonellina* KONINCK, 1881 based on *Turbonellina lepidus* (KONINCK, 1843) from Visé in Belgium the trochiform shell with flattened and rounded apex consists of many slender whorls and a deep and wide conical umbilicus. Margins of the outer lip go obliquely backward with a twist in the periphery forming a notch at the periphery which does not generate a selenizone. YOO (1994) described *Platyschisma lingua* from the Australian early Carboniferous which actually represents a member of the genus *Turbonellina* since it is spirally ornamented and has a long tongue-like anterior siphonal extention of the outer apertural lip. It is, thus, transferred to this genus as *Turbonellina lingua* (YOO, 1994). *Rhabdopleura solida* has a solid columella and stronger spiral ribs in more dense packing. *Portlockia* KONINCK, 1891 with the type selected by COSSMANN (1915) as *Turbo pygmaeus* KONINCK, 1843 from Tournai in Belgium represents a turbiniform shell with arched whorl profile between sutures and rounded base. The ornament consists of spiral ribs and a groove between them on the periphery. According to KNIGHT et al. (1960, Fig 124,5) the genus had been renamed by KNIGHT (1941, Pl.41, Fig.5) into *Portlockiella* KNIGHT,1941 because the name is preoccupied by *Portlockia* M'COY, 1846. But unfortunately KNIGHT suggested *Portlockiella kentuckyensis* as type which has a selenizone deep on the whorl, while *Portlockia pygmaea* has no slit. *Turbo pygmaeus* KONINCK, 1843 is thus here provided with the new generic name *Portlockomphalus* n. gen. with the type *P. pygmaeus* (KONINCK, 1843) from the early Carboniferous limestones of Tournai in Belgium.

Remarks: The subfamily Turbonellininae KNIGHT, 1956 was placed in the family Sinuopeinae WENZ, 1938, together with the genus *Platyschisma* (KNIGHT et al., 1960). But WENZ (1938) had created the Sinuopeinae as questionable subfamily to the Raphistomatidae KOKEN, 1896 to hold only the genus *Sinuopea* ULRICH, 1911 that occurs from the late Cambrian to the early Ordovician of North America. WENZ placed neither *Platyschisma* nor *Turbonellina* in his Sinuopeinae but regarded *Platyschisma* to represent a member of the subfamily Euomphalinae WENZ, 1938 of the Euomphalidae KONINCK, 1881 within the Euomphaloidea KONINCK, 1881 and *Turbonellina* to represent a somewhat questionable genus of the Trochonematinae of the Trochonematidae ZITTEL, 1895 in the Trochonematoidea ZITTEL, 1895. The diagnosis offered by WENZ for Sinuopeidae differs from that of KNIGHT et al. (1960). *Turbonellina* could also be considered to represent a trochoidean genus. The family Sinuopeidae should be restricted to the genus *Sinuopea* until it is better known and can presently not be defined to include *Platyschisma* and *Turbonellina* especially if we consider WENZ (1938) as the creator of this systematic unit into which these gastropods are to be placed.

13.7 Trochomorph group *Cassianastraea*

Spine bearing trochomorphs with nacreous shell and archaeogastropod protoconch.

Cassianastraea BANDEL, 1993 with the type *Pachypoma damon* LAUBE, 1869 from the late Triassic of the Alps has a conical shell ornamented by undulatung collabral ribs which form several rows of gutter like spines in the outer lip of the oblique aperture. The base is flattened and the aperture provided with a short anterior notch. The inner shell layer is nacreous and the embryonic shell of archaeogastropod,type. *Cassianastraea haueri* (KITTL, 1891) from the same locality has a more slender shell, and both species differ from *Ampezzalina* BANDEL, 1993 with the type *Pleurotomaria calcar* MÜNSTER, 1841 from the same late Triassic St. Cassian Formation that has two to three rows of hollow spines instead of gutter like scales. In contrast to *Spinulrichospira* BLODGETT & ROHR, 1989 from the Devonian *Ampezzalina* has several rows of spines. The modern *Pachypoma* GRAY, 1850 with type *Trochus inaequalis* MARTYN from the western Pacific Ocean resembles *Cassianastraea* and *Ampezzalina* in general shape, but differ in regard to the larger shell and flattened early shell portion. The shell of the early Carboniferous *Echinocirrus* RYCKHOLT, 1860 with type *Cirrus armatus* KONINCK, 1843 from Tournai is trochiform, discoidal with spiral ribs of which three terminate at the margin of the oblique outer lip in tubercular openings. The base is ornamented by revolving costae and has a widely open umbilicus. *Omphalocirrus* RYCKHOLT, 1860 with genotype from Givetian reefoid limestones of western Germany has a shell with flat spire and wide umbilicus. A row of tubular spines is found on the base if the shell is considered dextral. The whorls are rounded, and the umbilicus is wide. The aperture is rounded. *Coelocentrus* ZITTEL, 1882 with the type *Cirrus polyphemus* LAUBE, 1868 from the late Triassic has a low shell with marginal hollow spines and nacreous inner shell layer (BANDEL 1993). A member of this group is also the Silurian *Spinicharybdis* and *Hystricoceras* JAHN, 1894 from the Silurian of the Barrandium. The later according to KNIGHT (1941, Pl. 58, Fig.1) has trochiform shell with a row of large tubercular spines at the periphery. Both closely resemble modern *Guildfordia* GRAY, 1850 with its long marginal hollow spines, but their protoconch and shell structures are unknown.

Remarks: WENZ (1938) placed the Carboniferous *Echinocirrus* together with the Devonian *Omphalocirrus* and the Triassic *Coelocentrus* in the family Omphalocirridae WENZ, 1938 of the Euomphaloidea KONINCK, 1881. KNIGHT et al. (1960) placed *Omphalocirrus* in the family Macluritidae FISCHER, 1885 of the Macluritoidea FISCHER, 1885 with sinistral shells and considered *Coelocentrus* to represent a synonym to *Omphalocirrus*. KNIGHT et al. (1960), thus, abolished the family Omphalocirridae and placed *Echinocirrus* in the Luciellidae KNIGHT, 1956 of the Pleurotomarioidea even though it has no selenizone. Fossil shells of the type of *Coelocentrus* with shell resembling *Guildfordia* characterized by a basal edge or lamella and flat to concave base with triangular section like *Hystricoceras* are placed by KNIGHT et al. (1960) with the Craspedomatoidea WENZ, 1938.

13.8 Trochomorph group *Trochonema*

Turbiniform shell with a corner at the middle outer lip of the aperture and at the edge of the whorl flank to the base. These two principal carinate angulations may be substituted by spiral ornament. The inner shell layer is nacreous, and there is an archaeogastropod protoconch.

YOCHELSON (1956) noted that Ordovician representatives of the genus *Trochonema* SALTER, 1859 and *Loxoplocus* FISCHER, 1885 are almost identical in shell morphology with exception of the slit present in the latter. The genus *Eunema* SALTER, 1859 with type from the middle Ordovician has a turbiniform shell with a corner at the middle outer lip of the aperture and is not as high as *Trochonema*. BANDEL (1993) newly described *Eunema tyrolensis* KITTL, 1891 from the late Triassic of the Alps that has an inner nacreous layer. *Amberleya elegans* (MÜNSTER, 1841) from the early Jurassic of Englands is also similar (HICKMAN & McLEAN 1990, Fig. 38C). The genus *Gyronema* ULRICH, 1897 with the type *Gyronema pulchellum* ULRICH, 1897 from middle Ordovician of Minnesota USA has similar shell shape, but in addition to the two principal carinate angulations several minor ones. *Gyronema armata* (GOLDFUSS, 1832) from the middle Devonian of western Germany grew to 45 mm high and 44 mm width and formed a rather thick shell wall and is ornamented with 7 or up to 8 spiral rows of tubercles which have finer rows of tubercles between them. *Gyronema armata* resembles members of the genus *Turbonopsis* GRABAU & SHIMER, 1909 from the early Devonian Onondaga Limestone of Kentucky (KNIGHT 1941, Pl. 55, Fig. 2) and *Gyronema ormistoni* BLODGETT, 1992 from the mid Devonian of Alaska could very well represent the same species. BLODGETT (1992) found *Devononema* FRAUNFELDER, 1973 from the Givetian of Illinois to represent a synonym of *Gyronema*. The smaller and more delicate *Gyronema filicostatum* (SPRIESTERSBACH, 1942) from the Eifelian Ohler Schiefer of Western Germany which may be closely related to *Gyronema minutinodosa* BLODGETT & JOHNSON, 1992 from central Nevada has an ornament of numerous closely spaced collabral threads which form nodes at their point of intersection with the spiral cords. *Guidonia* DE STEFANI, 1880 with the type *Trochus rotulus* STOLICZKA, 1861 from the Lias of the northern Alps is also known from the late Triassic of Peru (Haas 1953) and the Early Jurassic of New Zealand. It closely resembles *Eunema* from the Paleozoic (BANDEL 1993, 1994)

Remarks: The superfamily Trochonematoidea according to YOCHELSON (1956) can be traced from the Ordovician to the Permian, but is not found in the Mesozoic. BANDEL (1993, 1994) in contrast placed late Triassic shells from the St. Cassian Formation and Jurassic shells from Europe, Peru and New Zealand near or into the genera *Trochonema* and *Eunema* and demonstrated their archaeogastropod nature. *Guidonia* also fits into the description of *Trochonema*. KNIGHT et al. (1960) reduced the taxon Trochonematidae to only a few genera while WENZ (1938) had originally united in it a large number of Paleozoic gastropods which resemble modern and Triassic Archaeogastropoda. This similarity had been noted by the scientists in the last century when they compared the large Devonian *Gyronema armata* to the modern *Turbo*. Extant *Turbo fluctuosus* WOOD, 1828 for example is very similar in the shape of its shell as had been noted by GOLDFUSS (1832).

13. 9 Trochomorph group *Brochidium*

The planispiral shell has an ornament of axial ribs, calcitic outer shell layer and archaeogastopod protoconch.

Brochidium KOKEN, 1889 with the type *B. cingulatum* (MÜNSTER, 1834) from the St. Cassian Formation from the late Triassic of the Alps has lamellar axial ribs. *Sorapisella* BANDEL, 1993 in addition to axial lamellae also has fine spiral threads in its ornament and cooccurs with *Brochidium* in the late Triassic St. Cassian Formation.

Remarks: The Liotiinae ADAMS & ADAMS, 1854 according to HICKMAN & MCLEAN (1990) hold the fossil taxa Brochidiinae YOCHELSON, 1956 and other representatives of the Craspedostomatidae WENZ, 1938. Thus, the Triassic genera *Brochidium*, *Dichostasia* YOCHELSON, 1956, *Anisostoma* KOKEN, 1889 and the Jurassic *Crossostoma* MORRIS & LYCETT, 1851 are grouped here. *Brochidium* also resembles modern *Cyclostrema* MARRYAT, 1818 and other planispiral members of the Skeneidae. YOCHELSON's (1956) Brochidiinae are based on a Permian species that resembles the Triassic *Cortinella* BANDEL, 1989 and not *Brochidium*. *Cortinella* has a larval shell that places it among the Neritimorpha. *Dichostasia* from the Permian resembles Triassic *Rolandomphalus* BANDEL, 1993 from St. Cassian Formation which represents an archaeogastropod with nacreous layer that is not related to *Brochidium* with its calcitic outer shell layer. *Anisostoma* with its characteristiclly widened aperture resembles *Zardinihelix* BANDEL, 1988 without such aperture but nacreous layer. Thus, the Brochidiinae YOCHELSON, 1956 interpreted as synonym to the Craspedomatidae by (KNIGHT et al. 1960) do most probably not represent a natural group.

13.10 Trochomorph group *Wöhrmannia*

The shell is discus-like with flattened apex and clearly dextral coiling and has one or several asymmetrically arranged marginal keels. The inner shell layer is nacreous and the protoconch that of an archaeogastropod.

The genus *Woehrmannia* BÖHM, 1895 with the type *Woehrmannia cirroides* BÖHM, 1895 from the Triassic of the Alps has a low discoidal shell and angular corner to the apical plate as well as to the rounded base. Two spiral keels feature the upper flank of the whorls, and there is a wide umbilicus. *Zardinihelix* BANDEL, 1988 has angular corners to the base as well as to the apical plate and a peripheral keel occurs together with *Woehrmannia*. *Rolandomphalus* BANDEl, 1993 from the same locality differs by twisting its aperture upwards in the fully grown shell.

Remarks: The Angariinae THIELE, 1921 only hold the modern genus *Angaria* RÖDING, 1798 but according to HICKMAN & MCLEAN (1990) also contain among others the fossil genus *Asperilla* KOKEN, 1896 with Jurassic type that resembles *Woehrmannia*. WENZ (1938) interpreted *Asperilla* to be a member of the Platyacridae WENZ, 1938 and, thus, a representative of the Euomphaloidea to which KNIGHT et al. (1960) classified only *Woehrmannia*, but not *Asperilla*. Mesozoic euomphaloids as interpreted by these authors like *Amphitomaria* KOKEN, 1997, *Weeksia* STEPHENSON, 1941, *Coelodiscus* BRÖSAMLEN, 1909, *Hippocampoides* WADE, 1916, *Nummocalcar* COSSMANN, 1896, and *Discohelix* DUNKER, 1848 proved to be members of quite a number of different groups, of which the first four genera do not even represent archaeogastropods (BANDEL 1988), and all are not related to the Carboniferous type species of the genus *Euomphalus* SOWERBY, 1814 (own data). Triassic *Woehrmannia*, *Zardinihelix* and *Frederikella* BANDEL, 1993 with nacreous inner structure could also be placed among the modern Liotiinae as characterized by HICKMAN & McLEAN (1990).

13.11 Trochomorph group *Triadoskenea*

Planispiral, small smooth archaeogastropods with shell composed of crossed lamellar structure.

Triadoskenea BANDEL, 1993 from the late Triassic is based on the type *T. ampezzana* BANDEL, 1993 and represents a small (3 mm wide) shell.

Remarks: Skeneidae CLARK, 1851 unite a goup of many species of usually small to minute Archaeogastropoda of which little is known. They commonly do not seem to have a nacreous shell. Among Triassic genera *Brochidium*, *Triadoskenea* BANDEL, 1993, and *Sorapisella* BANDEL, 1993 from the fauna of the St. Cassian Formation could be included in the Skeneidae. Perhaps the Silurian

Temnospira PERNER, 1903 could fit here, but it also resembles the Triassic *Cortinella* that represent a neritimorph species.

13.12 Trochomorph group *Tylotrochus*

The conical shell has a profile with flattened whorls separated by well developed sutures and provided with a sharp edge with the base. Ornament consists of spiral lirae and collabral threads, and the apertuere is oblique. The protoconch is of archaeogastropod type.

The Tegulinae with the only genus *Tegula* LESSON 1835 resemble *Tylotrochus* KOKEN, 1896 with the type *Trochus konincki* HOERNES, 1856 from the late Triassic of the northern Alps. *Tylotrochus semipunctatus* (MÜNSTER, 1841) and *T. elongatus* BANDEL, 1993 occured a little earlier in the southern Alps (BANDEL 1993).

Remarks: Trochinae RAFINESQUE, 1815 could have a representative in the Triassic *Tylotrochus*. Jurassic representatives of the genus *Ozodochilus* COSSMANN, 1918 and *Cochleochilus* COSSMANN, 1918 could connect with modern *Gibbula* RISSO, 1826 and *Monodonta* LAMARCK, 1799, which are considered to make their appearance in the Cretaceous by HICKMAN & McLEAN (1990). *Cantharidus* MONTFORT, 1910 and *Jujubinus* MONTEROSATO, 1884 according to these authors also go back to the Cretaceous. KASE (1984) includes *Discotectus* FAVRE, 1913 from the Jurassic and Cretaceous of the Tethys in this taxon. Ataphridae COSSMANN 1918 with genera like *Ataphrus* GABB, 1896 and *Zircia* SZABO, 1981 encompass rounded smooth Jurassic gastropods of trochinid shape which probably are Archaeogastropoda (SZABO 1981). That they really represent archaeogastropods is neither confirmed as jet by protoconch morphology nor by shell structure.

14. Selenimorpha

A taxon can successfully be used only when its description is clear enough to allow its differentiation from other taxa. Fossil groups can thus be separated from each other and put into relation with modern groups. Only in groups with living representatives the anatomy can be studied and taxonomy can be based on more reliable data than can be extracted from the shell alone. Modern slit bearing archaeogastropods can, thus, be classified into four well differentiated superfamilies, the Pleurotomarioidea SWAINSON, 1840, the Haliotioidea RAFINESQUE, 1815, the Seguenzioidea VERRILL, 1884 and the Fissurelloidea FLEMING, 1922. Among these the first three have a nacreous shell (BANDEL 1990), and the shells of the last consist only of crossed lamellar structure (BATTEN 1975).

As long as several of the Paleozoic "families" of slit bearing gastropods can be fitted into the diagnosis of the Pleurotomariidae with extant representatives, it is not possible to present a taxonomic scheme that may come close to the reality of evolution. Obviously WENZ (1938) distinguished the core groups of Paleozoic slit bearing shells like Eotomatiinae WENZ, 1938, Gosseletininae WENZ, 1938, Ptychomphalininae WENZ, 1938, and Ptychomphalinae WENZ, 1938, basically by their occurrence prior to the Triassic. Because judging from their diagnostic descriptions of all of them could be fitted with that presented by WENZ for the subfamily Pleurotomariinae. This *Pleurotomaria* DERANCE, 1826 relation is interpreted to have begun with the Triassic period, based on the assumption that higher taxonomy of the Selenimorpha changed with the transition from Paleozoic to Mesozoic times.

A similar appearance of the *Pleurotomaria* relation was assumed by KNIGHT et al. (1960). But these authors modified the classification of WENZ (1938) considerably and included in the Pleurotomariina COX & KNIGHT, 1960 the superfamilies Pleurotomarioidea, Trochonematoidea ZITTEL, 1895, and Fissurelloidea. Scissurellidae and Haliotidae are interpreted to represent families of the Pleurotomarioidea in the same rank as Pleurotomariidae. KNIGHT et al. (1960) use 22 families to differentiate the Pleurotomarioidea. Of these the Sinuopeidae WENZ, 1938 and Euomphalopteridae KOKEN, 1896 have no selenizone, but only a more or less distinct U-shaped sinus in the outer lip of their aperture. The other families are basically characterized by the width, depth, morphology and position of the slit and the selenizone arising from it. As in the classification of WENZ Pleurotomariidae could in their definition encompass many of the other families, were they allowed to occur in times before the Triassic.

As long as knowledge is based on scattered faunal assemblages of ecologically and paleogeographically widely separate fossils of quite different age of which very often not even the early shell portion and the composition of the mineral shell are known, the resulting system can not satisfy the evolutionary biologist. We therefore should begin more humbly by finding morphological groups, here phrased selenimorph groups (Selenimorpha according to BANDEL & FRYDA in print), that unite archaeogastropods with a slit and selenizone, contrasting from archaeogastropods without that feature (Trochomorpha, see BANDEL 1993b).

15. Groups of the Selenimorpha

15.1 Selenimorph group *Pleurotomaria*

Slit bearing Vetigastropoda with nacreous inner aragonitic shell layer and rhipidoglossate radula of the *Pleurotomaria* type and with conical large shells as found among the modern species of *Pleurotomaria* SWAINSON, 1840 and related genera (TROSCHEL 1856-1863).

15.2 Selenimorph group *Bembexia*

Conical shell with peripheral selenizone and lower and upper keel on flanks. Inner shell layer nacreous.

The group is characterized by a median selenizone accompanied by an angle above with a keel and an angle below with or without keel. The upper flank is flattened, and the lower edge to the base is rounded. The group can be traced from the Lower Devonian to the Upper Carboniferous. It includes the genus *Bembexia* OEHLERT, 1888 with the type *Pleurotomaria larteti* MUNIER-CHALMAS, 1876 from the early Devonian of the Bretagne. *Bembexia* closely resembles *Balbinipleura* BANDEL & FRYDA (in print) that has a more acute apical angle. The species of the genus *Borestus* Thomas, 1940 are also more acute in shape and have one more spiral lira on the lower flank (2 spiral lirae here instead of one). Its type *Borestus wrighti* THOMAS, 1940 comes from the Scottish early Carboniferous and *Borestus costatus* YOO, 1989 (YOO 1989, Figs. 25-28, 1994, Pl.10, Figs. 1-5) occurs in the Australian early Carboniferous. The mid Devonian genus *Quadricarina* BLODGETT & JOHNSON, 1992 has two additional spiral lirae present on the selenizone which are absent in the otherwise similar *Bembexia*. The genus *Catazona* GORDON & YOCHELSON, 1983 with the type *Catazona rudilirata* GORDON & YOCHELSON, 1983 from the Lower Carboniferous of Nevada is low spired, but has the typical outline of the flank with upper keel, vertical flank with selenizone in it, and rounded angle to the base (GORDON & YOCHELSON 1987). This ornament is similar to that of *Borestus* where the selenizone lies higher (middle of flank), and there are fewer spiral keels or lirae. The genus *Lancedellia* BANDEL, 1991 has a selenizone with undulating margins and shell is quite slender; otherwise its Triassic type *Paleunema costata* ZARDINI,1978 resembles in size and ornament *Balbinipleura*. The group can be traced from the early Devonian to the late Triassic.

Remarks: In the *Worthenia* group the selenizone lies higher up in the whorl profile, while in the *Wortheniella* group the early teleoconch is flattened. In both these groups the upper flank may have a spiral rib or not, and the spiral rib or keel below the selenizone forms the periphery (BANDEL 1991, SCHWARDT 1992). The *Rhineoderma* group differs by its ornament of many spiral ribs, keels or rows of tubercules, but has the same general shell shape and position of selenizone (GORDON & YOCHELSON 1987). The *Ptychomphalina* group has uninterrupted upper and lower flanks bordering the peripheral selenizone, which lies next to the suture (KNIGHT 1941, GORDON & YOCHELSON 1987, BLODGETT 1992, Pl. 7, Figs. 11-13). In the *Rhaphistomatella* group the selenizone lies above the periphery. Members of group of *Mourlonia* have a more rounded whorl profile with broad selenizone at the periphery and just above or within the suture on the spire (KNIGHT 1941, GORDON & YOCHELSON 1987).

