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Shell Microstructure and Systematics of *Sphaeriidae (Bivalvia, Eulamellibranchiata)*

[With 5 text-figs. and pls.VI—XXXVIII]

Systematyka małży z rodziny *Sphaeriidae (Bivalvia, Eulamellibranchiata)* na podstawie mikrostruktury muszli

Abstract. Seventeen species of the *Sphaeriidae* have been included in this study. In the members of this family the periostracum forms about 5% of the shell thickeness and on its inner and outer surfaces it bears sculpture, which is presumably a characteristic feature of particular species. Spherical or elongated conchiolin structures were observed on the inner surface of the periostracum of *Pisidium nitidum*; they strengthen its adhesion to the calcareous layers of the shell. The calcareo-organic portions of the shell are differentiated into layers distinguished by their homogeneous-granular, granular (homogeneous, Kobayashi, 1971), diagonal (composite prismatic, Kobayashi, 1971) and palisade (pallial myostracum) structures. In most species of the family studied canals, perpendicular to the shell surface and directed towards the inside of the shell, were seen in the calcareous layers. An analysis of microstructural characters indicates that the presence or lack of homogeneo-granular and granular structures, the value of angles between the lamellae of the diagonal layer, the shape of plates of the palisade layer and the pores are of essential taxonomic importance. The microstructural characters support the division of the *Sphaeriidae*, generally applied at present, and add new data to the issue of the systematic position of several taxa, e. g. *P. casertanum* f. *ponderosum* and *P. nitidum* f. *crassa*.

I. INTRODUCTION

The purpose of this work was to examine the shell microstructure of selected species and forms of the family *Sphaeriidae*, with special attention given to those whose taxonomic status had always raised doubt. The results of this study should permit us to answer the question whether the knowledge of the microstructure of shell will make it possible satisfactorily to determine the taxonomic status and degrees of relationship regarding the known taxa in this family.

The choice of the *Sphaeriidae* as the subject of this study was dictated by the fact of their being poorly known. The monographs by Herrington (1962) on the *Sphaeriidae* of North America, and by Zeissler (1971), who collected and arranged the data about their European members, may be regarded as exceptions. A monographic study was also given to the species of the genus *Pisidium* in Czechoslovakia (BRABENEC, 1973). Sure enough, the *Sphaeriidae* of France are best known; they were studied as early as the nineteenth century by BAUDON (1857) and recently by JAYET (1973) and KUIPER (1963a, 1964, 1965a, b, 1966, 1968, 1974). Much information about the *Sphaeriidae* of Great Britain is owed to ELLIS's (1962) work and interesting data concerning the systematics and ecology of the members of this group from the Soviet Union can be found in publications by ZHADIN (1952), PIROGOV and STAROBOGATOV (1974), TIMM (1975) and KRIVOSHEYNA (1978).

Apart from papers with physiographic data (e. g. PIECHOCKI, 1969, 1972; BERGER, 1973) there are scarcely several studies on the sphaeriid clams in Poland, among them papers by FELIKSIAK (1938), BERGER (1958, 1959, 1962), JACKIEWICZ (1962) and KASPRZAK (1975).

Finally, much information about morphological and anatomical variation in the *Sphaeriidae* can be found in works by ODHNER (1921), FAVRE (1927) and EHRMANN (1956), whereas their ecology is treated of by HEARD (1965), LADLE and BARON (1969), MACKIE, QADRI and CLARKE (1974a, b, 1976), MACKIE (1976a, b, 1978a), MACKIE and HUGGINS (1976) and HOLOPAINEN and RANTA (1977a, b).

The cause of poor knowledge of this group should be sought in its tremendous morphological and anatomical variation, which is probably due to self-fertilization, frequent in this group, and formation of populations that constitute pure lines. It is this fact, above all, that is responsible for a long list of synonyms within this family, collected and, in so far as possible, arranged by HERRINGTON (1962) and ZEISSLER (1971); BOETTGER (1961) critically discussed older attempts at systematic division of these clams. Some of the more frequently encountered divisions are summarized in Table I.

The application of shell microstructure as the basis for taxonomic studies was acknowledged to be expedient, because 1) none of the classificatory criteria used so far for this family has given satisfactory results and 2) the diversity of the microstructure of mineralized parts of invertebrates (KESSEL, 1933; KADO, 1953, 1960; KOBAYASHI, 1969, 1971; TOWE & THOMPSON, 1972; MORYCOWA, 1977; MACKIE, 1978b; CARTER, 1979) and the results of experimental studies on the modes of shell formation (BEEDHAM & TRUEMEN, 1958; KADO, 1960; FRETTER & GRAHAM, 1962; TOWE & HAMILTON, 1968a, b; TIMMERMANS, 1969; WATABE & WILBUR, 1960) permit the supposition that the diversity of the microstructure of shells is dependent on the biochemical specificity of the organism. In addition, the fact that the data on the microstructure of the biological mineral-organic elements may possibly be used also in studies of deposits prompted us to make attempts to utilize them. Investigations of this type have been carried out for higher systematic units (HOROWITZ and POTTER, 1971; KOBAYASHI, 1971; POPOV, 1977), but the trial to use the microstructure of shell as a systematic character ended in failure (MACKIE, 1978b).

Table I

Some taxonomic divisions of the *Sphaeriidae*

Author	Family	Subfamily	Genus	Subgenus
1	2	3	4	5
Baker (1928)	*Sphaeriidae*	*Sphaeriinae*	*Sphaerium* *Musculium*	
		Pisidiinae	*Eupera* *Pisidium*	
Herrington (1962)	*Sphaeriidae*		*Sphaerium* *Pisidium*	
(Klappenbach 1960)	....	....	*Byssanodonta* *Eupera*	
Boettger (1961) (tylko rodzaj *Pisidium*)			*Pisidium*	*Pisidium* s. str. *Galileja* *Neopisidium*
Meier-Brook (1970)	*Pisidiidae*		*Pisidium* *Afropisidium* *Neopisidium* *Rivulina* (= *Euglesa*)	
Zeissler (1971)	*Sphaeriidae*		*Sphaerium*	*Sphaerium* st. str. *Sphaeriastrum*
			Musculium	
			Pisidium	*Pisidium* s. str. *Cymatocycles* *Neopisidium* *Odhneripisidium*
Kuiper (1962) Brabenec (1973)	*Sphaeriidae*		*Sphaerium*	
			Pisidium	*Afropisidium* *Neopisidium* *Odhneripisidium* *Rivulina* *Pisidium* s. str.
Pirogov et Starobogatov (1974)	*Pisidiidae*	*Sphaheriinae*		
		Pisidiinae	*Pisidium* s. str. *Neopisidium* *Odheripididium*	
			Euglesa	*Henslowiana* *Cymatocyclas* *Casertiana* *Euglesa* s. str. *Cyclocalyx* *Pseudeupera* *Cingulipisidium* *Costopisidium* *Tetragonocyclas* *Arcteuglesa*

1	2	3	4	5
TIMM (1975) (ALIMOV et+ STAROBOGATOV 1968)	*Pisidiidae* (= *Sphaeriidae*)	*Sphaeriinae*		
		Pisidiinae	*Pisidium* *Lacustrina* *Parapisidium* *Afropisidium* *Euglesa* *Neopisidium* *Odhneripisidium*	

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II. MATERIAL AND METHOD

The clams of the family *Sphaeriidae* used in this study were collected by the authoress in 1973—1978. The assemblage contained, in addition, some specimens from Assist. Prof. Leszek BERGER'S collection and from the malacological collection of the Museum of Natural History, Polish Academy of Sciences, in Cracow. The sites of collection of the material are distributed all over the country and represent all categories of water habitats, from small periodical pools to rivers and lakes (Table II). A total of more than 4200 specimens belonging to 19 species were determined. Out of them, 17 species were included in this microstructural study, *P. pseudosphaerium* and *P. conventus* being omitted for lack of sufficient material. However, it seems that for the purposes of systematics it suffices to examine the other species of the same subgenera.

The material was preserved and stored in 75% ethyl alcohol. Part of the collection, removed from the alcohol, was kept in the dry state. Monographs by FAVRE (1927), EHRMANN (1956) and ZEISSLER (1971) and observations published by other authors in numerous specialistic papers were turned to account in determining specimens.

Table II

Material

Species	No. of specimens	Localities													
		Wolin Island	West Pomerania	East Pomerania	Białowieża Forest	Iława Lake District	Mazurian Lake District	Poznań region	Zielona Góra region	Nida River near Pińczów	Biała Przemsza River	Kraków region	Tatra Mts.	Low Beskid Mt.	Bieszczady Mts.
Sphaerium corneum	160	+	+		+	+	+			+		+			
— *rivicola*	30	+	+		+	+	+			+		+			
Musculium lacustre	300		+		+	+	+	+		+					+
Pisidium amnicum	300		+	+		+	+	+	+		+	+	+		
— *henslowanum*	500		+		+		+					+			
— *supinum*	40		+		+										
— *milium*	100	+	+		+		+	+			+				+
— *pseudosphaerium*	5							+							
— *subtruncatum*	230	+	+		+	+	+	+			+	+			
— *nitidum*	300	+	+		+						+	+			+
— *pulchellum*	20				+							+			
— *lilljeborgi*	4		(+)												
— *personatum*	400		+	+	+							+			
— *obtusale*	200		+		+		+					+	+		
— *casertanum*	1400		+		+	+	+		+	+	+	+	+	+	+
— *hibernicum*	100		+	+				+					+		
— *conventus*	5			+											
— *moitessierianum*	200		+					+							
— *tenuilineatum*	80							+			+				

+) subfossil specimens

In the list below the systematic arrangement has been adopted after ZEISSLER (1971) and the species and forms included in the present microstructural study are marked with an asterisk placed against their names.

Sphaeriidae

Genus *Sphaerium* SCOPOLI 1777

* *Sphaerium* (*Sphaerium*) *corneum* (LINNAEUS 1758)

* *Sphaerium* (*Sphaeriastrum*) *rivicola* (LAMARCK 1818)

Genus *Musculium* LINK 1807

* *Musculium lacustre* (C. F. MÜLLER 1774)

Genus *Pisidium* C. PFEIFFER 1821

* *Pisidium* (*Pisidium*) *amnicum* (O. F. MÜLLER 1774)
* *Pisidium* (*Cymatocyclas*) *henslowanum* (SHEPPARAD 1823)
* *Pisidium* (*Cymatocyclas*) *supinum* A. SCHMIDT 1851
* *Pisidium* (*Cymatocyclas*) *milium* HELD 1836
Pisidium (*Cymatocyclas*) *pseudosphaerium* BENTHEM, JUTTING et KUIPER 1947
* *Pisidium* (*Cymatocyclas*) *subtruncatum* MALM 1855
* *Pisidium* (*Cymatocyclas*) *nitidum* typ. JENYNS 1832
* *Pisidium* (*Cymatocyclas*) *nitidum* f. *bohemica* WESTERLUND 1890
* *Pisidium* (*Cymatocyclas*) *nitidum* f. *crassa* STELFOX 1918
* *Pisidium* (*Cymatocyclas*) *nitidum* A (see p. 271)
* *Pisidium* (*Cymatocyclas*) *pulchellum* JENYNS 1832
* *Pisidium* (*Cymatocyclas*) *lilljeborgi* CLESSIN 1886
* *Pisidium* (*Cymatocyclas*) *personatum* MALM 1855
* *Pisidium* (*Cymatocyclas*) *obtusale* typ. LAMARCK 1818
Pisidium (*Cymatocyclas*) *obtusale* f. *lapponicum* CLESSIN 1877
* *Pisidium* (*Cymatocyclas*) *casertanum* typ. (POLI 1791)
Pisidium (*Cymatocyclas*) *casertanum* f. *globulare* CLESSIN 1877
* *Pisidium* (*Cymatocyclas*) *casertanum* f. *ponderosum* STELFOX 1918
* *Pisidium* (*Cymatocyclas*) *hibernicum* WESTERLUND 1894
Pisidium (*Neopisidium*) *conventus* CLESSIN 1877
* *Pisidium* (*Neopisidium*) *moitessierianum* PALADJLHE 866
* *Pisidium* (*Odhneripisidium*) *tenuilineatum* STELFOX 1918

Microstructural examination was initially carried out using both a polarizing light microscope and a scanning electron microscope (SEM). After trials made with polarizing microscopes for reflected (Neophot-2) and passing light, light microscopy was given up, for, to be sure, magnifications obtained with them made it sometimes possible to identify some microstructural elements of the clam shells examined but not to describe them more closely. Observation of the surface and pores was possible only with the help of SEM. A Jeol JSM-35 scanning electron microscope was used at magnifications from 20 to 18000 times, most frequently 2000—6000 times, and at voltages of 15—35 kV.

Preparations were made from shells defatted in ethyl alcohol. Shells were broken in required planes and suitable fragments were chosen. Middle parts, situated on the internal side of the line connecting the marks of attachment of the muscles, distant from both the shell edge and the hinge, were chosen to describe sections parallel to the growth lines. They were digested in 0.1 n HCl for 8—12 seconds and rinsed in distilled water. The dried fragments were mounted on aluminium discs. At first only half the number of fragments were digested, the remaining ones being mounted immediately fater breating. Since the former preparations were more legible, the undigested ones had been abandoned. The preparations were sprayed with gold or platinum-gold alloy. About 600 photographs were taken.

The drawings of shells were made using a stereoscopic microscope with a microscopic drawing adapter (MNR-2).

The artifacts observed in preparations in SEM may have been caused 1. by fixation of the material and 2. by its digestion with HCl. In the course of fixation the substances that go into the making of the shell become precipitated from the extra-pallial fluid which is a colloidal solution present between the mantle and the shell. The structure of this precipitate, often very regular, seems to be independent of the shell structure. It is very spongy and loose, and more often than not falls off when the shell is being broken (Phot. 16). Sometimes, when the precipitates have the shape of regular or irregular large plates, they cling to the surface of the shell more closely. For this reason the observations of shell sections and the structures seen in the lumina of pores are very helpful in estimating the superficial structures. The digestion of the fracture surface with HCL aimed at removing fragments of the lamellae cracked while the shell was being broken. In consequence, the picture became more even and legible. The careful rinsing of shell pieces in distilled water after digestion prevented recrystallization.

III. RESULTS

Schematic structure of the shell of the *Sphaeriidae*

The schematic structure of the *Sphaeriidae* shell has been abstracted on the basis of the photographs of shell fragments of various species.

Its external layer is the conchiolin periostracum, the thickness of which forms about 5% of the shell thickness. Sculpturing, presumably characteristic of particular species, was observed on its surface. In *S. corneum* it consists of membranous ribs running parallel to the growth lines (Phot. 1), in *P. milium* of folds or wrinkles distributed in a disorderly manner (Phot. 81) and in *P. casertanum typ.* the surface is as a rule smooth and only in some of its fragments there are small protuberances (Phot. 169). Striae square to the growth lines were observed on the surface of juveniles of *P. casertanum* typ .(Phot. 168). A characteristic of grooves was found on the internal side, adhering to the calcareous layers, in the periostracum of *P. nitidum* typ. The mashen of the network are polygonal and where they adjoin the pores there occur spherical structures, about 3.5 μ in diameter, sculptured like the whole inner surface of the periostracum (Phot. 113). In the outer surface of the calcareous layers of the shell there are depressions (Phot. 114), usually filled with conchiolin spherical structures described above. Conchiolin fibres connecting the periostracum with the underlying layers (Phot. 110) were seen in *P. nitidum A* (see p. 271). At the edge of the shell the periostracum partly turns inside, thus protecting the marginal parts of the calcareous layer against action of external factors (Phot. 111).

The ligamentum, which in *P. personatum* is composed of bundles of fibres, parallel to each other and perpendicular to the shell surface, very much resembles the periostracum biochemically (Phot. 146).

The calcareo-organic layers, varying in structure, lie under the periostracum. In all the species examined the homogeneo-granular or the granular layer, or both these layers together or intermediate ones were found present. The homogeneo-granular structure contains considerable amounts of organic substance which cements the aggregates of calcium carbonate grains. The quantitative relations between the amounts of calcium carbonate and organic substance are various. The higher the proportion of organic substance, the more compact is the layer, whereas the higher calcium carbonate content is accompanied by an increase in the number of pores and, in consequence, the layer becomes spongy and, lastly, passes into the granular one (Fig. 1). This condition is well illustrated by the sections through the shells of *S. corneum* and *P. moitessierianum*. The described homogeneo-granular and granular layers correspond to KOBAYASHI'S homogenous structure (1971).

The appearance of the outer surfaces of the calcareous layers underlying the periostracum and composed of the structures described shows great interspecific variation. In *S. corneum* and *P. milium* these surfaces are granular and have pores, described earlier in *P. nitidum*, or shallow depressions. In *S. corneum* these structures are numerous and their diameter does not exceed 4 μ. In *P. milium* they are much smaller and not numerous. These two species differ also in the arrangement of grains and their size (Phots. 2. 3, 82). In *P. henslowanum* the grains are cemented together in rows and then the surface is built of somewhat irregularly, chaotically arranged bars (Phots. 59, 60). In another specimen of this species numerous bundles of fibrils, which it seems right to regard as strengthening structures, were uncovered by light digestion. On the basis of the picture obtained it is hard to make an opinion as to the relationship between these fibrils and the periostracum (Phots. 61, 62). *P. nitidum* typ. and *P. nitidum* f. *crassa* have this surface sculptured in a little different manner, but similar in both, composed of elongated plates arranged to from a herring-bone pattern (Phots. 115, 116).

In *S. rivicola* the outer surface of the calcareous layer is granular and has many holes and also pores situated in large shallow conchiolin depressions. In some pores there are plugs, whose structure resembles that of the depression walls (Phots. 22, 23). In *M. lacustre* the radially arranged grains sometimes form an irregular pattern round the shallow depressions (Phot. 36).

The diagonal layer, which often forms the nearly whole area of sections perpendicular to the growth lines becomes different gradually or by leaps from the granular or, directly, the homogeneo-granular layer. The angles between its lamellae are variable, less obtuse in the outer portions of shells than they are in the inner portions. Their values will be given in the descriptions of the microstructure of particular species. The free edges of the lamellae grow in

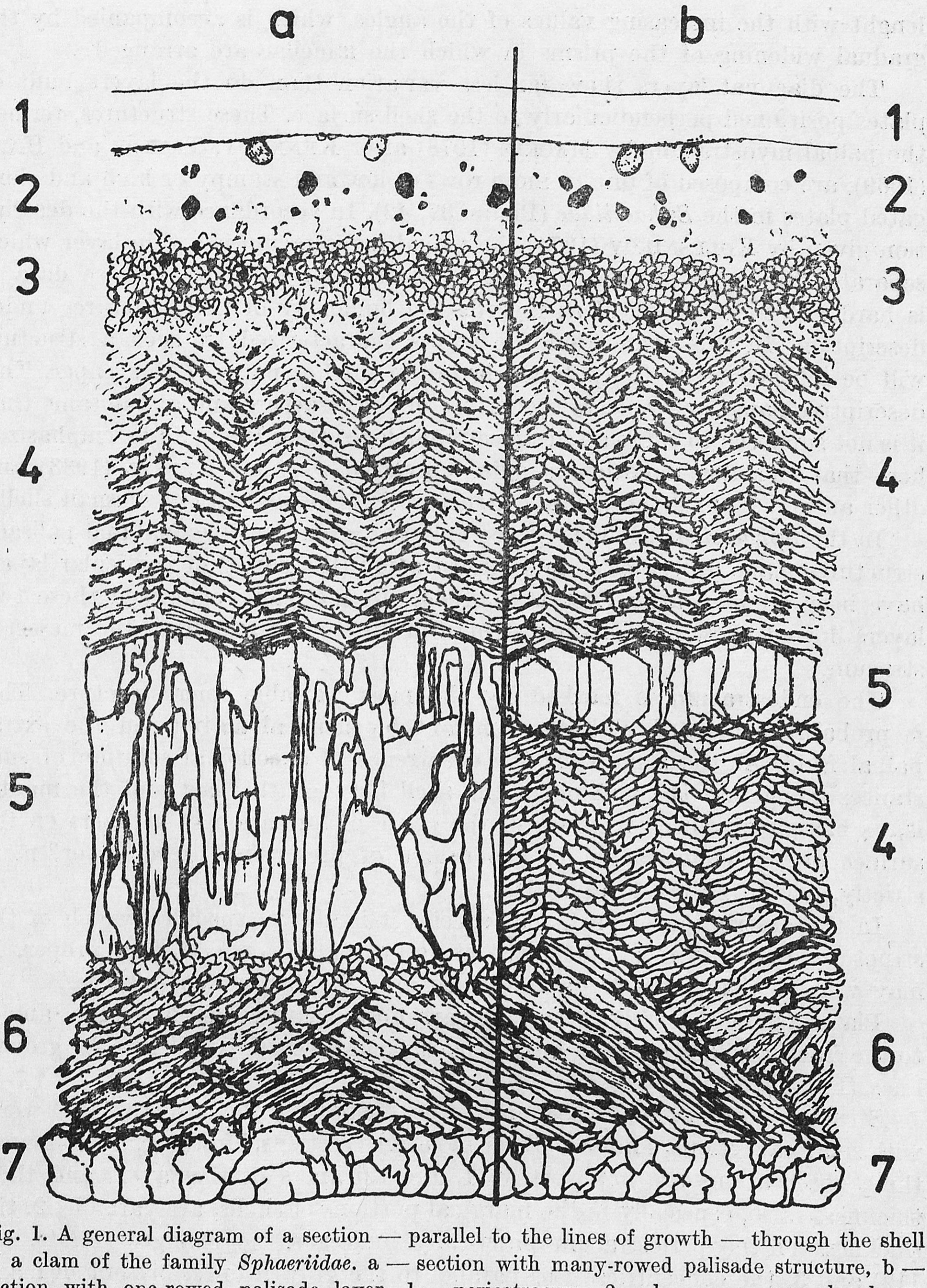

Fig. 1. A general diagram of a section — parallel to the lines of growth — through the shell of a clam of the family *Sphaeriidae*. a — section with many-rowed palisade structure, b — section with one-rowed palisade layer. 1 — periostracum, 2 — homogeneo-granular layer, with canals (hatched) parallel to the shell surface right under the periostracum, 3 — layer with granular structure, 4 — diagonal structure (composite prismatic structure), 5 — palisade structure, 6 — diagonal structure (crossed lamellar structure), only in shells of *S. corneum* and *S. rivicola*, 7 — endostracum

lenght with the increasing values of the angles, which is accompanied by the gradual widening of the prisms in which the lamellae are arranged.

The diagonal layers show far less variation than do the layers built of plates positioned perpendicularly to the shell surface. These structures, termed the pallial myostracum by MACKIE (1978) after KENNEDY, TAYLOR and HALL (1969), are composed of one or more rows of low and stumpy or high and elongated plates in the *Sphaeriidae* (Phots. 37, 42). In accordance with the description given by KOLESNIKOV (1974) the pallial myostracum is a thin layer which separates the mesostracum from the endostracum. In view of these data it is hard not to be sceptical as regards the homology of the structures under description. In this connection the layers characterized by such a structure will be referred to as the palisade layers in further parts of this paper. This descriptive name well reflects the nature of the structure and at the same time it is not supposed to cause an incorrect homologization. It should be emphasized here that this denomination is quite unrelated to what KESSEL (1933) and other authors termed the palisade structure in their desciptions of snail shells.

In the *Sphaeriidae* the homogeneo-granular, granular, diagonal and palisade structures make up the ecto- and mesostracum (the names of particular layers have been adopted after OBERLING, 1964). In the clams examined these two layers do not show any distinct structural differences and from the mesectostracum.

The endostracum is marked by the most variable microstructure. This is probably connected with the constant biochemical activity of the extrapallial fluid. At the same time the occurrence of a colloidal solution of substances going into the making of the shell between this last and the mantle is, as has already been mentioned, the cause of formation of artifacts on the surface of the endostracum in the course of preserving processes or, more strictly, at the killing of animals.

In the description of particular species it is always specified which of the structures above is most likely the structure of the endostracum proper. It may well be that some artifacts can be used for taxonomic purposes.

Plates arranged loosely, perpendicularly to the surface and at various angles to the fracture plane are seen in the endostracum section parallel to the growth lines (Fig. 1).

Structures observed on sections perpendicular to the growth lines were, with small exceptions, similar to those in parallel sections. However, the following three observations are noteworthy: 1. the thickness of the layers and their thickness ratio, especially in the marginal portions of shells, are variable, 2. the thickness of the periostracum practically undergoes no changes (Phots. 63, 112) and 3. the concentrical ribs parallel to the growth lines, present in many species of the family examined, are formed by ridges of the calcareous layers (Phots. 112, 196). This last observation is, in addition, supported by the photographs of the surfaces adjoining the periostracum (Phot. 36).

A comparison of digested and non-digested preparations permits conclusions as to the structure of elementary units of which the diagonal and palisade layers are built. They are, as is well known, organic-inorganic, i. e., calcareo-conchiolin lamellae. An analysis of these preparations shows that conchiolin forms a sort of sheath filled with calcium carbonate. Calcium carbonate also covers the conchiolin sheath on the outside and, in consequence, the lamellae of the diagonal layer and the plates of the palisade layer have the shape of regular rectangular parallelepipeds. They are joined together by conchiolin processes, which connect the conchiolin sheaths, giving rise to an organic, conchiolin matrix, covered by calcium carbonate on both sides.

The arrangement of the calcareous layers is heavily disturbed in the hinge region (Phot. 50), where there are some other structures beside those described above, e. g. a structure of tightly placed trabeculae, found in *P. casertanum* (Phot. 171). Moreover, in two species examined in this respect, *P. amnicum* and *P. casertanum* typ., a relatively aboundant network of canals was observed in the hinge region (Phot. 170). Similar canals occur in the calcareous layers of nearly all the sphaeriid species examined. The pores present in the outer surface of the shell join these canals, the diameter of which varies within wide limits in particular specimens. Processes of specialized cells of the mantle enter the canals (MUTVEI, 1964) and in most cases reach the periostracum. Similar canals were also observed in chitons and brachiopods (KOBAYASHI, 1969), but there they are situated in the marginal portions of the shell and in the they occur in the central part.

On account of its significance in palaeozoological studies, especially those of subfossil deposits, in this paper special attention is for the most part given to the microstucture of the calcareous layers, since, as has been pointed out, there are grounds to believe that their variability reflects the biochemica, specificity of the animals under study.

An analysis of sections and inner surfaces of shells and notes on systematics

At present the family *Sphaeriidae* is represented by 19 species in Poland (URBAŃSKI, 1957; BERGER, 1959). Sixteen of them are included in this microstructural study; *Pisidium lilljeborgi*, the species now encountered only in the subfossil state in Poland (KOWALKOWSKI and BERGER, 1972), has also been examined.

Genus *Sphaerium* SCOPOLI 1777

1. *Sphaerium* (*Sphaerium*) *corneum* (LINNAEUS 1758)

In Poland this common and variable species is represented by numerous conchological forms. In accordance with the data given by other authors (FAVRE, 1927; ADAM, 1947; EHRMANN, 1956; ZEISSLER, 1971), the differences chiefly concern the hinges, the situation of the umbo and the outlines and proportions of the shell. These forms are sometimes regarded as separate species (Žadin, 1952; Herrington, 1962), which opinion in view of the distinctly continuous nature of variation must be called in question. Shells obtained from Lake Sarąg and the River Rega were used in this microstructural study.

The shell thickness of *S. corneum* reaches 200 μ. The sections parallel to the growth lines are poorly differentiated (Phots. 4, 5). In this species the relatively thick periostracum (6 μ) overlies the considerably thicker homogeneo-granular layer. Its main constituent is organic matter, in which calcium carbonate crystals are distributed irregularly (Phot. 6). Right under the periostracum there are canals, which extend parallel to the shell surface. This layer passes fairly clearly into a layer which is granular in structure (Phot. 7) and contains far more $CaCO_3$ crystals. Here there are many gaps, which cause the spongy appearance of the granular layer.

The granular layer changes gradually into a layer with a regular herring-bone (diagonal) pattern. The angles between the lamellae of this layer range within relatively narrow limits, from about 90° in the region bordering upon the granular layer to about 110° in that adjoining the endostracum (Phot. 8). The lamellae which build the diagonal layer are joined together by processes, presumably conchiolin ones. The arrangement of gaps is regular here and they separate particular plates of this layer. A row of plates, about 5 μ in height and arranged like a palisade, runs at a distance of about 75 μ from the inner surface of the shell (Phot. 10). Lines parallel to the shell surface are often visible in this layer; they illustrate the successive stages of its growth in thickness (Phot. 3).

The innermost layer of the shell, the endostracum, is built of large irregular plates. They are fragments of plates of the diagonal layer, their arrangement in the endostracum being less compact and orientation independent of the growth lines (Phot. 9). The endostracum thickness in the examined shells of this species is around 8.3 μ.

The pictures of the inner surface of *S. corneum* shells and then those of the endostracum surface are very varied (Phots. 11, 12, 15, 16). The surface of the "endostracum proper" consists of irregular polygons, divided one from another by deep fissures (Phot. 11); a similar surface was observed in juvenile specimens of this species (Phots. 13, 14). The surface of the polygons is irregularly sculptured. The remaining pictures of the inner surface of the shell presented (Phots. 15, 16) seem to show artifacts produced by preservative procedures.

The diameter of pores, not numerous in the endostracum of *S. corneum*, ranges between 7 and 15 μ (Phots. 17—19). Their appearance confirms a close structural relation between the surface elements and the deeper layers of the shell.

2. *Sphaerium* (*Sphaeriastrum*) *rivicola* (LAMARCK 1818)

This species, marked by little conchological variation, was recorded from all fairly large rivers in Poland earlier (URBAŃSKI, 1957; ZEISSLER, 1971), but because of great changes that have taken place in its habitats in the last few years this information calls for verification. The material used in this study was collected in the Vistula and Nida.

The shell microstructure of members of these two populations is identical. The shell thickness is 200 μ and the picture of the surface of fracture parallel to the growth lines somewhat less differentiated than in *S. corneum*. As in *S. corneum*, the homogeneogranular layer with canals parallel to the shell surface underlies the periostracum. The granular zone is poorly marked and, as a result, the diagonal layer appears much closer to the outer surface of shell than it does in the previous species. The angles between the lamellae of the diagonal layer are obtuse (135—145°). This layer ends abruptly in a row of irregular triangular plates (Phot. 28), which lie in the fracture plane, and then passes into another layer with a diagonal pattern, corresponding to KOBAYASHI's (1971) description of the crossed lamellar structure (Phot. 26, 27). The edges of the innermost plates of this structure form the inner surface of the shell.

At low magnifications the inner surface of the *S. rivicola* shell is fine-grained (Phot. 34), composed of irregular plates (Phot. 35). Their sculpture (Phot. 33) suggests that they are built of irregular grains of inorganic matter cemented with conchiolin. These plates are sides of prisms, separated by deep fissures and joined toghether by not numerous conchiolin bridges.

The sculpture of the inner surface in the shell region void of the endostracum, close to the shell edge, is different. The irregular plates are elongated and nearly all of them are oriented in the same direction (Phot. 20).

The calcareous layers are penetrated by canals (Phots. 25, 27, 29), which run perpendicularly to the shell surface and connect the outer surface of these layers with the inside of the shell. They end in pores in the granular surface adjoining the periostracum (Phots. 21, 23). Pores leading to these canals occur also in the inner surface of the *S. rivicola* shell (Phots. 30, 32, 34). Their diameter ranges from 6.8 to 10.0 μ. Structures difficult to identify were observed near two pores (Phot. 31); Here we may be concerned with the contents of canals somewhat changed in the course of the preparation of specimens.

Genus *Musculium* LINK 1807

3. *Musculium lacustre* (O. F. MÜLLER 1774)

In Poland *M. lacustre* is a common and moderately stenotopic clam (URBAŃSKI, 1957; PIECHOCKI, 1969; BERGER and DZIĘCZKOWSKI, 1977; DYDUCH and FALNIOWSKI, 1979; JURKIEWICZ-KARNKOWSKA, in press).

An abundant population of *M. lacustre* with distinctly different, teratical shells was found in the fish breeding ponds of the Academy of Agriculture at Mydlniki near Cracow. Taking into consideration the great impact of human activity on this habitat (cultivation, fertilisation), in it we may seek the causes of these monstruosities. The shells of this species obtained from other localities, despite their great diversity, do not form distinctly separate groups. The variation observed is clearly continuous. The specimens used for this microstructural study were derived from Lake Sarąg in Mazuria.

The shells of *M. lacustre* are exceptionally thin, the ones examined being 54—64 μ in thickness. The homogeneo-granular layer of this species, about 9.3 μ thick, passes into a fairly broad though poorly distinguished granular layer. The amount of organic substance in both these layers is considerably larger than in *S. corneum*, *S. rivicola* and *P. amnicum* and the gaps are clearly fewer. The diagonal layer, situated deeper, is built of plates which are distinctly thinner than in the above-mentioned species (Phot. 39). In all the sections examined (Phots. 37, 38) there are single rows of plates with irregular sides at the base of this layer. No doubt, they are formed from plate fragments from the diagonal layer. The remaining portion of the section, from that described to the endostracum, is filled with a layer having a somewhat disturbed diagonal arrangement. There are few gaps here and the amount of organic substance is exceptionally large.

The cross-sections through these shells suggest that the chief constituent of their inner cover is organic (Phot. 38). This is confirmed by the picture of the inner surface of shell (Phot. 40), covered with fine, rectangular imbricate plates (Phot. 41). Not very large numbers of pores occurring in the endostracum have rather irregular edges and do not exceed 13 μ in diameter.

Genus *Pisidium* C. PFEIFFER 1821

4. *Pisidium* (*Pisidium* s. str.) *amnicum* (O. F. MÜLLER 1774)

In Poland, as in its whole distribution area (ADAM, 1947; ZEISSLER, 1971), *P. amnicum* occurs in all fairly large water-bodies and streams. Shells from Lake Sarąg and the Rivers Nida and Biała Przemsza were used in this microstructural study.

The shells of *P. amnicum* are thick (about 220 μ). Two kinds of sections parallel to the growth lines have been found, one very poorly differentiated and the other with six well-seen layers. In both cases the homogeneo-granular and granular layers underlying the periostracum, are very thin (Phot. 46). Owing to this the regular diagonal structure appears distinctly very close to the outer surface of shell. The angles between the lamellae of the diagonal layer are about 90° in the outer portion and grow gradually to 135° toward the shell inside. In some specimens the diagonal structure fills the whole section area and reaches the endostracum (Phot. 43), more often however it changes into a more or less complex palisade layer (Phots. 42, 45). In the first case it is built of elongated plates perpendicular to the shell surface, while in the second case the palisade layer consists of two rows of plates. A row of plates similar to those described above is separated from the diagonal layer by a row of short bars placed vertically (Phots. 48, 49).

The palisade (complex) layer passes gently into a zone composed of lamellae which lie parallel to each other and slantingly to the shell surface. In the regions adjacent to the canals this arrangement is somewhat disturbed.

The endostracum of *P. amnicum* is built of fairly regularly arranged plates which are fragments of lamellae of the previous layer. Three rows can be distinguished here. The first of them, bordering on the mesoectostracum, has a regular arrangement and the plates are turned by a certain constant angle in relation to their parental plates. The row lying under it is less regular and the third one, although distinguishable, is poorly legible.

The section through the shell of a juvenile specimen (Phot. 44) of this species does not differ essentially from the picture given above. The thickness of the shell examined is about 130 μ, the homogeneo-granular and granular layers are weakly marked, the angles between the lamellae of the diagonal layer are about 120°. The palisade layer appears at a distance of 110 μ from the external surface of shell, which distance is similar in adult specimens.

The pictures of the internal surfaces of this species are very varied, which should probably be ascribed to various phases of growth. Nevertheless, the differences between the sculpture of the inner shell surface in adult specimens (Phots. 51—53) are not smaller than those between them and the corresponding elements of shells of juvenile specimens (Phots. 54, 55). The appearance of the pores besides indicates a close relationship between the structures seen on the surface and the deeper layers of the shell (Phots. 56—58). Thus, the variation observed does not seem to be caused by artifacts, the more so, since Kobayashi (1971) found a similar structure to that photographed in *P. amnicum* from the Nida (Phots. 51, 52) in *Barbatia obtusoides*.

In *P. amnicum* the pores are fairly numerous, their diameter being about 12.5 μ in adults and about 5 μ in juveniles.

5. *Pisidium* (*Cymatocyclas*) *henslowanum* (Sheppard 1823)

This moderately eurytopic species, occurring all over the territory of Poland, more frequent in lowlands than in mountains and piedmont regions, inhabits permanent water-bodies with rich vegetation. The continuous exchange of water seems to be an indispensable condition of its existence (Piechocki, 1969; Kasprzak, 1975; Dyduch and Falniowski, 1979).

The variation of *P. henslowanum* is relatively small, it involves the shape of the shell and the partial reduction or complete lack of the umbonal fold. *P. henslowanum* v. *distans* Stelfox 1929 and *P. henslowanum* v. *inappendiculata* Steenberg 1917 have been described on the basis of the variation of these characters (Feliksiak, 1938). These forms are linked together by a continuous row of transitional forms (ZEISSLER, 1971; DYDUCH and FALNIOWSKI, 1979; JURKIEWICZ-KARNKOWSKA, in press). Out of the shells collected in littoral parts of lakes in Pomerania and Mazuria and in sluggish rivers (Drwinka, Narewka), the specimens with a well-developed umbonal fold from Lake Gardno were chosen for this microstructural study.

The shell thickness of this species is about 190 μ. The pictures of the sections parallel to the growth lines form two clear groups. One of them includes the sections which are very poorly differentiated (Phots. 65, 66) and the other consists of those exhibiting several distinct layers (Phot. 68).

In the poorly differentiated sections a layer with a high organic-substance content lies under the periostracum (Phots. 59, 60). Its nature is intermediate between the homogeneo-granular and the granular layer described for *S. corneum* (Phot. 69) and it passes into a layer with a diagonal pattern. The angles between the lamellae range from 90 to 125° and, as in other species, they are smaller in the outer portion of the shell than in the inner one. Such structure fills the whole remaining part of the section through the shell of a juvenile, about 91 μ thick.

Phot. 67 illustrates a further stage of the growth of a shell. The palisade layer, consisting of irregular elongate plates arranged perpendicularly to the shell surface in a plane parallel to the plane of section, appears at a distance of about 92 μ from the shell surface.

Shells with strongly differentiated sections parallel to the growth lines (Phots. 64, 68) have a relatively thick periostracum, which is underlain by a layer with a specific lamellar-granular structure. Here the lamellae have a diagonal arrangement, which is diversified by a large number of structures distributed chaotically in the section surface. They are connected with the plates of the layer being discussed, which rapidly passes into another layer, characteristic of *P. henslowanum* (Phot. 70). This is, as a rule, a palisade structure built of "torn bands" arranged perpendicularly to the shell surface. These bands also make up the next layer, which differs clearly in that they undergo a deflection by a certain angle (Phot. 71).

The inner surface of the *P. henslowanum* shell is generally smooth. In one case it was irregularly furrowed (Phot. 72), there being sometimes holes in the furrows (Phot. 73); in another case it was covered with plates resembling delicate (Phot. 74) or massive (Phot. 75) laminae.

6. *Pisidium* (*Cymatocyclas*) *supinum* A. SCHMIDT 1851

P. *supinum* often occurs in the waters of Poland, although in small numbers, if not singly (BERGER, 1960; PIECHOCKI, 1972). In general, it is more often encountered in the lowlands than in the waters of the southern part of the country; it is a stenotopic and rheophilous species. The specimens collected show slight variation. Clams from Lake Gardno were used in this microstructural study.

The thickness of shells of *P. supinum* ranges between 190 and 220 μ. The homogeneo-granular and granular structures form one layer, about 14 μ thick, in the sections parallel to the growth lines. It gradually merges into a layer with a diagonal arrangement, and this extends as far as the endostracum. The angles between the lamellae change gradually, from 100° in the surface layers to 140° in those adjacent to the palisade structure. The diagonal layer is divided by several lines parallel to the shell surface; their presence is presumably connected with the rhythm of the growth of the shell in thickness (Phots. 76—79). The above-mentioned palisade layer, which probably forms the endostracum, is composed of irregular plates, resembling the corresponding plates of *P. henslowanum* in shape (Phot. 67).

The inner surface of the shell of this species consists of plates with irregular, strongly indented margins (Phot. 80).

7. *Pisidium* (*Cymatocycles*) *milium* HELD 1836

This stenotopic clam of the genus *Pisidium* does not occur very often and in large numbers and is not thought to be very variable (ZEISSLER, 1971). However, an analysis of its characters indicates the well-marked conchological distinctness of some groups, which FAVRE (1927) considers to be separate forms.

In Poland *P. milium* occurs in small numbers but it is regularly distributed. Three conchological types have been distinguished in the material used in this study (Fig. 2). They correspond with the typical (Fig. 2,1), *contortum* PRIME (Fig. 2,3) and *pseudosphaerium* FAVRE (Fig. 2,2) forms given by FAVRE (1927). The specimens of this last form do not belong to *P. pseudosphaerium* BENTHEM JUTTING et KUIPER 1947 (KUIPER, 1962b), which has been ascertained by comparing them with the specimens of L. BERGER'S collection verified by J. KUIPER. There were no intermediate specimens between these three forms, but it may well be that this was due to the small representative value of the material in hand. The material for this microstructural study consisted of shells of the typical form and *P. milium* f. *contortum* from a lake in Wolin Island and Lake Gardno. No significant differences were found in internal structure between the shells of these forms.

The thickness of *P. milium* shells, which are much thinner than in other species, ranges from 33 to 70 μ. The distinct homogeneo-granular layer, 5.2 μ thick, underlies the relatively thick periostracum, which forms about 5% of the total shell thickness. It is separated from the deeper lying diagonal layer by a zone of very loose, spongy structure. Here, in addition to numerous openings there are processes, probably of conchiolin, which link the homogeneo-granular layer to the diagonal one. Some lamellae of the diagonal layer are connected directly with the homogeneo-granular layer (Phot. 88). The angles between the lamellae of the diagonal layer are mostly obtuse (up to 140°) and, as in other species, they vary, that is, are almost acute (about 90°) in the outer part and more obtuse in the inner part. The occurrence of polygonal plates oriented perpendicularly to the section plane was found only in *P. milium* (Phots. 83, 84). The presence of cavities, fairly regularly arranged, in some sections of this species (Phots. 85, 86) may be associated with the occurrence of those plates.

The endostracum of *P. milium* is built of polygonal, sometimes subcircular plates perpendicular to the shell surface (Phot. 87). The inner surfaces of several examined shells of this species had a very various appearance (Phots. 89—92). A single pore was found in one specimen (Phots. 93, 94), but the inner surface of this shell was quite smooth.

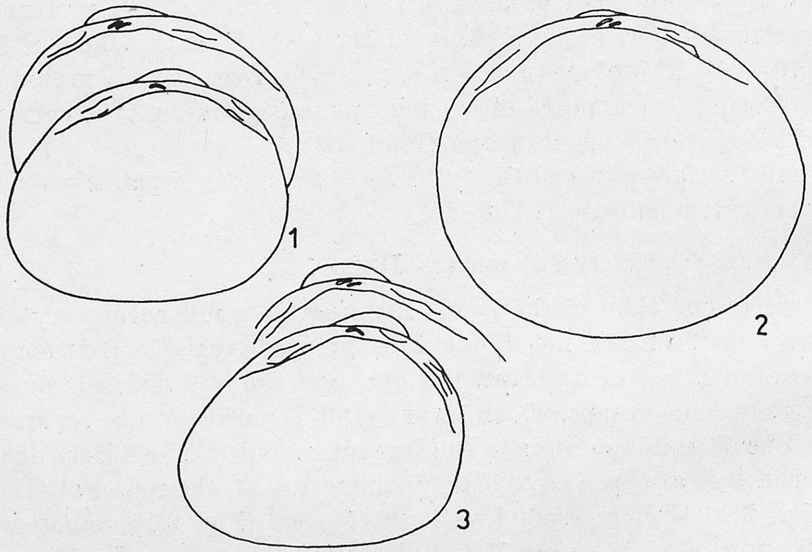

Fig. 2. Some forms of *P. milium* HELD 1836. 1 — *P. milium* typ., Stary Wisłok (from the collection of the Zoological Muzeum, P. A. o. Scs, in Cracow, undated); 2 — *P. milium* f. *pseudosphaerium* FAVRE, Drwinka 1976; 3 — *P. milium* f. *contortum* PRIME, Lake Sarąg, 1974

8. *Pisidium* (*Cymatocyclas*) *subtruncatum* MALM 1855

As in other countries of Central Europe (KUIPER, 1963 b), in Poland *P. subtruncatum* is a fairly common species and, as a rule, it occurs numerously (KASPRZAK, 1975; PIECHOCKI, 1972) in both stagnant and running waters.

This species is characterized by fairly great variation, but the range of variation is clearly smaller than in *P. casertanum* and *P. nitidum*, which only slightly surpass this species in eurytopicallity. The convexity, contour and surface sculpture of its shell undergoes the greatest changes. The variation of *P. subtruncatum* is more continuous than it is in other clams of the genus *Pisidium* (Fig. 3; Phots. 216, 217). The microstructural study material consisted of specimens collected in the rivers Biała Przemsza and Wełna and the collection, derived from the Stary Wisłok, in the Museum of Natural History, Polish Academy of Sciences, in Cracow.

The shell thickness of *P. subtruncatum* is between 35 and 77 μ. The well-developed granular layer (Phot. 98) extends under the thin periostracum, which forms somewhat less than 3% of the shell thickness. Conchiolin fibres, arranged chiefly perpendicularly to the shell surface were observed in it in one of the preparations. They may be strengthening structures, which connect the periostracum to the lower lying shell layers (Phot. 95).

The granular layer borders upon the diagonal one, which occupies the remaining part of all the sections examined (Phot. 99). Bands parallel to the shell surface can sometimes be seen in it. As in *P. supinum*, their origin is presumably due to the rhythm of growth of the shell (Phots. 96, 97, 102). The angles between the plates of the diagonal layer are 85—95° in the outer part of the shell and up to 120—125° in the inner part (Phots. 95, 100, 101).

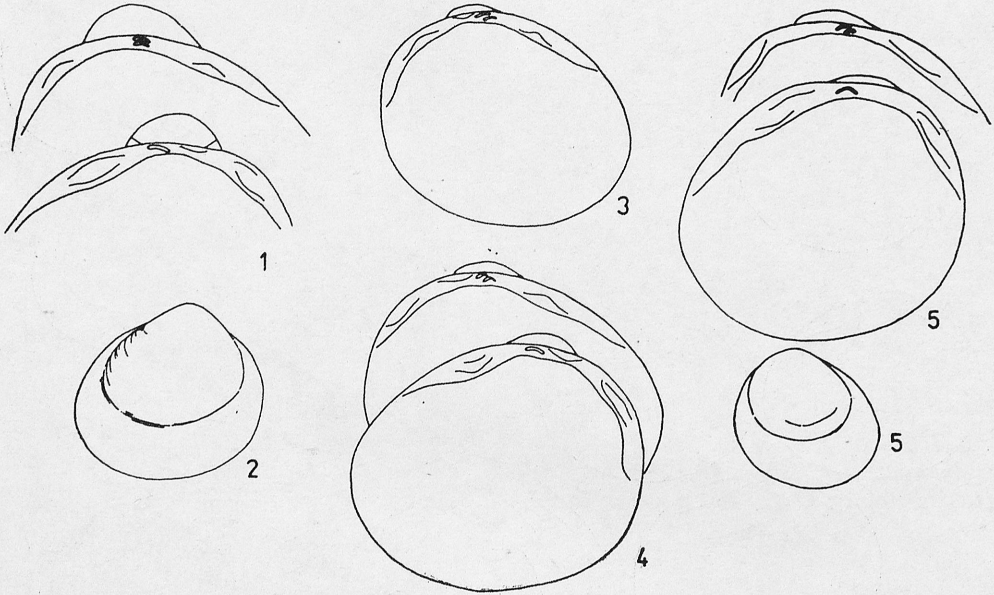

Fig. 3. Some conchological forms of *P. subtruncatum* Malm 1855, 1 — *P. subtruncatum* f. *pilens* Clessin, Stary Wisłok (from the collection of the Zoological Muzeum, P. A. o. Scs, in Cracow undated); 2 — very bulgy specien from Stary Wisłok (as above); 3 — *P. subtruncatum* typ, (Lake Sarąg, 1977); 4 — *P. subtruncatum*, thick-walled shell resembling that of *P. casertanum* f. *humeriferme* (Lake Gardno, 1975); 5 — *P. subtruncatum* with clearly broader hinge plate (Lake Sarąg, 1974)

Under low magnification the inner surface of shells of *P. subtruncatum* is fine-grained (Phots. 105, 108) and under higher power irregular polygonal or elongated plates, often with their surfaces richly sculptured, are visible. They are separated by deep fissures and linked by organic bridges.

The network of canals is ill developed in *P. subtruncatum* and none of its fragments was seen on transverse sections. The diameter of pores in the endostracum was very variable; it sometimes reached 16 μ and often was several times shorter (Phots. 103, 104, 107, 109). A wide range of pore diameters was observed in one and the same specimen (Phot. 106).

9. *Pisidium* (*Cymatocyclas*) *nitidum* JENYNS 1832

Many forms, frequently regarded as distinct species, have been described within this eurytopic species (PIROGOV & STAROBOGATOV, 1974).

In Poland *P. nitidum* occurs commonly, mostly in large aggregations (BERGER, 1962; PIECHOCKI, 1972; DYDUCH & FALNIOWSKI, 1979), although BERGER and DZIĘCZKOWSKI (1977) found that in the Konin lakes its specimens generally live singly. Apart from the typical specimens, three main forms of this species were distinguished in the material used for this study: *P. nitidum* f. *crassa* STELFOX (Phot. 220), *P. nitidum* f. *bohemica* WESTERLUND 1890 (Phot. 219), considered by PIROGOV and STAROBOGATOV (1974) to be a separate species, *Euglesa bohemica* (WESTERLUND 1890), and a group of small specimens more oval than the shells of the above-named forms and, except for three strongly marked concentrical ribs which separate the protoconch from the remaining

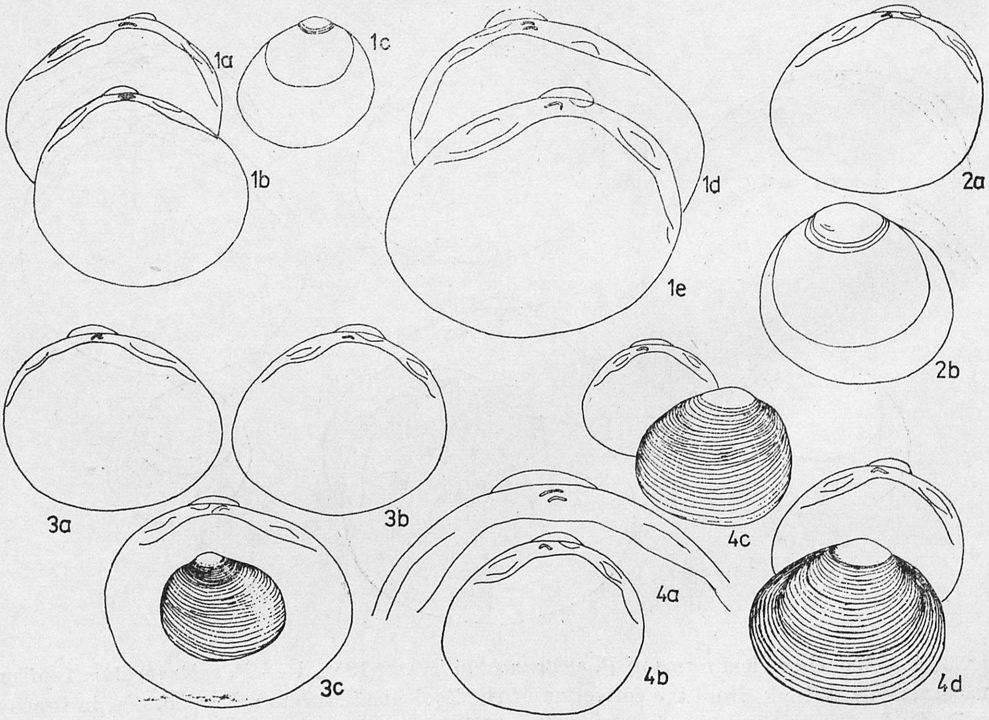

Fig. 4. Some conchological forms of *P. nitidum* JENYNS 1832. 1 a-c — *P. nitidum* typ. (Lake Gardno, 1975), d, e — *P. nitidum* typ., specimen with clearly broader hinge plate (Lake Gardno, 1975), 2a, b — *P. nitidum A*, dimensions: 1.2×1.5×0.9 mm (Gardno, 1975); 3a, b — *P. nitidum* f. *bohemica* (Gardno, 1975), c — *P. nitidum* f. *bohemica* (Biała Przemsza, 1978); 4a, b — *P. nitidum* f. *crassa* (Sarąg, 1974), c, d — *P. nitidum* f. *crassa* (Wolin Island, 1978)

part of the shell, having no sculpture seen under a magnifying glass but being smooth (Fig. 4, Phot. 218). Further in this paper I shall refer to this group of specimens as *P. nitidum A*.

The thickness of *P. nitidum* shells ranges within wide limites, from 21 μ in *P. nitidum A* to 90 μ in *P. nitidum* f. *crassa*. The sections trough the shells of *P. nitidum* typ., *P. nitidum* f. *bohemica* and *P. nitidum* f. *crassa* show many similarities, whereas the picture of the fracture surface in *P. nitidum A* is quite different.

In the typical form of *P. nitidum* the granular layer underlying the periostracum is well defined and about 21 μ thick, in *P. nitidum* f. *bohemica* and *P. nitidum* f. *crassa* it is, however, very poorly marked. The granular layer passes rather rapidly into the diagonal layer, in which, as in other species, the angles between the plates are smaller in the outer part of the shell (90—115°) than in the inner (130—145°). At the same time the free edges of the plates grow in lenght in the same direction (Phots. 118, 121—123).

At a distance of about 70—90 μ from the outer surface of the shell the system described above passes rapidly into a zone composed of characteristic plates, broad at the top and narrowing steeply towards the inside of the shell, thus resembling pickaxes in shape (Phots. 119—121). This layer is the last one in the sections of shells of *P. nitidum* f. *crassa*, whereas in *P. nitidum* typ. another layer built of lamellae lying obliquely to the shell surface is distinguishable (Phot. 119). The elongated plates (pallial myostracum) at the base of the diagonal layer are sometimes replaced by a row of loosely standing short plates which form the endostracum (Phot. 124).

The appearance of the section through the shell of *P. nitidum A* is completely different (Phot. 125). The periostracum is connected with the underlying layer by means of conchiolin fibres, which are visible in the photograph thanks to a slight displacement of the periostracum. The layer lying under the periostracum is composed of irregular plates, perpendicular to the shell surface. The remaining portion of the section is filled with laminated material of rather indistinct structure. The shells of these clams are exceptionally rich in conchiolin.

The inner surface of the above-mentioned forms of *P. nitidum* is smooth, furrowed by a network of grooves and fissures, varying in density (Phots. 126—128). It is supposed that pores occur in them sporadically. Their presence was found only in *P. nitidum* typ. (Phots. 129, 130). The fairly regular and decorative pattern seen on the inner surface of the shell of a *P. nitidum* f. *crassa* specimen seems to be an artifact produced during the preparation of material (Phot. 131).

10. *Pisidium* (*Cymatocyclas*) *pulchellum* JENYNS 1832

P. pulchellum is a poorly known, only slightly variable, stenotopic species. It occurs sporadically nearly all over the lowland (URBAŃSKI, 1957; BERGER, 1961, 1962; KASPRZAK, 1975).

A small number of specimens of *P. pulchellum* that I had collected included shells derived from the River Drwinka near Niepołomice. This is the south-easternmost locality of this species in Poland. The specimens from it were used in this ultrastructural study.

The inner structure of the relatively thin shell (about 50 μ) of this species is not much differentiated. The homogeneous layer, which underlies the periostracum, is very delicately marked and it merges into a layer of diagonal structure, which in the species under study filled up all the examined sections of shells. The angles between the lamellae vary from 110° in the outer part of the shell to 150° in the part adjacent to the endostracum (Phot. 132). The endostracum is composed of loosely, vertically arranged plates. All the layers mentioned are penetrated by canals, fairly numerous in this species, connecting the interior of the shell with the periostracum (Phot. 133).

The inner surface of *P. pulchellum* shells shows a great similarity to that of the shells described previously for *P. nitidum* typ. and *P. nitidum* f. *crassa*, but the furrows in the present species are somewhat shallower and distinctly oriented. As a result, the surface looks as if formed of irregular and elongated plates, which lie parallel to each other (Phots. 134, 136). The plates that surround the pores are ovel or polygonal (Phot. 137) and the diameter of pores is about 5 μ. The pores are fairly numerous, situated on the average about 100 μ from each other (Phot. 135).

11. *Pisidium* (*Cymatocyclas*) *lilljeborgi* Clessin 1886

This species of cool subpolar waters or deep alpine lakes, presumably occurs only as subfossil in Poland (Favre, 1927; Berger, 1962; Kowalkowski & Berger, 1972; Kuiper, 1974).

The microstructure of *P. lilljeborgi* shells was investigated on subfossil material. The periostracum of the fairly thick shells of this species (137 μ) overlies the rather indistinctly marked granular layer (Phot. 138), which changes gradually into the diagonal structure (Phot. 141). In *P. lilljeborgi* the angles between the lamellae lie within a narrow range from 120° in the outer layers to 130° in the inner ones. The diagonal structure passes gradually into a lamellar one, built of lamellae parallel to each other and oblique to the shell surface (Phots. 139, 140). They are adjacent to the palisade layer plates, which are perpendicular to the shell surface (Phot. 142). This is the endostracum, the innermost layer of the shell. Its surface and, thus, the inner surface of the shell is composed of polygonal plates separated by deep fissures (Phots. 144, 145). In the endostracum of this species there are pores, few in number and varying in diameter (Phots, 143, 144).

12. *Pisidium* (*Cymatocyclas*) *personatum* Malm 1855

As a typical species of small reservoirs, *P. personatum*, one of the least variable clams of the genus *Pisidium*, belongs to the commonest *Sphaeriidae* of Poland (Piechocki, 1972; Berger & Dzięczkowski, 1977). The specimens used in this microstructural study came from the Niepołomice Forest.

In the sections through the *P. personatum* shells, which are not very thick (50—90 μ), the very poorly marked homogeneo-granular layer occurs under the thin periostracum. The diagonal layer begins near the outer surface of the shell; the angles between its lamellae are exceptionally widely obtuse and, as in other species, increase gradually from 115° in the outer portion of the shell to more than 160° in the inner portion. No structure characteristic of the endostracum was observed in the sections examined (Phots. 147, 148). This agrees with the picture of the inner surface of the shell of this species. One of the fracture surfaces examined (Phot. 147) had different structure, its lamellae being arranged almost parallel to the fracture plane.

The inner surface of the *P. personatum* shell is covered by irregular plates (Phots. 151, 152) with a distinct granular structure. Numerous pores visible in it (Phot. 150) do not exceed 10 μ in diameter. They lead to canals, which reach the periostracum (Phot. 149).

13. *Pisidium* (*Cymatocyclas*) *obtusale* (LAMARCK 1818)

This is a clam of small reservoirs; it inhabits mostly periodical bodies of water and occurs sporadically in other water habitats (MEIER-BROOK, 1975). In view of the differences in the bulginess, contour, and surface sculpture of shells, the height and position of the umbo and the shape of the pseudocallus, several forms in the nature of ecophenotypes have been distinguished within the species *P. obtusale*. This species is common in Poland (FAVRE, 1927; URBAŃSKI, 1957).

The specimens of thin-walled shells, derived from a forest marsh in Mazuria were used as the basis for this study (Phots. 221—223). They are far bigger than other specimens of this species and there are many intermediate forms between them. The contour, bulginess and the development of the umbo in these thin-walled shells are analogous to those in *P. obtusale* f. *lapponicum* CLESSIN 1877, a form of small bodies of water, occurring in the north and in geological deposits of cold periods (SMULIKOWSKI, 1939; ZEISSLER, 1971), and often regarded as a separate species (KUIPER, 1975). On the other hand, similar specimens with somewhat elongated shells are characteristic of puddles and flood waters of high-mountain brooks (KUIPER, 1974). For studying the microstructure of the shell of *P. obtusale*, I used the material from Toporowy Staw in the Tatras, the peatbogs near Ostrów and forest marshes in Mazuria. No essential differences in microstructure were observed between the shells of typical specimens (From Toporowy Staw and the peatbogs near Ostrów) and the thin-walled shells of specimens from the forest marshes in Mazuria.

The sections of relatively thin shells (30—46 μ) of *P. obtusale* are poorly differentiated. The granular structure forms a hardly distinguishable broad layer (Phot. 153). It changes gradually into a diagonal structure, in which the angles between the lamellae grow with the distance from the inner surface of the shell from 85° (in specimens from Toporowy Staw) or 100° (in those from the peatbogs near Ostrów) to 130° (Phots. 154, 155). The diagonal structure extends to the inner surface of the shell.

The inner surfaces of the specimens examined had numerous deep pores. Their diameter was 6—10 μ. The network of pores is very dense, the distance between the edges of pores being sometimes below 7.5 μ (Phots. 156, 163, 165, 166).

Particular forms and, often, specimens differ very much in the sculpture of the inner surface. In *P. obtusale* from the peatbogs irregular plates lie one on another and their structure suggests that they have been formed of fine carbonate grains cemented with organic matter (Phot. 164). This is also evidenced by Phots. 157 and 158, which probably show an earlier stage of shell formation.