15.3 Selenimorph group *Rhineoderma*

The conical shell has a peripheral selenizone and ornament of spiral and collabral lirae. The inner shell layer consists of nacre.

In the trochiform shell of members of *Rhineoderma* KONINCK, 1883 with the type *Pleurotomaria radula* KONINCK, 1843 from the Lower Carboniferous of Belgium has more or less flattened whorls flanks and the ornamentation consists of opistocline collabral lirae and spiral threads or ribs commonly with nodes in intersections. The selenizone is generated by a slit in the middle of the outer lip and usually has regularly spaced lunulae. Succeeding whorls are attached directly adjacent or a little below the selenizone. Gradation into species of *Dictyotomaria* KNIGHT, 1945 with the type *D. scitula* (MEEK & WORTHEN, 1861) from the Late Carboniferous of Texas are present which connects Devonian species with such in the late Triassic like *Dictyotomaria subcancellata* (ORBIGNY,1849) and perhaps later Mesozoic ones (BANDEL 1991). The genus *Glabrocingulum* THOMAS, 1940 with the type *G. beggi* THOMAS from the Carboniferous of Scotland clearly repesents an archaeogastropod as was shown by YOO (1988, 1994) in case of two early Carboniferous species *Glabrocingulum obesum* YOO, 1988 and *G. pustulum* YOO, 1994 from eastern Australia which have the protoconch preserved. The genera *Phymatopleura* GIRTY, 1939 (= *Orestes* GIRTY), and *Deseretospira* GORDON & YOCHELSON, 1987, both from the Carboniferous of USA belong here as well. This seems to be a predominantly Carboniferous-Permian group with some species in the Devonian as well as in the Triassic.

Remarks: If ornamental patterns become less apparent, a transition to the *Ptychomphalina* Group is also seen.

15.4 Selenimorph group *Worthenia*

The conical shell has a flattened flank and selenizone on its upper corner. The inner shell layer is nacreous.

Members of the genus *Worthenia* KONINCK, 1883 (= *Ananias* KNIGHT, 1945) with *Turbo tabulatus* CONRAD, 1835 from the late Carboniferous of Indiana (WENZ 1938, KNIGHT 1941) have a characteristically conical shell with flattened vertical median portion of whorl profile flanked by two keels, with the selenizone forming the upper keel. Ornament of collabral growth increments and lirae and spiral lirae and ribs. The genus *Baylea* KONINCK, 1883 with the type *Trochus yvanii* LÈVEILLÈ, 1835 from the early Carboniferous of Belgium differs by having the selenizone not as raised keel as is the case with *Worthenia*. In addition *Baylea* is covered by spiral ribs. *Ruedemannia* FOERSTE, 1914 is close to *Worthenia* and has the Ordovician type *Lophospira lirata* ULRICH, 1897. The selenizone of an Australian species of *Ruedemannia* from the early Carboniferous described by YOO (1994) is like that of *Worthenia*. The Devonian genus *Oehlertia* PERNER, 1907 with early Devonian type *Pleurotomaria senilis* PERNER, 1907 from Pragian Koneprus-Limestone resemble a mid Devonian species from western Germany (own observations). The Permian *Eirlysia* BATTEN, 1956 is turbiniform with rounded angulation and selenizone between two threads slightly above mid-whorl. The type is *Eirlysia exquisita* BATTEN, 1956 from the Permian of Texas.
Remarks: The *Worthenia* group can be traced to the Ordovician and may grade into the Triassic *Wortheniella* group. With the lower angulation of the profile of the whorl of *Worthenia* becoming more rounded the shell resembles those of the *Rhineoderma* group. Transitions between these two groups can easily be consťructed. If the selenizone wanders a little down, members of the *Worthenia* group would change in such of the *Bembexia* group.

15.5 Selenimorph group *Wortheniella*

Like *Worthenia*, but with flattened apex that is in early whorls planispirally coiled. The shell is nacreous and the protoconch of the archaeogastropod type.

SCHWARDT (1992) described a number of species of *Wortheniella* SCHWARDT, 1992 present in the late Triassic St. Cassian Formation alongside with the genus *Bandelium* SCHWARDT, 1992. They resemble the Paleozoic representatives of the *Worthenia* group regarding ornament of the teleoconch and position of the selenizone, but not in regard to the flat early shell whorls. These are trochospiral in members of the *Worthenia* group which has been illustrated by YOO (1994). Nothing is known about the continuation of *Wortheniella*-like selenimorphs in the Jurassic or later times, while a derivation from *Worthenia*-like forms of the Late Paleozoic is possible.

15.6 Selenimorph group *Rhaphistomella*

The low shell has a subsutural row of nodules and upper peripheral slit. Inner shell layer nacreous, and the embryonic shell is of archaeogastropod type.

The shell with narrow base and flatted upper surface has a labral sinus in a shallow notch that generates a selenizone. It is characterized by the median selenizone, the subsutural row of nodes or ribs, and the structure of its shell with disected crossed lamellar aragonitic structure on the outer layer, and nacreous structure in the inner layer. The group is based on the genus *Rhaphistomella* KITTL, 1891 with Triassic genotype and holds *Trepospira* ULRICH & SCOFIELD, 1897 based on *Pleurotomaria sphaerulata* CONRAD, 1842 with Upper Carboniferous genotype, and *Angyomphalus* COSSMANN, 1916 with *Euomphalus radians* KONINCK, 1843 from the Lower Carboniferous as genotype. The group can be traced from the Lower Devonian to the Upper Triassic and species are recognized from Lower Carboniferous of North America (KNIGHT 1933, GORDON & YOCHELSON 1987) and Europe (KONINCK, 1843) as well as Australia (YOO, 1989) to the Upper Triassic of the Alps (BANDEL 1991).

Remarks: WENZ (1938) included *Trepospira*, *Angyomphalus* and *Rhaphistomella* in the family Pleurotomariidae, subfamily Ptychomphalinae together with rather different genera like *Büchelia*. KNIGHT et al. (1960) utilized the family Raphistomatidae KOKEN, 1896 with subfamily Liospirinae KNIGHT, 1956 holding *Trepospira* and *Angyomphalus*. But they included *Rhaphistomella* in the Eotomariidae subfamily Eotomariinae. Nothing is known about possible survivors of the group from the Jurassic onwards.

15.7 Selenimorph group *Mourlonia*

The biconical to globular shell has a peripheral selenizone, next to suture. The inner shell layer is nacreous, and the protoconch is of the archaeogastropod type.

The shell has uninterupted upper and lower flanks bordering the peripheral selenizone, which lies next to the suture. Such species are common in the Carboniferous of North America and Europe (KNIGHT 1941, GORDON & YOCHELSON 1987). Here the genus *Ptychomphalina* (= *Ptychomphalus* of KONINCK, 1881) is based on *Helix ? striatus* SOWERBY, 1817 from the early Carboniferous of England. It is extremely similar to the genotype of *Mourlonia* KONINCK which is *Helix carinatus* SOWERBY, 1812 also from the early Carboniferous of England. The genus *Ptychomphalus* AGASSIZ, 1839 with early Jurassic type species *Helicina compressa* SOWERBY, 1813 was noted with *Ptychomphalus protei* (LAUBE,1868) from the Triassic St. Cassian Formation (BANDEL 1991). Here the slit lies above the periphery with its lower margin forming the edge of the flattened flanks in the biconical shell. The genus *Euzone* KOKEN, 1896 has a globular shell with low whorl profile and increments of growth prominent and bent toward the selenizone that arised from a short slit in median position in the rounded aperture. The type *Euzone alauna* KOKEN from the Upper Triassic of the northern Alps with selenizone on the rounded whorls in median position resembles *Euzone calypso* (LAUBE, 1868) (BANDEL 1991). The Triassic *Euzone* closely resembles those members of *Mourlonia* that have an indistinct selenizone in median position and fine spiral liration as background ornament and the group can, thus, be traced from mid Paleozoic to the Upper Triassic.

Remarks: GORDON & YOCHELSON (1987) placed *Mourlonia* and *Ptychomphalina* in different subfamily level taxa - Ptychomphalinae (*Mourlonia*) and Eotomariinae (*Ptychomphalina*) - even though both genera differ only in regard to a more flattened upper flank in *Ptychomphalina*. They also thought that *Mourlonia* had a wider selenizone than *Ptychomphalina* which is not so when the types of both genera are compared with each other (BATTEN 1967, and own observations on the type-species as well as on related species from the Lower Carboniferous of Belgium). The suggestion of WENZ (1938) to place both in the same subfamily Ptychomphalininae has more creditibility and even the suggestion of KNIGHT et al. (1960) placing both genera in one and the same genus *Mourlonia* could be accepted.

15.8 Selenimorph group *Stuorella*

The conical shell has a flattened whorls and selenizone near the peripheral edge to a flattened base. Inner shell structure is nacreous and the embryonic shell of the archaeogastropod type.

Stuorella KITTL, 1891 has an acutely conical shell with flattened whorl profile and indistinct sutures. The selenizone lies above the peripheral edge in the lower or central portion of the outer lip of the aperture. The base is flattened or concave. The type is *Stuorella subconcava* (MÜNSTER, 1841) from the late Triassic St. Cassian Formation (BANDEL 1991). Rather similar, but with selenizone slightly higher in more central position of the flattened whorl flank occurs in the same stratigraphical and ecological position *Codinella* KITTL, 1899. Similar shell shapes are found among Jurassic predecessors of modern Pleurotomariidae as well as with the Permian *Lamellospira* (BATTEN, 1972) and Carboniferous *Glyptotomaria* KNIGHT, 1945. *Glyptotomaria* with the type *Glyptotomaria apiarium* KNIGHT, 1945 comes from the Pennsylvanian of Texas and is turbiniform to high trochiform beehive-shaped with flattened base and ornament of collabral and spiral lirae. Its selinizone is depressed and bordered by cords.

Remarks: KNIGHT et al. (1960) placed *Codinella* along with *Glyptotomaria* in the family Phymatopleuridae while *Stuorella* is considered to represent a member of the Pleurotomariidae. Genera like *Peruvispira* CHRONIC, 1949 and *Pagodina* WANNER, 1942 both from the Permian could intermediate between members of the *Stuorella* group and those of the *Bembexia* or *Worthenia* group.

15.9 Selenimorph group *Gosseletina*

The rounded shell has the selenizone high up on the whorl. The embryonic shell is of the archaeogastropod type.

Gosseletina BAYLE, 1885 with the type *Pleurotomaria callosa* KONINCK, 1843 from the Visé of Belgium has a globular shell of medium size with rounded whorl faces with selenizone high up on the flank. Whorls overlap so much that the suture lies close to the selenizone. Ornament consists of very fine spiral striation on smooth background. A species from the late Triassic St. Cassian Formation is *Gosseletina fasciolata* (MÜNSTER, 1841) (BANDEL, 1991). The genus *Rhaphischisma* Knight, 1936 (=*Rotellina* KONINCK, 1881) with the type *Rotellina planorbiformis* KONINCK, 1881 from the Tournai of Belgium has a rotelliform shell with depressed spire. The selenizone lies close to the upper suture, and a callus covers the umbilicus. *Platyloron* OEHLERT, 1888 with type *Pleurotomaria bischofi* GOLDFUSS,1844 from the mid Devonian of western Germany has a flatly rotelliform shell with the selenizone on the upper side of its whorls and smooth shell. The early Devonian *Planozone* PERNER, 1907 from the Barrandium is a little higher than *Platyloron* and has a wider selenizone. In the similar *Umbotropis albicans* PERNER, 1903 from the same Pragian limestones the selenizone is partly covered by the suture (KNIGHT 1941). The genus *Stenoloron* OEHLERT, 1888 is based on *Pleurotomaria viennayi* OEHLERT, 1888 from the mid Devonian of northern France is also rotelliform with slit just above the suture. The *Gosseletina* morphogroup can therefore be traced from early Devonian to late Triassic.

Remarks: KNIGHT et al. (1960) consider the genus *Rhaphischisma* to represent the only member of the Rhaphischismatidae KNIGHT, 1956 of the Pleurotomarioidea. WENZ (1938) placed *Gosseletina* in the Gosseletininae, a taxon that was raised to family status by KNIGHT et al. (1960) and considered to have been in existence from the mid Ordovician to the late Triassic.

15.10 Selenimorph group *Luciella*

The frilled margin carries the selenizone below it and ornament on upper whorl surface includes strongly prosocline threads and growth lines. The base is covered with spiral cords.

Luciella KONINCK, 1883 with the type *Pleurotomaria eliana* KONINCK, 1843 from Visé in Belgium. The genus *Rhombella* BRIDGE & CLOUD, 1947 represents a *Luciella* without crenulated fill and ornament with growth lines and probably can be regarded as a synonym to *Prosolarium* PERNER, 1903 which is quite like *Rhombella,* but of Silurian and not Ordovician age. *Epiptychia* PERNER, 1907 is much higher and of early Devonian age.

Remarks: WENZ (1938) placed the genus *Luciella* in the subfamily Gosseletininae of the Pleurotomariidae. According to KNIGHT et al. (1960) it belongs to the Luciellidae KNIGHT, 1956 of the Pleurotomariioidea which is also thought to contain *Echinocirrus* RYCKHOLT, 1860 that has no clearly demarcated selenizone and spinose flanks.

15.11 Selenimorph group *Buechelia*

The shell has a flattened apex and conical base with peripheral selenizone.

Buechelia SCHLÜTER, ,1894 with the type *Buechelia goldfussi* SCHLÜTER, 1894 from the mid Devonian of Western Germany has a reversed conical shape with flattened apex and sharp peripheral angulation that carries the selenizone. The conical base is partly covered by the thickned inner lip of the aperture which is continuous into the channelled columella. *Buechelia* resembles the Ordovician *Raphistoma* HALL, 1847, which according to KNIGHT (1941) had a shorter slit. *Scalites* EMMONS, 1842 with the type *Scalites angulatus* EMMONS, 1842 from the Ordovician of New York State, USA carries a selenizone on the periphery that originates in a deep labral sinus present on the edge between the broad flattened apical ramp and the vertical flank extending into a base with subconical shape (KNIGHT 1941). The Carboniferous genus *Ampulloscalites* WENZ, 1938 with the type *A. tabulatus* PHILLIPS from the early Carboniferous of Belgium has a slit (KONINCK 1881) and selenizone on its periphery. The shell has a flat apical spire and conical base without open umbilicus. Members of the morphogroup *Buechelia* occur from the Ordovician to the Carboniferous and have no known relatives in the Mezoizoic period. Since their shell structure is not yet known, the relation to the Pleurotomarioidea remains unsolved.

Remarks: According to KNIGHT et al. (1960) *Buechelia* is considered a relative to *Raphistoma* and thus placed in the Raphistomatidae KOKEN, 1896 within the Pleurotomarioidea. The subfamily Omospirinae WENZ, 1938 holds the genera *Omospira* and *Buechelia* but not *Ampulloscalites.* WENZ (1938) interpreted the Omospirinae to represent members of the Murchisoniidae.

15.12 Selenimorph group *Catantostoma*

The aperture of fully grown small shell deviates from the trochospiral coiling and may have slit and aperture differentiated into holes in *Catantostoma*, or bearing a sinus in *Anarconcha*, a slit in *Brilonella*, no slit in *Mitchellia* and *Scoliostoma*. These small shells are ornamented by a network formed by equally strong spiral and axial ribs.
Catantostoma SANDBERGER, 1842 is a conical shell with rounded whorls that carries the selenizone below the periphery. The final whorl deviates and bends in anterior direction displacing the umbilicus between the lips of the aperture. Thus the aperture is narrowed, and its margins are thickened. The slit ends before reaching the shell margin and there is a key hole shaped final

opening. The anterior notch of the aperture also forms a hole (KNIGHT 1941). *Anarconcha* HORNY, 1964 based on *Pseudomurchisonia pulchra* PERNER,1903 from the Pragian limestones of the Barrandium has a more highly coiled shell than *Brilonella* KAYSER, 1873. It could represent a species of *Brilonella* with the type *Scoliostoma serpens* KAYSER, 1872 from the mid Devonian of Western Germany. It also has the slit forming a deep indentation without clear selenizone behind it like the type of *Brilonella*: *Cosminia complacens* PERNER,1903 from the Pragian limestone presents the regularly coiled early shell portion of a *Michellia* KONINCK, 1877 in which the last whorl is usually twisted off (HORNY 1991). Thus, *Mitchellia complacens* (PERNER,1903) belongs to a genus with the type *M. striatula* KONINCK, 1877 from the Devonian of Australia. The genus *Scoliostoma* BRAUN, 1838 with the type *S. dannenbergi* from the mid Devonian of western Germany has a conical shell which in fully grown shells twists to the left. Perhaps *Odontomaria* ROEMER, 1876 with the type *O. elephantina* ROEMER, 1876 from the mid Devonian of western Germany belongs here as well. It represents an uncoiled selenimorph shell with unknown early portion and shell structure (KNIGHT 1941).

Remarks: KNIGHT (1941) interpreted the second opening in the apertural notch of the fully grown *Catantostoma* as ingestive opening to water entering the pallial cavity and the hole at the end of the selenizone as egestive opening. Such a current through the pallial cavity suggests the presence of one gill only. Similar currents are seen in the Seguenziidae where we have species with and without slit (MARSHALL 1988). The slit bearing and slit-less Devonian species here united in the group *Cantatostoma* coud represent a similar case. *Anarconcha* could be a precursor of *Brilonella* with sinus in the outer lip. *Brilonella* deepened the slit to such a degree that a selenizone formed behind it. With the Barrandian and Australian species of *Mitchellia* there are related species of the early Devonian *Anarconcha* with uninterrupted apertural margins, which in the mid Devonian *Scoliostoma* twist to the left when fully grown. In the case of *Catantostoma* the slit became closed to form a hole and the shell twist resulted in a second hole.

These small gastropods of similar whorl dimensions, ornament and shape may, thus, form an interrelated group in which *Brilonella* has been placed with the Murchisoniidae by KNIGHT et al. (1960), *Catantostoma* to the Catantostomatidae of the Pleurotomarioidea, *Scoliostoma* (= *Mitchellia*) to the Codonocheilidae S.A.MILLER, 1889 of the Craspedostomatoidea WENZ, 1938. All these genera could be placed with the Catantostomatidae WENZ, 1938 representing an independent group of which we still do not know the early ontogenetic shell and the shell structure.

15.13 Selenimorph group *Laubella* KITTL, 1891

The small trochispiral shell is ornamented with axial and spiral lirae resembles slit bearing species of the modern Seguenziidae. Like these they carry the selenizone high up on the whorl, and whorl profile is rounded. Like modern *Seguenzia* JEFFREYS, 1876 the inner shell layer is nacreous and the embryonic shell of the archaeogastropod type.

The superfamily Seguenzioidea consists of usually small (around 2-5 mm) species of which some have a slit and selenizone and others not (MARSHALL 1983, 1988, QUINN, 1983). BANDEL (1991) recognized in the genus *Laubella* KITTL, 1891 from the Late Triassic a probable fossil representative of this group of nacreous archaeogastropods (BANDEL 1979) which may be related to the Trochoidea, but not to the Pleurotomarioidea. BANDEL (1991) reconstructed the function of the mantle cavity of *Laubella* and *Schizogonium* KOKEN, 1889 from the Triassic as connected to one gill, and similar reconstructions could be applied to several Paleozoic selenimorph groups with species that have a slit in another than central position of the outer lip.

15.14 Selenimorph group *Schizogonium*

The flat and spiny shell has a planispiral juvenile whorls and slit on the upper side and periphery with keel and spines. The inner shell is nacreous and the embryonic shell that of the archaeogastropod type.

Representatives of the genus *Schizogonium* KOKEN, 1889 are known from the late Triassic and are based on the type *S. scalare* (MÜNSTER, 1841) from the southern Alps. A similar shell is found in the genus *Spinulrichospira* BLODGETT & ROHR, 1989 with moderately high-spired minutely phaneromphalous shape and tube-like spines just below mid whorl height. There is probably a selenizone above the spines. The type is *S. cheeneetnukensis* BLODGETT & ROHR, 1989 from the early Eifelian of Alaska.

Remarks: The Schizogoniidae COX, 1960 have been placed with the Pleurotomarioidea. But BANDEL (1991) interpreted the presence of a channel near the peripheral keel alongside with the slit as indication of a siphonal canal formed by the mantle fold. Thus, water would have entered the pallial cavity via this canal and left it through the slit, in a similar way as is found in the Seguenziidae.

15.15 Selenimorph group *Temnotropis* LAUBE, 1870

The *Haliotis* like shell has a rapidly enlarging shell diameter and slit above periphery. The inner shell layer consists of nacre.

The Haliotioidea with ear- shaped nacreous shells with a row of tremata may or may not have ancestors in the nacreous slit bearing *Temnotropis* LAUBE, 1870 group (Temnotropidae COX, 1960) of the Late Triassic (BANDEL 1991). The genus *Haliotis* LINNÉ, 1758 is not clearly recognizable before Late Cretaceous time.

15.16 Selenimorph group *Scissurella* ORBIGNY, 1824

The small trochoidal shells have a selenizone with open and closed slit, grading into limpets of emarginulid and key hole limpet (fissurellid) shape. The shell consists predominantly of crossed lamellar structure.

Similarities of the anatomy and shell structure connects the scissurellids with the key hole limpets of the Fissurellidae FLEMING, 1822 (HASZPRUNAR 1988, 1989). Thus, we may connect Scissurellidae and Fissurellidae in the Fissuelloidea and see in them a monophyletic group, even though they are well differentiated from each other since late Triassic times (BANDEL 1994). The Scissurelloidea/Fissurelloidea have their earliest representative in the late Triassic St. Cassian Formation (Bandel 1994).