The rims that surround the pores are a specific character of *P. obtusale* (Phots. 159, 162, 167). In the specimens from Makruty they have a very regular shape (Phot. 167), a certain regularity can also be found in the development of the plates which cover the inner surface in the members of this population. Rich though irregular sculpture of the inner surface was observed in several specimens of this species (Phots. 160, 161). It may be supposed to be an artifact brought about during the preparation of material.

14. *Pisidium* (*Cymatocyclas*) *casertanum* (POLI 1791)

The vast range of *P. casertanum* is in keeping with its uncommon eurytopicality and morphological variability. It occurs in numerous forms, many a time described as distinct species (HERRINGTON, 1962; KUIPER, 1966, 1974; JAYET, 1973), connected by rows of intermediate forms.

The great variation of *P. casertanum* is well illustrated by the specimens from rivers and fresh-water reservoirs of Poland (Fig. 5.1—5.6). Three groups are distinguishable in the material collected. The first of them consists of specimens with thin-walled shells characterized by numerous pores and the various position of the umbo in relation to the middle of the shell. The shell outlines are elliptic, ovate and, sometimes, slightly triangular, the hinge plates are narrow. The thickness (bulginess) of shells is variable and clearly correlated with environmental conditions. In general, the shells are less bulgy in small brooks with cool water (e. g. the Prądnik at Sułoszowa) than in forest marshes in the lowland, The extreme form, *P. casertanum* f. *globulare*, is characteristic of high-mountain puddles, although I found its specimens also in a forest marsh near Lake Sarąg in Mazuria. An interesting relationship was observed between the specimens of *P. casertanum* from this forest marsh and those from the brook flowing from it to the lake. The shells from the marsh were very bulgy (their dimensions: 4.2—4.7 × 3.5—4.0 × 2.7—3.2), those from the lake quite flat, whereas the specimens from the brook had intermediate proportions.

Another group of specimens is characterized by somewhat smaller shells with a smaller number of pores, their umbos situated close to the middle, and regular oval outlines. The specimens of this group inhabit highly stable habitats, like lakes, ponds, etc. This group is the least variable as regards conchology and it includes clams with shells typical of the species.

The third group comprises specimens with thick-walled and massive shells which have broad hinge plates. Their umbos are broad and shifted to the rear. The shell outlines vary from triangulo-oval to triangular. I gathered such specimens in medium-sized rivers and reservoirs, often marked by specific chemical properties, e. g. in waters on a chalk substratum. Relatively numerous ecophenotypes were described from Lake Gardno, and then from a body of water with decidedly unstable physico-chemical conditions (STRZELECKI & PÓŁTORAK, 1971). *P. casertanum* f. *humeriforme* and *P. casertanum* f. *ponderosum* are extreme forms in this group.

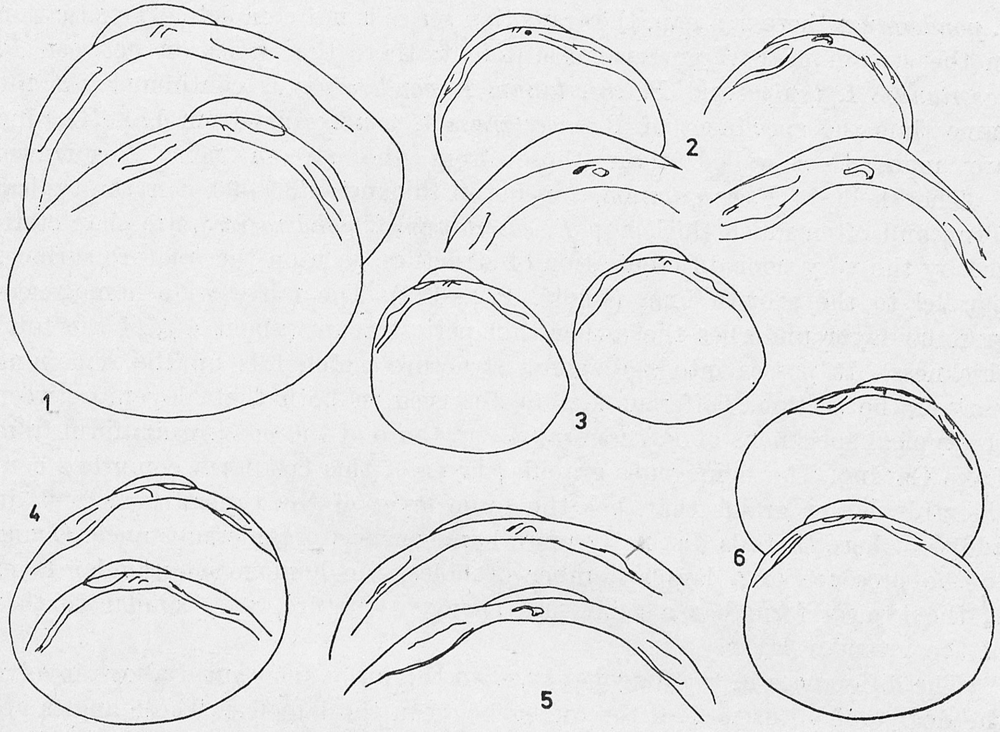

Fig. 5. Some conchological forms of *P. casertanum* (POLI 1791). 1 — *P. casertanum* typ., specimen with clearly broader hinge plate, thick-walled (Lake Gardno, 1975); 2 — *P. ponderosum* (Lake Sarąg, 1974); 3 — *P. casertanum* f. *humeriforme* (Jeziorak, 1976); 4 — *P. casertanum* typ. (Lake Sarąg, 1977); 5 — *P. casertanum* f. *globulare*, Stary Wisłok (from the collection of the Zoological Muzeum, P. A. o. Scs, in Cracow, undated), 6 — *P. casertanum* typ. (Bieszczady Mts., 1974)

Out of the numerous forms of this species, two groups of shells were chosen for close microstructural examination: specimens typical of the species and those of *P. casertanum* f. *ponderosum* from small brooks at Zielona Góra, the River Prądnik, a stream near Węgorzewo, the River Biała Przemsza and Lake

Gardno. The specimens of the *ponderosum* form from Lake Gardno and the stream near Węgorzewo do not correspond fully with each other. Between the specimens from Lake Gardno belonging to the typical form and *P. casertanum* f. *ponderosum* from the same locality there is a series of intermediate forms but it is incomplete (Dyduch & Falniowski, 1979). The continuity of transition exists between the typical form and *P. casertatum* f. *humeriforme*, whereas between the members of this last form and those of *P. casertatum* f. *ponderosum* there is a gap, the transition series is not complete. The situation in the stream near Węgorzewo is different; there the transition between *P. casertanum* f. *typica* and *P. casertanum* f. *ponderosum* is continuous. At the same time the specimens of *P. casertanum* f. *ponderosum* from Lake Gardno are more thick-walled than those from the stream near Węgorzewo.

The shells of *P. casertanum*, varying in thickness (35—90 μ in the typical form, and often much thicker in *P. casertanum* f. *ponderosum*), are characterized by the very poor differentiation of structure, seen on the fracture surfaces parallel to the growth lines (Phots. 172—177). The fairly wide homogeneo-granular layer underlies the rather thin periostracum (about 4% of the total thickness). It passes into a diagonal structure which fills up the remaining part of the section. Differences were observed in both these layers between the typical specimens of *P. casertanum* and those of the *ponderosum* form from Lake Gardno. The homogeneo-granular layer of this last form comprises considerably larger grains than has the same layer of the typical form and, in addition, here there is distinctly more homogeneous organic substance. Owing to the presence of a larger number of holes, the homogeneo-granular layer of the typical form has a somewhat spongy structure, very similar to that of the granular layer.

The differences in the diagonal layer in the forms mentioned above involve the degree of obtuseness of the angles between the lamellae. These angles are larger in the outer parts of the shell than in the inner parts, they change gradually from 100° to 130° in the typical form and from 140° to 160° in *P. casertanum* f. *ponderosum*. The foregoing is true of the allopatrically occurring specimens (176, 190, 191).

The inner shell surface of *P. casertanum* typ. is covered with irregular jagged plates, joined by bridges. Pores rather often occur in specimens of this species, their diameter being around 10 μ (Phot. 187). Some structures, arising presumably as a result of the inertia of reactions taking place in the extrapallial fluid, observed in several specimens of this species from different localities, have a marked resemblance (Phots. 188, 189, 192). They are formed of plates in the shape of flat cones with furrows, varying in depth, arranged radially on their edges. The furrows are distinctly deeper in *P. casertanum* f. *ponderosum* (Phot. 192) than in other forms (Phot. 189).

An analysis of the same characters in the sympatrically occurring specimens of *P. casertanum* typ. and *P. casertanum* f. *ponderosum* from the stream near Wegorzewo shows slight differences in their development. This concerns the homogeneo-granular and diagonal structures (Phots. 178, 181). The angles between lamellae are also similar (130—140° and 120—140°, Phots. 177, 180) and so are the usually very variable shapes of the plates of the palisade layer (Phots. 179, 182).

The great similarity of the shell surfaces (Phots. 183, 185) and pores (Phots. 184, 186) is striking.

15. *Pisidium* (*Cymatocyclas*) *hibernicum* WESTERLUND 1894

In Poland *P. hibernicum* is a probably fairly regularly but rarely occurring clam, which shows small conchological variation. In the assemblages used for this study it occurred in small numbers (Table II); the specimens from Lake Gardno were chosen for microstructural examination.

The transverse sections, parallel to the growth lines, through the thin (about 30 μ) and delicate shells of *P. hibernicum* are little differentiated (Phot. 193). The well-marked homogeneous layer with only few holes in it seems to be a characteristic feature of this species (Phot. 194). It passes via a poorly marked layer with a granular structure into the diagonal layer, in which the angles between the lamellae are exceptionally obtuse and, as in other species, increase rapidly from 105° to 150° (160°).

The endostracum is composed of very elongate plates, which, as in other species, are arranged perpendicularly to the shell surface, to which their long axes are parallel.

The pictures of the inner surfaces examined are various, mostly irregularly wrinkled and furrowed (Phot. 195). The pores in the endostracum are few in number, their diameter being about 7.5 μ.

16. *Pisidium* (*Neopisidium*) *moitessierianum* PALADILHE 1866

This stenotopic species inhabits stagnant or slow-running waters. In Poland- as in other parts of its range, it is not often met with (BERGER, 1958; KASPRZAK, 1975; MEIER-BROOK, 1975; BERGER & DZIĘCZKOWSKI, 1977). The results of investigations carried out so far show that the occurrence of *P. moitessierianum* is limited to the lowland. The specimens from Lake Gardno were used in this microstructural study (Phot. 224).

In *P. moitessierianum* the shell thickness ranges from 60 to 80 μ. The broad homogeneo-granular layer (about 7.5 μ), containing much organic matter with not numerous large holes, lies under the periostracum (Phots. 198, 207); sometimes the amount of organic matter is somewhat smaller and the holes are more numerous and, besides, much smaller (Phot. 202). Moreover, there are some sections void of any distinct and well-developed homogeneo-granular layer and then right under the periostracum is the very weakly marked granular layer, which further passes into another structure (Phots. 200, 203). In both these cases the said layers are underlain by structures, which seem to be specific of *P. moitessierianum* and are composed of bars arranged slantingly to the fracture plane. Their arrangement in the outer portion of the shell is less regular

(Phot. 204) than in the inner (Phot. 205). This layer fills the nearly whole section of the shell and reaches the endostracum of palisade structure (Phot. 201).

Unlike the above-described sections, the sections with a distinct homogeneogranular layer (Phot. 197) have a regular diagonal layer, in which the angles between the lamellae vary from 115° in the outer part to 150° in the inner and which passes into the endostracum built of loosely arranged plates perpendicular to the shell surface (Phots. 197, 199, 200).

This observation corresponds closely with the picture of the situation under the inner surface of the endostracum (Phots. 208, 209), which is covered by a rosette-like arrangement of plates. It may well be that this structure is an artifact and that the other type of inner structure observed in *P. moitessierianum* constitutes the actual surface of the endostracum (Phot. 210). It is formed of irregular plates separated by deep furrows.

17. *Pisidium* (*Odhneripisidium*) *tenuilineatum* Stelfox 1918

P. tenuilineatum is a stenotopic, slightly variable clam, found rarely and in small numbers in Poland (Kuiper, 1962a; Piechocki, 1972). The material used for this microstructural study comes from the collection of Assist. Prof. Leszek Berger.

The exceptionally thin shell of *P. tenuilineatum* (Phots. 211, 214) are marked by poorly differentiated sections. Under the periostracum is the wide granular layer (about a third of the section) of uncommonly loose and spongy structure (Phot. 212). It passes fairly decidedly into the diagonal layer, in which, as in other species, the angles between the lamellae vary from 110° to 160°.

The endostracum is built of vertically placed, elongate plates (Phot. 213). Its surface, i. e. the inner shell surface, is formed of irregular polygonal plates separated by fissures (Phot. 215).

IV DISCUSSION

1. The differentiation of the shell microstructure in the *Sphaeriidae*

In this work an attempt was made to establish the relationship of some forms within the family *Sphaeriidae* on the basis of the microstructure of their shells. In view of the lack of exact descriptions of the microstructure of freshwater clam shells, a general scheme of their structure in the species of the family *Sphaeriidae* (Fig. 1) and detailed descriptions of the sections parallel to the growth lines and structures of the inner shell surface were worked out on the basis of SEM pictures.

Special attention was given to the microstructural characters which can be of use in taxonomic studies. The sculpture found on the surface of the periostracum, presumably specific of definite groups, belongs to such characters

(Phots. 1, 81, 168). Its usefulness was not examined more closely because of limitations in our access to SEM. It may however be supposed that these and other details concerning the conchiolin structures associated with the periostracum may turn out applicable in studies of the relationships between the species of the *Sphaeriidae*. This is also suggested by GIUSTI'S (1973) observations on the glochids *Unio*, *Potamide* and *Anodonta* and by the distinct biochemical specificity of the periostracum found in some prosobranchiate snails (KOLESNIKOV, 1974). The same is true of other microstructural elements associated with the periostracum, i. e. the sculpture of the inner surface of the periostracum and elements binding it to the underlying lime layers. Among these we should number the spherical or elongated (fibrous) conchiolin structures found in *P. nitidum*. No information about the occurrence of such structures in other clams has been found in literature. The ascription of mechanical role to their presence seems to be the best explanation. It may be supposed, namely, that they are points which strengthen the adhesion of the periostracum to the calcareous layers. In other mussels there may be differently developed structures which do a similar job.

Lack of comparative data does not permit us to draw definitive conclusions as to the scale of variation of the surface structure, adjacent to the periostracum. Observations indicate a wide range of this variation (Phots. 2, 3, 59, 82 and others), and the completely different development of this character in *S. corneum*, *S. rivicola* and *M. lacustre* evidences its usefulness at least at subgeneric level (Phot. 3, 20, 21, 36). Its possible utilization in considerations on the problems concerning lower systematic units needs further study.

The presence of the homogeneo-granular structure (sometimes termed simply "homogeneous") was observed in most species, *P. subtruncatum*, *P. nitidum*, *P. pulchellum* and *P. obtusale* being exceptions in this respect. In *P. personatum* it is very poorly marked and the subfossil shells of *P. lilljeborgi* had their surface layers somewhat destroyed, which made their identification impossible. No normally developed homogeneo-granular structure was found in *P. henslowanum* and *P. supinum*, either. In these species the periostracum overlies a layer with an intermediate structure between the homogeneo-granular and granular ones, which differs them clearly from the other clams of the family under study and agrees with the opinion on their close kinship (HERRINGTON, 1962).

The layers with a granular structure occur more regularly in the species of the family *Sphaeriidae*. They are absent only from *P. pulchellum*, *P. personatum* and *P. casertanum* and sometimes are very narrow, e. g. in *S. rivicola* and *P. hibernicum*.

Maintaining their specific character, both the homogeneo-granular and the granular structure differ somewhat in form between particular species. Attention is attracted by the strongly spongy granular structure of *P. milium* and the granular structure, which does not stand out very distinctly against the adjacent layers, in *M. lacustre*.

The diagonal structure, included by MACKIE (1978b) in the "crossed-lamellar structure" (KOBAYASHI, 1971), predominates clearly in the shells of the *Sphaeriidae*. In view of the results of the study here presented, it however seems more justified to regard it as the "composite prismatic structure" (KOBAYASHI, 1971).

Only the innermost portions of the sections of *S. corneum* and *S. rivicola* agree with the description of the crossed-lamellar structure. In connection with the presence of this structure in the shells of clams of the family *Corbiculidae* (KOBAYASHI, 1971), it may be thought that the occurrence of the crossed-lamellar structure in the shells of the genus *Sphaerium* is an atavistic character. This gives evidence of the close relationship of the clams of those two families and agrees with the opinions on their systematic position (GOTTING, 1974). Moreover, it permits the supposition that the evolution of the *Sphaeriidae* connected with their expansion in fresh waters was accompanied by the replacement of the crossed-lamellar structure by the composite prismatic one. This statement is supported by the great resemblance of the conchiolin matrix of these structures (KOBAYASHI, 1969, 1971).

The angles between the lamellae of the composite prismatic structure are very variable within the family examined but, which has been checked on the shells of *S. corneum* and *P. casertanum*, they vary within constant limits in particular species and are generally smaller in the outer portion of the shell than in the inner (Table III). It seems that this character can be widely used in studies of the affinities within the homogeneous systematic groups of mussels comprising a number of species, whereas its usefulness in such investigations at supraspecific level is questionable. Measurability is a great practical advantage of this character.

Remarkable inter- and intraspecific variation has been observed in the degree of compactness of the diagonal structure (composite prismatic structure). This observation agrees with MACKIE's (1978b) results, but because of the immeasurability and unstability of such criteria their application in practice is restricted very much. Layers with a structure referred to as the palisade structure in this paper often occur in the sections parallel to the growth lines. As I have already mentioned, this term is used as vicarious for the elements which MACKIE (1978b) called the pallial myostracum. It should be emphasized that the name used here, the palisade structure, does not at all correspond with that used by KESSEL (1944) and other investigators in their descriptions of the inner structure of snail shells. The layer of palisade structure shows great variety as regards the shape and size of plates of which it is built, their arrangement and the situation of the whole layer in relation to the other microstructural elements of shell. Some of these characters are decidedly typical of these species and they will probably turn out helpful in the studies of supraspecific relations. This is especially true of the shape, size and arrangement of plates.

The palisade layer was never observed right under the periostracum, from

Table III

Selected characters of the shell microstructure in the *Sphaeriidae*

No.	Species		Layer		Angles (°)	Pores
			homogeneo-granular	granular		
1	*Sphaerium*	*corneum*	+	+	90—100	+*
2	—	*rivicola*	+	(+)	135—145	+*
3	*Musculium*	*lacustre*	+	[+]	120—145	+
4	*Pisidium*	*amnicum*	+	+	90—135	+
5	—	*henslowanum*	+		90—125	?
6	—	*supinum*	+		100—140	?
7	—	*milium*	+	(+)g	90—140	+
8	—	*subtruncatum*	—	+	85—125	+
9	—	*nitidum*	—	+	90—145	+
10	—	*pulchellum*	(+)	—	110—150	+*
11	—	*lilljeborgi*	?	—	120—130	+
12	—	*personatum*	(+)	—	115—160	+*
13	—	*obtusale*	—	+	85—130	+
14	—	*casertanum*	+	—		+
		f. casertanum S			100—130	
		f. ponderesum			140—160	
		f. casertanum A			130—140	
		f. ponderosum			120—140	
15	—	*hibernicum*	+	(+)	105—160	+
16	—	*moitessieranum*	±	∓	115—150	—
17	—	*tenuilineatum*	—	+	110—160	—

Symbols used in Table III

\+ — presence of the structure named in the caption of the appropriate column
— — lack of the structure named in the caption of the appropriate column
* — canals perpendicular to the shell surface, ending in pores right under the periostracum
(+) — very narrow layer
[+] — layer very weakly marked off from the adjacent layers
g — narrow layer, strongly spongy structure
? — no data
∓, ± — layers with homogeneo-granular and granular structures occurring alternatively in *Pisidium moitessierianum*
S — values of angles (in diagonal layer) given for sympatrically living specimens
A — values of angles (in diagonal layer) given for allopatrically living specimens

which it was always separated by another structure. It occurred mostly in the inner portions of the shell, where it formed the endostracum in adult specimens. This coincides with Mackie's (1978b) observations; examining the Canadian sphaeriid species, he found that the pallial myostracum occurs mostly in the inner part of the shell.

Out of the structures examined, the inner shell surface appeared the most variable. The basic causes of this variation are the ontogenetic development and the inertia of reactions taking place in the extrapallial fluid. The variation brought about by these factors has a very wide range (Phots. 52, 57, 58, etc.). The usefulness of this phenomenon in systematic studies, if there is any, cannot be established before carrying out adequate experiments on the modes of formation of shells and examining this process in the aspect of ontogenetic development.

The sculpture of the surface of the endostracum proper (i. e. in adult specimens, void of the structures arising in fixation owing to the biochemical inertia of the extrapallial fluid) is much less variable. This surface is composed of polygonal plates, separated by deep fissures and covered by characteristic sculpture (e. g. Phots. 11, 128, 185). It may be supposed that this is a fairly common development of this element, which is supported by the observations of the inner surface of the shell in *Cardita leana*, *Monia* sp., *Mytilus* sp. and other mussels (KOBAYASHI, 1971).

The variation of the endostracum proper at least partly corresponds with the variation of the palisade structure, which would indicate the similar informative value of these characters in systematic studies. This opinion is well illustrated by the photographs of the appropriate structures of *P. nitidum* and *P. casertanum* (e. g. Phots. 112, 117, 119, 120, 124, 126—128, 131, 176, 177, 180, 182, 183, 185, 188, 189).

At the present state of knowledge of the problems being considered here it is difficult to make precise conclusions. The estimation of the influence of various ecological factors on the above mentioned structures, especially the endostracum, which remains in the state of dynamic equilibrium with the extrapallial fluid as should be thought on the basis of what we know about the formation of the shell, (FRETTER & GRAHAM, 1962). Analogously to the types of inner structure it would perhaps be possible to distinguish those of the shell surface. Although the number of observations of these structures is small as yet, the above-quoted example of the correspondence of observations concerning the shell inside in the genera *Cardita*, *Monia* and *Mytilus*, and the resemblance of the surfaces of the endostracum in *P. amnicum* (Phot. 51) and *Barbatia obtusoides* (KOBAYASHI, 1971) rather indicate that the nature of variation in this structure is none too accidental.

In my microstructural studies of the shells of the *Sphaeriidae* I gave much attention to pores and canals in the calcareous layers of the shell. They occur in the shells of the mussels of the families *Arcidae*, *Glycimeridae*, *Spondylidae*, *Mytylidae* and *Chamidae*, and have also been found in the fossil members of the *Monoplacophora*, *Tryblidum reticulatum* (MUTVEI, 1964; KOBAYASHI, 1969). While in the shells of the families mentioned the pores in the endostracum lead to canals perpendicular to the shell surface and confined to the inner and pearl layers (inner and pellucid shell layers, acc. to KOBAYASHI, 1969), in the shells of sphaeriids they reach the periostracum. Corresponding pores in the outer surface of the calcareous layers of the shell (adjacent to the periostracum) were found in *S. corneum*, *S. rivicola*, *P. pulchellum* and *P. personatum*. In the shells of other species examined the course of the canals in the transverse sections parallel to the growth lines is similar to that in the species mentioned, which permits the supposition that in them the canals also reach the periostracum.

The number of pores and the network of canals differ in particular species. They were not found in *P. henslowanum*, *P. supinum* and *P. moitessierianum*, while in *P. milium* their presence was questionable — out of the four shells examined, only one had pores. In *P. casertanum* differences were found between particular forms in the number and density of canals. The shells of thin-shelled specimens living in small streams and reservoirs have generally a richer network of canals. The structures under discussion occur particularly abundantly in the clam populations of periodical high-mountain puddles (e. g. in the Tatra Mts.).

The diameters of canals are larger in the endostracum than in the layers bordering on it and thus the canals become narrower in the direction from the endostracum towards the periostracum. Apart from that, their diameters are very various: in the *Arcidae*, *Glycimeridae* and *Spondylidae* they are from 4 to 6 μ, in the *Mytilidae* smaller than 1 μ (KOBAYASHI, 1969) and in the examined species of the *Sphaeriidae* between 5 and 16 μ.

The significance of these canals to the clam organism is not clear. In the mantle epithelium of *Musculium* two types of cell have been distinguished, a low and broad and a high and pyramidal. These last cells have a kind of processes which enter the shell canals and reach the periostracum. In MUTVEI's (1964) opinion, this confirms the thesis maintained by TAYLOR et al. (1969) that the epithelium increases by growing in the periostracal groove, when the calcareous layers are not yet being secreted. KOBAYASHI (1969) does not accept this opinion and KNIPRATH (1978) claims that the epithelium grows owing to mitoses which take place all over the mantle surface.

In taxonomic studies of the family *Sphaeriidae* the data on the development of the canals and their network seem to be as important as the adequate information concerning the endostracum and the palisade layer.

In addition to the above-described canals perpendicular to the lines of growth, in the homogeneo-granular layer, directly under the periostracum in the shells of *S. corneum* and *S. rivicola* there are canals parallel to the shell surface. No information on similar structures in other clams has been found in available literature.

2. The shell microstructure and the systematics of the *Sphaeriidae*

As has already been mentioned, 17 clam species of the family *Sphaeriidae* and, according to ZEISSLER (1971), belonging to three genera, *Sphaerium* SCOPOLI 1777, *Musculium* LINK 1807 and *Pisidium* S. PFEIFFER 1821, were embraced in this study. A juxtaposition of the generic anatomic characters given by that authoress (Table IV) permits the inference that, as stated by HERRINGTON

(1962), except for the conchological criteria (calyculism, Mackie & Qadri, 1974) there are no grounds to separe *Musculium* Link 1807 as a distinct genus. Moreover, Mackie and Qadri (1974) question the diagnostic value of calyculism.

A comparison of *S. corneum*, *S. rivicola* and *M. lacustre* with respect to their microstructure shows that 1. there are differences between them in the formation of the granular (Table III) and palisade layers (Phots. 9, 10, 28, 37—39), 2. unlike the other two species, *M. lacustre* has no canals parallel to the shell surface in the homogeneo-granular layer, and 3. pores were found present under the periostracum in *S. corneum* and *S. rivicola* and then the canals perpendicular to the shell surface reach the periostracum directly in these species, whereas in *M. lacustre* they seem to terminate in the homogeneo-granular layer.

The first observation agrees with anyway undoubtful specific distinctness of the clams discussed, whereas the others indicate the existence of greater differences between *M. lacustre*, on the one hand, and *S. corneum* and *S. rivicola*, on the other hand, than between these last two species. Considering the membership of *S. corneum* and *S. rivicola* in two separate subgenera, *Sphaerium* s. str. and *Sphaeriastrum* Bourguinat 1854 (Žadin, 1952; Ehrmann, 1956; Zeissler, 1971), these microstructural differences in shell seem to justify the retention of the genus *Musculium*. The presence of the crossed-lamellar structure in *S. corneum* and *S. rivicola* is an additional argument supporting this opinion.

It must be stated that the criteria used here should be verified by anatomical studies, since differences of similar status often occur between groups of species within the genus *Pisidium*, but they are accompanied by slight anatomic distinctness, used mostly as the basis for the erection of subgenera in this genus (Heard, 1965; Zeissler, 1971).

The microstructural variation of shells in the genus *Pisidium* includes all the elements described by me. Only in *P. amnicum* both layers underlying the *periostracum*, the homogeneo-granular and the granular, are distinctly marked. In the remaining species either the homogeneo-granular or the granular layer is present; only in the shells of *P. milium* and *P. hibernicum* a very thin granular layer can be distinguished beside the well-developed homogeneo-granular layer. *P. henslowanum* and *P. supinum*, as has already been mentioned, are exceptions with an intermediate structure.

The distinctness of the microstructure of shells of *P. amnicum* corresponds with the membership of this species in the subgenus *Pisidium* s. str., monotypical in Central Europe (Zeissler, 1971), whereas the presence of a specific structure in the shells of both *P. henslowanum* and *P. supinum* emphasizes their close relationship.

The remaining species examined in the genus *Pisidium* can be divided with respect to the development of the homogeneo-granular and granular layers into four groups. The most numerous group consists of species that have only the granular layer, i. e. *P. subtruncatum*, *P. nitidum*, *P. obtusale* and *P. tenuilineatum*.

P. pulchellum, *P. personatum* and presumably *P. lilljeborgi* have their homogeneo-granular layer poorly marked and no granular layer at all, whereas *P. casertanum* differs from the other species of this genus in that it has no granular layer but a distinct homogeneo-granular layer. Only in *P. moitessierianum* the occurrence of these layers seems to be alternative.

The fact that the presence of pores is taken into consideration in divisions within the genus *Pisidium* (Table IV) results in laying emphasis on the distinctness of *P. moitessierianum* and separating *P. tenuilineatum* from the first of the groups mentioned. This agrees with their membership in two different subgenera, occurring in small numbers in Europe, *Neopisidium* ODHNER 1921 (*P. moitessierianum*) and *Odhneripisidium* KUIPER 1962 (*P. tenuilineatum*).

Table IV

Anatomical criteria in the generic systematics in the family *Sphaeriidae* (tabulated after ZEISSLER, 1971)

Genus Body part	*Sphaerium* + *Musculium*	*Pisidium*
siphons	2	1
nephridium	inner (pericardial) tube forms a loop directed forward and downwards	no loop, pericardial tube rising upwards and somewhat bent
gills	both gills well developed and occurring on either side as an inner and outer gill, each with an inner and an outer lamella	gills shifted farther to the back, in most species the posterior gill loses its inner or ascending lamella so that the outer lamella by itself represents the whole gill; the posterior gill undergoes a further reduction within the genus

The occurrence of pores in the outer surface of the calcareous layers, right under the periostracum, differs *P. pulchellum* and *P. personatum* from the other species of the subgenus *Cymatocyclas* DALL 1903 and confirms their above-signalled close relationship. On the other hand, the inclusion of these species, as suggested by PIROGOV and STAROBOGATOV (1974), in separate subgenera (*Costopisidium* PIROGOV & STAROBOGATOV 1974 and *Euglesa* s. str.) excites doubt. The anatomic characters of *P. pulchellum*, *P. lilljeborgi* and *P. personatum* (EHRMANN, 1956; ZEISSLER, 1971) and the data on the microstructure of their shell, summarized in Table III, permit the supposition that these species are closely related to each other and that they are probably links of the same evolutionary line. This line presumably led from *P. personatum* through *P. lilljeborgi* to *P. pulchellum*. Here took place a reduction of the posterior gills, enlargement of the aperture for the foot and shortening and broadening of the siphon ending (ZEISSLER, 1971). These anatomic changes were accompanied by much smaller changes in the microstructure. All the three species retain the inner structure of shell similar, but the mean value of angles in the diagonal layer and seemingly the number of pores increase gradually. This last character, as has been pointed out for *P. casertanum*, is probably correlated with environmental conditions. The foregoing data probably constitute the basis of the isolation of the species mentioned from the subgenus *Cymatocyclas*. Before additional anatomical studies have been made, I propose tentatively to call this group of species *Cymatocyclas* DALL 1903 "A".