16. Classification of the gastropods according to their mode of ontogeny

Only the Docoglossa among the gastropods own a "trochophora" stage of larval development during which there is a mouth and anus, but no shell (Pseudotrochophora according to SALVINI-PLAWÉN 1980, Praeveliger according to FIORONI 1970). Among the other gastropods such a phase occurs only in yolk feeding forms. JÄGERSTEN (1972) suggested that recent pelagic larvae represent the result of the adaptation of juvenile forms in order to live in the open water. Direct development should be the original process. According to this theory metamorphosis arose when the life cycle of the early Metazoa became partly pelagic and partly benthic. In this case the juveniles remained in the pelagic zone, where they continued to swim about with the aid of their ciliary cover, while the adults became bottom dwellers and bilaterally symmetrical. The continued evolution of both pelagic young and the benthic adult implied that metamorphosis became more extreme. Thus, the two development stages diverged, and the juvenile form became a larva.

The larva of the Docoglossa and the simple larva of *Teredo* (BANDEL 1987) can be taken as evidence for the presence of an original planktotrophic phase in the development of conchiferen molluscs. But they can not be used to construct a direct homology between the metatrochal ciliary bands of the veliger larva and the annelid/ echiurid trochophore as suggested by NIELSEN (1985, 1987). If this is so, both Vetigastropoda and Protobranchia have lost their planktotrophic feeding and

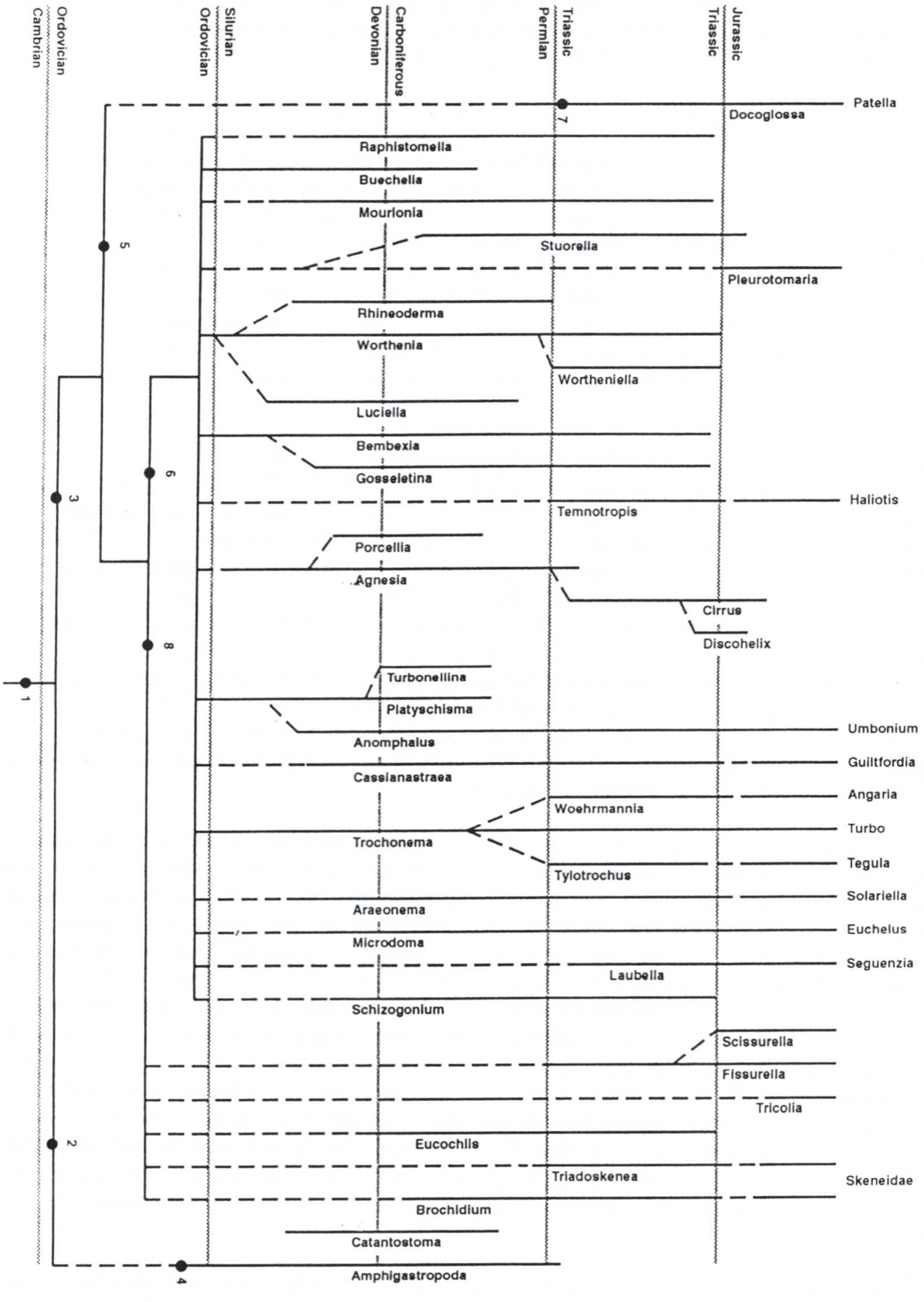


Figure 9: Hypothetical relation of Morphogroups of Archaeogastropoda connected with their occurrence in time. Interrupted lines are only suggestion.

Fig. 8

1. Torsion of the soft body (Gastropoda). 2. Torsion after emryogenesis. 3. Torsion during emryogenesis. 4. Torsion after formation of the embryonic shell. 5. Addition of larval shell during late embryonic development. 6. Convolute dextral larval shell surrounding untorted embryonic shell. 7. Shell formation after soft body torsion. 8. Embryonic and larval shell same coiling mode as teleoconch. 9. Embryonic shell and larval shell different coiling mode as teleoconch.

substituted it by yolk reserves. Docoglossa and Scaphopoda still have simple planktotrophic larvae (SCHARENBERG in prep), the eulamellibranchiate bivalves and higher gastopods can still activate this old constructional plan, if needed (BANDEL 1982, 1987).

Torsion in Gastropoda amounts to a twisting of the body so that the shell is rotated through 180°. Its presence defines a snail. GARSTANG (1929) arrived at the opinion that the torsion made its first appearance in the veliger larva. He suggested that torsion arose as a larval adaptation that it was carried over into the adult stage, the adults being then compelled to cope with the resulting situation. Thus, torsion should be more advantageous to the larva than to the adult. GARSTANG considered the gastropods to be the outcome of a sudden jump in the evolution of the veliger larva. With its visceral mass reversed this new larva settled down and grew into a torted mature specimen that had untorted parents. The handicap in GARSTANG's idea is that he thought that prior to torsion the protective value of the larval shell was limited because the delicate head and velum could not be withdrawn into the posterior mantle cavity until the foot had been withdrawn. Torsion supposedly facilitated the withdrawal of the head and velum, because the mantle cavity moved into a more favourabel position.

As was shown conclusively by BANDEL (1982), the theory is wrong because the head foot is not retracted into the mantle cavity and, thus, the argument of GARSTANG (1929) has lost its base. JÄGERSTEN (1972) had regarded this scenario as an unlikely one, but suggested that the phylogenetic appearance of the phenomenon occurred gradually in the adult phase to be shifted later to the pelagic larva. His view was confirmed by BANDEL (1982) when the embryonic development of several archaeogastropods was analysed. Also STANLEY's (1979) ideas can not be correct according to which it is nearly impossible for an untorted gastropod-like mollusc to evolve an operculum. STANLEY's problem can be comprehended when his Fig.6 is taken into reconsideration. Here the operculum and head foot has to enter the mantle cavity when the retractor muscle contracts. They do not have to do this as assumed by GARSTANG and CROFTS since in real life the whole mantle cavity is also withdrawn deeper into the shell, and the cavity is thus closed when the head foot are pulled in. Thus, in contrast to STANLEY´s theory an untorted pregastropod could well have had an operculum and be able to withdraw in its shell.

The embryo of an archaeogastropods forms first a bilaterally symmetrical primary shell that detaches from the glandular cells of the mantle as soon as it has grown to a size that is sufficient to contain the soft body in its shelter (BANDEL 1982). Only afterwards the visceral mass is twisted by about 180° due to differential growth of its epidermis. Thus, head food are rotated in relation to the shell. During the process of body torsion the growing foot changes its position from lateral/dorsal to ventral. The shell is later transformed into the trochospiral, usually dextral coil aided by the activity of muscles. Two muscle bundles are usually attached to the inner side of the shell and continue into body and foot. When the foot with its dorsal operculum is pressed against the outer side of the shell while muscle fibres attached to the inner side pull the shell is deformed. Since muscles are usually not attached symmetrically to the inside of the shell but assymetrically a lateral twist results in a dextral, rarely in a sinistral coil during the deformation. After the shell has been pulled into spiral shape it is mineralized from within and, thus, fixed in shape. During this rapid process aragonitic crystallites grow into the organic material of the primary shell which is mineralized thoroughly. The weaker of the two muscle bundles detaches from the shell and the stronger transforms into the columellar retractor muscle.

Archaeogastropods perform torsion of the body after the shell has been formed. All other extant gastropods secrete a shell only after the shell-less soft body has been torted due to differential growth of its tissues. Thus, archaeogastropods differ from all other gastropods by the timing of torsion of the visceral mass in relation to shell formation. The sister group of the Gastropoda, the Cephalopoda still have retained the type of mineralization that is found among the archaeogastropods (BANDEL 1982, 1986). Archaeogastropods reflect in their ontogeny still the difference in timing between torsion of the soft body and spiralization of the shell. Thus, a stage of gastropod evolution can be imagined in which the soft body torsion occurred even later in ontogeny as is the case in Archaeogastropods. NAEF (1911) considered the bellerophontids (Amphigastropoda) to represent gastropods in which torsion occured during the early benthic stage and resulted in a totally symmetrical shell. Thus, bellerophontids may represent such gastropods where the soft body torted after embryogenesis was completed and the shell mineralized. According to PEEL (1991) *Bellerophon* is more easily reconstructed as torted gastropod than as untorted bilaterally symmetrical monoplacophoran-like mollusc which supports NAEF's hypothesis. The Amphigastropoda could in this case be regarded as one of five subclasses of the Gastropoda.

If *Bellerophon* and its relation is a gastropod the presence of crossed lamellar structure in Fissurellidae/ Scissurellidae as well as the Phasianellidae and relation and some Skeneidae could represent a very old character of shell structure that formed very early in gastropod evolution.

The primary or embryonic shell of the archaeogastropoda is succeeded by the teleoconch. In all other gastropod groups an additional shell may be secreted between embryonic primary shell and the teleoconch. In these cases ontogeny is extended, and the larval shell differs from the primary shell and from the postmetamorphic shell. Such larval shells can be found on Paleozoic gastropods (HERHOLZ 1992, YOO 1989,1994, BANDEL 1991, 1993, 1994). The adult shells belonging to these can be grouped according to KNIGHT et al. (1960) with the Platyceratoidea, the Murchisonioidea, the Loxonematoidea, the Subulitoidea, the Cerithioidea and the Pyramidelloidea, all of which can be traced to the Ordovician by their teleoconch morphology (WENZ 1938, KNIGHT et al. 1960).

The larval shell enables marine species to construct a shell that serves and grows on a free-swimming larva that feeds on planktonic organisms. This differs from *Patella* and *Acmaea* which may feed in the plankton without having velar lobes and without growing a larval shell (KESSEL 1964, DODD 1957). Members of the Vetigastropoda, as far as is known, have no planktonic feeding stage. JÄGERSTEN (1972) and STRATHMANN (1978) emphasized the concept that an evolutionary loss of the planktotrophic larva is irreversible. This could distinguish the Vetigastropoda that have lost the pelagic feeding capacity from the more primitive Docoglossa which feed with simple ciliary corona and some cilia surrounding the mouth.

Planktotrophic larvae of the Neritimorpha, Caenogastropoda and Heterostropha in contrast have ciliary bands oriented on the outer margins of the velum (FRETTER & MONTGOMERY 1968). These larvae move through the water and at the same time collect particles which become entrapped between the ciliary bands. The cilia of the outer band drive particles downward to the ciliated groove. Here cilia transport the particles to the mouth. Transition from embryonic stage into larval stage and metamorphosis in the adult stage in gastropods is an important step in the life history. This transformation process from the larva and from the later to the adult organization distinguishes the subclasses of the Gastropoda. Neritimorpha secrete during the embryonic development a shallow concave and smooth primary shell. The shell is mineralized and attached with a tissue at the same place where the later differentiated retractor muscle connects to the interior of the shell, and further growth is connected with the secretion of shell increments until the embryonic shell resembles an egg with the upper part cut off laterally. With this shell planktotrophic life begins during which a convolutely coiled shell is secreted which in Neritidae is transformed into a simple hollow sphere by dissolution of the inner walls. No caenogastropod is known where smooth whorls of the larval shell overlap as much onto the embryonic shell and following whorls (BANDEL 1982, 1991b).

While HASZPRUNAR (1988) proposed a common ancestor of Caenogastropoda and Heterobranchia (=Heterostropha) with metatrochal ciliary bands present in the veligers of both groups directly homologous, PONDER (1991) proposed the derival of the Heterostropha from a small sized stem species with lecithotrophic development. Accordingly PONDER assumed an independent evolution of larval planktotrophy in Caenogastropoda and Heterostropha. The later interpretation can not be supported with fossils and there is also no evidence to support the first interpretation.

Four distinct features in the ontogeny of the Archaeogastropoda separate them from the other three subclasses of extant Gastropoda:

a. The change from external to internal fertilization as a fixed ontogenetic trend caused a change in the morphology of the spermatozoa which did not occur in the archaeogastropods. Three types of basic morphologies are evidence for independent development of the three internally fertilizing groups of Neritimorpha, Caenogastropoda and Heterostropha.

b. External fertilization postulates the accessability of spermatophores to the eggs and thus inhibits the enclosure of eggs within a capsule that can hold back salt and yolk. This limits the Archaeogastropoda to water of normal marine salinity and inhibits to enclose eggs in liquid yolk. Internal fertilization allows to cover fertilized eggs with an egg capsule that can prevent salts and yolk from leaking out.,Thus, environments with higher or lower salinity can be conquered as has been the case among some of the groups contained within the Neritimorpha, Caenogastropoda and Heterostropha.

c. The first body opening appears as mouth only in very special cases of yolk feeding intracapsular ontogenies (BANDEL 1982, 1987). The planktotrophic case displays the construction of a complete intestine with mouth stomach and anus coming into function at the same time. This case still without shell in a free swimming larva is encountered among gastropods only in the Docoglossa. It is also seen in Bivalvia (*Teredo*), and Scaphopoda. Its presence only in the Docoglossa indicates the very basal position of this group among the Gastropoda.

d. The primary shell of the Archaeogastropoda is deformed before it becomes mineralized. Aragonite crystallites grow into the organic shell here as well as in the ammonites among the cephalopods. Other gastropods have an embryonic and larval periostracum that forms the base to mineral deposits, but is not mineralized in itselve.

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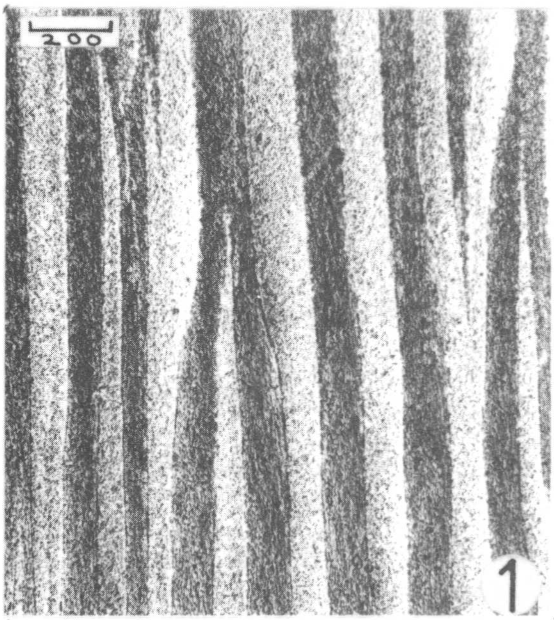
Plate 1:	The outer calcitic crossed lamellar layer of *Patella crenata*. The included scale is in microns.
Fig.1 & 2:	Section oblique to the shell surface.
Fig. 1:	Light-dark alternation of first order lamellae. x 50.
Fig. 2:	The first order lamellae twist to the right side upon approaching the outer surface of the shell. x 33.
Fig.3:	View onto the shell surface near the rim of a juvenile shell with lamellae of the first order parallel to the rim. Second order lamellae crop out with right angle or oblique to the boundaries of first order lamellae. x 200.
Fig.4:	Fracture oriented as in Fig.1 with dark-grey alternation of first order lamellae. x 100.
Fig.5:	The detail to Fig. 4 with lamellae of the second order nearly horizontally broken, forming steps. The fine vertical striations on the surface of the second order lamellae represent the boundaries of third order lamellae. x 370.
Fig. 6:	The oblique fracture demonstrates in diagonal direction four lamellae of the first order. x 350.



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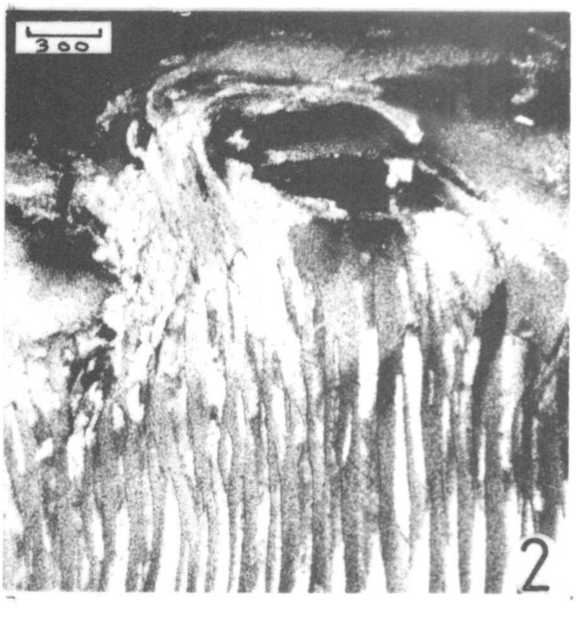

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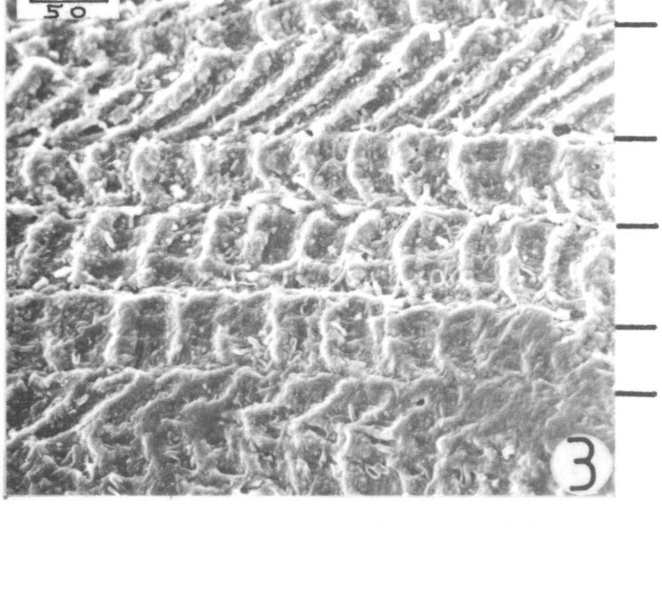

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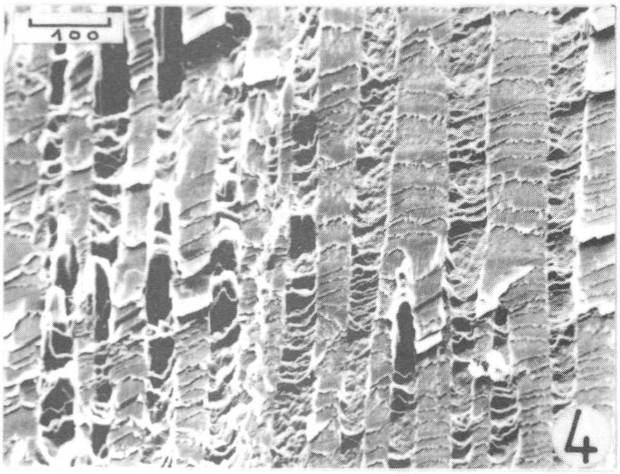

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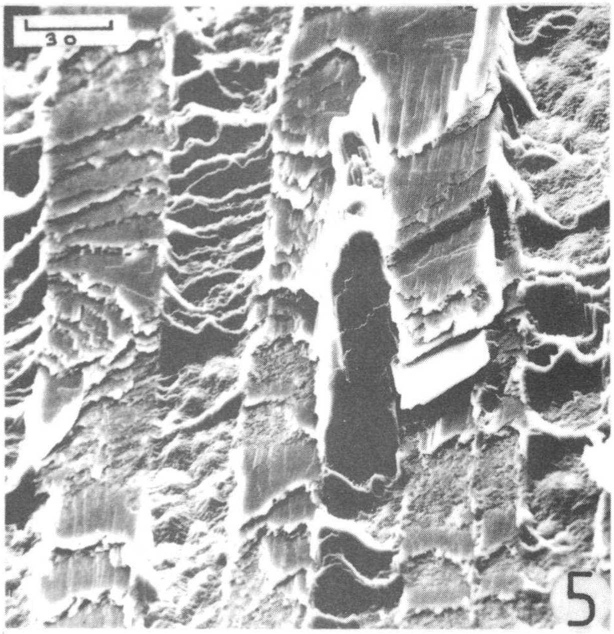

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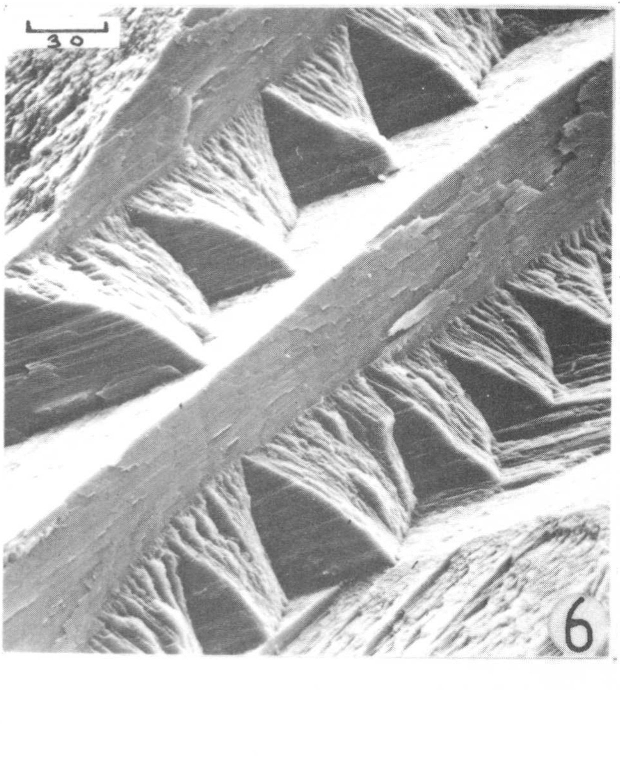

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Plate 2: The outer calcitic crossed lamellar layer of *Patella crenata*. The included scale is in microns.