Interesting conclusions can be drawn from a microstructural analysis of three very variable species, *P. nitidum*, *P. obtusale* and *P. casertanum*, of which each comprises numerous conchological forms. As has already been mentioned, in the study material *P. nitidum* is represented by *P. nitidum* typ., *P. nitidum* f. *bohemica* and *P. nitidum* f. *crassa*. The clearly marked conchological and microstructural distinctness of the group of *P. nitidum* A specimens from slightly brackish Lake Gardno (PÓŁTORAK & STRZELECKI, 1971; DYDUCH & FALNIOWSKI, 1979) provides no bases to shake the systematic position of these clams. Lack of descriptions of similar forms in literature permits the supposition that the distinctness observed is connected with the specific physicochemical properties of water in Lake Gardno.

P. nitidum typ., *P. nitidum* f. *bohemica* and *P. nitidum* f. *crassa* occur beside this form in Lake Gardno. Despite the unquestionable differences between these three forms it seems right to retain them in one species. The recognition of *P. nitidum* f. *bohemica* and *P. nitidum* f. *crassa* as distinct species, as proposed by PIROGOV and STAROBOGATOV, has not been supported by their anatomy, and the present data on the distribution of the first of these forms indicate that it is a lacustrine ecophenotype of *P. nitidum* (PIECHOCKI, 1969; BERGER & DZIĘCZKOWSKI, 1977). The very close affinity of *P. nitidum* typ., *P. nitidum* f. *bohemica* and *P. nitidum* f. *crassa* is suggested by the similar values of angles in the diagonal structure and the resemblance of the shapes of plates in the palisade layer.

Much less variation was observed in the microstructure of *P. obtusale*. As mentioned above, this species produces several conchological forms connected by continuous series of intermediate forms. No essential differences were noted in the structure of the granular and diagonal layers between the typical and thin-walled specimens of large shells gathered in the forest marsh by Lake Sarąg. The presence of more or less regular rims round the pores is a characteristic feature of the inner surface of shells in *P. obtusale*; apart from that, the sculpture of the surface is very diversified.

The last of the species mentioned, *P. casertanum*, is one of the most cosmopolitan, eurytopic clams, variable in respect of its conchology. Out of the numerous forms, two, the typical and *P. casertanum* f. *ponderosum*, were chosen for close examination of the shell microstructure. In the material examined distinct differences in some microstructural elements were observed between the members of these forms from different localities. They concern the homogeneo-granular layer, the angles in the diagonal layer and the sculpture of the inner shell surface. This last character is marked by great intra- and supraspecific variation and so it has a limited value in systematic considerations. No differences were found between the members of these forms derived from the same locality, even as regards the sculpture of their inner shell surface. Thus, the issue of the systematic value of the shell microstructure becomes more complicated than in the cases described previously. The resemblance of the shell microstructure of *P. casertanum* typ. from the Biała Przemsza (Klucze) and that from Zielona Góra, and then the specimens occurring allopatrically, does not allow the acceptance of the opinion that the above-described situation is caused by ecological factors.

In the discussion of *P. casertanum* in the Systematic Part attention was given to the fact that the transition between the typical form of *P. casertanum* and *P. casertanum* f. *ponderosum* may differ from locality to locality. In view of these data and the differences found in the shell microstructure one should agree with ŽADIN (1952) and EHRMANN (1956), who propose to acknowledge *P. casertanum* f. *ponderosum* STELFOX 1918 as a distinct species, *P. ponderosum* (STELFOX 1918) (Fig. 5.2). At the same time, it should be stated that in *P. casertanum* itself it may come to the development of the ponderosum form, distinguished in the sense in which FAVRE (1927) distinguished it in various species, e. g. in *P. milinum* or *P. personatum*. It may be supposed that this tendency to form ponderosum-type shells is of the ecophenotypic nature in the meaning used by HUBENDICK (1951) with regard to the *Lymnaeidae*.

The anatomical criteria, presented in Table IV, and the shape and position of the umbo make the basis for the division of the family *Sphaeriidae* into three genera: *Sphaerium*, *Musculium* and *Pisidium*. The determination of species within these genera is based on the external and internal characters of shells. According to ZEISSLER (1971), the most important of them are the outline and convexity of the shell, the shape and position of the umbo, the sculpture of the surface and the structure of the hinge (mainly the shape of the hinge plate, the teeth and the fossa for the ligament). These characters as a rule stand the test, nevertheless their fluency often limits their usefulness. Another difficulty is that they undergo great changes under the influence of ecological factors, like temperature, chemism, speed of water flow, etc. The ranges of this phenotypic variation often overlap, e. g. in the Alpine members of *P. casertanum*, *P. hibernicum* and *P. personatum* (JAYET, 1973). JAYET (1973) and KUIPER (1974) write that the specimens of the Alpine populations are characterized by very thin and delicate (small amount of mineral salts, especially $CaCO_3$, in water) and exceptionally bulgy shells. This is probably connected with the thermal conditions prevailing in these biotopes; because of low temperatures the progeny stay somewhat longer in the mother's organism and the juveniles that begin independent life are larger than in other biotopes. This hypothesis is supported by the observations of MEIER-BROOK (1970), who studied the effect of temperature on the dynamics of populations of the *Pisidium* species.

The data from the Tatra Mts. (Wierzejski, 1883) only partly agree with the regularities observed by Jayet (1973) and Kuiper (1974) in the Alpine *Pisidium*. In the Tatra ponds Wierzejski (1883) collected the following species: *P. fossarinum* Clessin (most probably *P. casertanum* Poli), *P. pallidum* Jeffr., *P. obtusale* Pff. and *Calyculina lacustris* var. *Steinii* A. Schmidt (most probably *Musculium lacustre* O. F. Müller). The above-mentioned *Pisidium* species differed, according to Clessin, from the typical (lowland) ones only in size, that is, they were smaller; on the other hand, the specimens of the last species named were marked by their "uncommon largeness", which would agree with the observations from the Alps. Wierzejski's (1883) observations are corroborated by the scanty material collected by the authoress in the Tatra Mts. The taking into consideration of ontogenic variation causes much trouble, although some shell parameters of the species of this family, e. g. the length: height ratio, are exceptionally stable (Thomas, 1965).

An analysis of the sphaeriid shell microstructure suggests that it can provide some new characters, more stable, precise and less sensitive to ecological factors than are the macroconchological characters. The presence or lack of the homogeneo-granular and granular layers, the structure of the diagonal layer and that of the palisade layer plates and poress to be the most essential microstructural characters. We may cherish hopes that after their being verified in histological-anatomical studies, it will be possible to apply microstructural analyses more widely in palaeozoological and biological investigations.

V. CONCLUSIONS

A. Shell microstructure

The conchiolin periostracum, which overlies the calcareous layers in the *Sphaeriidae*, has its both outer and inner surfaces sculptured, the sculpture being presumably typical of species. Spherical or elongate conchiolin structures were observed on the inner surface of the periostracum in *P. nitidum*; they probably strengthen its adhesion to the calcareous layers.

The surface to which the periostracum adheres is very variable. The calcareous part of the sphaeriid shell is differentiated into the homogeneo-granular and granular layers (both included in the homogenous structure of Kobayashi, 1971), the diagonal layer (Kobayashi's crossed-lamellar and composite prismatic structures) and the palisade layer (pallial myostracum).

The sculpture of the inner surface of the shell of the *Sphaeriidae* is heterogeneous; now, it is difficult to estimate it from the systematic point of view, especially because of difficulties connected with making allowances for ontogenetic variation.

The calcareous layers of the *Sphaeriidae* are penetrated by canals perpendicular to the surface; the pores leading to them occur in the inner shell surfce.

B. Taxonomic conclusions

The present microstructural analysis of the clam shells examined has confirmed

— the distinctness of ***Musculium lacustre***, as a member of the genus ***Musculium***, from the remaining species,

— the distinctness of *P.* (*Pisidium* s. str.) *amnicum*, *P.* (*Neopisidium*) *moitessierianum* and *P.* (*Odheripisidium*) *tenuilineatum*, as members of three different subgenera, and

— the close affinity of *P. henslowanum* and *P. supinum* within the subgenus *Cymatocyclas* DALL 1903, which fact became the basis for the distinction of two groups of species: *P. subtruncatum*, *P. nitidum* and *P. obtusale*, and *P. pulchellum*, *P. lilljeborgi* and *P. personatum*. On the basis of anatomical observations the last three species have been included in the group *Cymatocyclas* DALL 1903 A of undetermined systematic status. In order to establish its relation to the remaining species of the genus it is necessary to carry out further detailed anatomical studies.

Finally, the analysis of the shell microstructure in *P. casertanum* typ. and *P. casertanum* f. *ponderosum* suggests the specific distinctness of the specimens of this last form. This concerns the individuals with distinctly triangular thick-walled shells, corresponding with the distinctly triangular thick-walled shells, corresponding with the description given by EHRMANN (1956). *P. ponderosum* seems to be a typical lacustrine species. Apart from that, specimens resembling *P. ponderosum* conchologically but different in microstructure may occur in other types of habitats. These should be regarded as members of *P. casertanum* f. *ponderosum*.

If the foregoing conclusions have been taken into consideration, the taxomic system given by ZEISSLER (1971) should be modified as follows:

Family *Sphaeriidae*

Genus *Sphaerium* SCOPOLI 1777
  S. (*Sphaerium* s. str.) *corneum* (LINNAEUS 1758)
  S. (*Sphaeriastrum*) *rivicola* (LAMARCK 1818)
Genus *Musculium* LINK 1807
  M. lacustre (O. F. MÜLLER 1774)
Genus *Pisidium* C. PFEIFFER 1821
  P. (*Pisidium* s. str.) *amnicum* (O. F. MÜLLER 1774)
  P. (*Cymatocyclas*) *henslowanum* (SHEPPARD 1823)
  P. (*Cymatocyclas*) *supinum* A. SCHMIDT 1851
  P. (*Cymatocyclas*) *milium* HELD 1836
  P. (*Cymatocyclas*) *pseudosphaerium* BENTHEM, JUTTING et KUIPER 1947
  P. (*Cymatocyclas*) *subtruncatum* MALM 1855

P. (*Cymatocyclas*) *nitidum* Jenyns 1832
P. (*Cymatocyclas*) *obtusale* (Lamarck 1818)
P. (*Cymatocyclas*) *casertanum* (Poli 1791)
P. (*Cymatocyclas*) *ponderosum* (Stelfox 1918)
P. (*Cymatocyclas*) *hibernicum* Westerlund 1894
P. (*Cymatocyclas A*) *pulchellum* Jenyns 1832
P. (*Cymatocyclas A*) *lilljeborgi* Clessin 1866
P. (*Cymatocyclas A*) *personatum* Malm 1855
P. (*Neopisidium*) *conventus* Clessin 1877
P. (*Neopisidium*) *moitessierianum* Paladilhe 1866
P. (*Odhneripisidium*) *stewarti* Preston 1909
P. (*Odhneripisidium*) *tenuilineatum* Stelfox 1918

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REFERENCES

Adam W. 1947. Revision des Mollusques de la Belgique. I. Mollusques terrestres et dulciceles. Mém. Musée. Royal D'Hist. Natur. Belg. Bruxelles **106** : 1—298.

Baudon A. 1857. Essai monographique sur les pisidies Francaises. Mém. Soc. Acad. Oise, Beauvais **3**: 315—67.

Beedham G. E., Trueman E. R., 1958. The Utilization of J^{131} by Certain Lamellibranchs, with Particular Reference to Shell Secretion. Quart. Jour. Microscop. Sc. London **99**, 2: 199—204.

Berger L. 1958. Nowe stanowiska *Pisidium moitessierianum* Paladilhe 1866. Pr. Kom. biol. Pozn. TPN, Poznań **19**: 5—9.

Berger L. 1959. Wyniki wstępnych badań nad groszówkami *(Pisidium)* Wielkopolski. Przyr. Polski zach. Poznań **2**: 279—284.

Berger L. 1960. Badania nad mięczakami *(Mollusca)* Pojezierza Mazurskiego. Badania Fizjogr. Polski zach. Poznań **4**: 7—49.

Berger L. 1961. Mięczaki pogranicza Wielkopolski, Śląska i Jury Krakowsko-Wieluńskiej. Pr. Kom. biol. Pozn. TPN, Poznań **25**, 1: 1—123.

Berger L. 1962. Uwagi o rozmieszczeniu małżów *Sphaeriidae* w Krutyni na Pojezierzu Mazurskim. Fragm. Faun. Warszawa **10**: 1—9.

Berger L. 1973. *Mollusca* of the river Raba and some of its tributaries. Acta Hydrobiol. Kraków **15**, 4: 401—411.

Berger L., Dzięczkowski A. 1977. VI. *Mollusca,* in the Bottom Fauna of the Heated Konin Lakes. Monogr. faun. pol. Warszawa — Kraków **7**: 151—179.

Boettger C. 1961. Zur Systematic der in die Gattung *Pisidium* C. Pfeiffer gerechneten Muscheln. Arch. Moll. Frankfurt am Main **90**: 227—248.

Brabenec J. 1973. Československé druhy rodu *Pisidium* C. Pf. — hrachovky (Moll. Biw.). Prace a studie — Přir. Pardubice **5**: 147—176.

Carter I. G. 1979. Comparative shell microstructure of the *Mollusca. Brachiopoda* and *Bryozoa.* Scanning Electron Microscopy 2, SEM inc., AMF O'Hare, I **1:** 439—446+456.

Dyduch A., Falniowski A. 1979. Mięczaki Jeziora Gardno i konieczność ich ochrony (*Mollusca* of Gardno Lake and necessity of their protection) — Ochr. Przyr. Kraków **42:** 151—181.

Ehrmann P. 1956. *Mollusca,* Weichtiere. Die Tierwelt Mitteleuropas. Leipzig, **1:** 1—257.

Ellis A. E. 1962. British freshwater bivalve Molluscs. Linnean Soc. Synopses Brit. Fauna 13, London.

Favre J. 1927. Les mollusques post-glaciaires et actuels du Bassin de Geneve. Mém. Soc. Phys. Hist. Nat. Geneve, **40** (1): 171—434.

Feliksiak S. 1938. *Pisidium subtruncatum* Malm v. *tenuilineatiformis* v. n. oraz kilka nowych lub rzadkich dla Polski groszówek (*Pisidium* C. Pfeiffer). *Pisidium subtruncatum* Malm v. *tenuilienatiformis* v. n. und einige für Polen neue oder seltene Pisidien (*Pisidium* C. Pfeiffer). Fragm. Faun. Musei Zoologici Polonici, Warszawa **3,** 24: 485—493.

Fretter V., Graham A. 1962. British Prosobranch Molluscs. Their functional anatomy and ecology. London Society, pp. 755.

Giusti F. 1973. The minute shell structure of the glochidium of some species of the genera *Unio, Potomida* and *Anodonta (Bivalvia, Unionacea).* Malacologia, **14:** 291—301.

Götting K.-J. 1974. Malakozoologie. Stuttgart.

Heard W. H. 1965. Comparative life histories of the north American pill clams *(Sphaeriidae: Pisidium).* Malacologia, Michigan **2,** (3): 381—411.

Herrington H. B. 1962. A Revision of the *Sphaeriidae* of North America *(Mollusca: Polecypoda).* Miscell. Publ. Mus. Zool. Michigan **118:** 1—74.

Holopainen I. J., Ranta E., 1977a. Carbon Dioxide Output in the Respiration of Three *Pisidium* Species *(Bivalvia, Sphaeriidae).* Oecologia (Berl.), Berlin **30:** 1—8.

Holopainen I. J., Ranta E. 1977b. Respiration of *Pisidium amnicum (Bivalvia)* measured by infrared gas analysis. Oikos, Copenhagen **28:** 196—200.

Horowitz A. S., Potter P. E. 1971. Introductory Petrography of Fossils. Berlin. 210 pp.

Hubendick B. 1951. Recent *Lymnaeidae,* their Variation, Morphology, Taxonomy, Nomenclature and Distribution. Kungl. Svenska Vetensk. Akad. Handl., Stockholm **3,** 1: 1—223.

Jackiewicz M. 1962 Występowanie *Pisidium personatum* Malm *(Mollusca, Bivalvia)* w biotopach lądowych. Ekol. pol. ser. B. Warszawa **8,** 1: 75—78.

Jayet A. 1973. Sur quelques *Pisidium* Haut-Alpins. Malacologia, Michigan **14:** 415—418.

Jurkiewicz-Karnkowska E. w druku: Mięczaki *(Mollusca)* drobnych zbiorników wodnych i ścieków Puszczy Białowieskiej i Puszczy Niepołomickiej. Ochr. Przyr. Kraków R. **44.**

Kado Y. 1953. On the Scheme of the Shell Structure of Lamellibranchs. Jour. Sc. Univ. Ser. B, Hiroshima 1, **14,** 18: 243—254.

Kado Y. 1960. Studies on Shell Formation in Molluscs. Jour. Sc. Univ. Ser. B, Hiroshima 1, **19,** 4: 163—210.

Kasprzak K. 1975. Zgrupowania małży z rodzaju *Pisidium* sensu lato *(Bivalvia, Mollusca)* w różnych typach zbiorników wodnych. Fragm. Faun., Warszawa **20,** 9: 131—141.

Kennedy W. J., Taylor J. D., Hall A. 1969. Environmental and biological controls on bivalve shell mineralogy. Biol. Rev. Cambridge Philos. Soc., **44:** 449—530.

Kessel E. 1933. Über Periostracum-Bildung. Z. Morph. Ökol. Tiere, 40, Berlin **3:** 348—360.

Kniprath E. 1978. Growth of the Shell-field in *Mytilus (Bivalvia).* Zool. Ser., Stockholm **7,** 2: 119—121.

Kobayashi I. 1969. Internal Microstructure of the Shell of Bivalve Molluscs. Am. Zool., **9:** 663—672.

Kobayashi I. 1971. Internal shell microstructure of recent Bivalvian Molluscs. Sc. Rep. Niigata Univ. Ser. E, Geol. Mineralogy, Niigata **2,** 27—50.

Kolesnikov C. M. 1974. Paleobiochemičeskie i mikrostrukturnye issledovanija v paleolimnologii (Teoretičeskie i metodologičeskie aspekty). „Nauka". Leningrad: 1—160.

Kowalkowski A., Berger L. 1972. Die Bedeutung der Conchylienfaunen für die spätpleistezäne und holozäne sediment — und Bodenstratigraphie. Bull. Amis. Sci. Lett. Poznań, ser. D, Poznań **12 13:** 215—224.

Krivošejna L. V. 1978. Melkie dvustvorčatye moljuski semejstva *Pisiidae* (podsemejstvo *Euglesinae*) basejna vjerchnego Irtyša. Zool. Z., Moskwa **57,** 10: 1489—1500.

Kuiper J. G. J. 1962 a. Systematische Stellung und geographische Verbreitung von *Pisidium tenuilineatum*. Arch. Moll., Frankfurt am Main. **91,** 4/6: 173—181.

Kuiper J. G. J. 1962 b. Zur Nomenklatur und Verbreitung von *Pisidium pseudosphaerium*. Arch. Moll., Frankfurt am Main **91,** 4/6: 183—189.

Kuiper J. G. J. 1963 a. Auguste Bandon, Seine Systematik der Pisidien, nebest biographischen Notizen. Arch. Moll., Frankfurt am Main **92,** 1/2: 49—54.

Kuiper J. G. J. 1963 b. Hauptzüge der Verbreitung des Genus Pisidinen in Europa. Arch. Moll., Frankfurt am Main **92,** 5/6: 247—252.

Kuiper J. G. J. 1964. Ist *Galileja tenebrosa* ein *Pisidium*? Arch. Moll., Frankfurt am Main **93,** 181—185.

Kuiper J. G. J. 1965 a. Familie — *Pisidiidae.* Zoetwatermollusken von Nederland, Den Haag 1—19.

Kuiper J. G. J. 1965 b. The status of *Pisidium hibernicum* Westereund. Jour. Conch., London **26,** 42—46.

Kuiper J. G. J. 1966. La distribution des espèces vivantes du genere *Pisidium* C. Pf. en France. Jour. Conch., London **105,** 181—215.

Kuiper J. G. J. 1968. Die spätpleistozänen Pisiden des ehemaligen Aschersleben. Sees. Arch. Moll., Frankfurt am Main **98,** 23—38.

Kuiper J. G. J. 1974. Die Pisidien der Hochalpengewässer. Arch. Moll. Frankfurt am Main **104,** 1 (3): 1—29.

Kuiper J. G. J. 1975. Zwei neue boreale *Pisidium*-Arten: *P. hinzi* und *P. waldeni*. Arch. Moll. Frankfurt am Main **106,** 1/3: 27—39.

Lade M., Baron F. 1969. Studies on three species of *Pisidium (Mollusca: Bivalvia)* from a chalk stream. J. Anim. Ecol. Cambridge **38,** 407—413.

Mackie G. L. 1976 a. Contributed papers at the 1976 meeting. *Sphaeriidae* natality and its significance in water quality studies. Bull. Amer. Malacol. Un.

Mackie G. L. 1976 b. Trematode parasitiam in the *Sphaeriidae* clams, and the effects in three Ottawa river species. Nautilus. Philadelphia 30, **90** (1): 36—41.

Mackie G. L. 1978 a. Effects of Pollutants on Natality of *Musculinum securis (Bivalvia: Sphaeriidae)*. Nautilus, Philadelphia **92** (1): 25—33.

Mackie G. L. 1978 b. Shell structure in freshwater *Sphaeriaceae (Bivalvia: Heterondonta)*. Can. Jour. Zool., Ottawa **56,** 1: 1—6.

Mackie G. L., Huggins D. G. 1976. Biological Notes on *Eupera cubensis (Bivalvia: Sphaeriidae)* from Kansas. Jour. Pis. Res. Board of Canada, Ottawa **33,** 7: 1652—1656.

Mackie G. L., Qadri S. U. 1974. Calyculism in *Musculium securis (Pelecypoda: Sphaeriidae)* and its significance. Can. Jour. Zool, Ottawa **52,** 8: 977—980.

Mackie G. L. Qadri S. U. Clarke A. H. 1974 a. Byssus structure of larval forms of the fingernail clam, *Musculium securis* (Prime). Can. Jour. Zool., Ottawa **52,** 7: 945—946.

Mackie G. L., Qadri S. U., Clarke A. M. 1974 b. Development of brood sacs in *Musculium securis Bivalvia: Sphaeriidae*. Nautilus, Philadelphia **88** (4): 109—111.

Mackie G. L., Qadri S. U., Clarke A. M. 1976. Intraspecific variations in growth, birth periode and longevity of *Musculium securis (Bivalvia: Sphaeriidae)* near Ottawa, Canada. Malacologia, Cambridge **15** (2): 433—446.

Meier-Brook C. 1970. Untersuchungen zur Biologie einiger *Pisidium*-Arten. Arch. Hydrobiol. Suppl. Stuttgart **38:** 73—150.

Meier-Brook C. 1975. Der ökologische Indikatorwert mitteleuropäischer *Pisidium*-Arten

(*Mollusca, Eulamellibranchiata*). Eiszeitalter u. Gegenwart, Öbringen/Württ. **26**: 190—195.

Morycowa E. 1977. L'ultra-microstructure du squelette des *Helioporidae* fissiles (*Octocorallia*). Second Sym. international sur les coraux et récifs. Paris 1975. Mém. du B. R. G. M. N° 89.

Mutvei H. 1964. On the shells of *Nautilus* and *Spirula* with notes on the shell secretion in non-cephalopod molluscs. Ark. Zool., Stockholm **16**, 14: 221—278.

Oberling J. J. 1964. Observations on some structural features of pelecypod shell. Mitt. Naturforsch. Ges. Bern. N. Folge, Bern **20**: 1—60.

Odhner N. H. J. 1921. On some species of *Pisidium* in the Swedish state museum. Jour. Conchol., London **16**, 7: 218—223.

Piechocki A. 1969. Mięczaki (*Mollusca*) rzeki Grabi i jej terenu zalewowego. Fragm. Faun. Warszawa **15**, 10: 111—197.

Piechocki A. 1972. Materiały do poznania mięczaków (*Mollusca*) rzeki Pasłęki. Materialen zur Kenntnis der Molluskenfauna das Flusses Pasłęka. Fragm. Faun. Warszawa **18**, 7: 121—139.

Pirogow V. V. Starobogatow J. I. 1974. Melkie dvustvorčatye molljuski semejstva *Pisidiidae* ilmenka Bolšej Karabulak v delte Volgi. Zool. Z., Moskwa **53**, 3: 325—337.

Popow S. V. 1977. Mikrostruktura rakoviny i sistematika kardiid. Trudy Paleontologičeskogo Instituta A. N. SSSR, Moskwa **153**: 1—124.

Smulikowski B. 1939. Przyczynek do znajomości morfologicznego zróżnicowania muszli *Pisidium casertanum* Poli i *Pisidium obtusale* C. Pfeif. — Contribution à l'étude de la différentiation morphologique de la coquille chez les *Pisidium casertanum* Poli et *Pisidium obtusale* C. Pfeif. Odb. z: Spr. Tow. Nauk. Warszawa, **32**: 83—84.

Strzelecki J., Półtorak T. 1971. Plankton przymorskiego jeziora Gardno w okresie letnim. The plankton of Lake Gardno the Baltic Sea during the Summer season. Acta Hydrob., Kraków **13**, 3: 269—294.

Taylor J. D., Kennedy W. I., Hall A. 1969. The shell structure and mineralogy of *Bivalvia. Nucelacea — Trigonacea.* Bull. Brit. Mus. (Natur. Hist.) Zool. suppl., London **3**: 1—125.

Thomas G. J. 1965. Growth in one species of *Sphaeriidae* clam. Nautilus, Philadelphia **79**, 2: 47—57.

Timm V. 1975. The *Pisidiidae* of lake Vörtsjärv. Estonian Contribution IBP Tallin, **4**: 201—262.

Timmermans L. P. M. 1969. Studies on shell formation in Molluscs. Nether. Jour. Zool., Leiden **19**, 4: 417—523.

Towe K. M. 1972. Invertebrate shell structure and the organic matrix concept. Biomineralization. Research raports, Stuttgart — New York **4**: 1—14.

Towe K. M., Hamilton G. H., 1968 a. Ultramicrotome-Induced Deformation Artifacts in Densely Calcified Material. J. Ultrast. Res., **22**, 274—281.

Towe K. M., Hamilton G. H. 1968 b. Ultrastructure and Inferred of the Nature and Developing Nacre in Bivalve Mollusks. Calc. Tiss. Res. Berlin **1**, 306—318.

Towe K. M., Thompson G. R. 1972. The Structure of Some Bivalve Shell Carbonates Prepared by Ion-Beam Thinning, A. Comparison Study. Calc. Tiss. Res. Berlin **10**, 38—48.

Urbański J., 1957. Krajowe ślimaki i małże. PZWS, Warszawa, 276 pp.

Watabe N. 1965. Studies on shell formation. XI. J. Ultrastr. Res., **12**, 3—4: 351—370.

Watabe N., Wilbur K. 1960. Influence of the Organic Matrix on Crystal Type in Molluscs. Nature London **188**, 4747: 334.

Wierzejski A. 1883. Zarys fauny stawów tatrzańskich. Odb. z: VIII t. „Pamiętnika Tatrzańskiego", Kraków 1—31.

Zeissler H. 1971. Bestimmungstabelle für die mitteleuropäischen *Sphaeriaceae*. Limnologica (Berlin) **8**, 2: 459—503.

Žadin W. I. 1952. Molljuski presnych i solonowatych vod SSSR. Moskva—Leningrad, 376 pp.

STRESZCZENIE

Celem pracy było zbadanie mikrostruktury muszli wybranych gatunków i form małży z rodziny *Sphaeriidae*, ze szczególnym uwzględnieniem tych, których status taksonomiczny zawsze budził wątpliwości.

W pracy wykorzystano materiały zbierane przez autorkę w latach 1973—1978 na terenie Polski (tabela II). Uzupełniono je okazami z kolekcji doc. dra hab. L. Bergera i zbiorów Muzeum Zoologicznego PAN w Krakowie. Ogółem oznaczono ponad 4200 okazów należących do 19 gatunków. Spośród nich 17 objęto badaniami mikrostruktury. Badania prowadzono głównie przy użyciu skaningowego mikroskopu elektronowego (SEM) Jeol JSM 35 w Pracowni Mikroskopii Elektronowej UJ.

Przygotowanie materiału do SEM obejmowało kolejno: łamanie muszli wzdłuż wyznaczonych płaszczyzn, płukanie wybranych fragmentów w alkoholu etylowym i wodzie destylowanej, trawienie 0,1 n HCL (10—12 sek.), ponowne płukanie ciągłe w wodzie destylowanej i suszenie. Preparaty napylane były złotem lub stopem złota i platyny. Używano napięć 15—35 kV i powiększeń 20—18 000 ×, najczęściej korzystano z obrazów o powiększeniach 2000—6000 ×. Wykonano ponad 600 zdjęć.

Na podstawie otrzymanych informacji opracowano schemat budowy muszli małży z rodziny *Sphaeriidae* (ryc. 1). Periostracum — zewnętrzna, konchiolinowa warstwa muszli — jest stosunkowo gruba i stanowi około 5% grubości muszli. Na jego powierzchni stwierdzono obecność struktur prawdopodobnie charakterystycznych dla poszczególnych gatunków (fot. 1, 81, 168, 169). Na wewnętrznej, przylegającej do warstw wapiennych stronie periostracum znaleziono u *Pisidium nitidum* typ. charakterystyczną siatkę bruzd. Oka tej siatki są wielokątne, gdzieniegdzie na opisywanej powierzchni występują kuliste twory o średnicy 3,5 μm, mające skulpturę podobną do całej powierzchni wewnętrznej periostracum (fot. 113). Na zewnętrznej powierzchni warstw wapiennych znajdują się wgłębienia (fot. 114), normalnie wypełnione opisanymi powyżej strukturami konchiolinowymi. Należy przypuszczać, że wzmacniają one przyleganie periostracum do warstw wapiennych. Podobną funkcję przypisać można konchiolinowym włókienkom łączącym periostracum z warstwami wapiennymi u *P. nitidum* A (fot. 110). Na brzegach muszli periostracum częściowo wchodzi do jej wnętrza (fot. 111).

Strukturę ligamentum badano u *P. personatum*. Budują je równolegle do siebie a prostopadle do powierzchni muszli ułożone pęczki konchiolinowych włókien (fot. 146).

Pod periostracum znajdują się warstwy wapienno-organiczne o różnej strukturze. U badanych gatunków stwierdzono obecność warstw homogenno-ziarnistej lub ziarnistej, obu równocześnie lub też pośrednich. Struktura homogenno-ziarnista zawiera znaczne ilości substancji organicznej, spajającej agregaty granul wapnia (fot. 207). W strukturze ziarnistej substancja orga-

niczna występuje w znacznie mniejszych ilościach. Opisane struktury zaliczyć należy do „homogeneous structure” KOBAYASHIEGO (1971).