Fig. 1: Shell broken nearly perpendicular to the surface. In the centre of the figure the boundary between two lamellae of the first order is oriented vertically. Thin sheets on the left side are second order lamellae. x 2400.

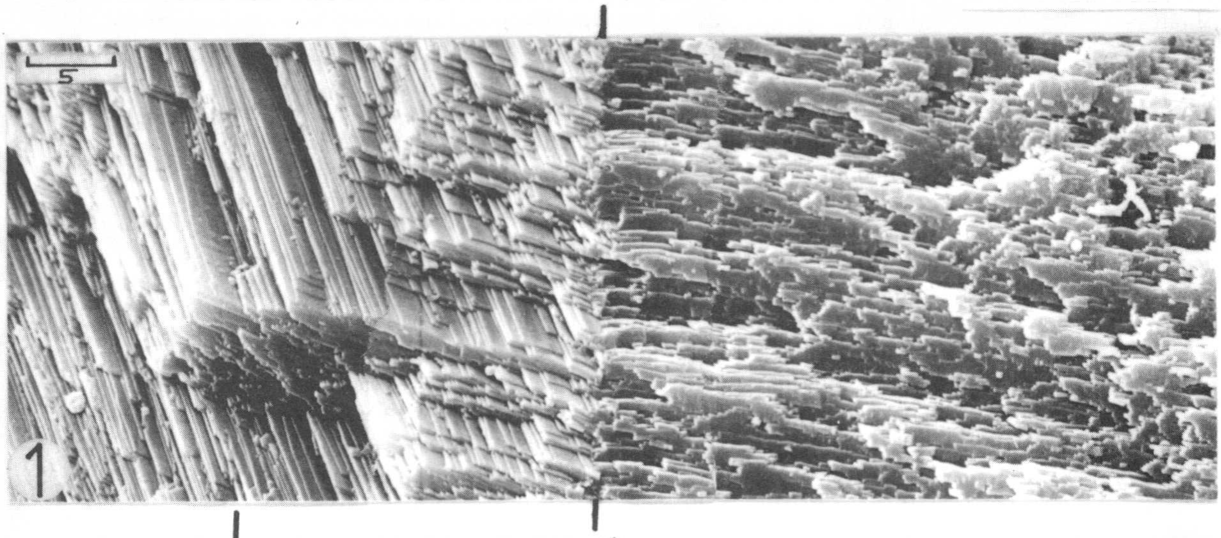
Fig. 2: In the detail to Fig. 1 lamellae of the second order consist of third order lamellae with lath-like shape. x 3700.

Fig: 3: View of the inner side of a juvenile shell with the vertical boundary between lamellae of the first order exposed. The flat lamellae of second order crop out as zig-zag shaped blades with direction of growth is indicated by the points of the lamellae, and increments of growth are visible as small wrinkles (arrows). x 8000.

Fig. 4: As in Fig. 3 on the upper left side vertical alternation of light grey to dark grey ribbons indicate folding of second order lamellae, similar as in a sheet of corrugated iron. See also Fig. 6. x 4700.

Fig. 5: View onto the inner side of a juvenile shell in direction parallel to the long axis of the second order lamellae with zig-zag alternation of third order lamellae that form an angle of about 156° (360°) to each other. x 12500

Fig. 6: Situation similar to Fig. 3 in which the frequency of depressions and heights formed by lamellae of third order increases in direction to the upper side of the figure representing the direction of growth. x 6000.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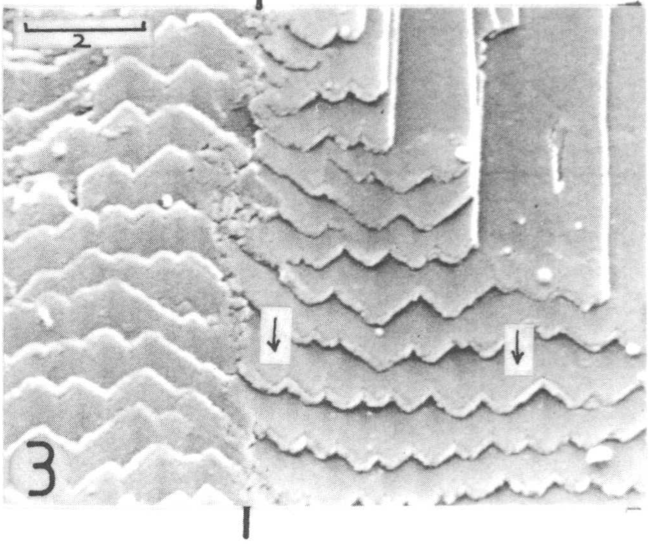
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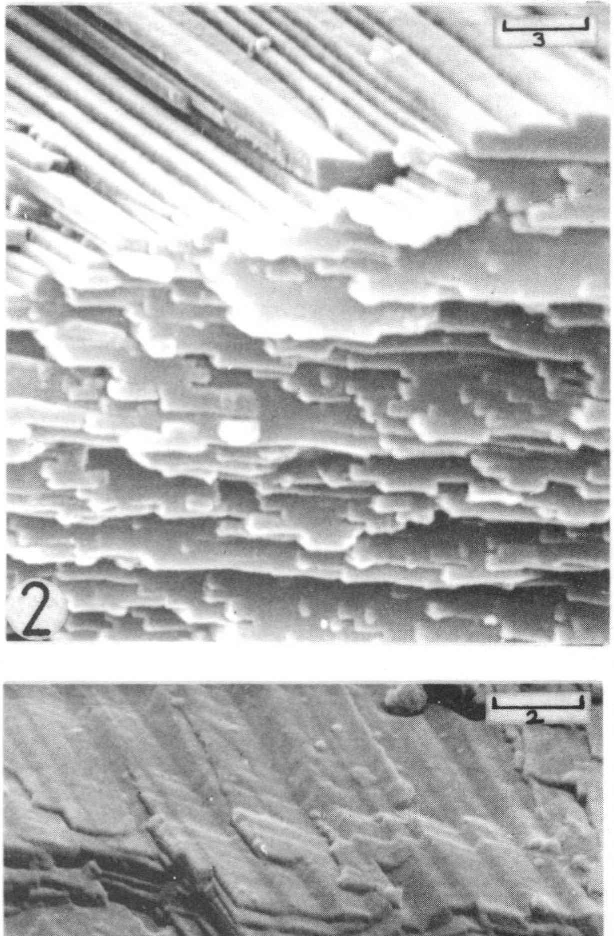
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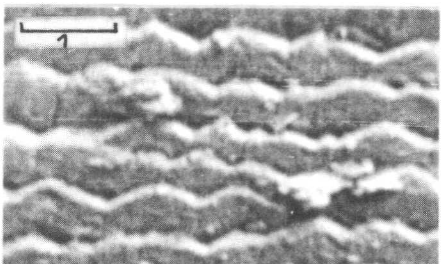
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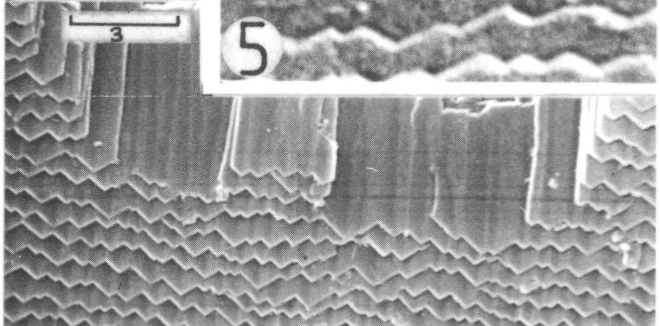
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Plate 3: Inclusions within the calcitic crossed lamellar layer and the myostracum. The included scale is in microns.

Fig.1: Oblique section perpendicular to the plane of symmetry near the region of the apex with crossed lamellar layer that grew around the shell of an ostracod. x 80.

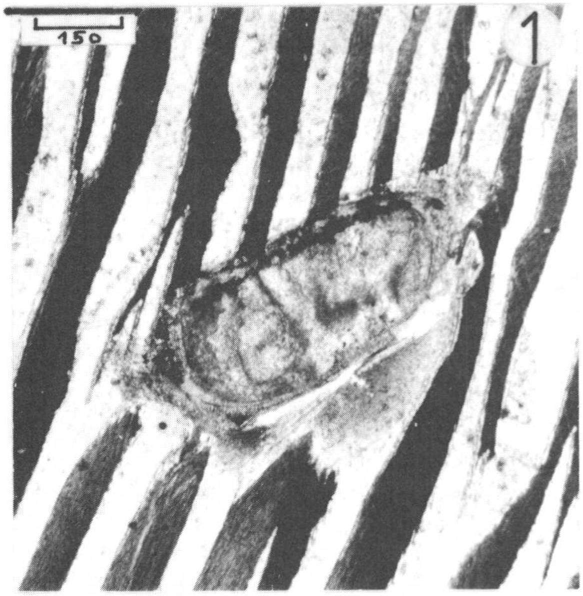
Fig.2: The calcitic crossed lamellar layer (lower part) is overlain by spherulite sectors (Brewster crosses) of the myostracum (upper part), and here four sand grains are included. x 30.

Fig.3: Near the inner surface of the shell a foraminifera (cf. *Elphidium* sp.) has been overgrown, and lamellae of the second order bent around it. This section parallel to the outer margin and vertical to shell surface shows a rhombic pattern of lamellae of the 2nd order of different lamellae of the first order in the lower half of the figure. x 50.

Fig.4: The detail to Fig. 3 with the smooth surface of the foraminifera coated by vertically oriented needles of aragonite, representing cement formed within the shell cavity present between the object and the surrounding shell layers. x 950

Fig.5: A similar fraction as in Fig. 3 with the spine of a sea urchin included in the shell and the inner surface of the shell seen at the right base of the picture. x 100.

Fig.6: The detail to Fig. 5 with cement formation of aragonitic needles seen on the cavity roof formed by the calcitic lamellae as well as on the calcitic surface of the sea urchins spine. x 500.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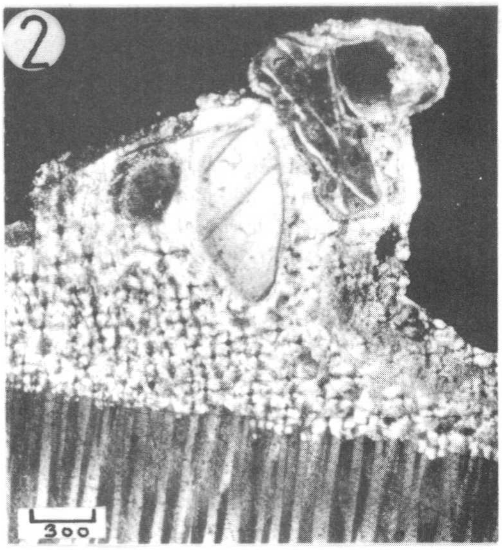
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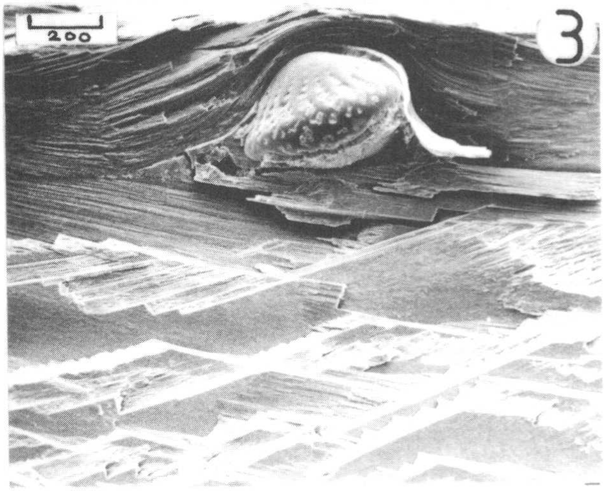
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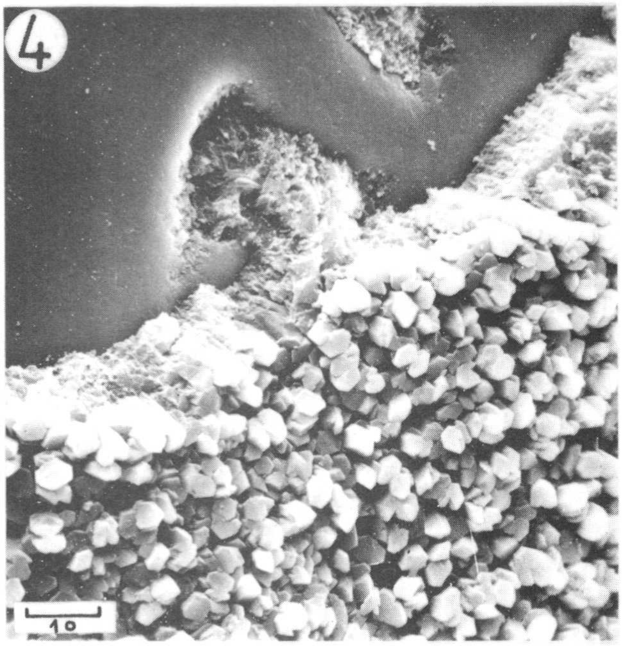
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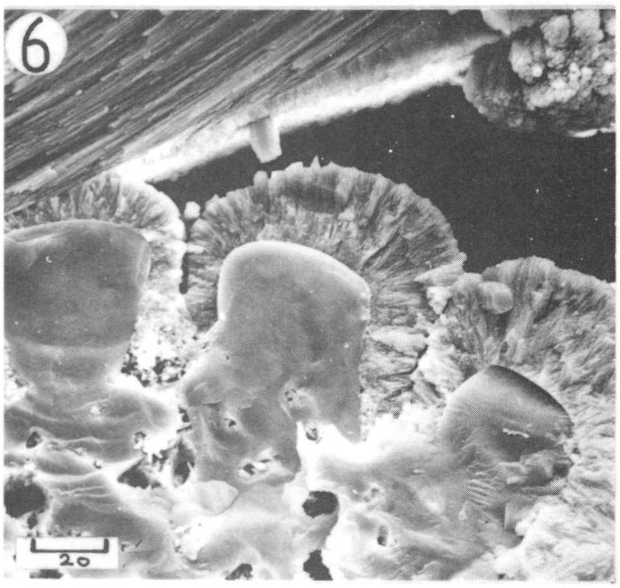
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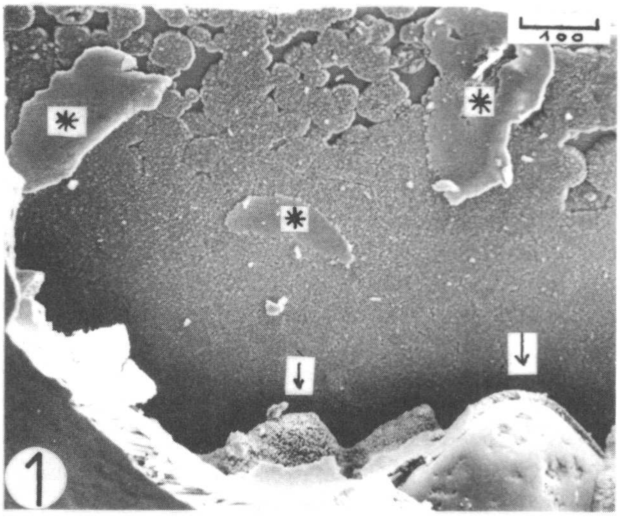
Plate 4:	Morphology of the crystallites of the pore cement that grew up around inclusions within calcitic and aragonitic layers in the shell of *Patella crenata*. The included scale is in microns.
Fig. 1:	Opened pocket within the shell that is filled with sand (arrows). The inner shell surface is exposed in the lower left of the picture. The surface of the pocket as well as that of the sand grains is covered by aragonitic crystallite coats. x 100.
Fig.2:	The detail to, Fig. 1 with clusters of twinned aragonite crystallites forming pockets of cement that grew on the calcitic surface. x 700.
Fig.3:	In a subfossil shell the etched surface of the aragonitic crystallites displays the pseudohexagonal shape of the twinned crystal well. x 5800.
Fig.4:	Here aragonitic twin crystallites have intergrown to form a pseuohexangonal column of the pore cement. x 5000.
Fig.5:	Sand grains included in the aragonitic hypostracal layers are coated with pore cement forming a layer of needle-like crystallites. x 250.
Fig.6:	Aragonitic multi-twin composed of four pseudohexagonal twins. x 12000.
Fig.7:	Another crystallite of the pore cement demonstrating the multitudes of crystal shapes found here. x 6700.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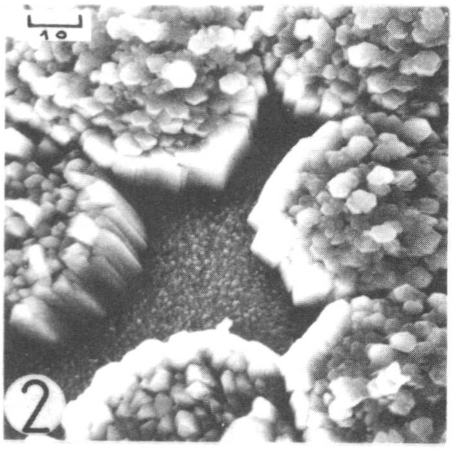
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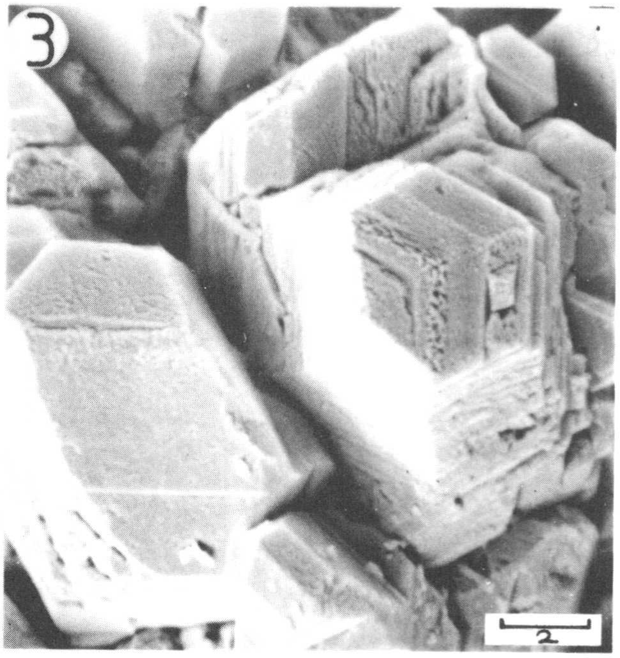
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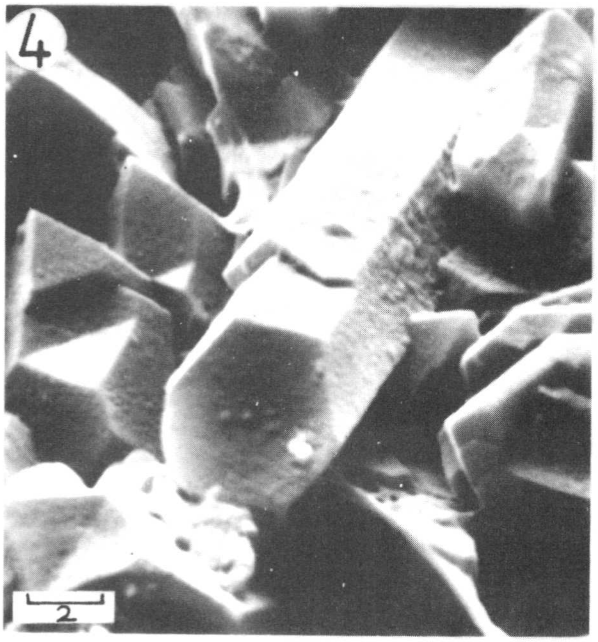
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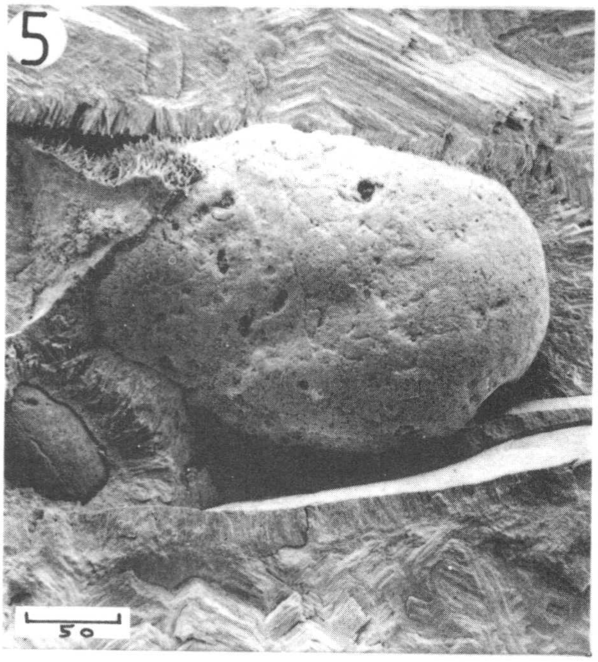
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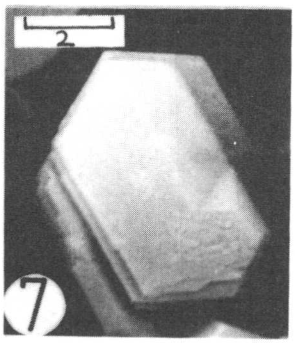
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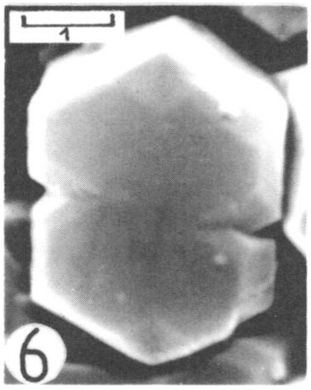
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Plate 5: The myostracum. The included scale is in microns.