Obrazy powierzchni zewnętrznych warstw wapiennych wykazują dużą zmienność, niekiedy znajdowano w nich pory (fot. 2, 3, 59, 60, 61, 62, 82, 115, 116). Powierzchnie te są tworzone przez opisane powyżej struktury zaliczane do „homogeneous structure”. Z warstw o strukturze ziarnistej lub homogenno-ziarnistej wyróżnicowuje się stopniowo lub skokowo struktura diagonalna, która tworzy często prawie cały przekrój. Zaliczono ją do „composite prismatic structure” (KOBAYASHI 1971), natomiast opisowi „crossed lamellar structure” (KOBAYASHI 1971) odpowiadają obrazy najbardziej wewnętrznych warstw *Sphaerium corneum* i *S. rivicola*.

W muszlach badanych małży często występuje struktura zwana w pracy palisadową, a przez MACKIEGO (1978b) za KENNEDYM, TAYLOREM i HALLEM (1969) nazywana „pallial myostracum”. Warstwy o takiej strukturze są jedno- lub wielorzędowe, zbudowane z płytek niskich i krępych, lub wysokich i wydłużonych (fot. 42, 48). Struktury: homogenno-ziarnista, ziarnista, diagonalne i palisadowa budują u *Sphaeriidae* ecto- i mesostracum. Te dwie warstwy nie wykazują tu wyraźnej odrębności strukturalnej i tworzą mesoectostracum. Endostracum jest prawdopodobnie warstwą o najbardziej zmiennej mikrostrukturze, co pozostaje w związku ze stałą aktywnością biochemiczną „extrapalliai fluid” (FRETTER i GRAHAM 1962). Budują tę warstwę płytki ułożone luźno w płaszczyznach prostopadłych do powierzchni wewnętrznej muszli (ryc. 1).

Porównanie preparatów trawionych i nie trawionych sugeruje, że płytki wchodzące w skład poszczególnych warstw powstają w wyniku wypełnienia przez węglan wapnia organicznej matrycy, tworzącej swoistą pochwę. Związek ten pokrywa także konchiolinową pochwę od zewnątrz (fot. 172, 173, 174, 177). Płytki, a ściślej ich pochwy, połączone są konchiolinowymi wypustkami.

Układ warstw wapiennych w okolicy zamka ulega zaburzeniu (fot. 50), a występują tu także struktury odmienne od powyżej opisanych (fot. 171). U dwóch badanych pod tym względem gatunków — *P. amnicum* i *P. casertanum* w okolicy zamków stwierdzono bogatą sieć kanałów (fot. 170). Podobne kanały o przebiegu prostopadłym do powierzchni muszli występowały u większości badanych gatunków (tabela III). Prowadzą do nich pory znajdujące się na wewnętrznej powierzchni muszli. Kanały dochodzą do periostracum, lub też kończą się w warstwach bezpośrednio do periostracum przylegających. Do kanałów wchodzą, zdaniem MUTVEIA (1964), wypustki płaszcza.

W dalszej części pracy opisano zróżnicowanie odpowiadających sobie przekrojów równoległych do linii przyrostów oraz powierzchni wewnętrznych muszli 17 gatunków. Omówiono także skalę zmienności powierzchni wewnętrznych warstw wapiennych, struktur homogenno-ziarnistej, ziarnistej, diagonalnej i palisadowej oraz endostracum i porów na tle systematyki *Sphaeriidae* (tabela III). Analiza tych danych potwierdziła:

— odrębność *Musculium lacustre*, jako przedstawiciela rodzaju *Musculium*, w stosunku do pozostałych *Sphaeriidae*;

— odrębność *Pisidium* (*Pisidium* s. str.) *amnicum*, *P.* (*Neopisidium*, *moitessierianum* i *P.* (*Odhneripisidium*) *tenuilineatum*, jako przedstawicieli trzech różnych podrodzajów.

W obrębie podrodzaju *Cymatocyclas* Dall 1903 dane o mikrostrukturze potwierdziły bliskie pokrewieństwo *P. henslowanum* i *P. supinum* oraz stały się podstawą wyodrębnienia dwóch grup gatunków — pierwszą z nich tworzą: *P. subtruncatum*, *P. nitidum* i *P. obtusale*, drugą: *P. pulchellum*, *P. lilljeborgi* oraz *P. personatum*. Biorąc pod uwagę obserwacje anatomiczne trzy ostatnie gatunki zaliczono do grupy *Cymatocyclas* Dall 1903 A, o nie ustalonej randze systematycznej. Dla określenia jej stosunku do pozostałych gatunków rodzaju konieczne jest przeprowadzenie dokładnych badań anatomicznych.

Analiza mikrostruktury muszli *P. casertanum* typ. i *P. casertanum* f. *ponderosum* przemawia za gatunkową odrębnością tej ostatniej formy. Dotyczy to osobników o wyraźnie trójkątnych, grubościennych muszlach, odpowiadających opisowi podanemu przez Ehrmanna (1956). *P. ponderosum* wydaje się być gatunkiem typowo jeziornym. Niezależnie od tego w siedliskach innego typu mogą występować osobniki zbliżone konchologicznie do *P. ponderosum*, lecz odmienne pod względem mikrostruktury. Należy je uznać za przedstawicieli *P. casertanum* f. *ponderosum*.

Przeprowadzona analiza użyteczności taksonomicznej mikrostruktury *Sphaeriidae* wykazała, iż są to dobre cechy taksonomiczne, przydatne zwłaszcza w sytuacjach budzących wątpliwości.

Redaktor pracy: doc. dr L. Sych

Plate VI

1. Outer surface of periostracum of *S. corneum* (L. Sarąg, 1977), ×2000. 2. Outer surface of calcareous layers of *S. corneum* (Riv. Rega, 1978), ×430. 3. Pores in outer surface of calcareous layers in *S. corneum* (L. Sarąg), 1977, ×6000. 4. Section of shell of *S. corneum* juv., 8 mm long (Riv. Rega, 1978), taken parallel to lines of growth. ×600. 5. Section of shell of *S. corneum* (L. Sarąg, 1977), parallel to lines of growth. ×540. 6. A portion of Phot. 5. Section parallel to lines ot growth — periostracum (P), homogeneo-granular layer (H). ×4800. 7. A portion of Phot. 5. Section paralle to lines of growth — granular layer. ×6000

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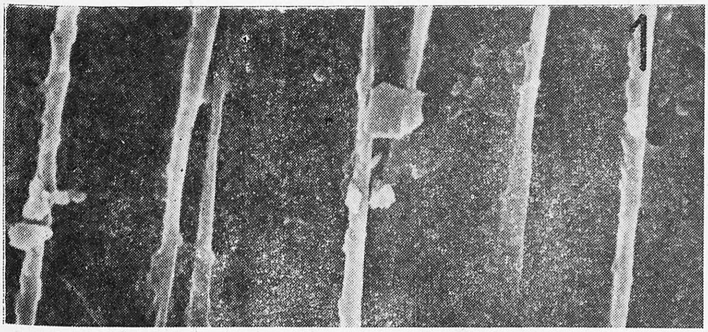
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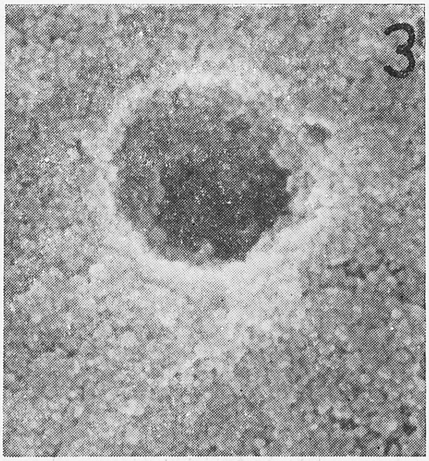
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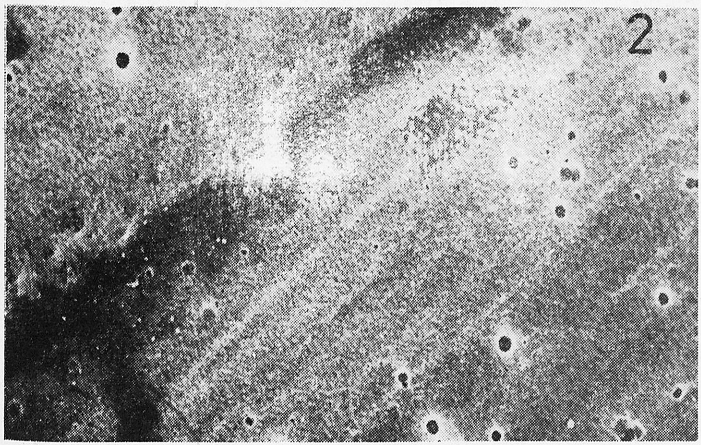
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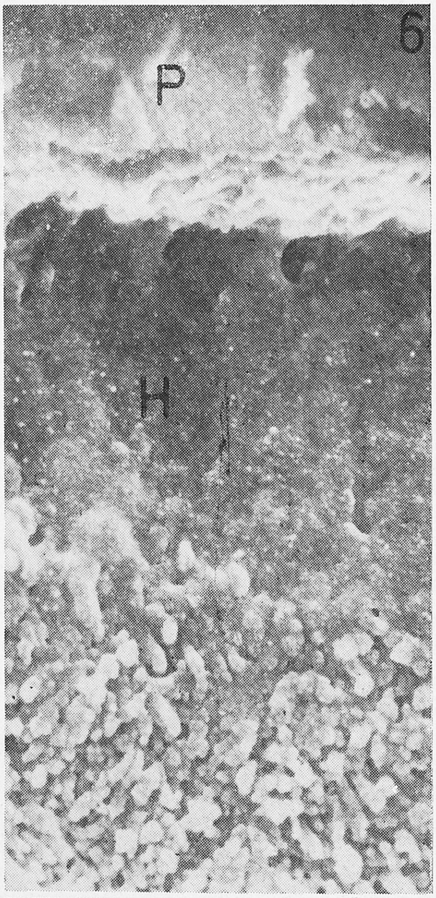
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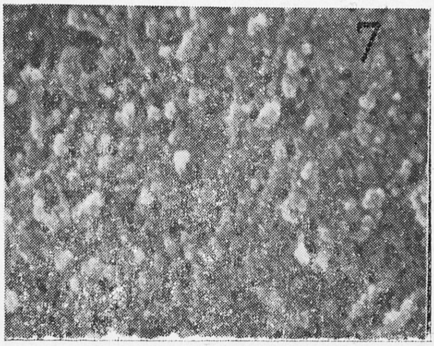
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Plate VII

8. A portion of Phot. 5. Section parallel to lines of growth — diagonal layer. ×6000. 9. A portion of Phot. 5. Section of endostracum, parallel to lines of growth. ×4800. 10. A portion of section of shell in *S. corneum* (L. Sarąg, 1977), parallel to lines of growth and showing one-rowed palisade layer (Pa). ×1000. 11. Inner shell surface (endostracum) in adult *S. corneum* (L. Sarąg, 1977). ×6000. 12. Inner shell surface (endostracum) in *S. corneum* juv., 8 mm long (Riv. Rega, 1978). ×400. 13. A portion of Phot. 12. Inner shell surface (endostracum) of juvenile, 8 mm long. ×6000. 14. A portion of Phot. 12. Inner shell surface (endostracum) of juvenile, 8 mm long. ×6000. 15. Inner shell surface of *S. corneum* (L. Sarąg, 1977). ×6000

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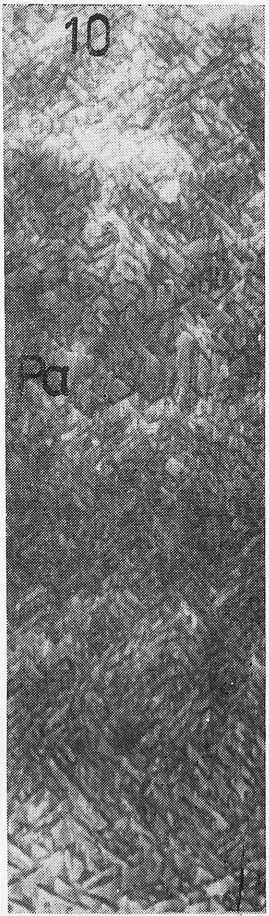
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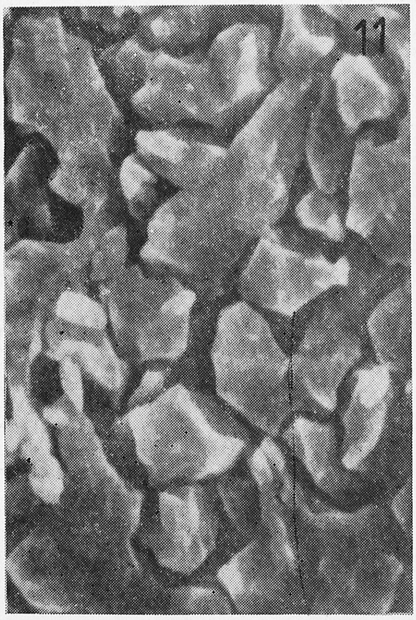
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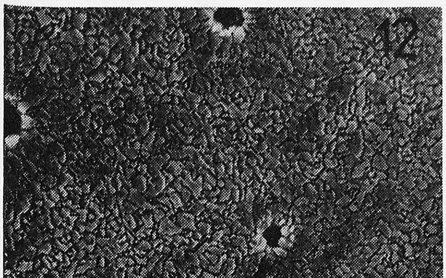
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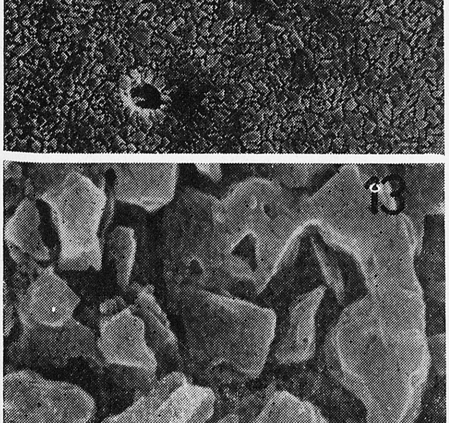
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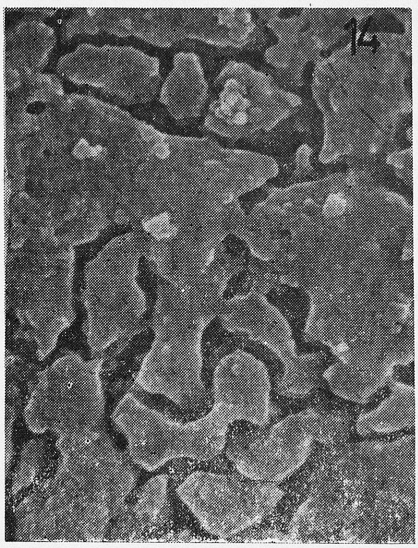
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Plate VIII

16. Inner shell surface (endostracum) of *S. corneum* (L. Sarąg, 1977). ×6000. 17. A pore in endostracum of *S. corneum* (Riv. Rega, 1978). ×2000. 18. A pore in endostracum of *S. corneum* juv., c. 8.0 mm long (Riv. Rega, 1978), ×2000. 19. A pore in endostracum of *S. corneum* juv., c. 8.0 mm long (Riv. Rega, 1978). ×2000. 20. Outer surface of calcareous layers of *S. rivicola* (Riv. Vistula, 1972). ×2000. 21. Outer surface of calcareous layers of *S. rivicola* (Riv. Nida, 1977). ×600

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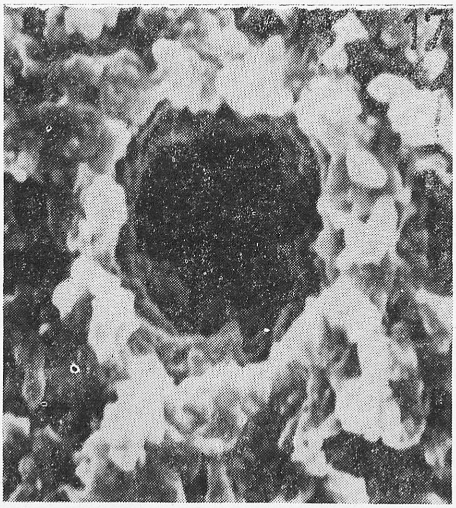
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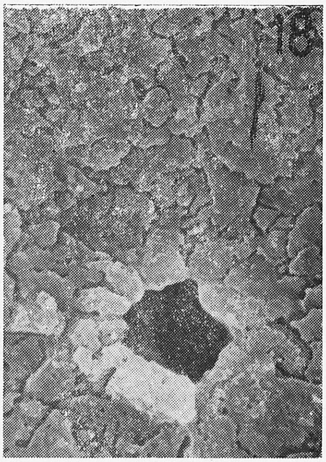
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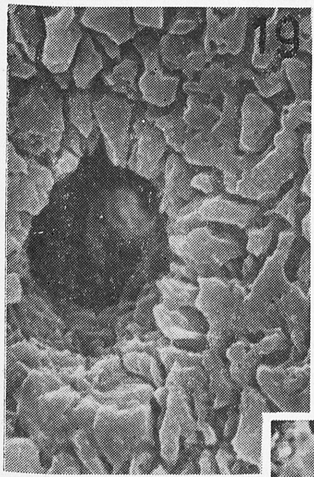
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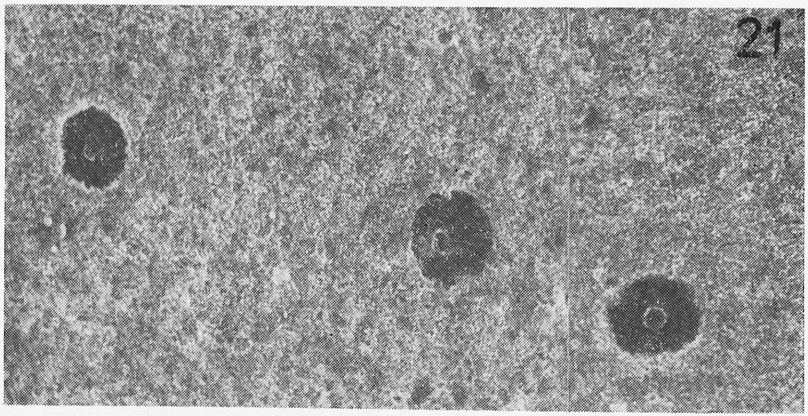
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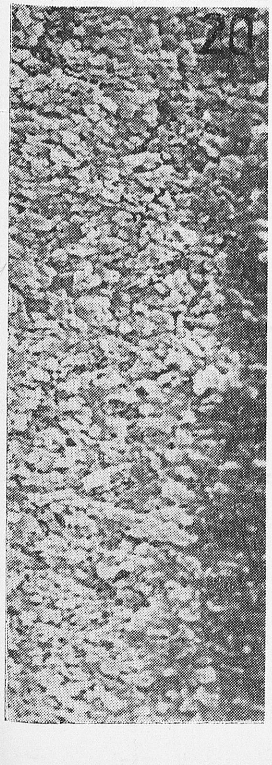
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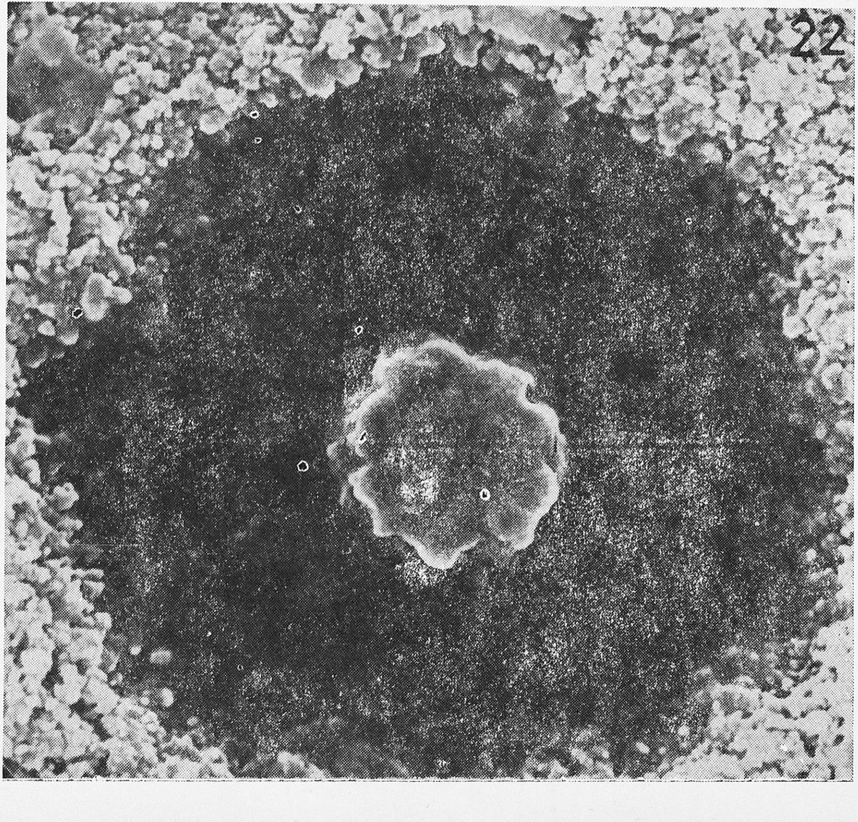
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Plate IX

22. A pore with plug in outer surface of calcareous layers of *S. rivicola* (Riv. Nida, 1977). × 5400. 23. A pore in outer surface of calcareous layers of *S. rivicola* (Riv. Nida, 1977). × 3000. 24. Section of shell of *S. rivicola* (Riv. Vistula, 1972), parallel to lines of growth. × 480. 25. Section of shell of *S. rivicola* (Riv. Nida, 1977), parallel to lines of growth. × 300. 26. Section of shell of *S. rivicola* (Riv. Nida ,1977), parallel to lines of growth. × 300. 27. Section of shell of *S. rivicola* (Riv. Nida, 1977), parallel to lines of growth. × 400

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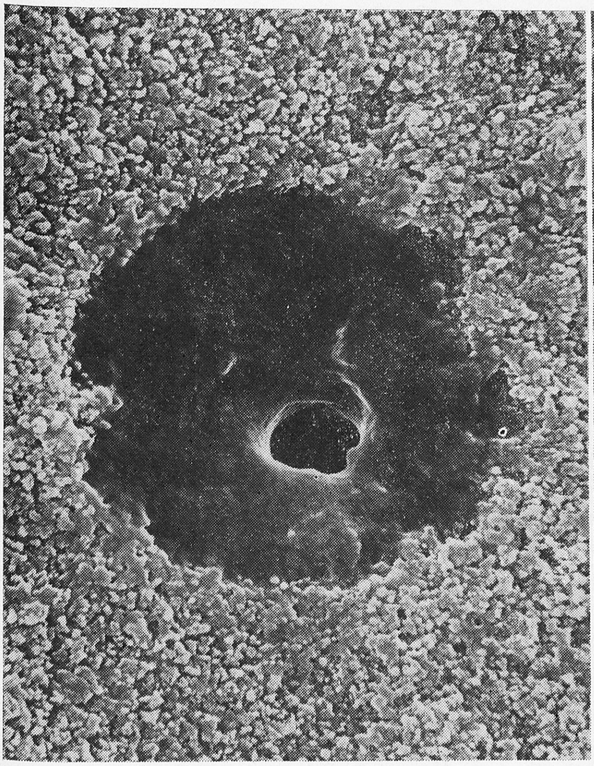
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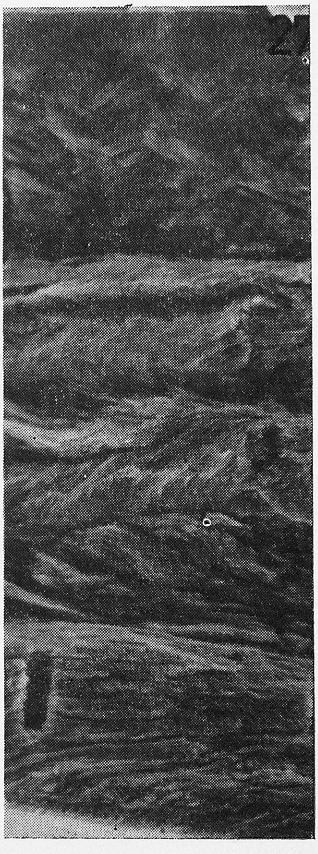
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Plate X

28. A portion of Phot. 26. Section of shell of *S. rivicola*, parallel to lines of growth, showing the transition of the composite prismatic structure into the crossed lamellar structure in the diagonal layer. × 3000. 29. A portion of Phot. 25. A canal in crossed lamellar structure. × 1300. 30. Inner shell surface (endostracum) of *S. rivicola* (Riv. Nida, 1977). × 400. 31. A portion of Phot. 30. Inner shell surface (endostracum) of *S. rivicola* (Riv. Nida, 1977). × 2000. 32. A pore in endostracum of *S. rivicola* (Riv. Nida, 1977). × 4000. 33. A portion of Phot. 32. Inner shell surface (endostracum) of *S. rivicola*. × 13000. 34. Inner shell surface (endostracum) of *S. rivicola* (Riv. Vistula, 1972). × 600. 35. A pore in inner shell surface of *S. rivicola* juv. (Riv. Vistula, 1978). × 2000

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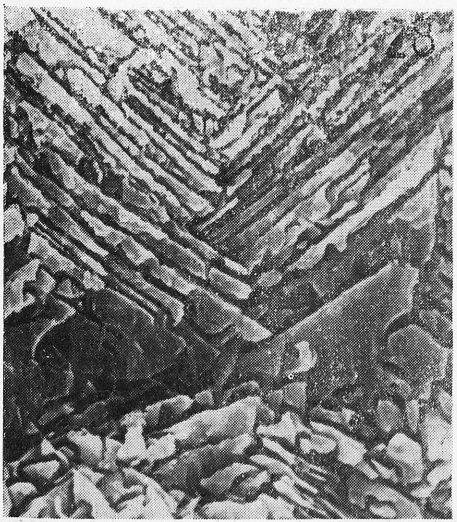

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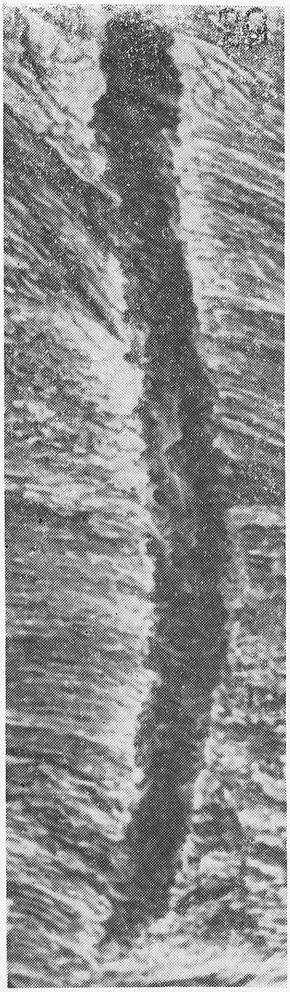

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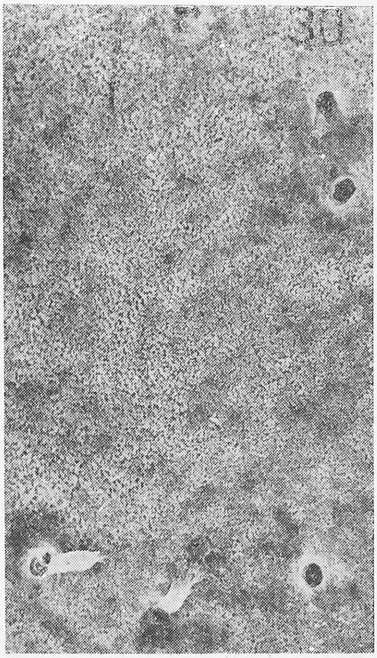

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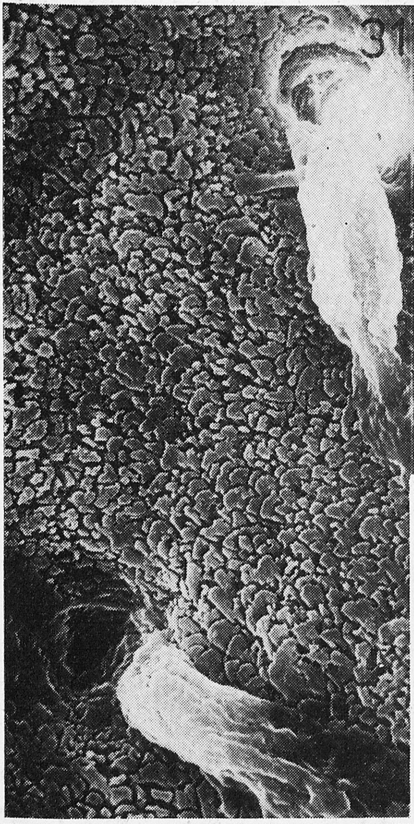

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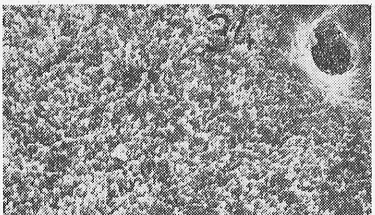

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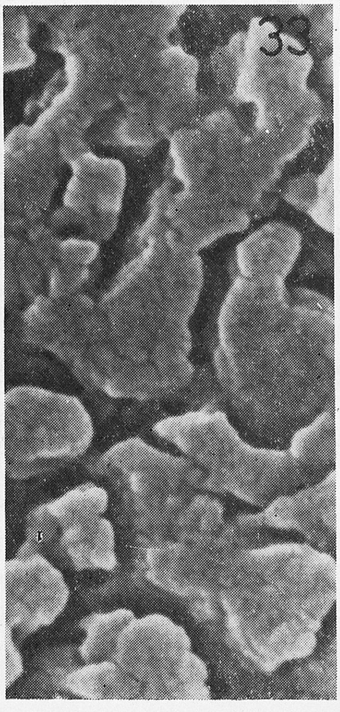

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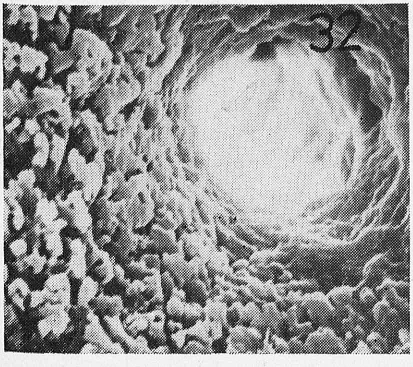