Fig. 1: The thin section perpendicular to the plane of symmetry and to the shells surface near the apex with different shell layers marked at the margin. E represents a part of the calcitic crossed lamellar layer. M represents the myostracum, and H the hypostracum. x 200.

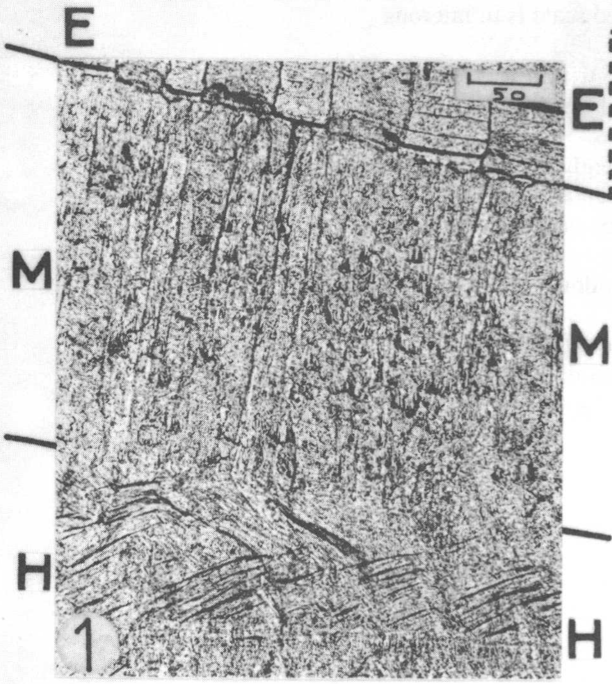
Fig.2: Thin section as in Fig 1 seen with crossed Nichols displays at the border between M (myostracum) and E (calcitic crossed lamellar layer). Four lobes representing spherulite sectors of the myostracum extend into the calcitic outer layers. x 320.

Fig.3: Similar section as in Fig.2 seen with the SEM as fractured shell demonstates the two parts of the myostracum, a layer with spherulite sectors (SM) and a lower one of prismatic structure (PM). x 350.

Fig.4: Fracture as in Fig. 3 with the crystallites of the spherulite sectors (SM) grading without interruption into those of the prismatic portion of the myostracum (PM). x 4800.

Fig.5: Inclined thin section parallel to shell surface with the dark-light alternation of the lamellae of the outer calcitic crossed lamellar layer at the left and the spherulite sectors cut vertical to their long axis of the myostracum at the right. x 85.

Fig.6: The detail to Fig. 5 with Brewster-crosses (crossed Nichols) revealing the spherulitic structure of the spherulite sector columns. x 180.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E
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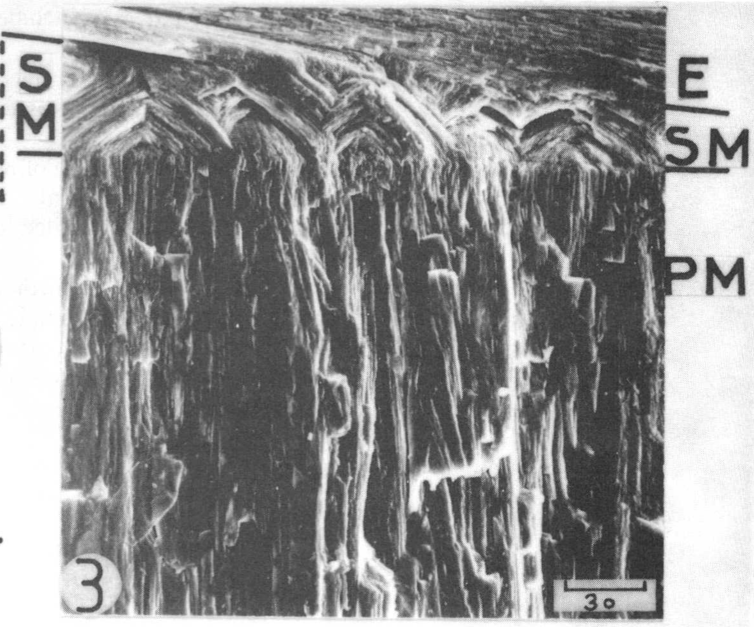
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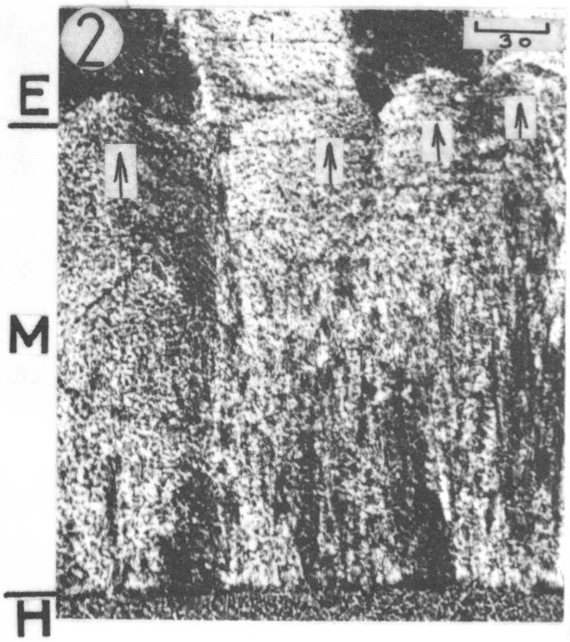
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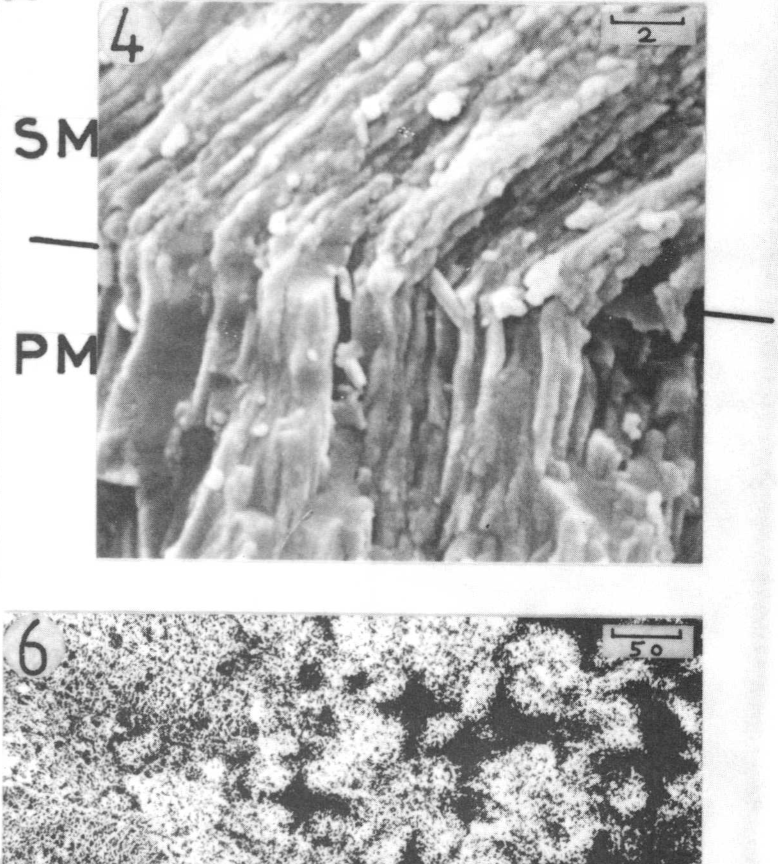
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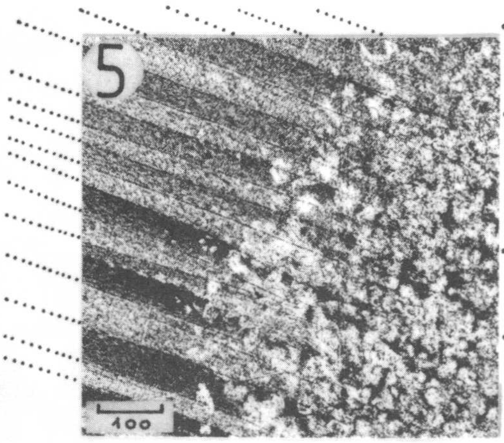
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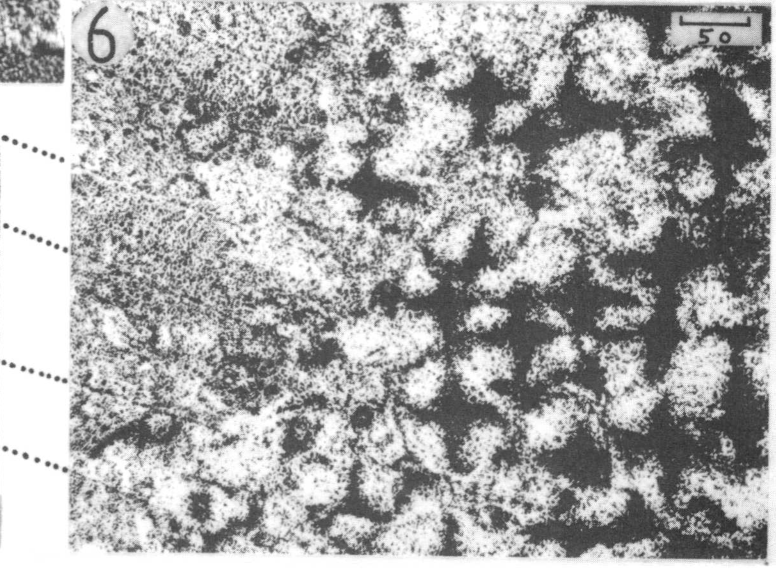
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Plate 6: The myostracum of *Patella crenata*. The included scale is in microns.

Fig.1: The etched section parallel to the shell surface within the myostracal layer shows the spherulite sectors resting on the calcitic crossed lamellar layer seen in the right upper corner. x 170.

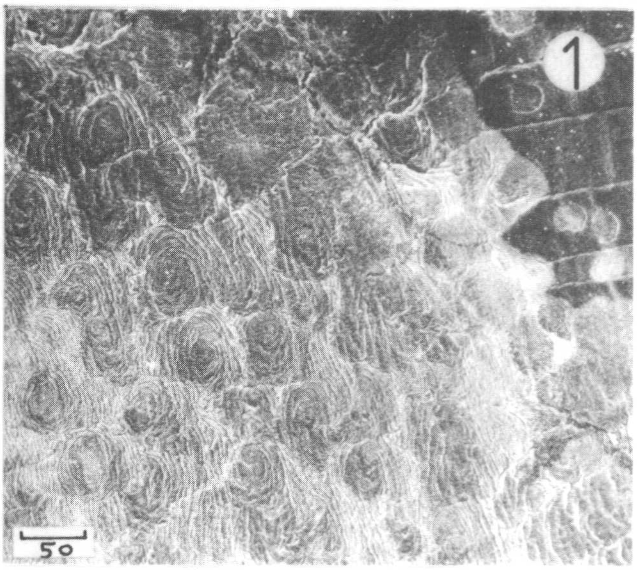
Fig.2: The detail to Fig.1 shows the interfingering of neighbouring spherulite sectors. x 400.

Fig.3: The detail to Fig.2 demonstrates the radial orientation of the elements of third order consisting of aragonitic needles that are united to cone-like elements of the second order. x 1000.

Fig.4: The etched section as in Fig.1, but a little further down in the prismatic myostracum demonstrates the radial orientation of the single prisms. x 300.

Fig.5: The detail to Fig.4 shows the radial arrangement of the bundle of prisms. x 1300.

Fig.6: The detail to Fig.5 demonstrates that each crystallite in the myostracal prisms represents a single crystal with characteristic etching marks. x 6600.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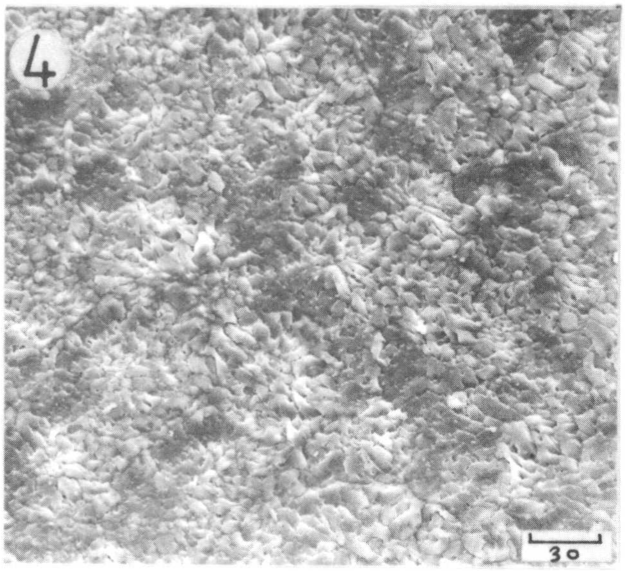
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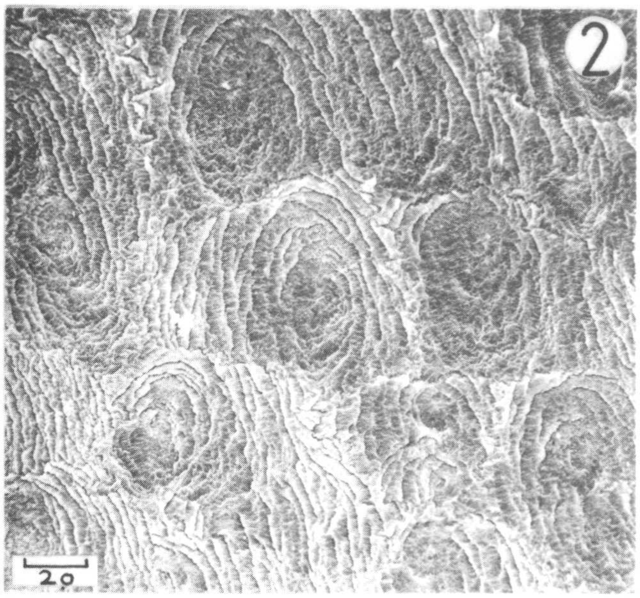
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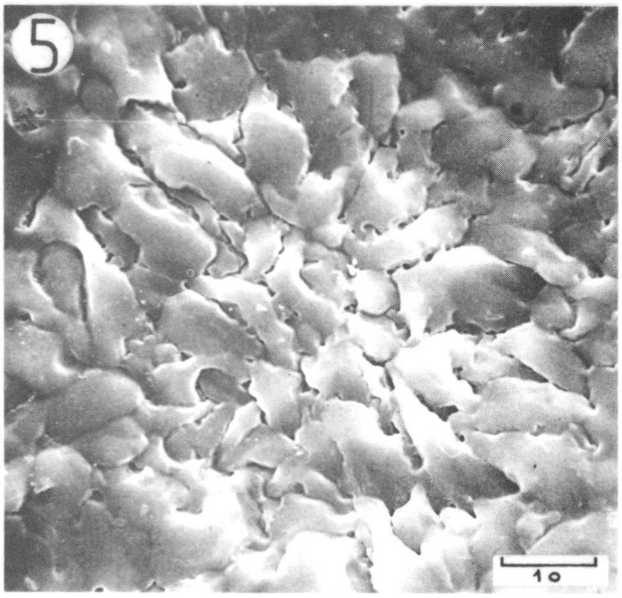
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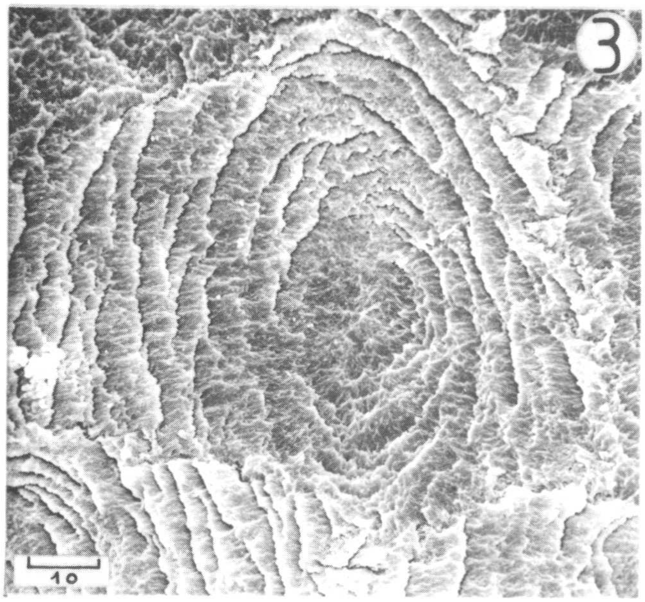
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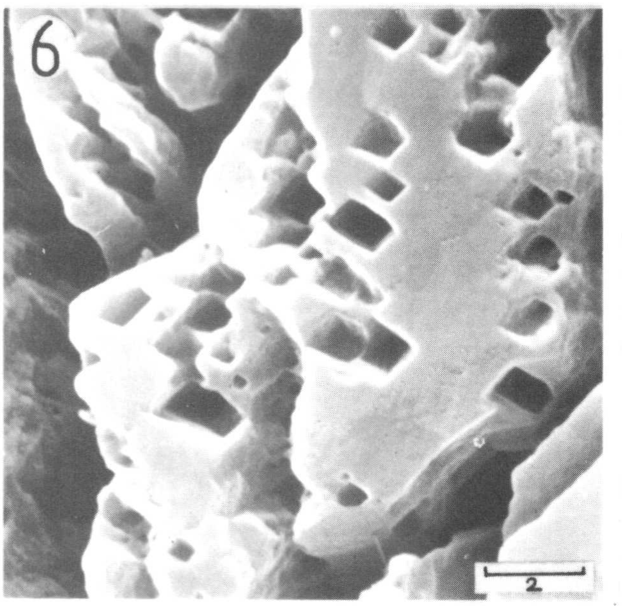
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Plate 7: The myostracum of *Patella crenata*. The included scale is in microns.

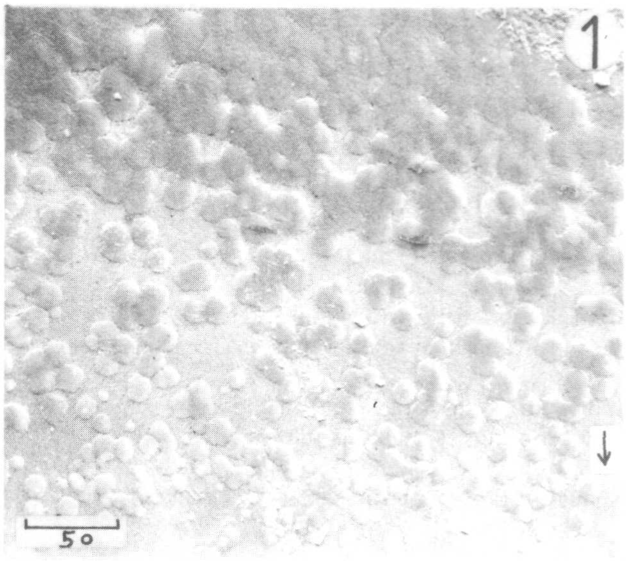
Fig.1: The inner surface of the myostracal layer in a juvenile shell cleaned and coated shows the growth fronts of spherulite sectors (detail in Figs.2-4). The arrow points in the direction of beginning growth. x 240.

Fig.2: The begin of myostracum formation on the surface of the calcitic crossed lamellar layer consists largely of organic material (lower side of Fig.1). x 1700.

Fig.3: The small cussion-like aggregates grow on calcitic crossed lamellar structure forming pseudohexagonal crystalline bodies. (central part of Fig.1). x 450.

Fig.4: With further growth the cussion-like aggregates fuse to each other, and there is only a Y-like groove present that shows their borders (upper part of Fig.1). x 2200.

Fig.5: The etched radial section vertical to the shell surface of a juvenile shell shows the two layered myostracum, M1 with aragonitic crossed lamellar structure (Pl.8, Figs.1-3) and M2 with aragonitic prismatic structure deposited later (Pl. 8, Figs.5,6). x 1100.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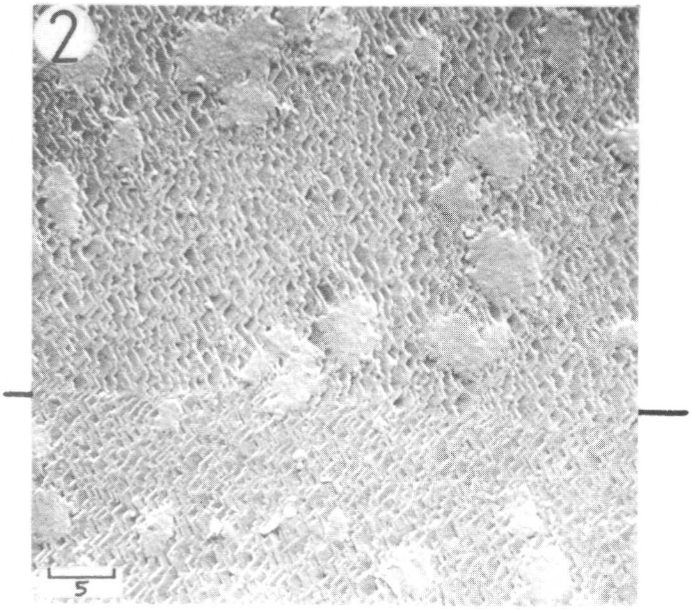
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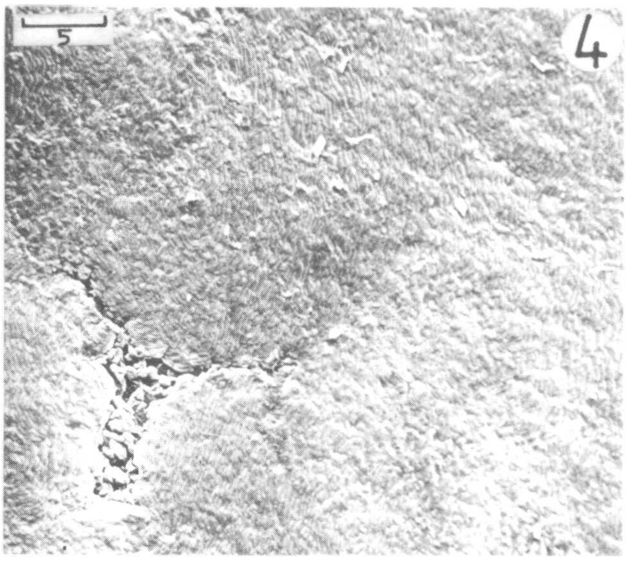
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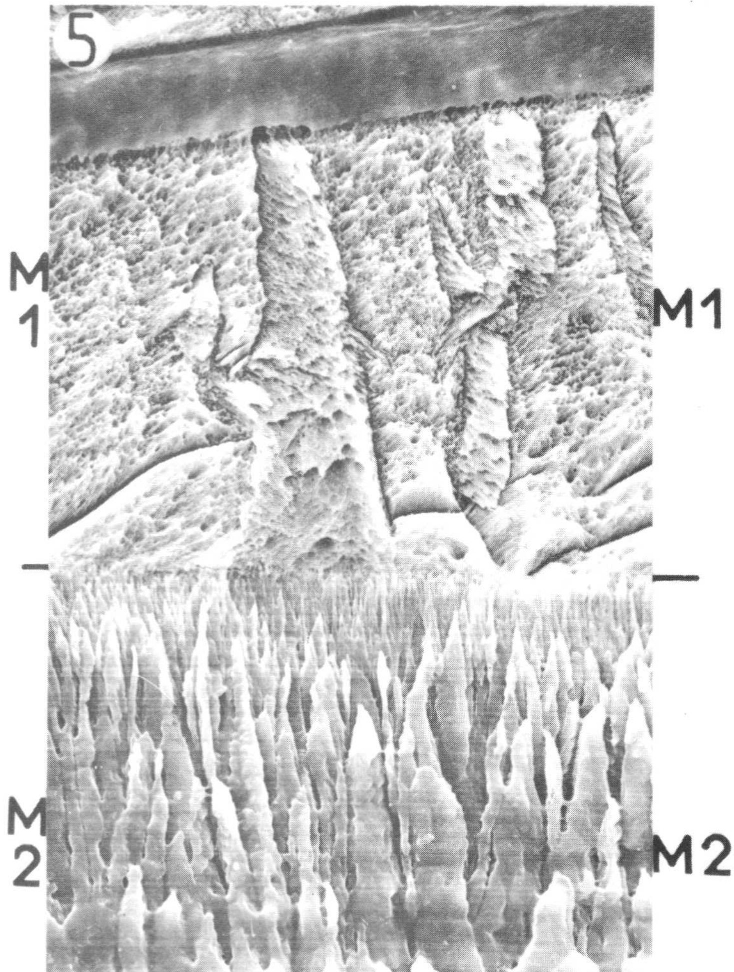
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M 1
M1
M 2
M2
10

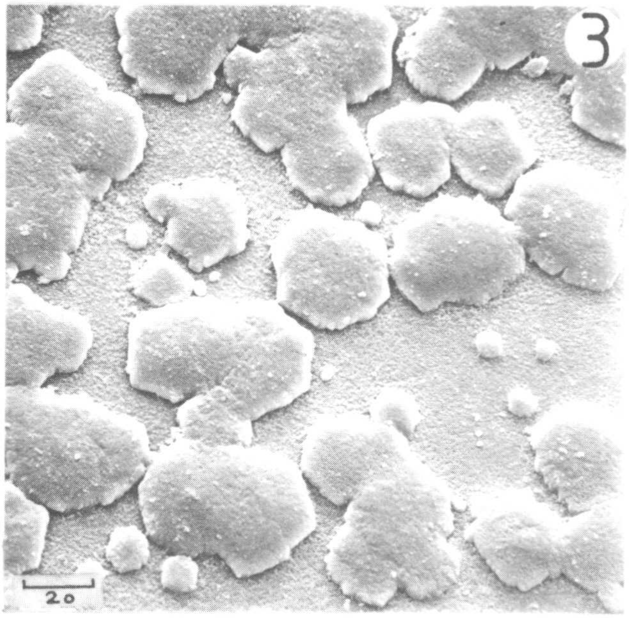
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Plate 8: The myostracum in juvenile *Patella*. The included scale is in microns.

Fig. 1: The etched radial section vertical to shell surface shows the outer calcitic crossed lamellar layer (E) that has been bored by endoliths and settled by epiphytes is underlain by the aragonitic crossed lamellar myostracum (M1) holding two layers rich on organic material (arrows). Hypostracum is not present. x 120.

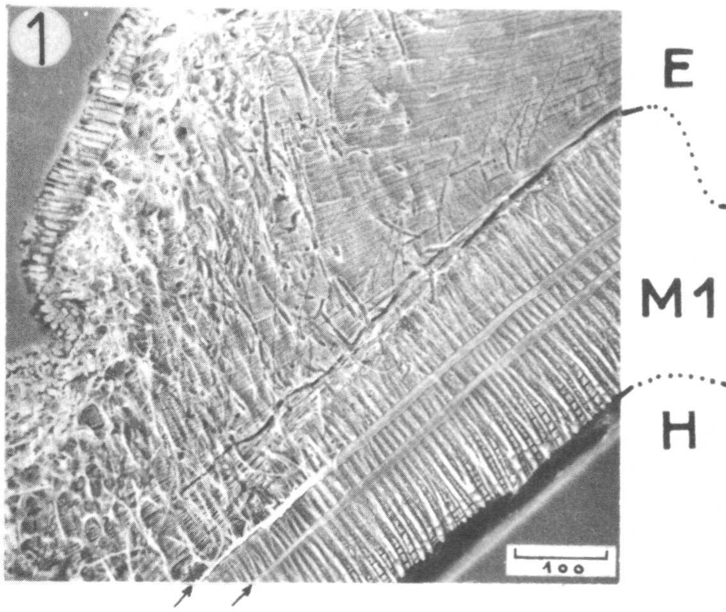
Fig. 2: Like in Fig. 1, but cut near the apex of the shell and, thus, with thin layer of aragonitic crossed lamellar structure of the hypostracum (H). x. 310.

Fig. 3: The detail to Fig. 2 shows that the number of aragonitic crossed lamellae of the first order in M1 decreases with shell growth. x 840.

Fig. 4: Almost radial and almost vertical and etched section with arrow indicating organic intercalations reflecting intermissions in shell growth which are continuous from the outer layer (E) to the myostracal layer (M1). x 220.

Fig. 5: Adapical section of the same individual shown in Fig. 6 with begin and increase in thickness of the prismatic myostracum (from left to right, M2) and its intercalation with the hypostracum (H). x 330.

Fig. 6: Adapical section of the same individual as shown in Fig. 5 with increase in thickness of M1 and decrease and end of the hypostracal layers (H) along with the exposed myostracum of the shell interior (M2). x 310.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E
M1
H
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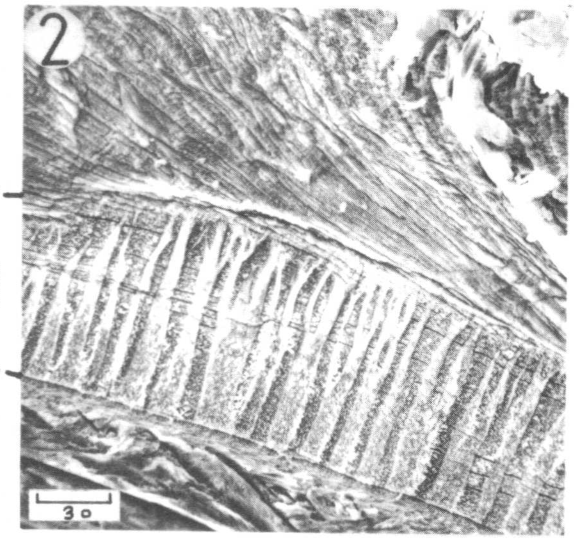
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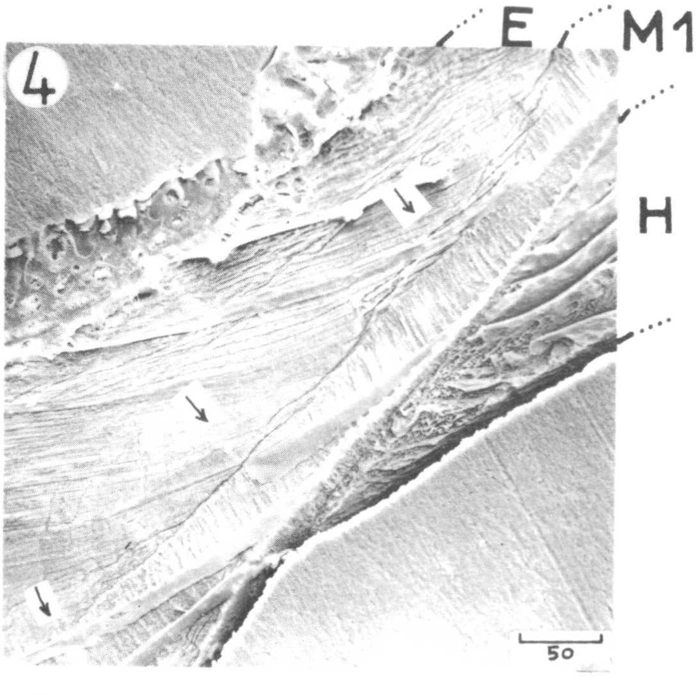
E
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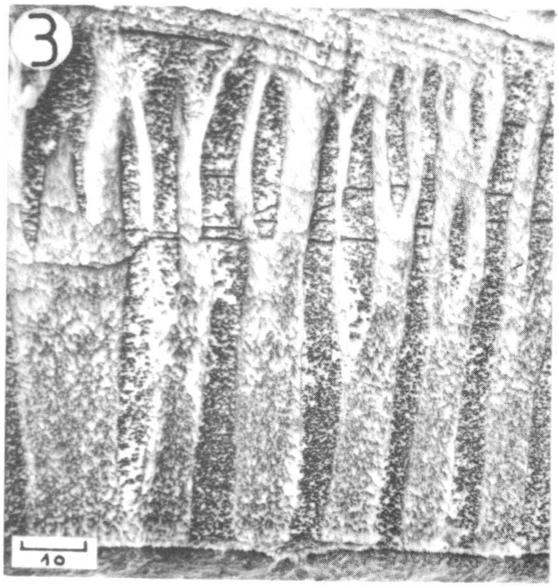
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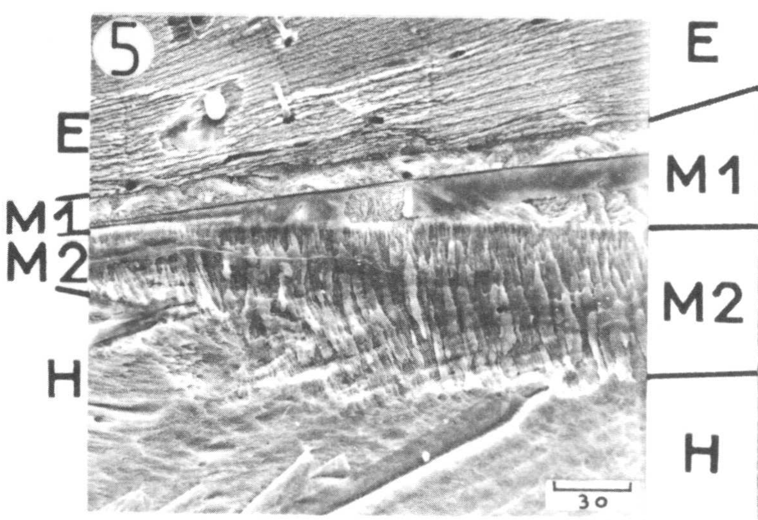
5
E
E
M1
M1
M2
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H
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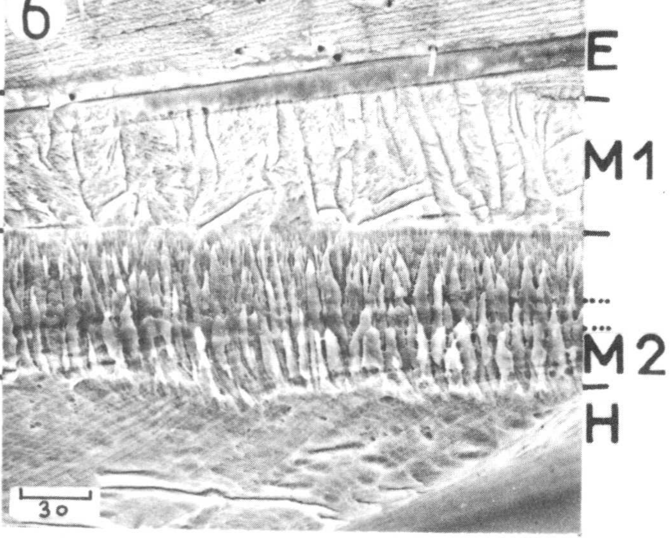
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Plate 9: The aragonitic myostracum of *Patella crenata*. The included scale is in microns.

Fig. The thin section parallel to the plane of symmetry of the shell and vertical to the shell surface shows an intercalation of aragonitic crossed lamellae (KL) and aragonitic prismatic layers (P). x 160.

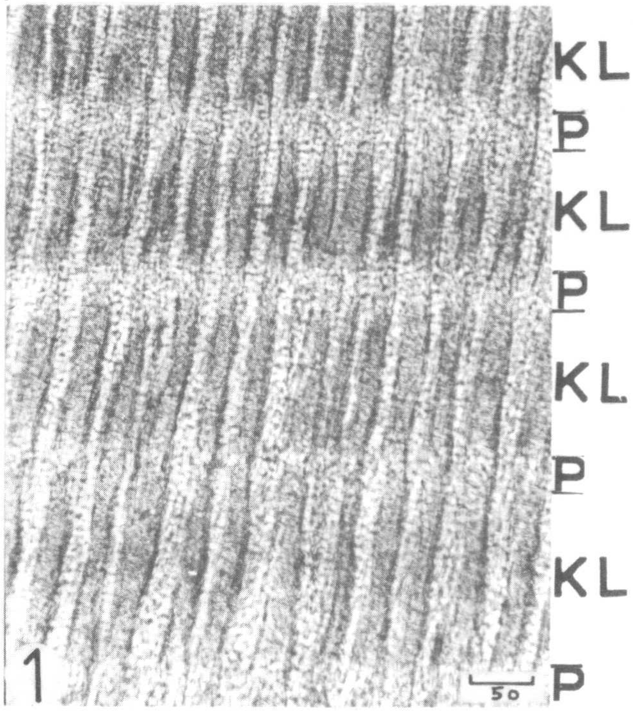
Fig.2: Same situation as in Fig.1, but seen in fracture with dark lamellae of the first order in which lamellae of the second order have been broken parallel to the plane of the picture. The marks on the side indicate the position of prismatic intercalations. x 110.

Fig.3: The etched section shows vertical lamellae of the first order with the lamellae of the third order sticking out of the plane and two prismatic layers with organic material exposed. x 560.

Fig.4: The detail to Fig.2 shows three lamellae of the first order and in the central one lamellae of the second order parallel to the plane of the picture. A prismatic layer crosses from left to right in the centre of the picture. x 1100.

Fig.5: The detail to Fig.4 shows the lamellae of the third order which compose the lamellae of the second order, and the dark lines indicate fine growth striations, thus, fine differences in content of organic material. x 2250.

Fig.6: In a lamella of the first order a new lamella of first order originates. Lamellae of the second and third order are visible. x 2400.


KL
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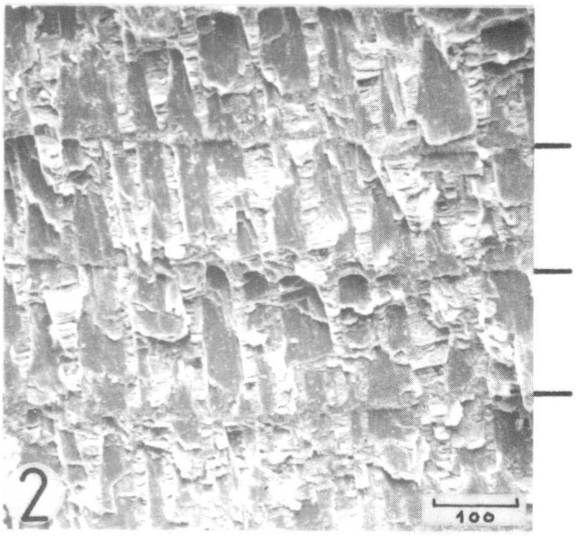
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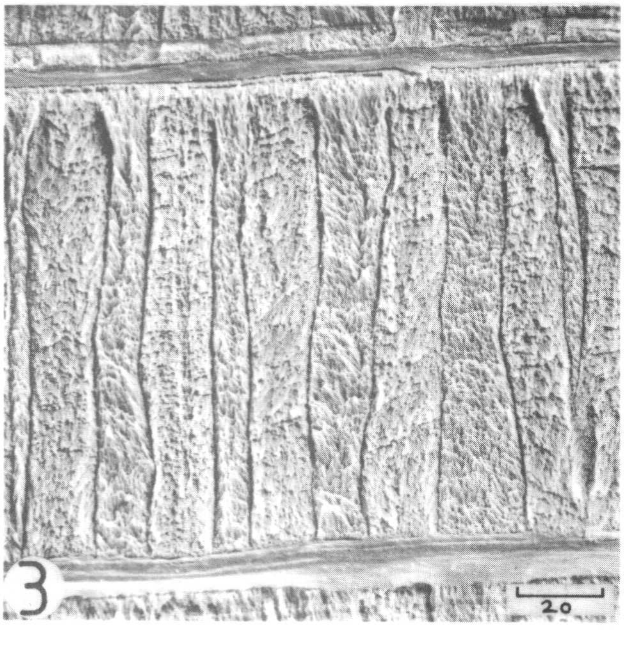
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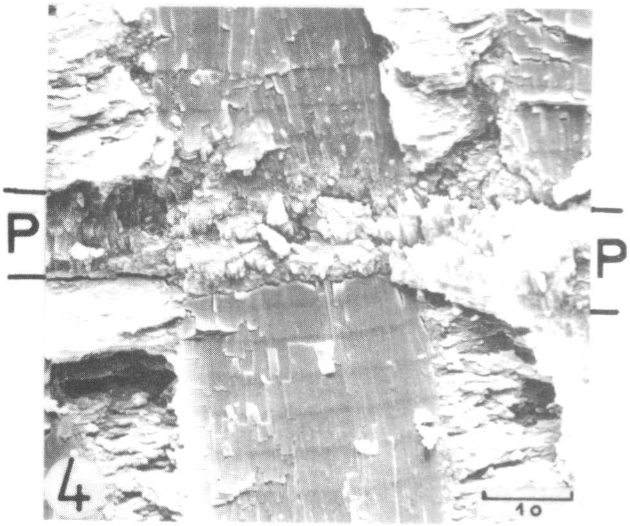
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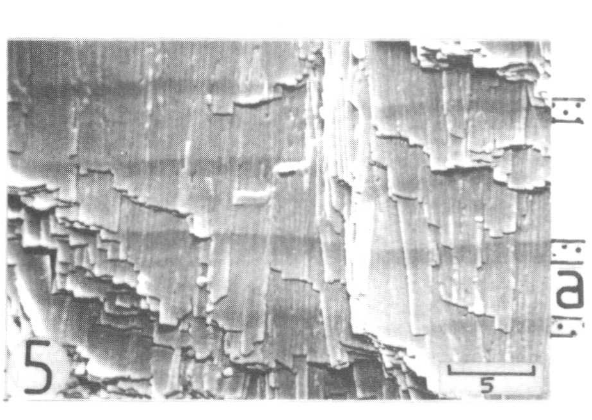
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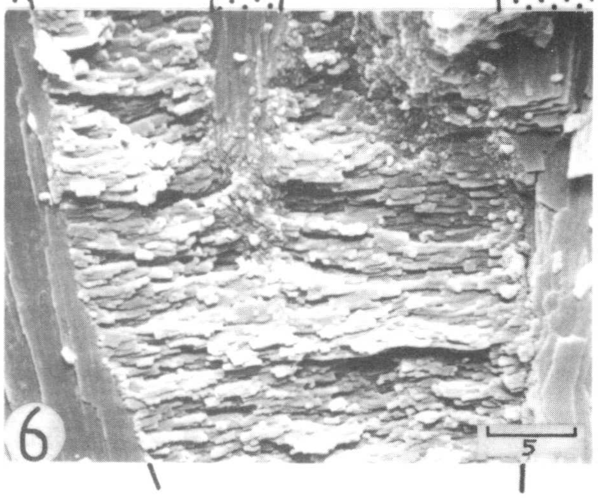
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Plate 10: The aragonitic hypostracum of *Patella crenata*. The included scale is in microns.

Fig.1: The fracture vertical to the surface of the shell and nearly parallel to the boundaries between first order lamellae shows the prisms of the myostracum (M) on which the hypostracum has grown with crossed lamellar layers intercalated by prismatic layer (marginal lines). The arrow points toward the inner surface of the shell. x 65.