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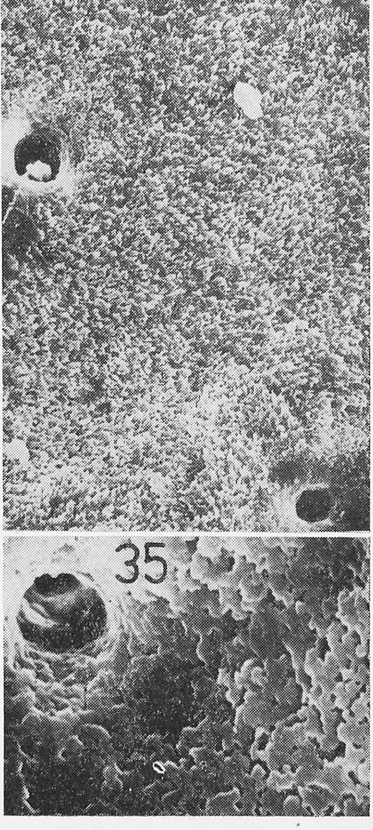

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Plate XI

36. Outer of calcareous layers in *M. lacustre* (L. Sarąg, 1974). × 400. 37. Section of shell of *M. lacustre,* parallel to lines of growth (L. Sarąg, 1974). × 2000. 38. Section of shell of *M. lacustre* (L. Sarąg, 1974), parallel to lines of growth. × 1800. 39. Homogeneo-granular (H) and granular (G) layers of *M. lacustre* (L. Sarąg, 1974). × 5400. 40. Inner shell surface in *M. lacustre* (L. Sarąg, 1974), × 240

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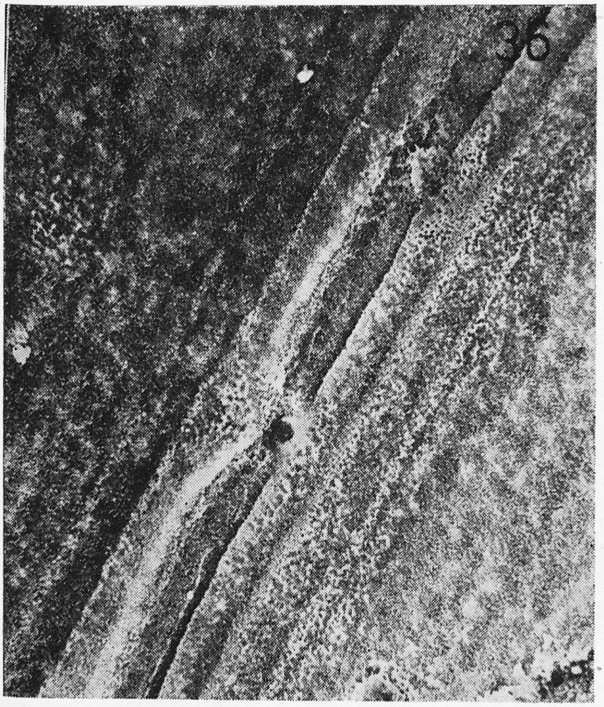
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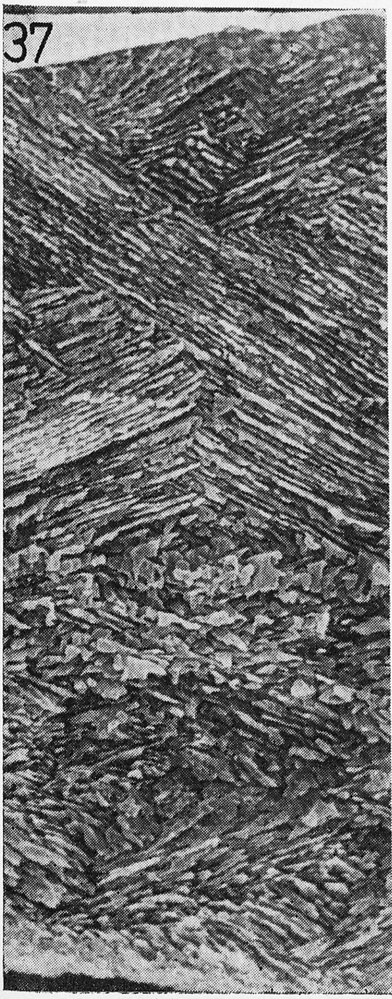
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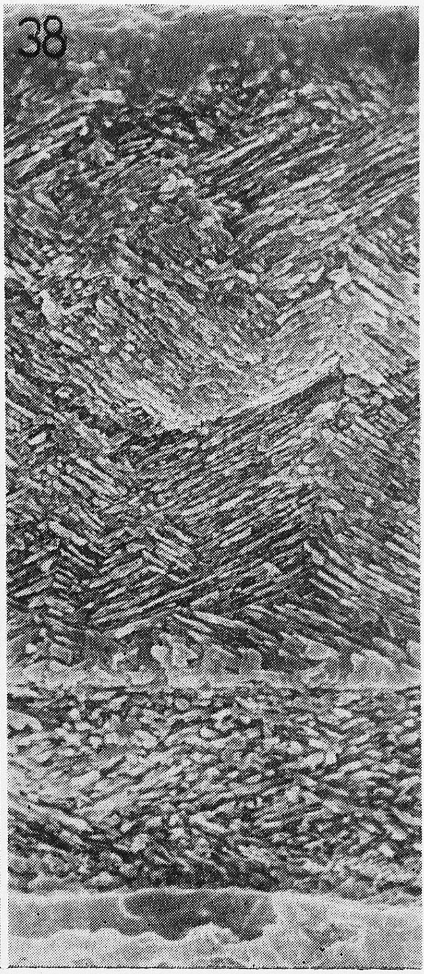
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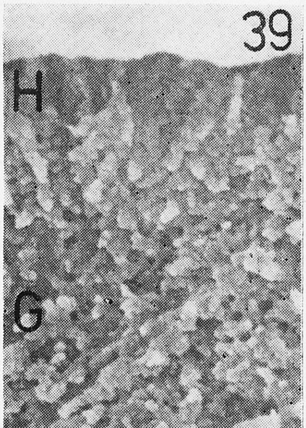
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Plate XII

41. Pores in endostracum of *M. lacustre* (L. Sarąg, 1974). × 3000. 42. Section of shell of *P. amnicum* (L. Sarąg, 1977), parallel to lines of growth. × 440. 43. Section of shell of *P. amnicum* Sarąg, 1977), parallel to lines of growth. × 660. 44. Section of shell of *P. amnicum* juv. (L. Sarąg, 1977), parallel to lines of growth. × 780, undigested. 45. Section of shell of *P. amnicum* juv. (Riv. Biała Przemsza at Jaroszowiec, 1978). × 3000. 46. A portion of Phot. 43. Granular structure of *P. amnicum*. ×4400. 48. A portion of Phot. 42. Transition of diagonal structure into palisade structure. ×1600

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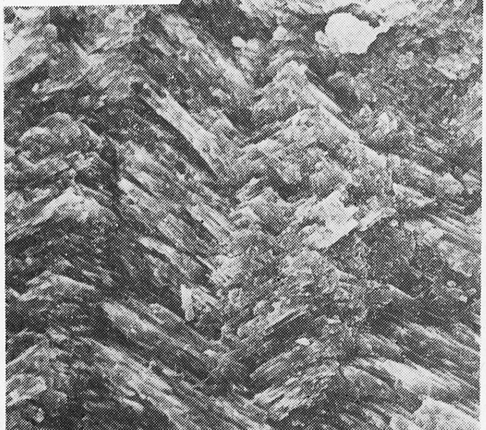

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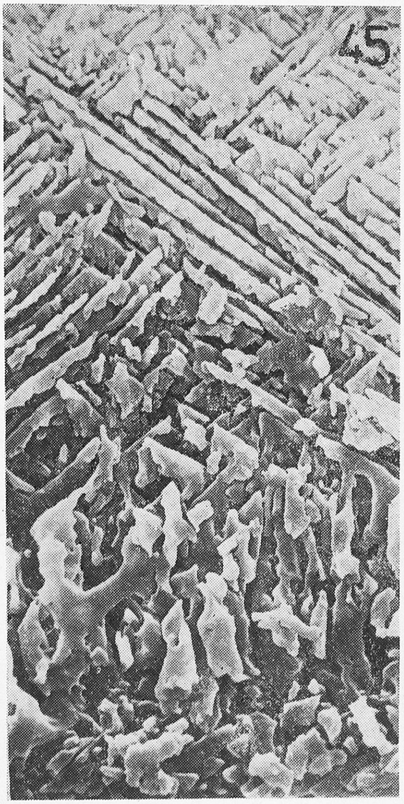

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Plate XIII

48. A portion of Phot. 47. Transition of diagonal structure into palisade structure. × 15000. 49. A portion of Phot. 45. Palisade structure of P. *amnicum* juv. × 6000. 50. Section of shell of *P. amnicum* in hinge region, (L. Sarąg, 1977) parallel to lines of growth. × 1200. 51. Outer shell surface of *P. amnicum* (Riv. Nida, 1977). × 400. 52. A portion of Phot. 51. Outer shell surface in *P. amnicum*. × 2000. 53. Inner shell surface and a pore of *P. amnicum* (L. Sarąg, 1977), × 2000. 54. Inner shell surface of *P. amnicum* (Riv. Biała Przemsza at Jaroszowiec, 1978). × 6000.

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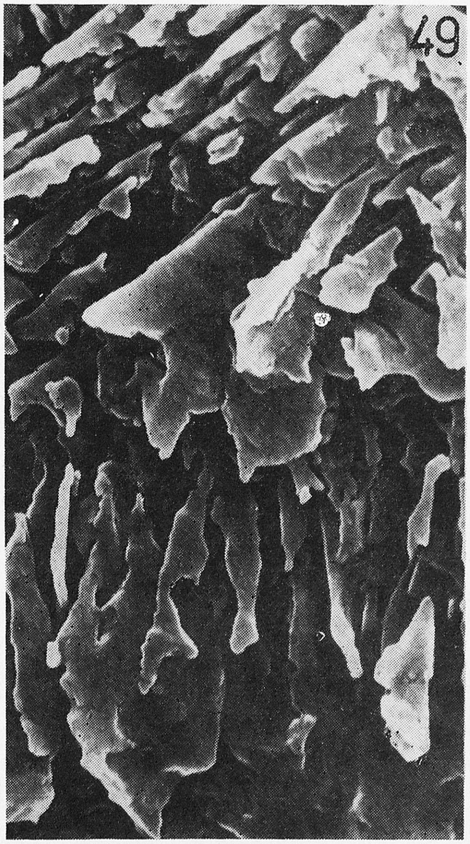
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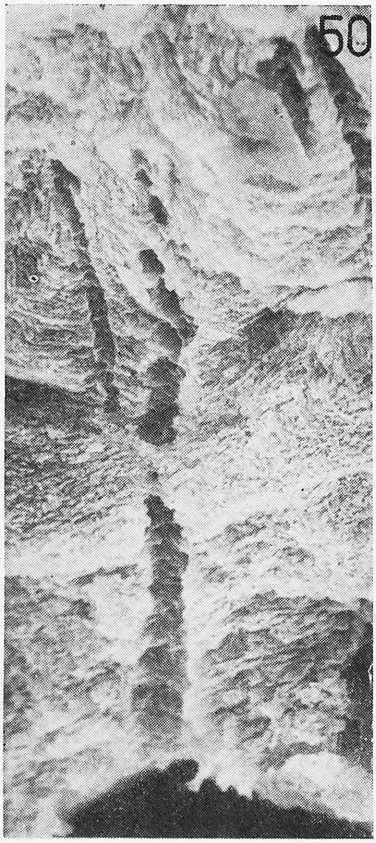
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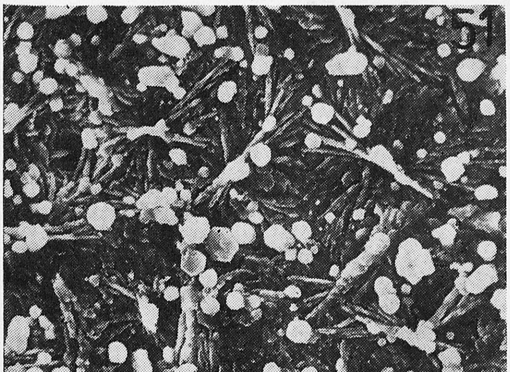
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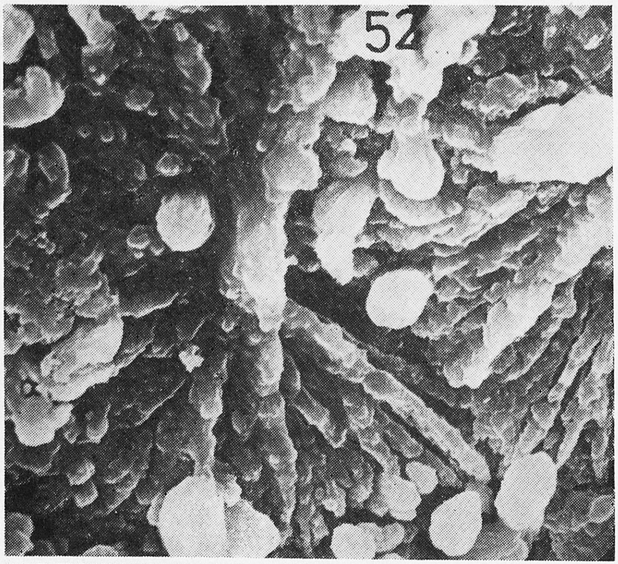
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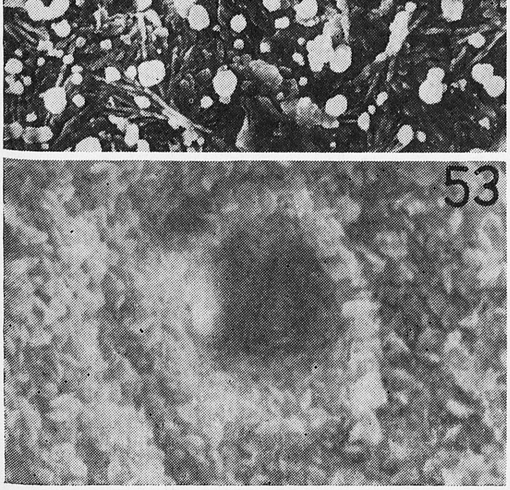
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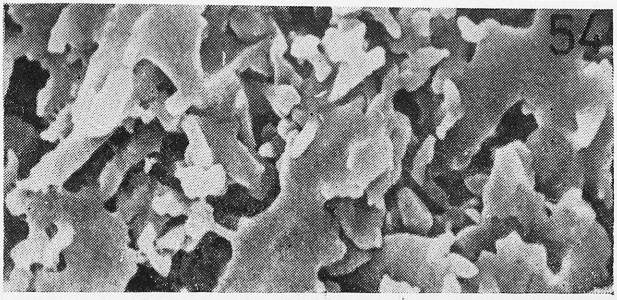
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Plate XIV

55. Inner shell surface of *P. amnicum* juv. (L. Sarąg, 1977). × 4800. 56. A pore in endostracum of *P. amnicum* (Riv. Nida, 1977). × 2000. 57. A pore in endostracum of *P. amnicum* juv. (Riv. Biała Przemsza at Jaroszowiec, 1978). × 4000. 58. A pore in inner shell surface of *P. amnicum* juv. (L. Sarąg, 1977). × 4000. 59. Inner surface of calcareous layers of *P. henslowanum* (L. Gardno, 1975). × 720. 60. Outer surface of calcareous layers of *P. henslowanum* (L. Gardno). × 10 000. 61. Outer surface of calcareous layers of *P. henslowanum* (L. Gardno, 1975). × 300. 62. A portion of Phot. 61. Fibrils on outer surface of calcareous layers in *P. henslowanum* × 15 000

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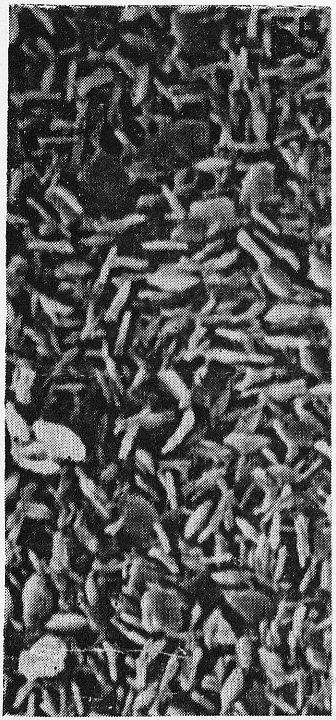
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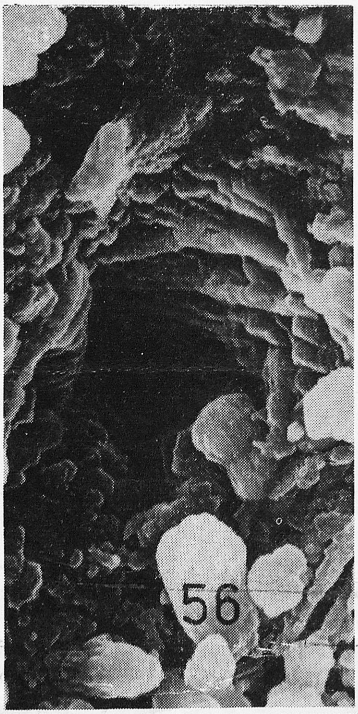
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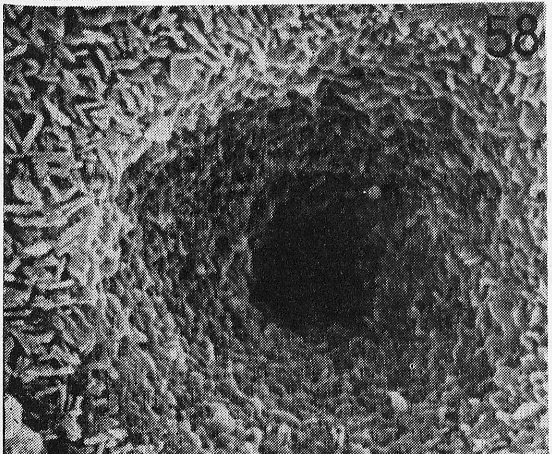
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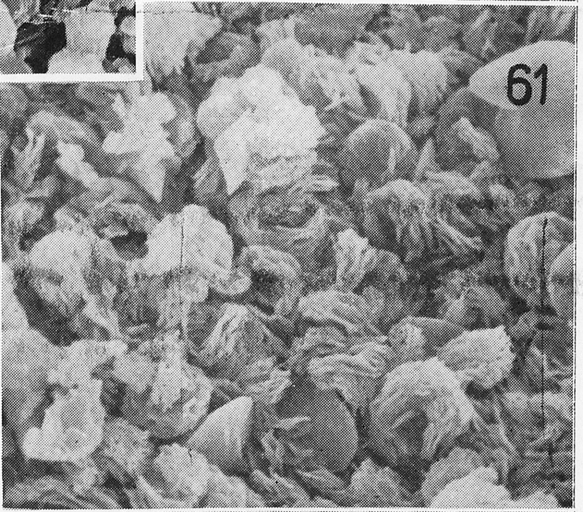
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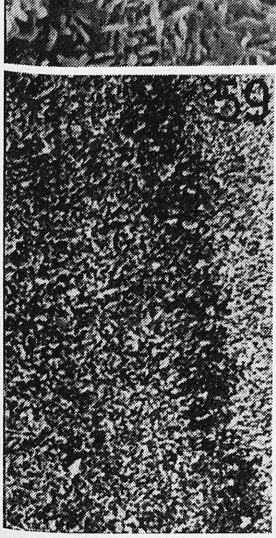
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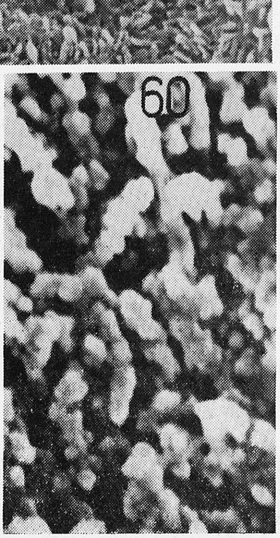
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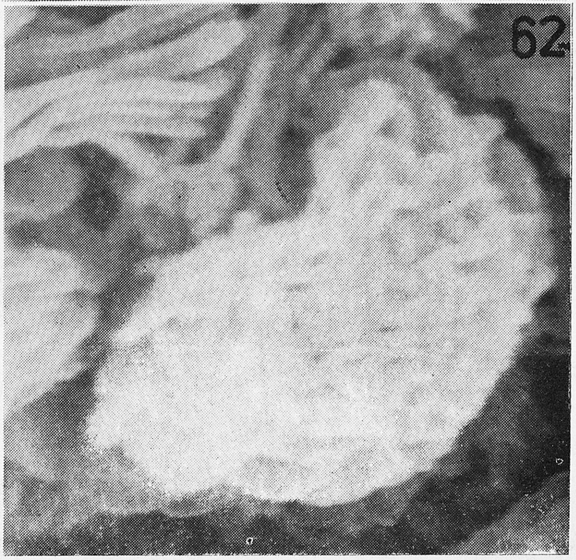
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Plate XV

63. Section of shell of *P. henslowanum*, rectangular to lines of growth (L. Gardno, 1975). × 540. 64. Section of shell of *P. henslowanum* (L. Gardno, 1975), perpendicular (somewhat oblique) to lines of growth. × 540. 65. Section of shell of *P. henslowanum* (L. Gardno, 1975), parallel to lines of growth. × 720. 66. Section of shell of *P. henslowanum* (L. Gardno, 1975), parallel to lines of growth. × 1100. 67. Section of shell of *P. henslowanum* (L. Gardno parallel to lines of growth. × 600. 68. Section of shell of *P. henslowanum* (L. Gardno, 1975), parallel to lines of growth. × 480. 69. A portion of Phot. 68. „Granular" layer. × 3000. 70. A portion of Phot. 68. Palisade structure, „torn bands", in *P. henslowanum*. × 3000.

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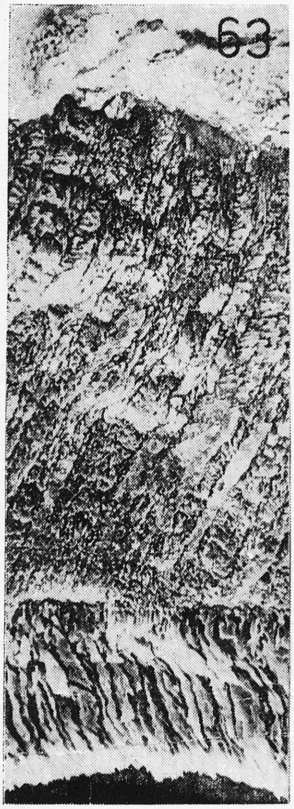
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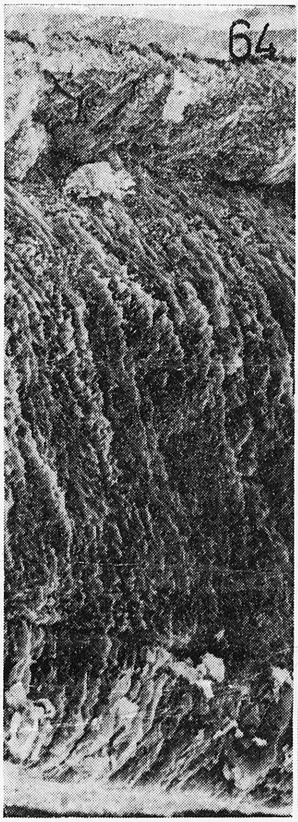
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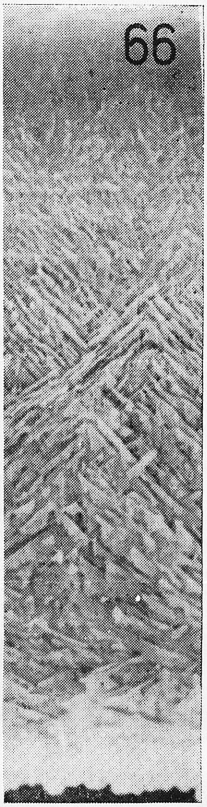
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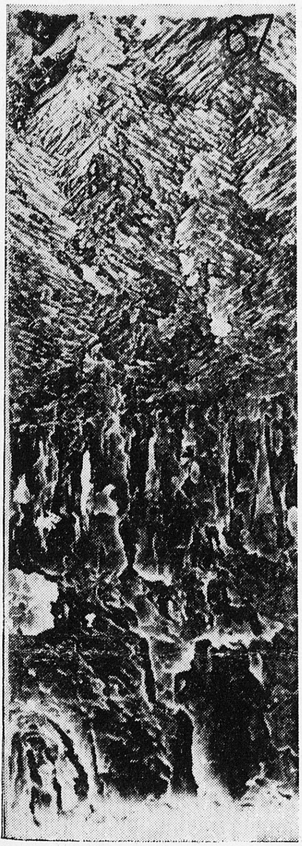
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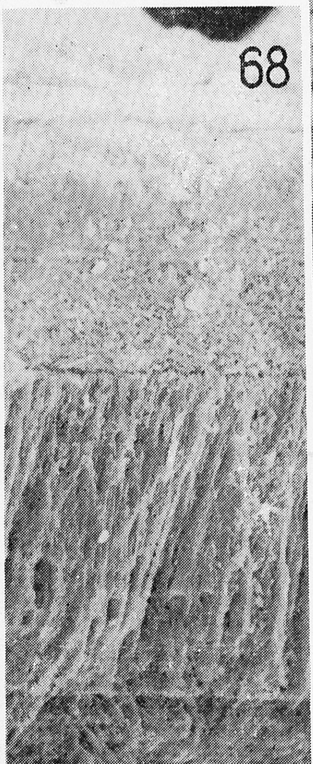
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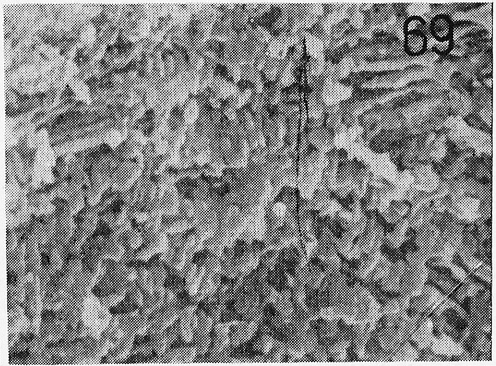
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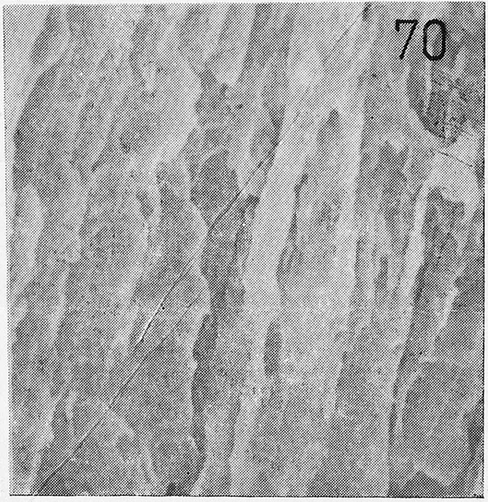
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Plate XVI

71. A portion of Phot. 68. Section through endostracum of *P. henslowanum.* × 3000. 72. Inner shell surface of *P. henslowanum* (L. Gardno, 1975), × 2000. 73. Inner shell surface of *P. henslowanum* (L. Gardno, 1975). × 6000. 74. Inner shell surface of *P. henslowanum* (L. Gardno, 1975). × 2000. 75. Inner shell surface of *P. henslowanum* (L. Gardno, 1975). × 2000. 76. Section of shell of *P. supinum* (L. Gardno, 1975), parallel to lines of growth. × 540. 77. Outer portion of section in Phot. 76. Section through shell of *P. supinum,* parallel to lines of growth. × 1100

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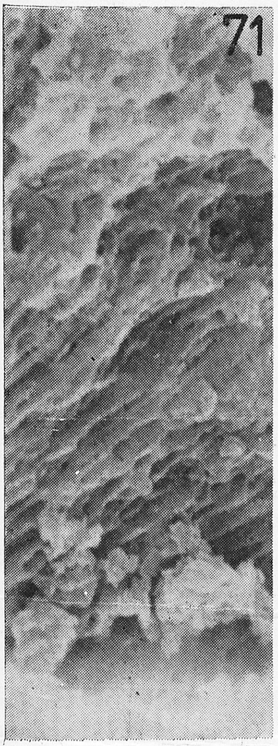
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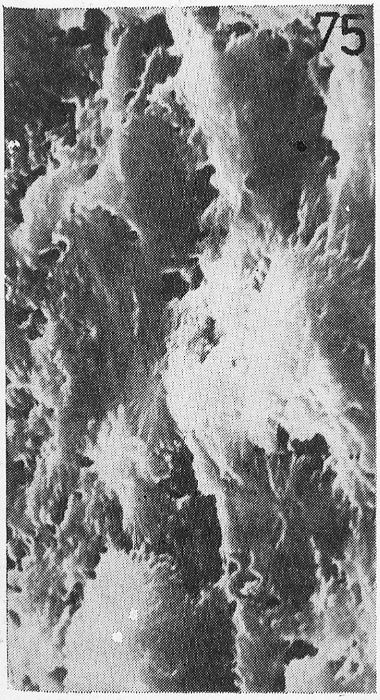
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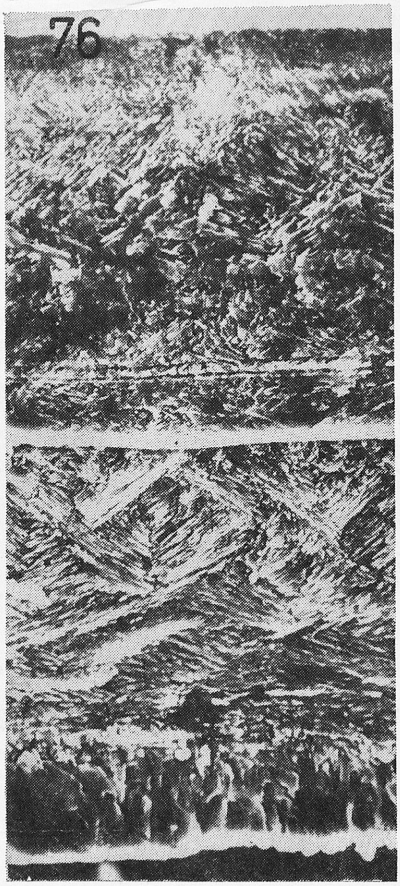
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Plate XVII

78. Inner portion of section in Phot. 76. Section of shell of *P. supinum*, parallel to lines of growth. × 1100. 79. Section of shell of *P. supinum* (L. Gardno, 1975), parallel to lines of growth. × 480. 80. Inner shell surface of *P. supinum* (L. Gardno, 1975). × 6000. 81. Outer surface of periostracum of *P. milium* (L. Gardno, 1975). × 2000. 82. Outer surface of calcareous layers of shell in *P. milium* (L. Gardno, 1975). × 2000. 83. Section of shell of *P. milium* (L. Gardno, 1975), parallel to lines of growth. × 3200. 84. A portion of Phot. 83. Section of shell of *P. milium*, parallel to lines of growth. × 6000.