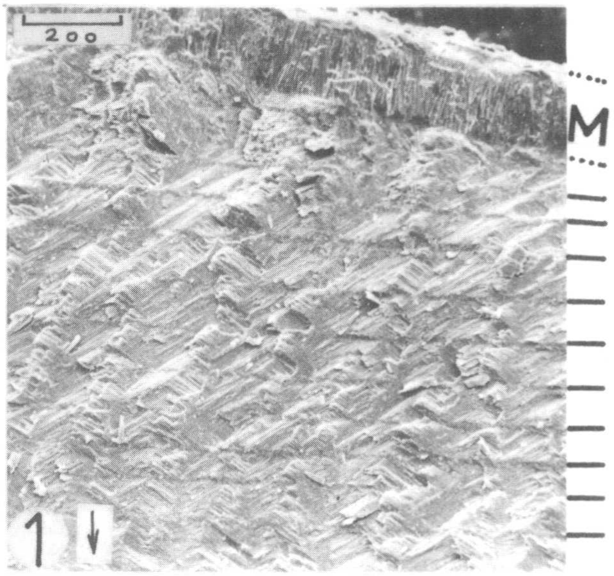
Fig.2: The etched section parallel to the surface of the shell shows that the aragonitic lamellae of the first order of the crossed lamellar structure interfinger more than is the case in the calcitic crossed lamellar structure. x 500.

Fig.3: The detail to Fig.1 shows second order lamellae of several lamellae of the first order which interfinger. The angle of the needles of the third order of two lamellae of the first order form 109° to each other, and the median axis of this angle is vertical to growth surface and the intercalated prismatic layers. x 200.

Fig.4: The detail to Fig.3 shows an enlargement of crossed lamellae and intercalated prismatic layer. x 500.

Fig.5: The detail to Fig.4 shows the continuation of the lamellae of the third order of the crossed lamellar structure with the prisms of the prismatic layer (arrows). x 5000.

Fig.6: View onto the growing hypostracum on the inner shell surface in which the lumps represent the base to the prisms of a prismatic intercalation which was growing when life ended. x 12500.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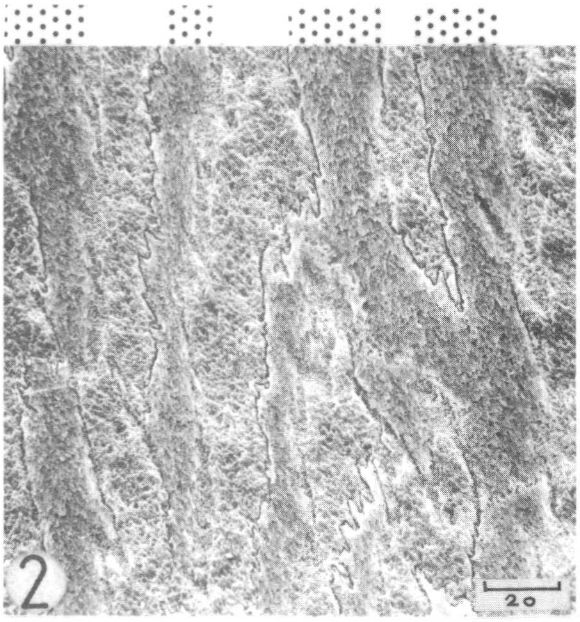
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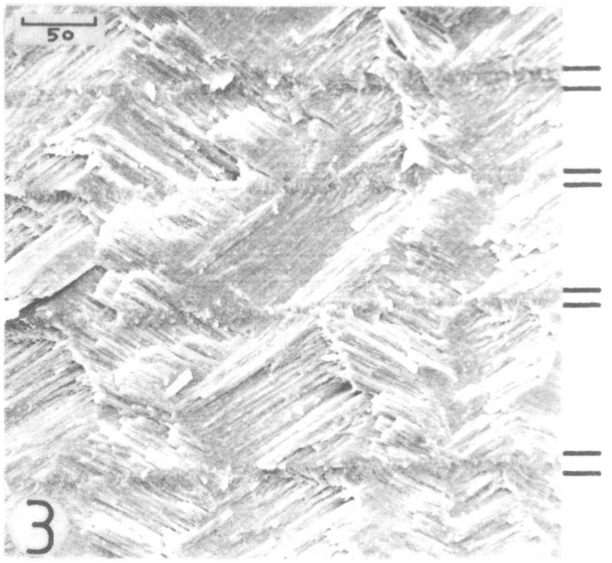
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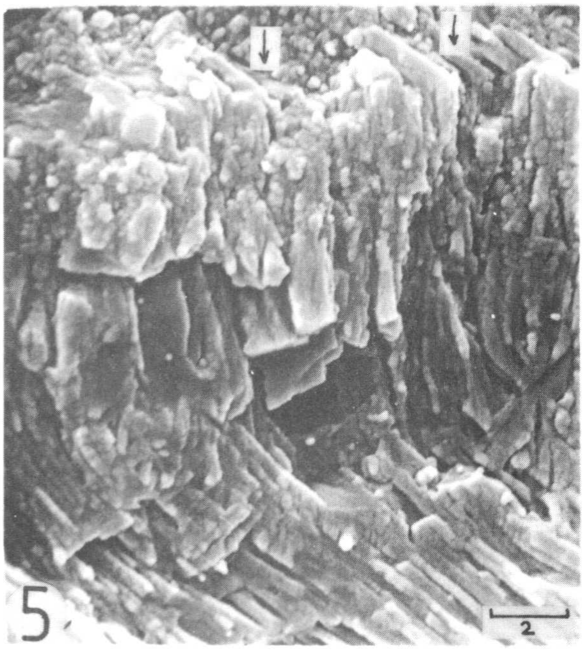
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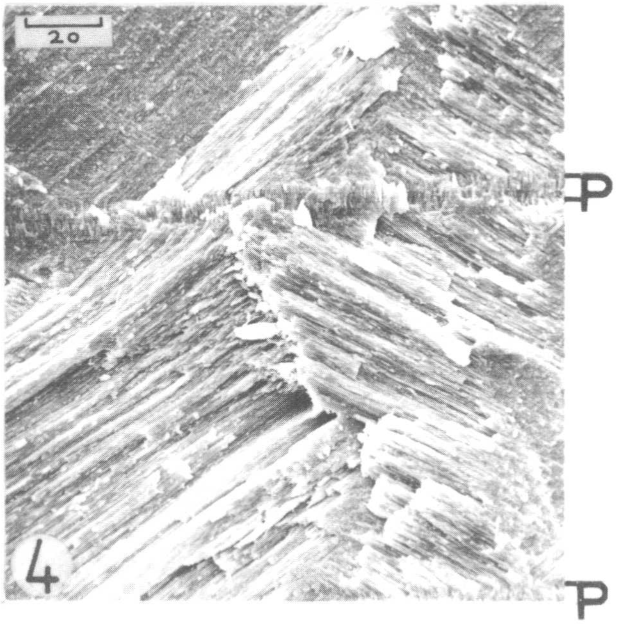
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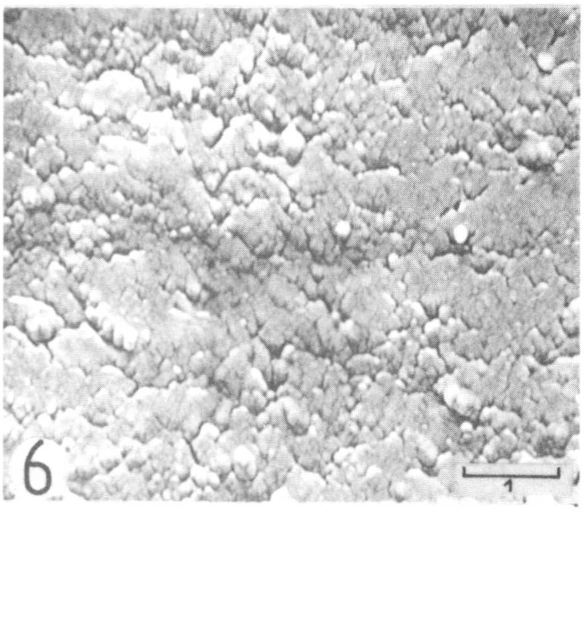
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Plate 11: Calcitic lamellae of the hypostracum of *Patella crenata*. The included scale is in microns.

Fig.1: The thin section vertical to the plane of symmetry of the shell and vertical to the shell surface in the area of the apex shows a calcitic inclusion in the aragonitic layers forming the dark trapezoidal central portion. x 200.

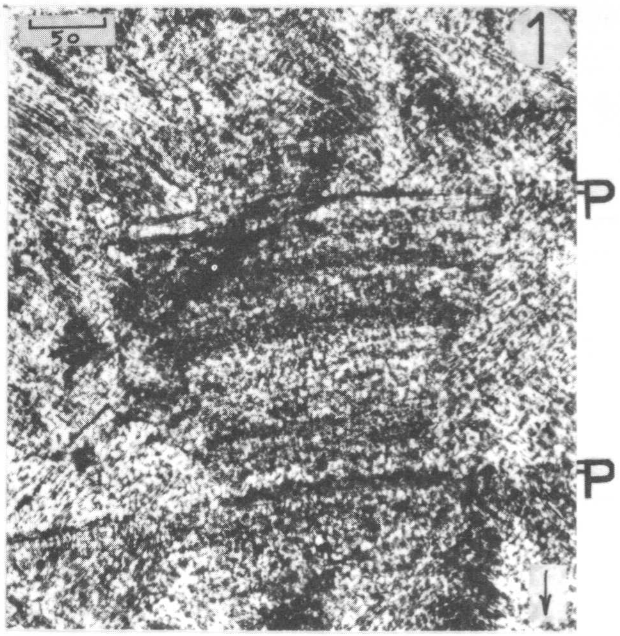
Fig.2: The etched section vertical to shell surface and vertical to the orientation of lamellae of the first order in the aragonitic crossed lamellar structure shows the same type of calcitic inclusion as seen in Fig.1. Calcitic lamellae seen in the central part of the picture are about parallel to the prismatic intercalations in the crossed lamellar structure. The arrow points toward the surface of growth. x 225.

Fig.3: The fracture vertical to the shell surface shows the lamellae of the calcitic hypostracum. x 1100.

Fig.4: The fracture nearly parallel to the inner surface of the shell shows the calcitic lamellae of the hypostracum. Parallel to the surface of the picture are the lamellae of the second order and those of the third order are vertical to them and produce the corrugated pattern. The rims of lamellae from left to lower right indicate the predominant pattern of cleavage within the calcitic layer. x 2000.

Fig.5: Fracture as in Fig.4 with calcitic lamellae of the second order overgrown by the crystallites of a prismatic layer. x 1500.

Fig.6: The detail to Fig.5 shows the base crystallites to a prismatic layer. x 17000.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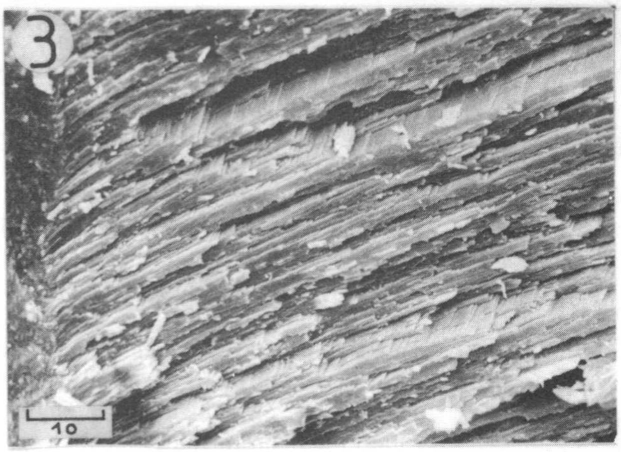
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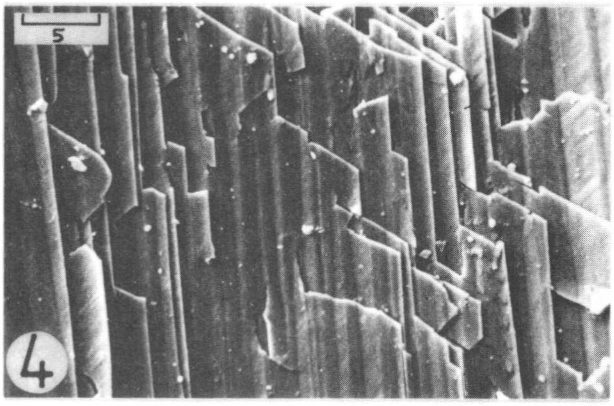
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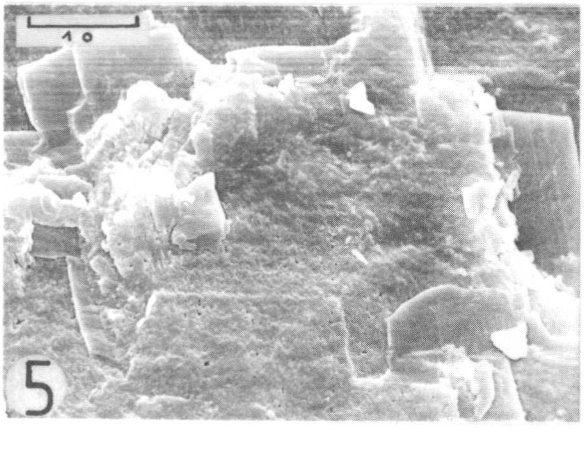
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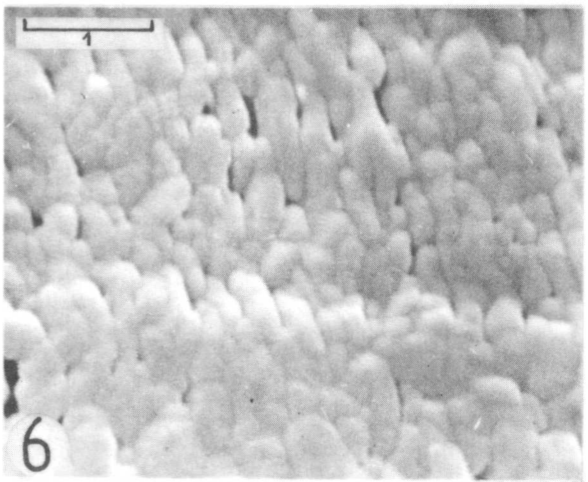
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Plate 12: Aragonitic spherulithic sectors within the calcitic hypostracum in *Patella crenata*. The included scale is in microns.

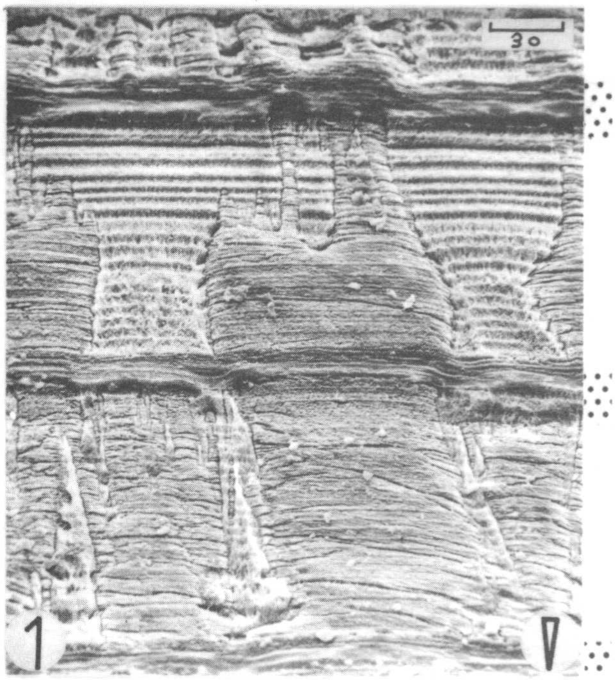
Fig.1: The etched section vertical to shell surface shows spherulite sectors coming from above and continuous through prismatic layers that are intercalated and rich in organic matter. The prismatic layers are marked at the picture margin. Between the aragonitic spherulite sectors are calcitic lamellae. x 310.

Fig.2: The etched section vertical to the shell surface shows plait-like spherulite sectors in the upper layer that end further inward. Just above a layer rich with organic material a spherulite sector begins and continues below. x 700.

Fig.3: Thin section parallel to the surface of the shell exposes hypostracum that is of mixed composition. The Brewster crosses reveal the spherulitic nature of the aragonitic portions within a calcitic matrix. x 80.

Fig.4: The fracture at right angle through the shell exhibits an aragonitic spherulite sector within the hypostracum. Lamellae of the second order are parallel to the surface of the picture. and the intercalations represent growth increments. x 2000.

Fig.5. The fracture similar to that shown in Fig.4 demonstrates the spherical organization of this aragonitic body in the hypostracum. x 750.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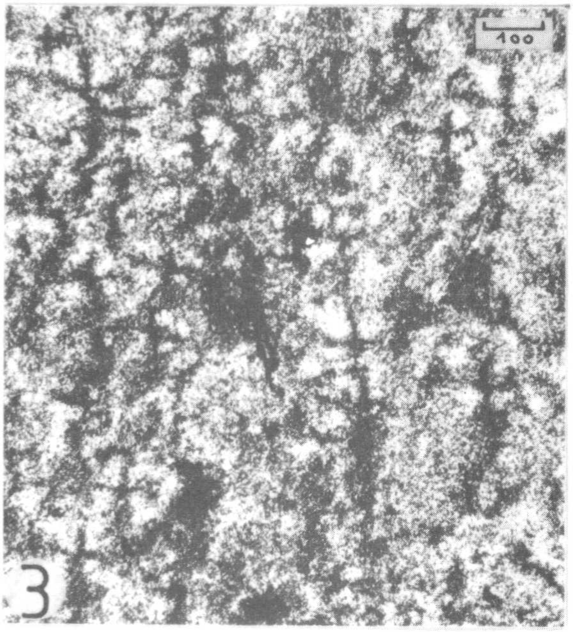
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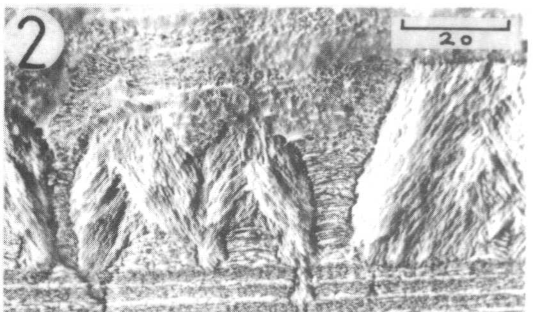
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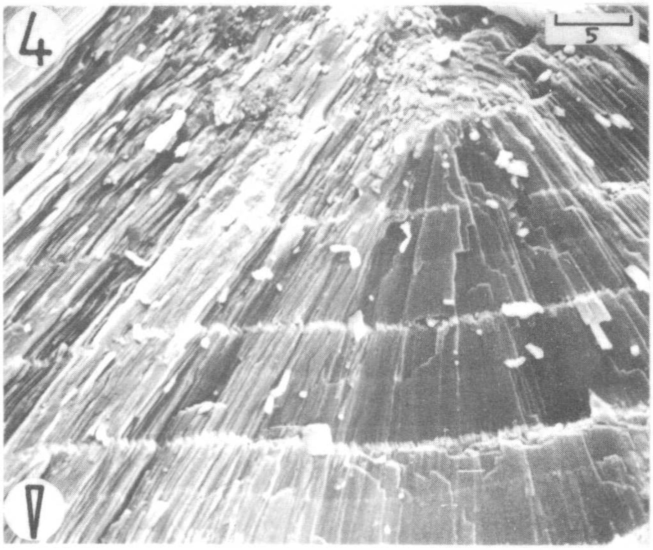
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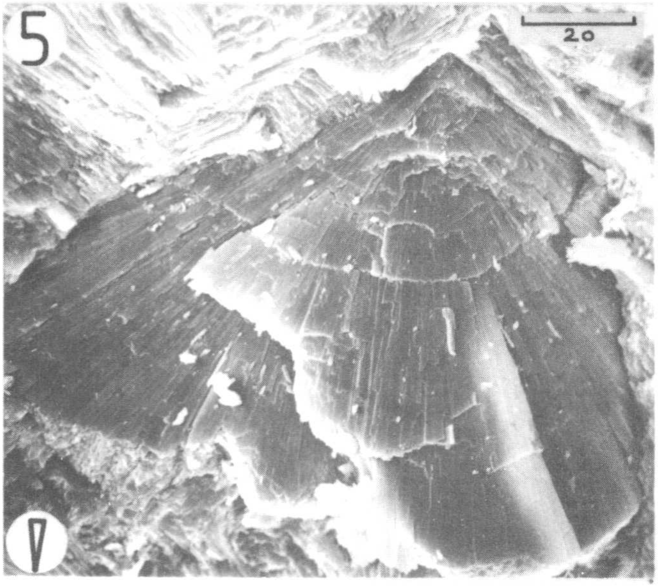
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Plate 13: Aragonitic spherulite sectors in the calcitic hypostracum. The included scale is in microns.

Fig.1: The fracture normal to the inner surface of the shell (the inner surface of the shell is seen below the arrow) presents a view onto a cavity from which a spherulite sector has broken loose. x 160.

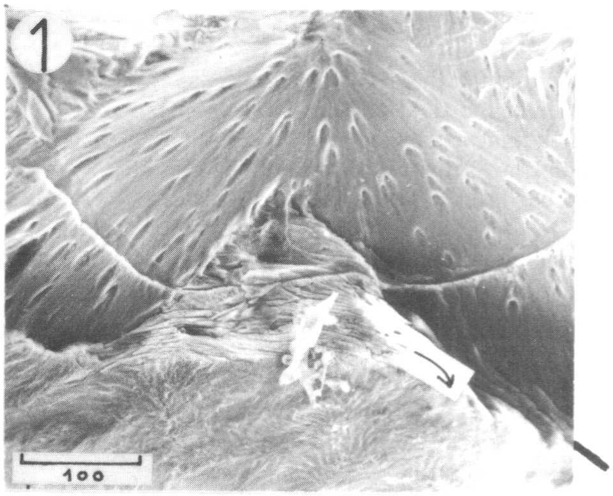
Fig.2: The detail to Fig.1 shows pits where small new spherulite sectors initiated. x 530.

Fig.3: The detail from the lower part of Fig.1 with structures seen on the inner shell surface that reflect the growth of spherulite sectors. x 190.