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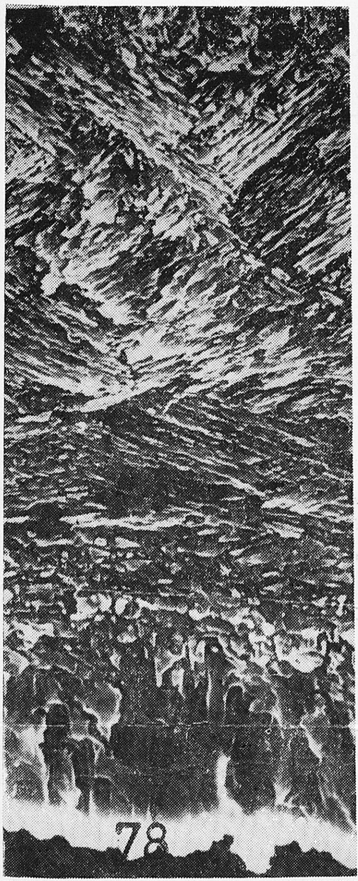
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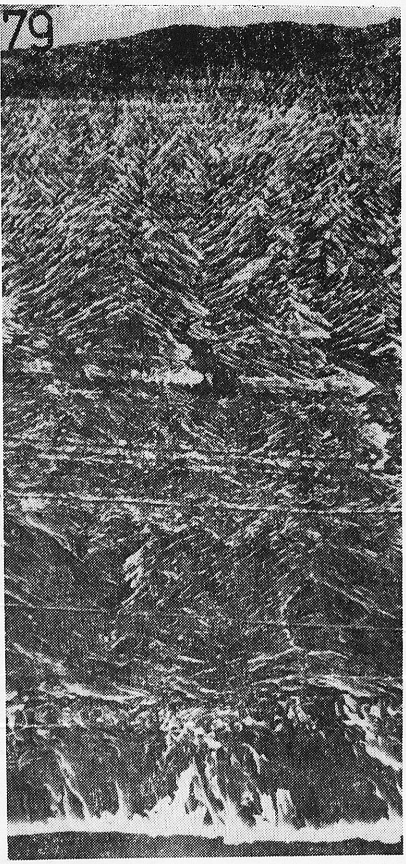
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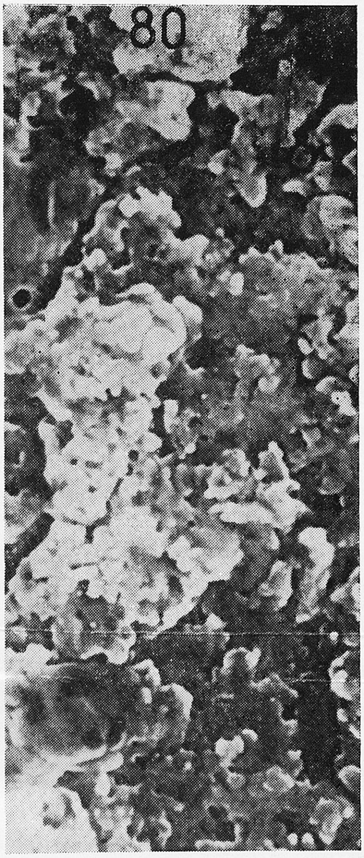
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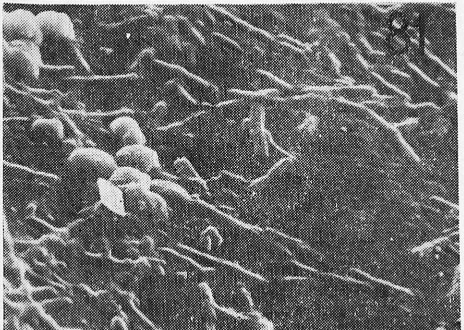
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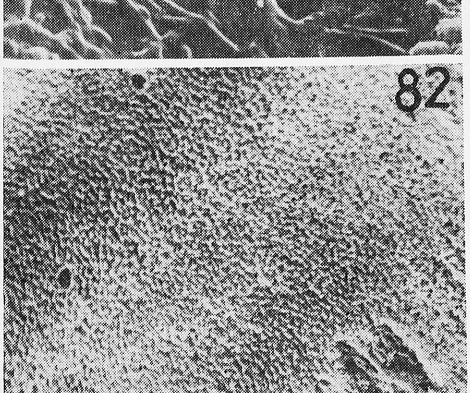
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Plate XVIII

85. Section of shell of *P. milium* (Wolin I., 1978), parallel to lines of growth. × 2400. 86. Section of shell of *P. milium* (Wolin I., 1978), parallel to lines of growth. × 2400. 87. Section of shell *P. milium* (L. Gardno, 1975), parallel to lines of growth. × 3200. 88. A portion of Phot. 87. Section of *P. milium* shell, parallel to lines of growth; periostracum (P), homogeneogranular layer (H). × 8600. 89. Inner shell surface of *P. milium* (Wolin I., 1978). × 400. 90. A portion of Phot. 89. Inner shell surface of *P. milium*. × 2000

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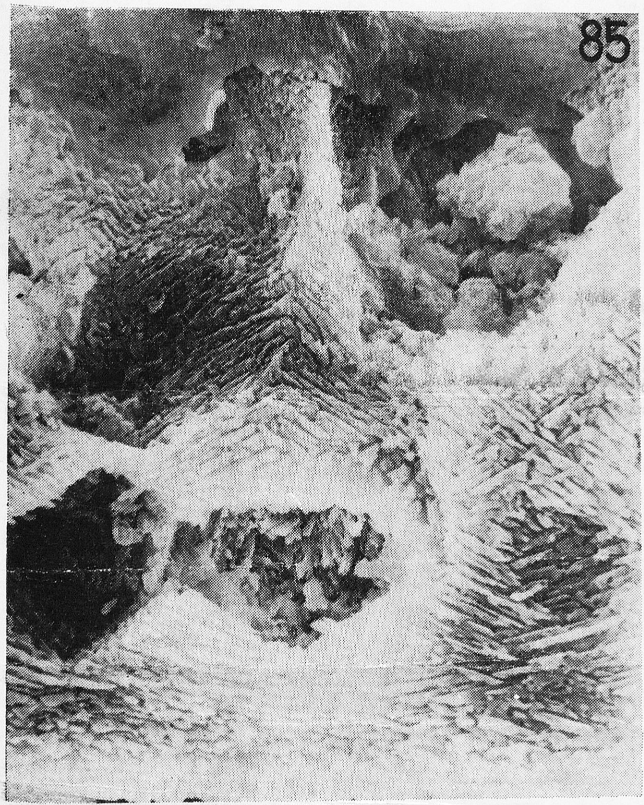
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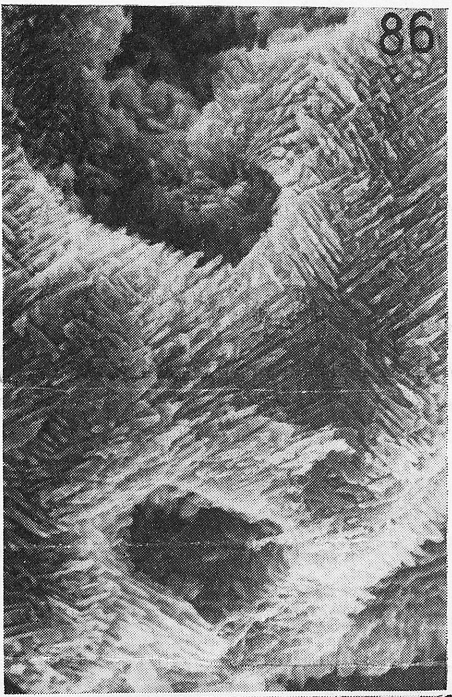
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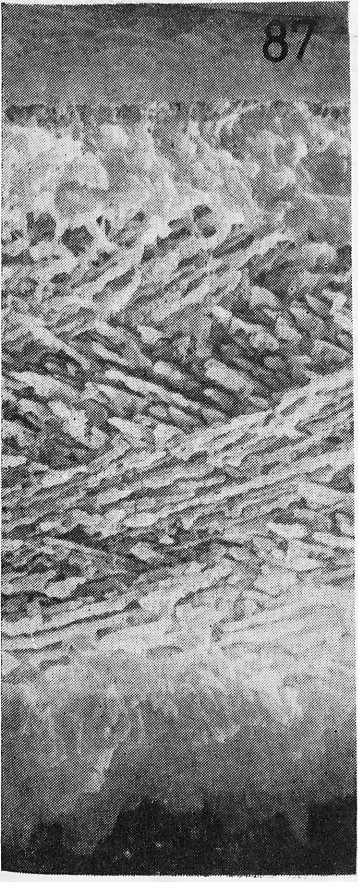
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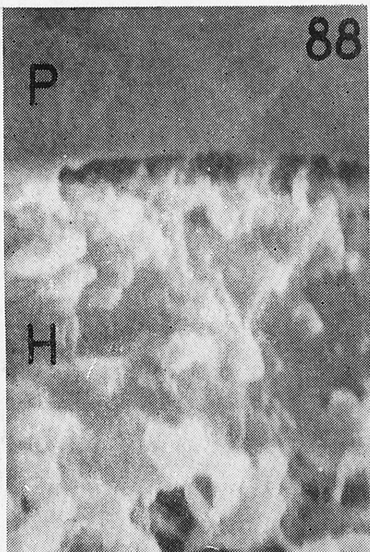
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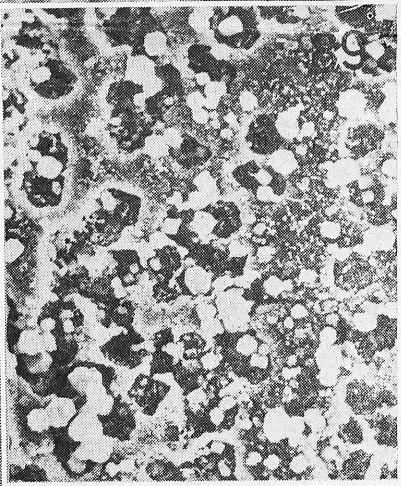
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Plate XIX

91. A portion of Phot. 90. Inner shell surface of *P. milium*. × 6000. 92. Inner shell surface of *P. milium* (L. Gardno, 1975). × 2200. 93. Inner shell surface of *P. milium* (L. Gardno, 1975). × 1000. 94. A portion of Phot. 93. Inner shell surface of *P. milium*. × 4800. 95. Section of shell of *P. subtruncatum* (Riv. Biała Przemsza at Jaroszowiec, 1978), parallel to lines of growth. × 1300. 96. Section of shell of *P. subtruncatum* (Riv. Biała Przemsza at Jaroszowiec, 1978), parallel to lines of growth. × 1500

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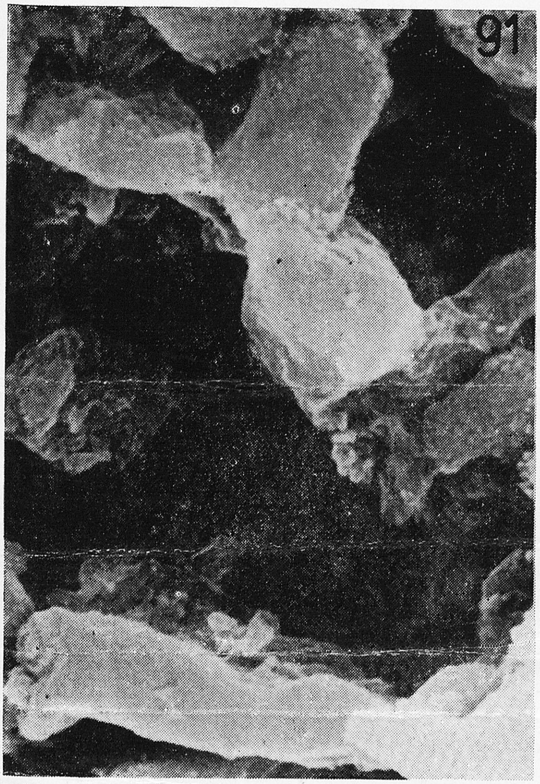
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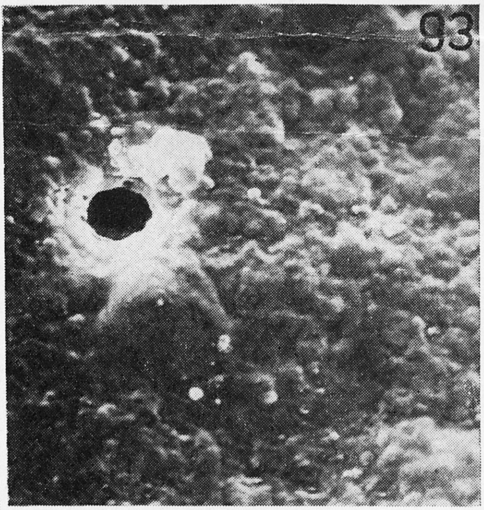
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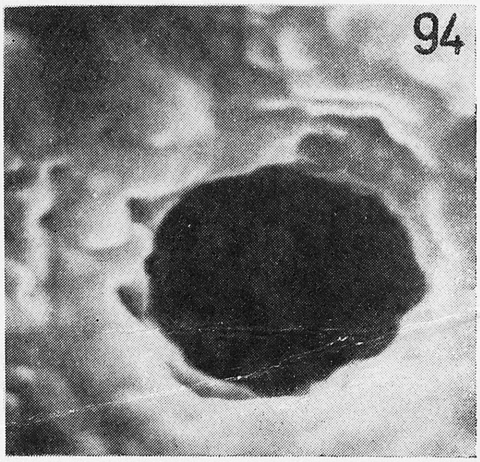
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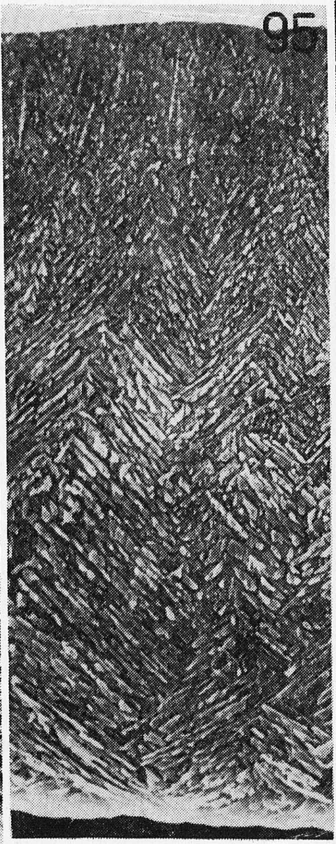
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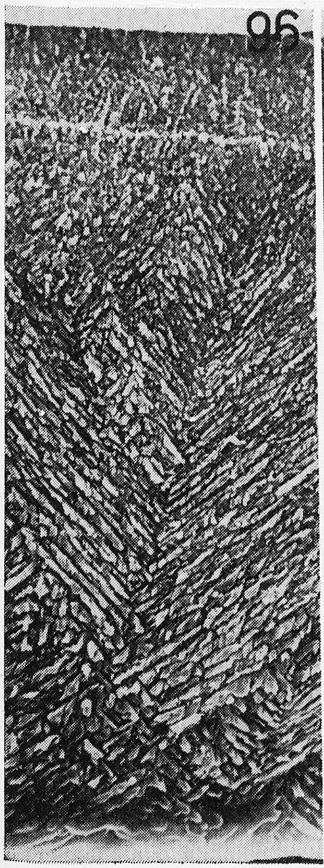
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Plate XX

97. Section of shell of *P. subtruncatum* juv. (Riv. Biała Przemsza at Jaroszowiec, 1978), parallel to lines of growth. × 2000. 98. A portion of Phot. 96. Section of shell of *P. subtruncatum*, parallel to lines of growth, showing granular layer. × 8600. 99. A portion of Phot. 97. Section of shell of *P. subtruncatum*, parallel to lines of growth, showing granular structure and outer portions of diagonal layer. × 10 000. 100. A portion of Phot. 96. Section of shell of *P. subtruncatum*, parallel to lines of growth, showing diagonal layer. × 3000. 101. A portion of Phot. 100. Section of shell of *P. subtruncatum*, parallel to lines of growth. × 7200

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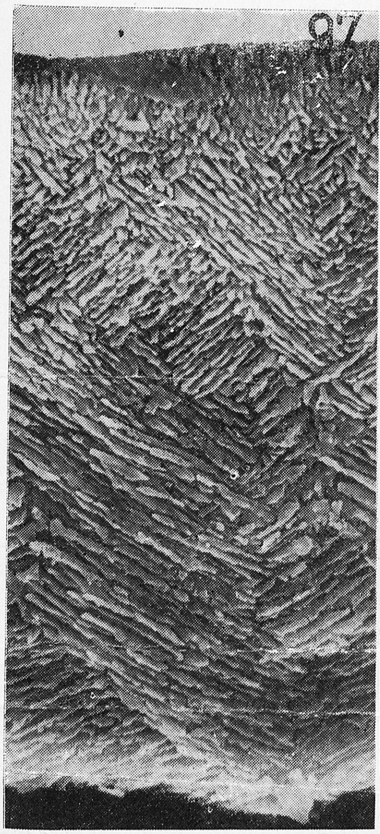
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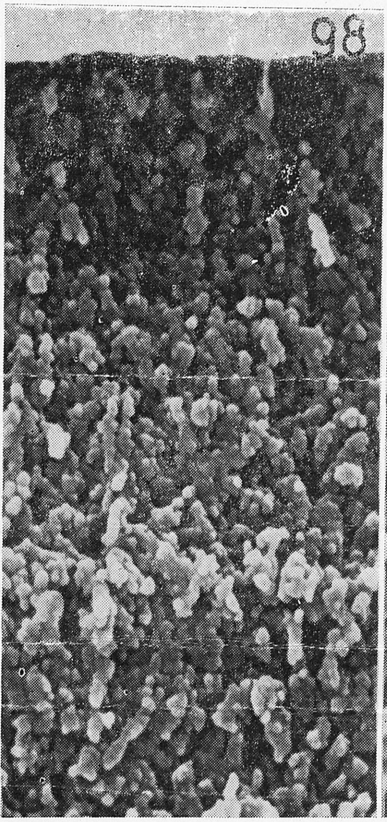
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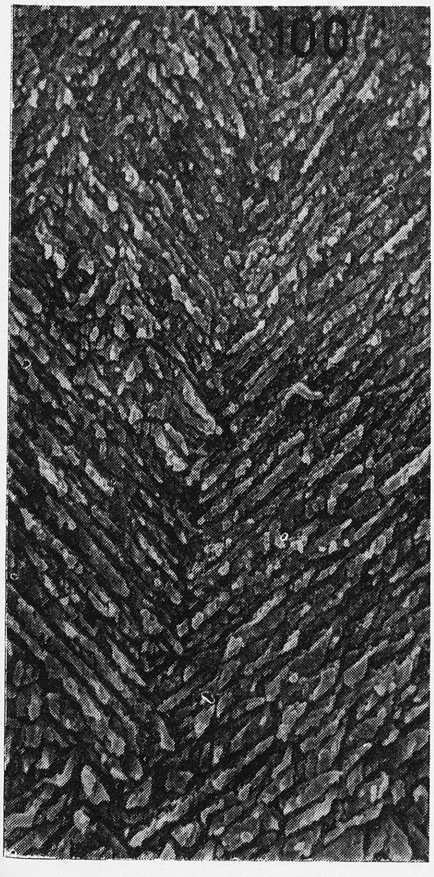
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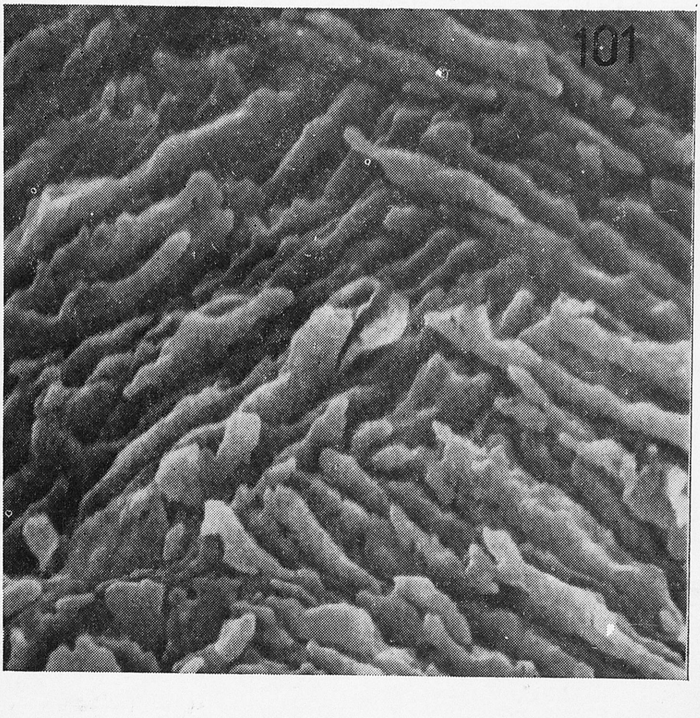
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Plate XXI

102. Section of shell of *P. subtruncatum* (Stary Wisłok, collection of P. A. o. Scs), parallel to lines of growth. × 1500. 103. Inner surface and pore in shell of *P. subtruncatum* (Stary Wisłok, collection of P. A. o. Scs). × 1000. 104. A portion of Phot. 103. A pore in endostracum of *P. subtruncatum*. × 4000. 105. Inner shell surface of *P. subtruncatum* (Riv. Biała Przemsza at Jaroszowiec, (1978). × 400. 106. A portion of Phot. 105. Inner shell surface of *P. subtruncatum*. × 2000. 107. A portion of Phot. 106. A pore in endostracum of *P. subtruncatum*. × 4000. 108. Inner shell surface of *P. subtruncatum* (Riv. Wełna, 1978). × 400. 109. A portion of Phot. 108. A pore in endostracum of *P. subtruncatum*. × 2000

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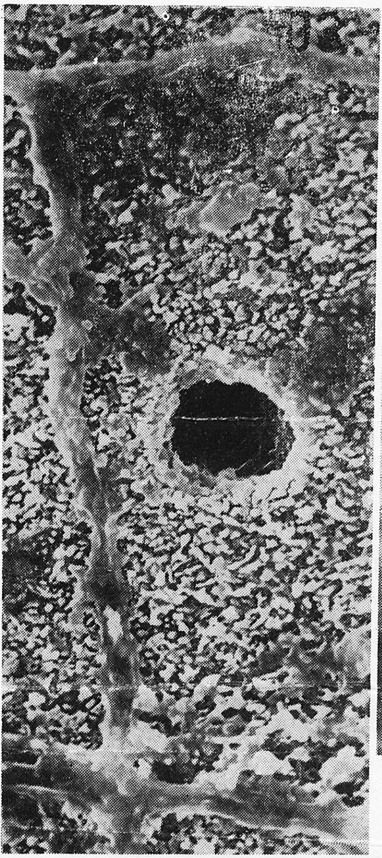
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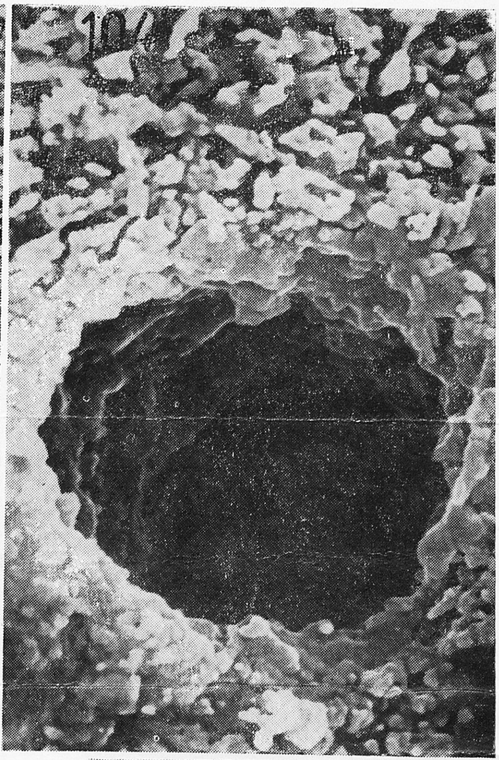
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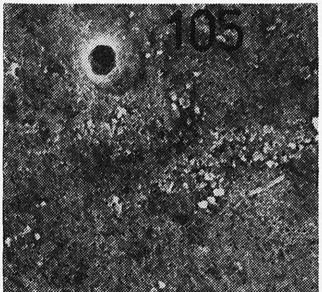
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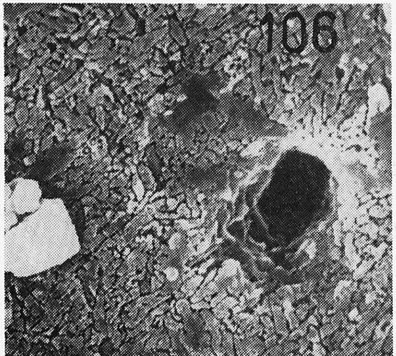
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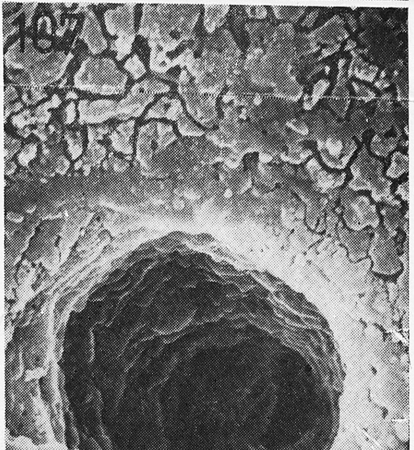
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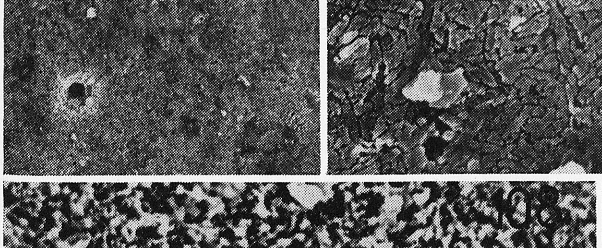
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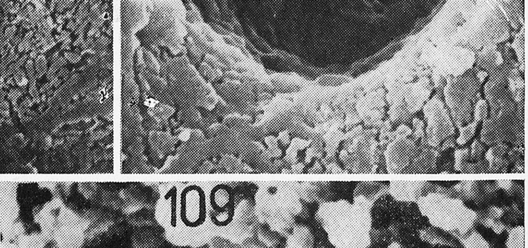
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Plate XXII

110. A piece of shell of *P. nitidum* (L. Gardno, 1975), with its periostracum partly turned back to show fibrils connecting it with calcareous layers. × 4000. 111. Edge of shell of *P. nitidum A* (L. Gardno, 1975). × 2200. 112. Section of shell of *P. nitidum* (L. Gardno, 1975), rectangular to lines of growth. × 2200. 113. Inner surface (contiguous to calcareous layers) of periostracum of *P. nitidum* typ. (L. Gardno, 1975). × 15 000. 114. Outer surface of calcareous layers in *P. nitidum* typ. (L. Gardno, 1975), with a spherical depression which was filled with the spherical structure visible in Phot. 113. × 15 000. 115. Outer surface of calcareous layers of *P. nitidum* typ. (L. Gardno, 1975). × 1000. 116. Outer surface of calcareous layers of *P. nitidum* f. *crassa* (L. Sarąg, 1974). × 1800. 117. Section of shell of *P. nitidum* typ., (L. Gardno, 1975), parallel to lines of growth. × 1500

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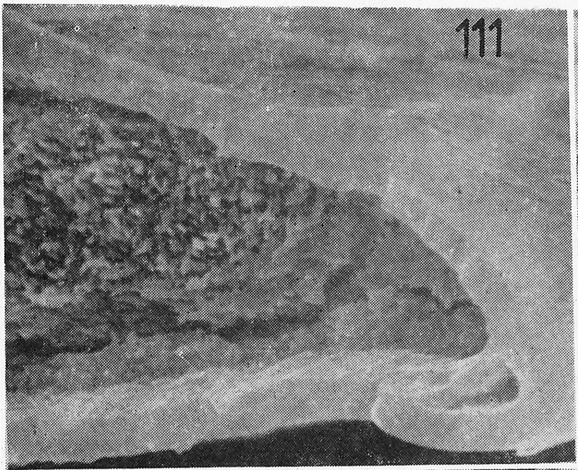
110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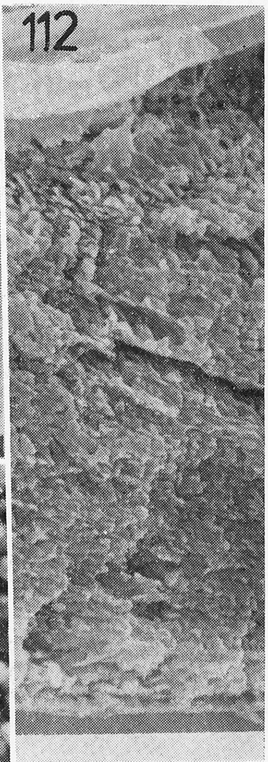
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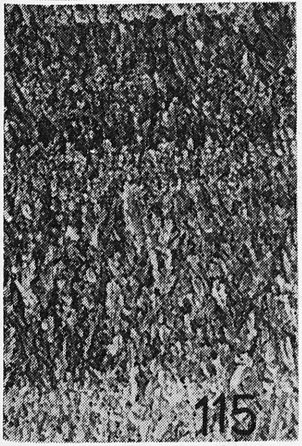
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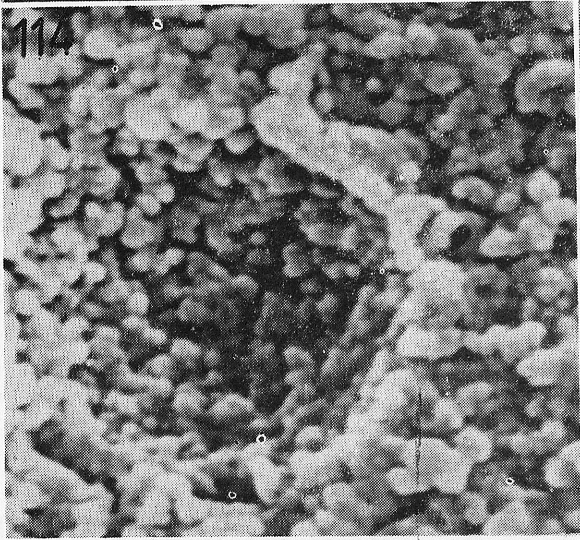
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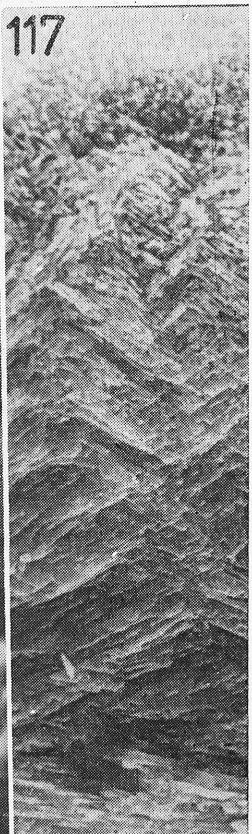
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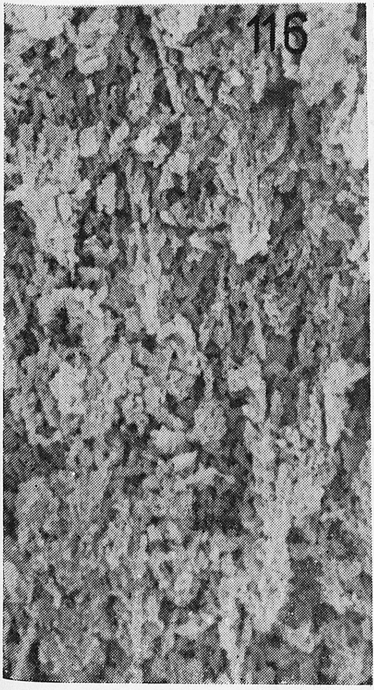
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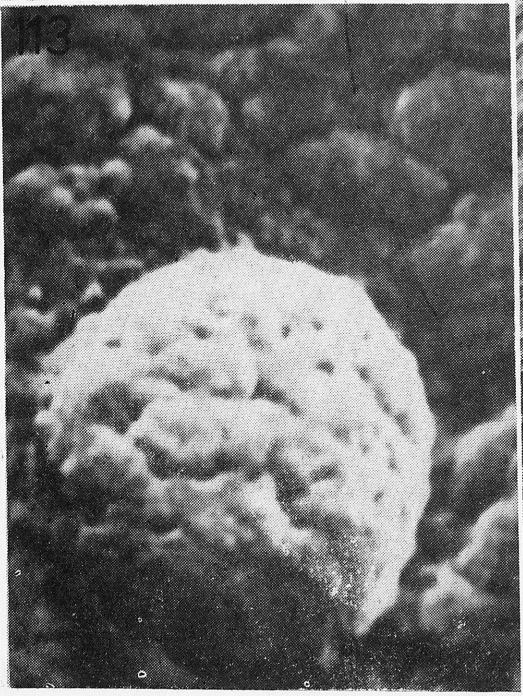
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Plate XXIII