Fig.4: The detail to Fig.3 with the inner surface of the shell showing second order lamellae cropping out as polycuspid thin sheets. The central elevation may represent the begin of formation of a new lamella of the first order. x 1900.

Fig.5: The fracture normal to the surface of the shell shows lamellae of the second order crossed by increments of growth (asterix indicates the position of the detail in Fig.6) and with arrow pointing toward growth surface. x 950.

Fig.6: Detail to Fig.5 at the area indicated by the asterix shows fine vertical ribbons (marked at the margin) that represent increments of growth and fine vertical lines which are traces of the third order lamellae. x 5600.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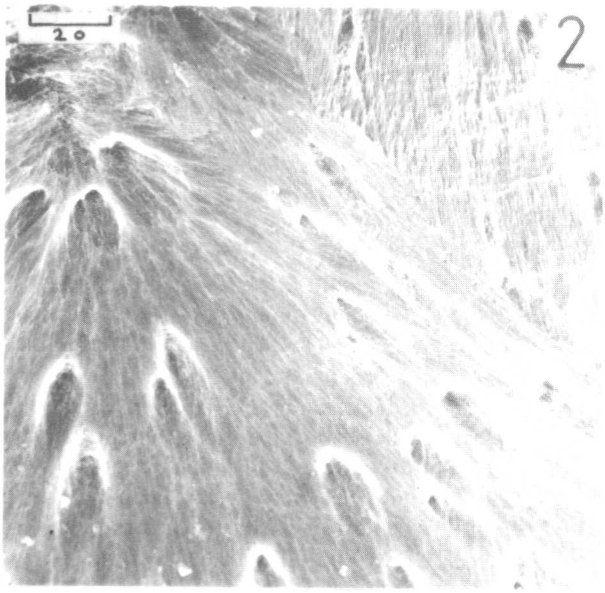
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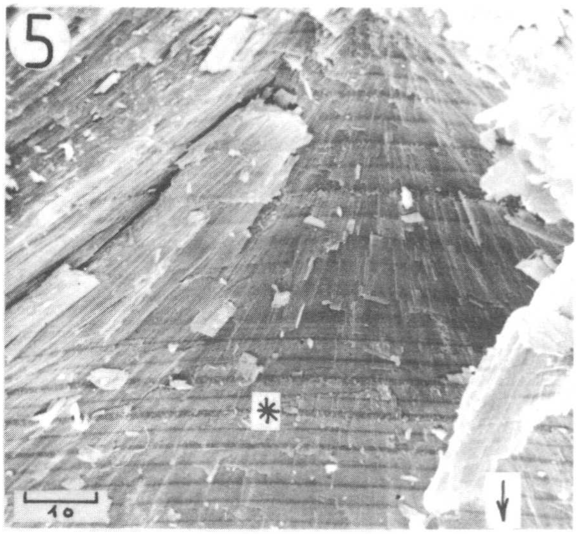
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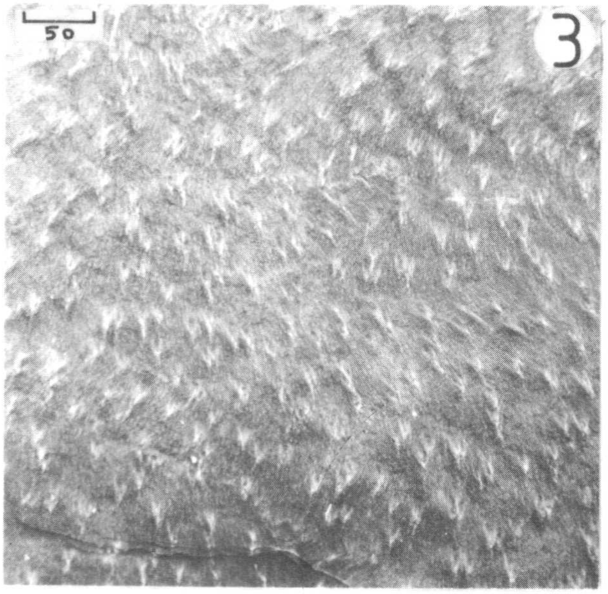
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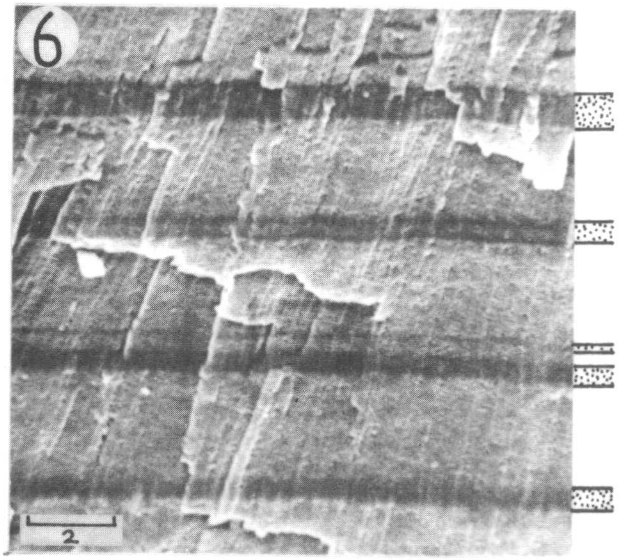
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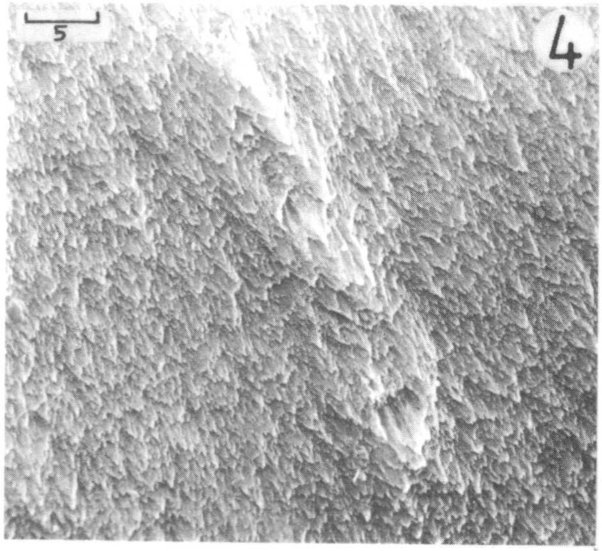
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Plate 14: Organic lamellae of the shell. The included scale is in microns.

Fig.1: The section parallel to the surface of the shell and through the hypostracal layers shows horizontally oriented lamellae of the second order in the right corner and a prismatic layer to the right, with fibrillar matrix between both indicated by the arrow. x 2500.

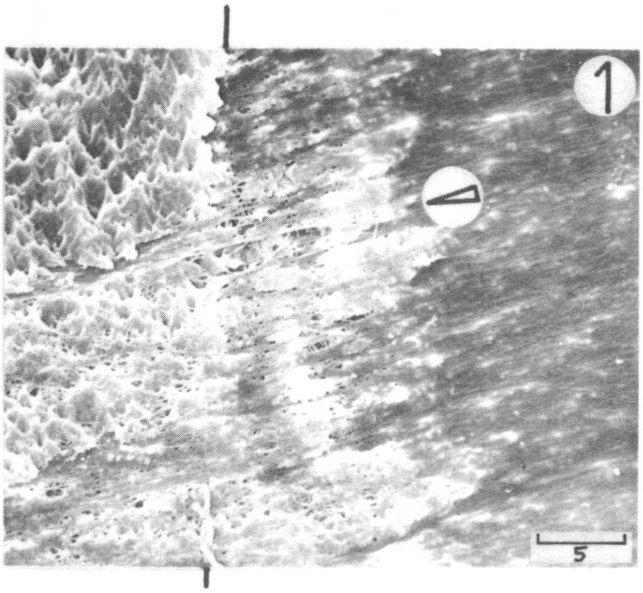
Fig.2: Similar section as in Fig.1 with an organic fibrillar layer that follows the orientation of the prismatic layer that overlies the crossed lamellar layer exposed in the lower part. x 4500.

Fig.3: The section perpendicular to the shell shows at the upper left side and lower right side aragonitic crossed lamellar structure of the juvenile myostracum. The organic sheet in the centre represents a layer that has folded down onto the fracture surface from a line indicated by the arrows. x 2700.

Fig.4: The detail to Fig.3 shows the fibrillar structure of the organic sheet and a preferred orientation of the fibres indicated by the arrows. x 13000.

Fig.5: The section parallel to the surface within the myostracal layer exposes a sheet without structure and with the traces of the spherulites imprinted on it. The organic sheet rests on the calcitic crossed lamellar layer and forms the base of the myostracum. x 4500.

Fig.6: The shiny layer that covers the hypostracum on the inner surface of the shell was dissolved off with hot KOH solution and fixed on a glass. Its structure reveals a pattern of fibres. x 12000.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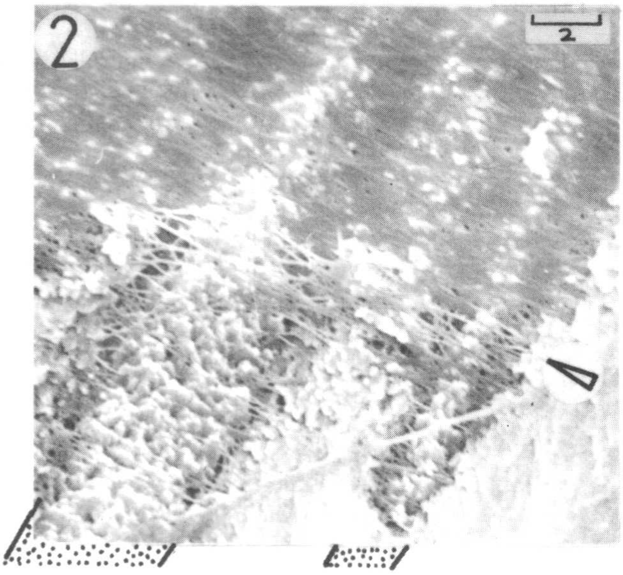
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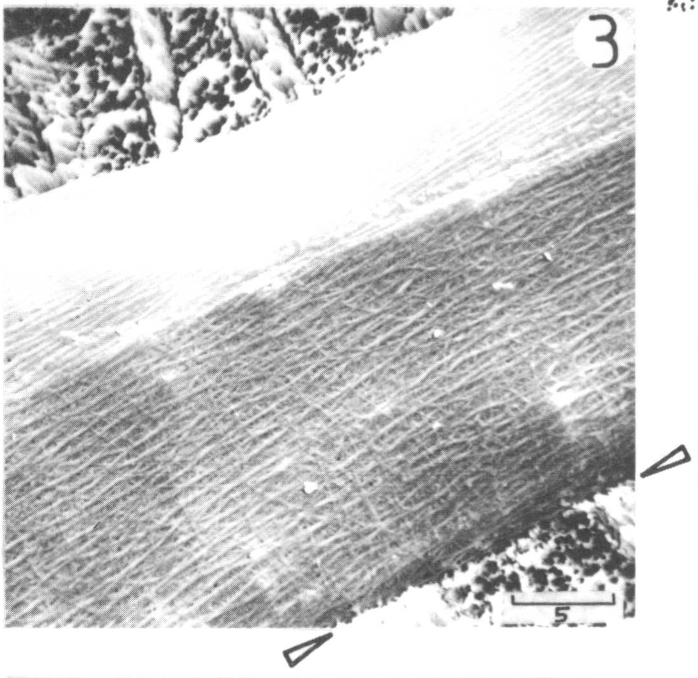
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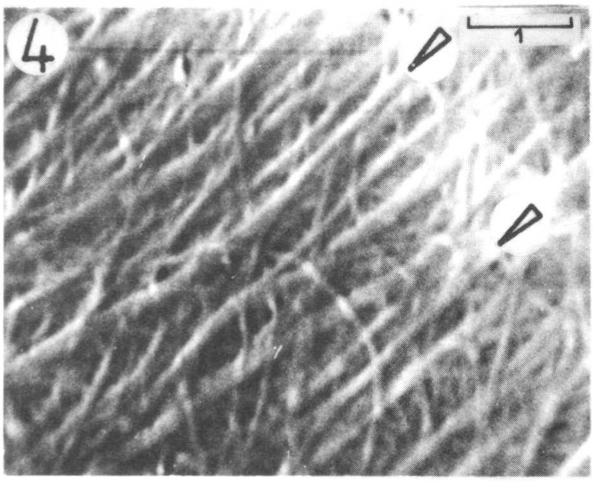
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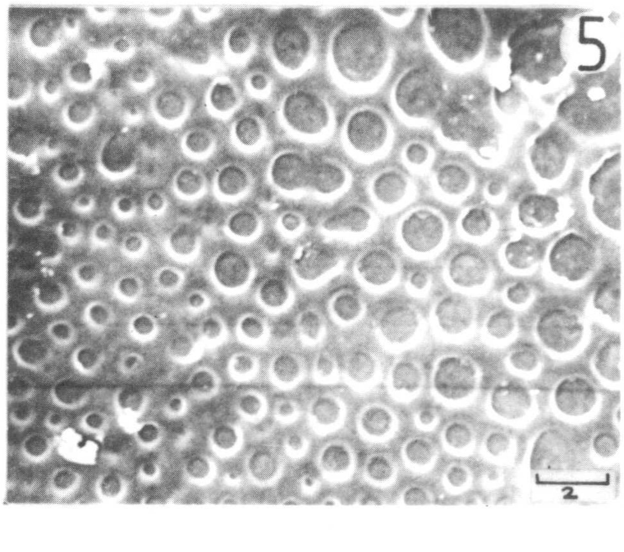
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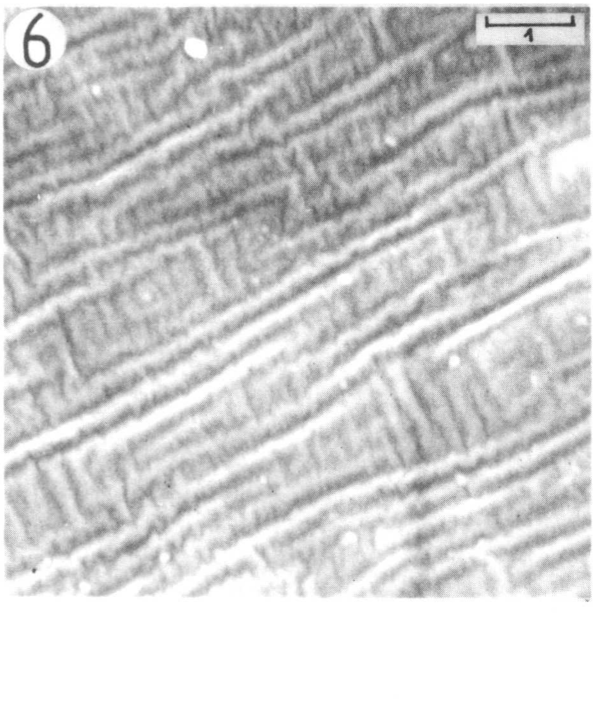
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Plate 15: Biogene corrosion due to epilithic and endolithic organisms. The included scale is in microns.

Fig.1: The section vertically through the surface of the shell and through the calcitic crossed lamellar layer shows intensive perforation due to the activity of endoliths producing a micritic shell part and beneath that zone tubular dissolution channels that may end with a widening (arrow).x 300.

Fig.2: Intensively bored calcitic shell portion that has almost totally lost its original structure. x 630.

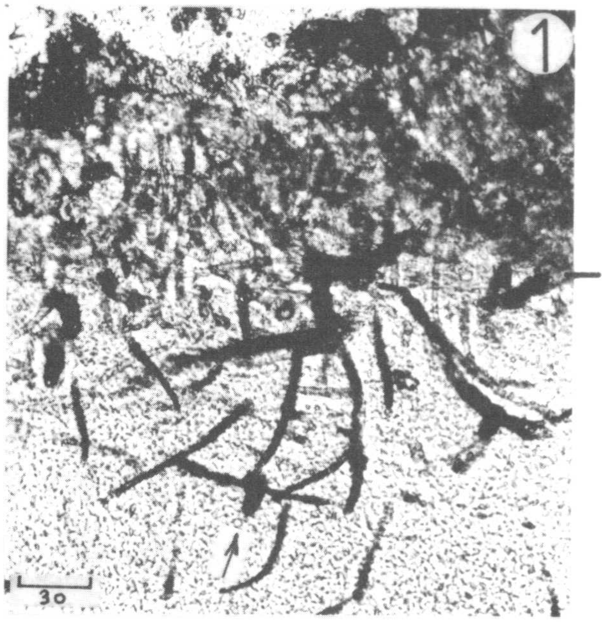
Fig.3: The detail from Fig.2 shows a relict of the original boring organism (probably a fungus) still within its tube. x 2500.

Fig.4: The etched radial section vertical to the surface of a juvenile shell shows micritization beginning at the surface of the shell and continuing into the calcitic layer as well as into the aragonitic crossed lamellae of the inner layers as boring tunnels. x 310.

Fig.5: The fracture parallel to the surface of the shell through the calcitic shell layer shows nearly round tubes which still hold relicts of the endolithic organisms which excavated them. x 1300.

Fig.6: Etched section perpendicular to the surface of the shell that is covered by a crust of red algae below which there are endoliths that penetrate the shell (arrow). x 310.

Fig.7: Thallus of a red alga of the type seen in Fig.6. x 800.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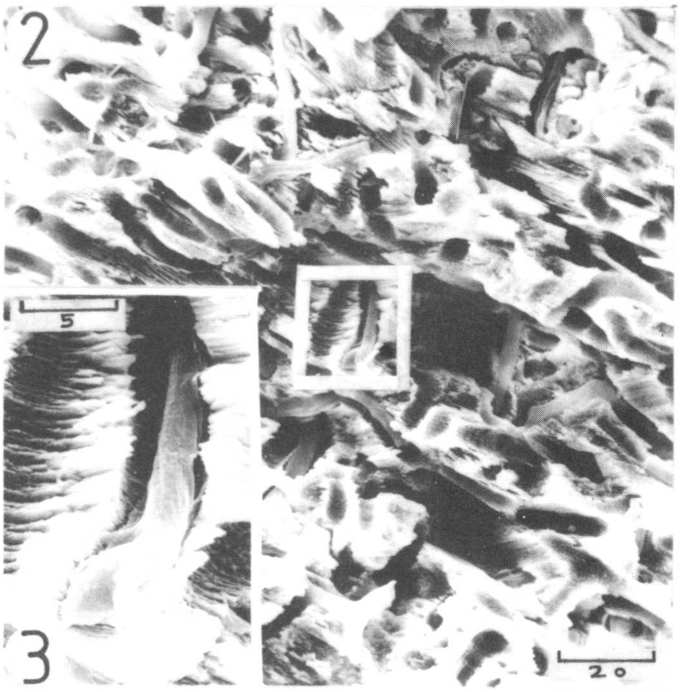
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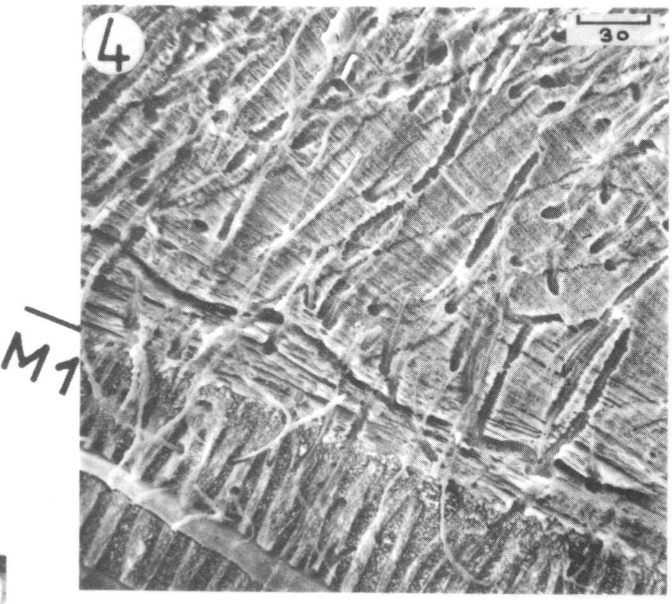
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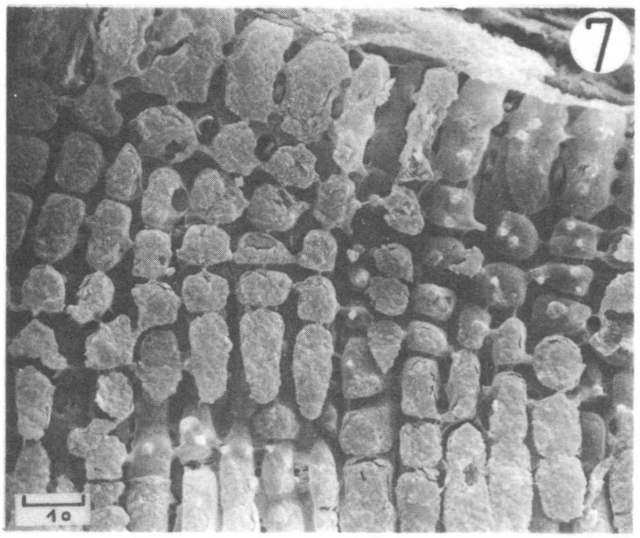
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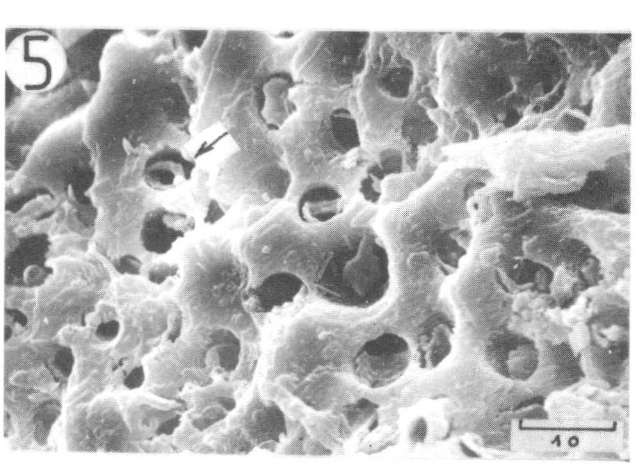
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