118. Outer half of section through shell of *P. nitidum* typ., parallel to lines of growth (L. Gardno, 1975). × 1200. 119. Inner half of section through shell of *P. nitidum* typ. (same shell as in Phot. 118), parallel to lines of growth. × 1200. 120. A portion of Phot. 119. Section through *P. nitidum* typ. shell, parallel to lines of growth, showing transition of diagonal structure into palisade structure. × 3300. 121. Section of shell of *P. nitidum* f. *crassa*, (L. Sarąg, 1974), parallel to lines of growth. × 1300. 122. Section of shell of *P. nitidum* f. *bohemica* (L. Gardno, 1975), parallel to lines of growth. × 3200. 123. Section of shell of *P. nitidum* f. *bohemica* (L. Gardno, 1975) parallel to lines of growth. × 2000. 124. Section through endostracum of *P. nitidum* f. *bohemica* (L. Gardno, 1975) parallel to lines of growth. × 6000

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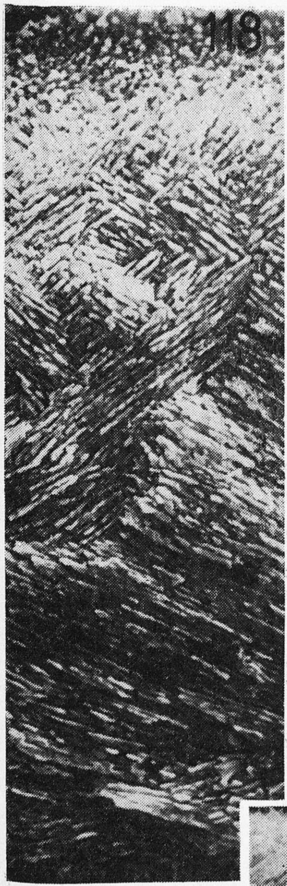

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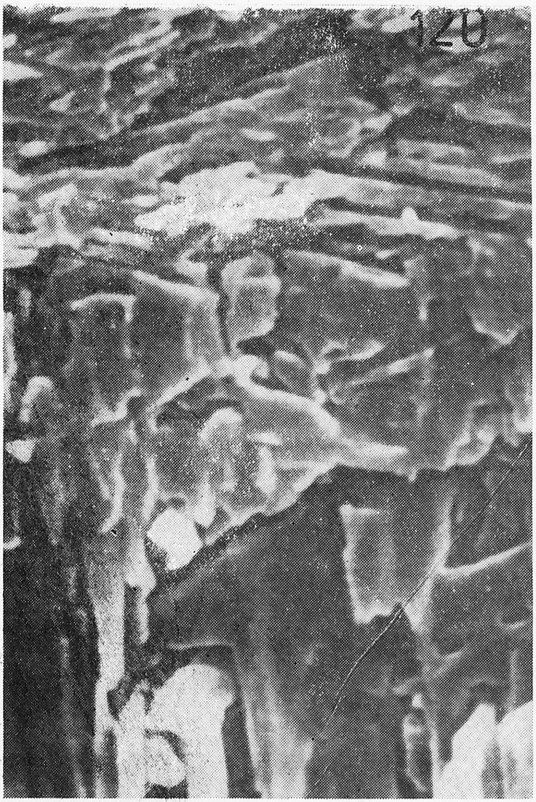

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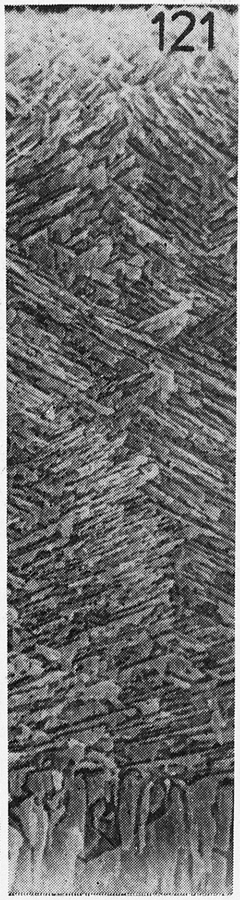

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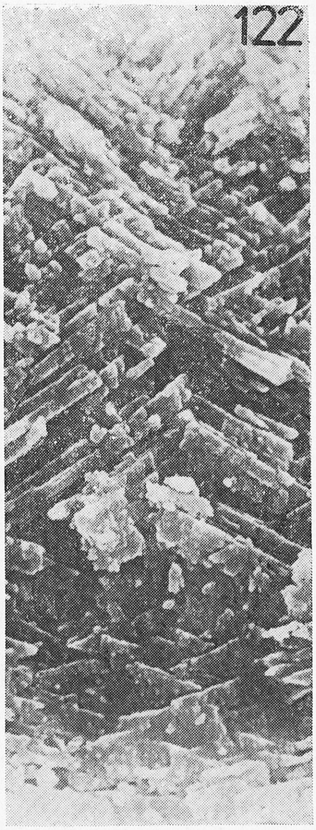

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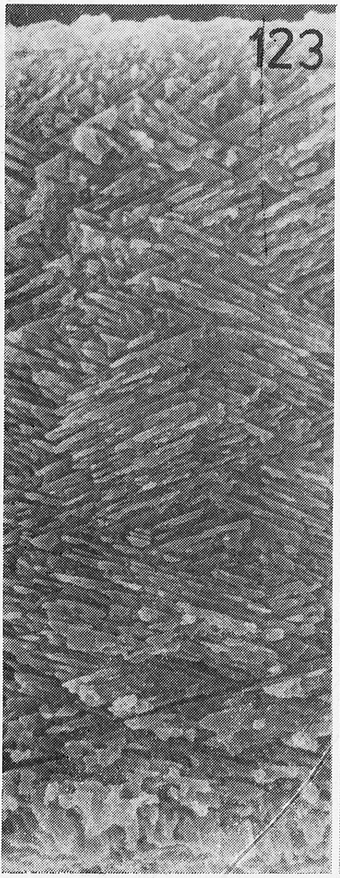

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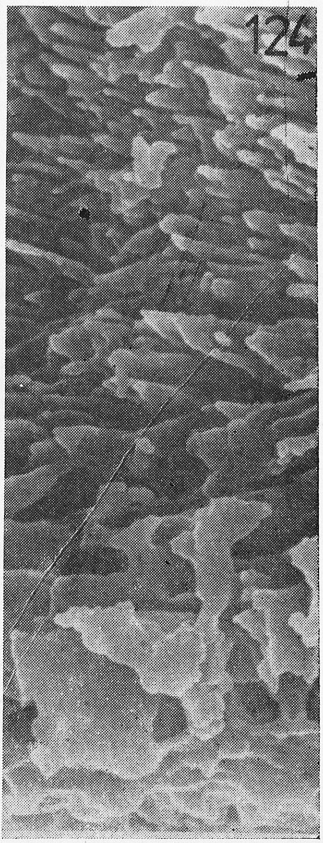

124

Plate XXIV

125. Section of shell of *P. nitidum A* (L. Gardno, 1975), parallel to lines of growth. × 4800 126. Inner shell surface of *P. nitidum* f. *bohemica* (L. Gardno, 1975). × 2000. 127. Inner surface of shell of *P. nitidum* f. *bohemica* (L. Gardno, 1975). × 2000. 128. Inner shell surface of *P. nitidum* f. *crassa* (L. Sarąg, 1974). × 4800. 129. Inner shell surface of *P. nitidum* typ. (L. Gardno, 1975). × 400. 130. A pore in endostracum of *P. nitidum* typ. A; portion of Phot. 129. × 2000. 131. Inner shell surface of *P. nitidum* f. *crassa* (Wolin I., 1978). × 2000

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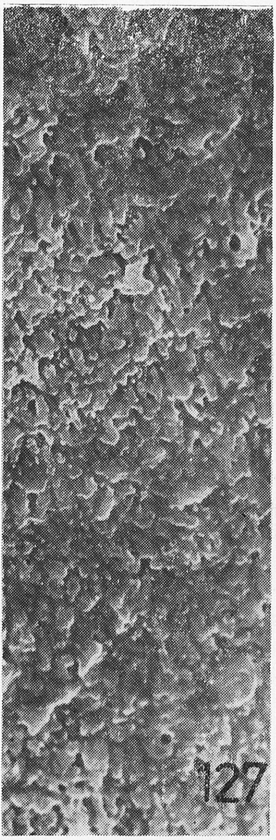
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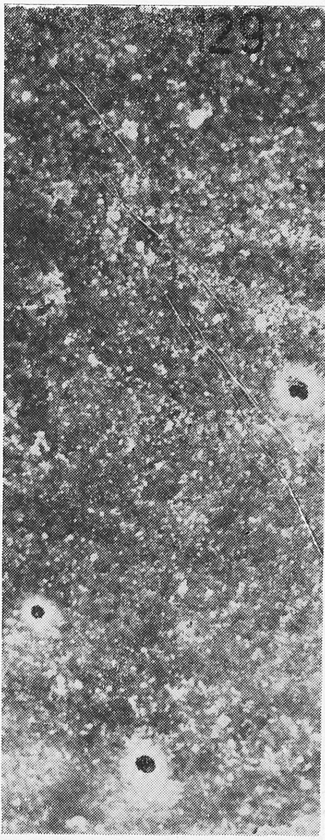
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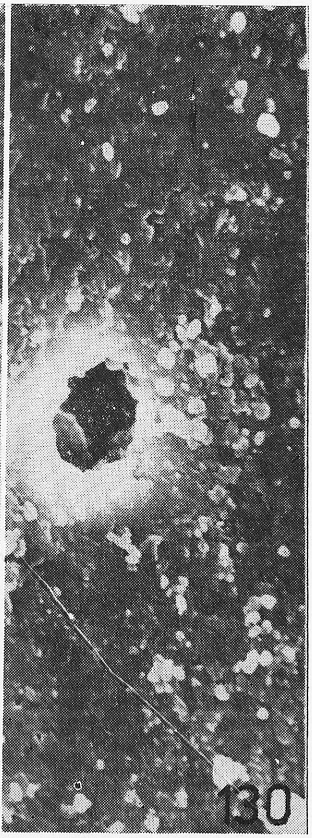
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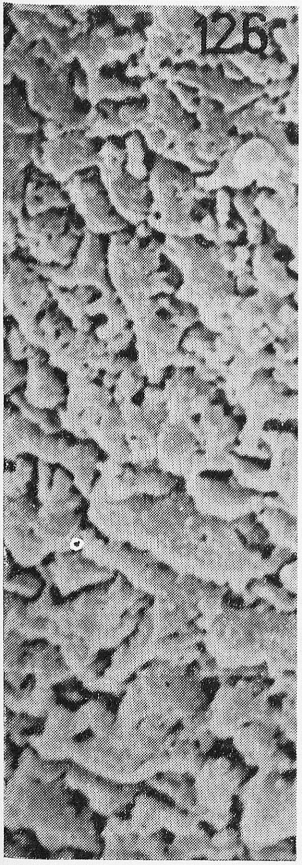
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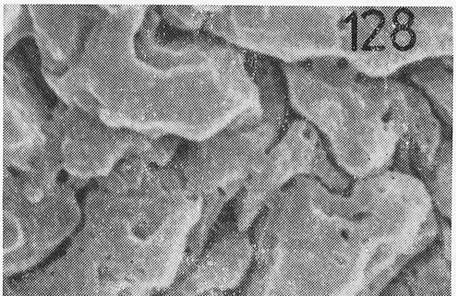
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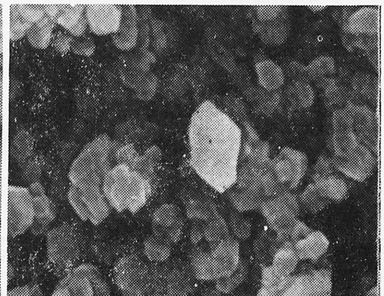
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Plate XXV

132. Section of shell of *P. pulchellum* (Riv. Drwinka, 1977), parallel to lines of growth. × 2200. 133. Section of shell of *P. pulchellum* (Riv. Drwinka, 1977), parallel to lines of growth. × 2600. 134. Inner shell surface of *P. pulchellum* (Riv. Drwinka, 1977). × 1000. 135. Inner shell surface of *P. pulchellum* (Riv. Drwinka, 1977). × 430. 136. A portion of Phot. 135. Inner shell surface of *P. pulchellum.* × 2000. 137. A portion of Phot. 136. A pore in endostracum of *P. pulchellum.* × 6000. 138. Outer part of section through shell of *P. lilljeborgi* (L. Miedwie, 1963), parallel to lines of growth; leg. L. Berger, det. K. Kasprzak. × 1500. 139. Inner part of section throught shell of *P. lilljeborgi* (other part of same shell as in Phot. 138). × 1500

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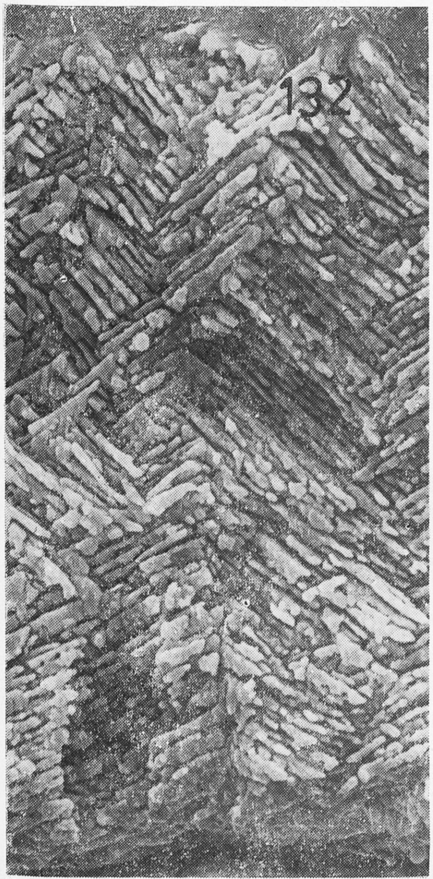
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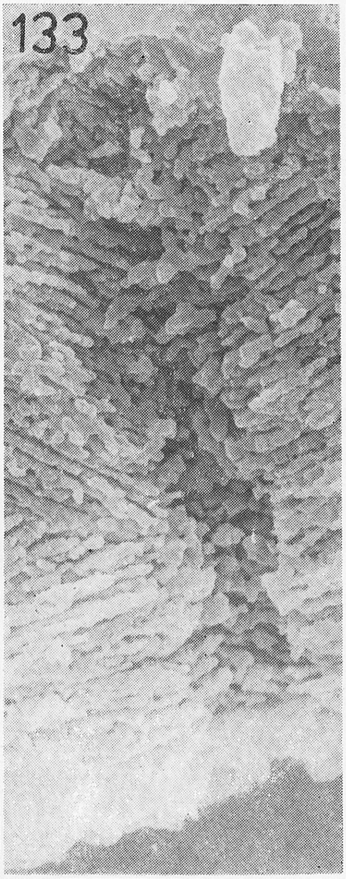
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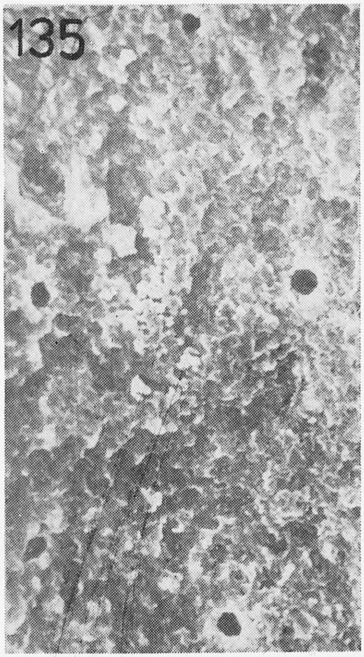
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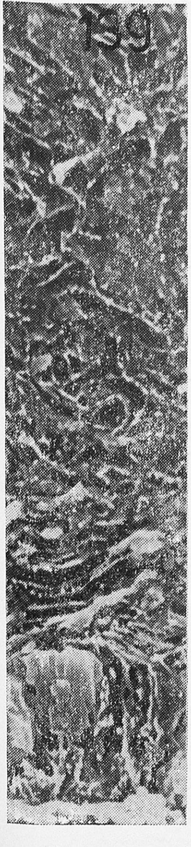
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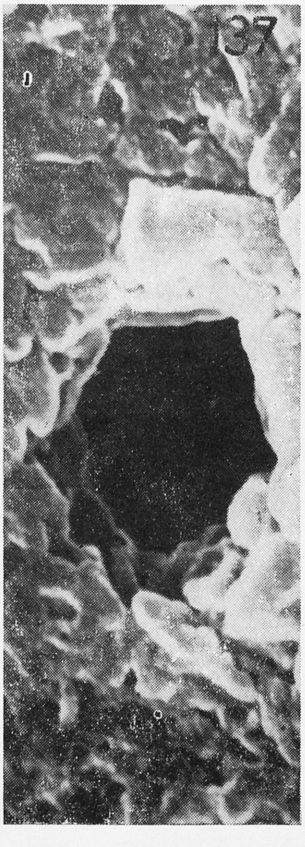
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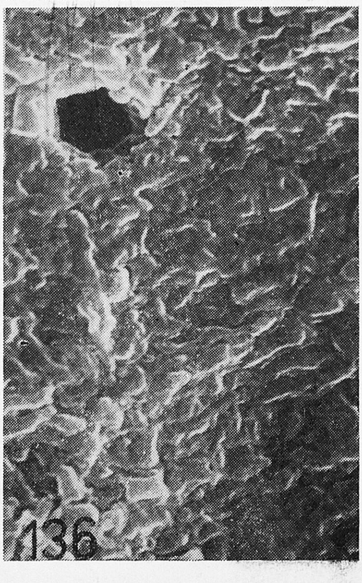
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Plate XXVI

140. Section of shell of *P. lilljeborgi* (L. Miedwie, 1963), parallel to lines of growth; leg. L. BERGER, det. K. KASPRZAK. × 1000. 141. Section of shell of *P. lilljeborgi* (L. Miedwie, 1963), parallel to lines of growth; leg. L. BERGER, det. K. KASPRZAK. × 1200. 142. A portion of Phot. 140. Section through endostracum of *P. lilljeborgi*, parallel to lines of growth. × 6000. 143. Inner shell surface of *P. lilljeborgi* (L. Miedwie, 1963), leg. L. BERGER, det. K. KASPRZAK. × 400. 144. Inner shell surface of *P. lilljeborgi* (L. Miedwie, 1963), leg. L. BERGER, det. K. KASPRZAK. × 2000. 145. Inner shell surface of *P. lilljeborgi* (L. Miedwie, 1963), leg. L. BERGER, det. K. KASPRZAK. × 2000. 146. Section through ligament of *P. personatum* (Niepołomice Forest, 1976), parallel to hinge axis. × 1000

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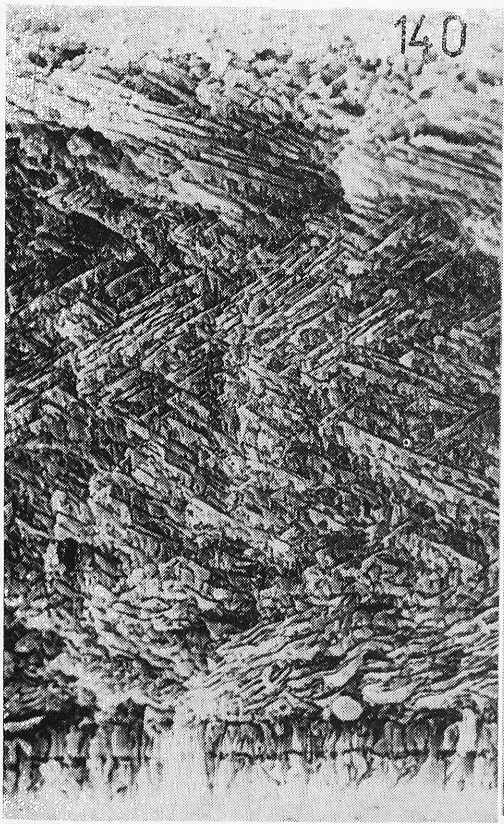
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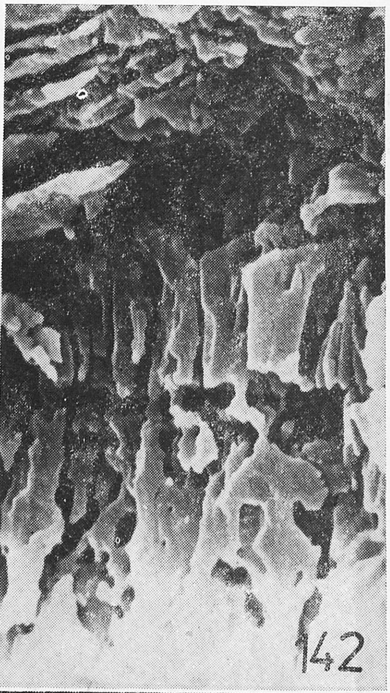
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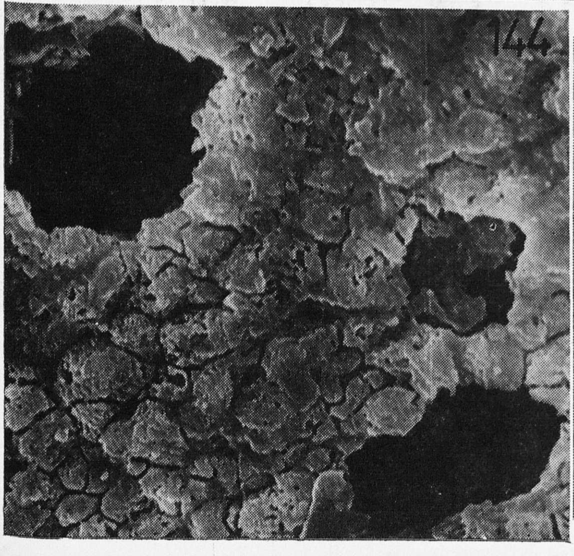
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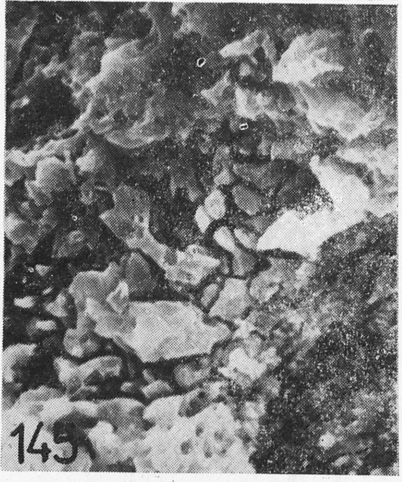
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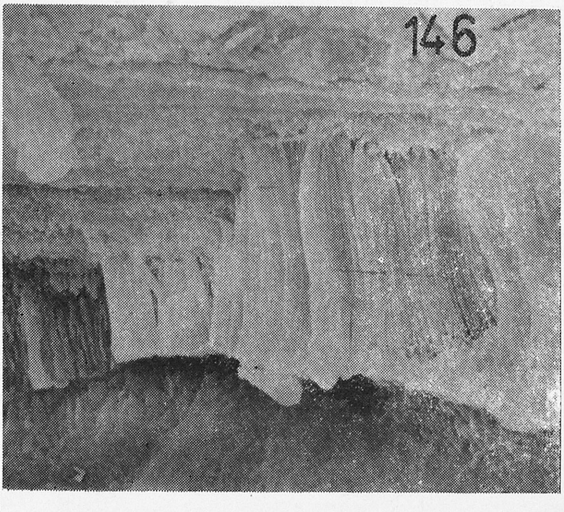
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Plate XXVII

147. Section of shell of *P. personatum* (Niepołomice Forest, 1976), parallel to lines of growth. × 1200. 148. Section of shell of *P. personatum* (Niepołomice Forest, 1976), parallel to lines of growth. × 1800. 149. Inner shell surface of *P. personatum* (Niepołomice Forest, 1976), × 200. 150. Inner shell surface of *P. personatum* (Niepołomice Forest, 1976). × 600. 151. A pore in endostracum of *P. personatum* (Niepołomice Forest, 1976). × 6000. 152. A pore in endostracum of *P. personatum* (Niepołomice Forest, 1976). × 4000. 153. An outer portion of section through shell of *P. obtusale* (Toporowy Staw in the Tatras, 1978), parallel to lines of growth. × 2400

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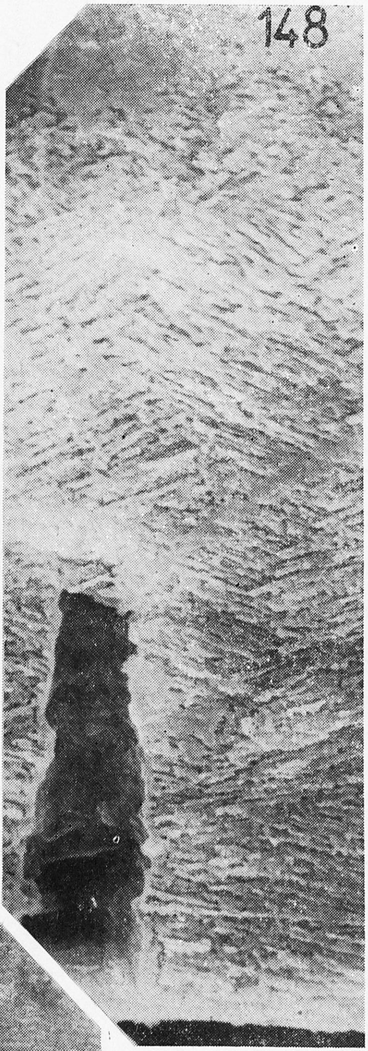
147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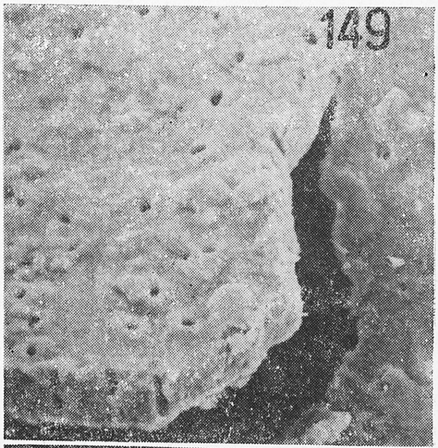
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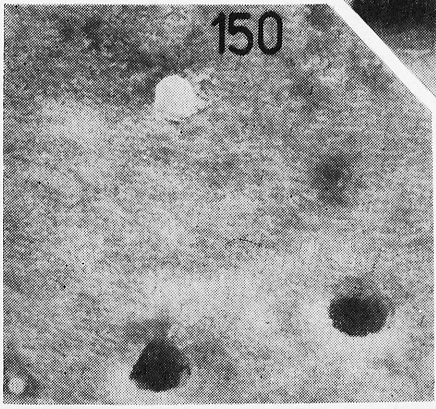
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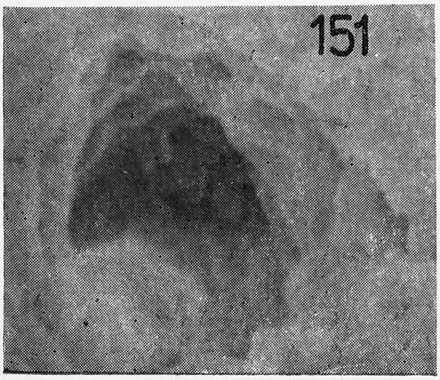
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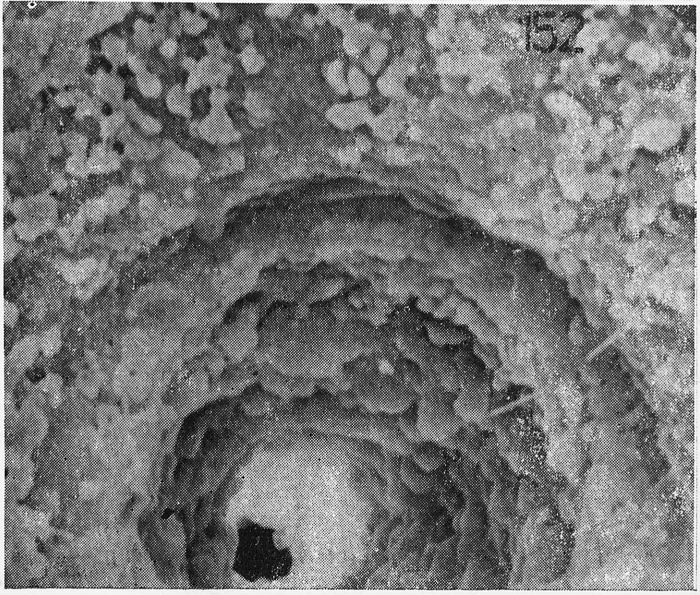
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Plate XXVIII

154. Inner portion of section through shell of *P. obtusale*, parallel to lines of growth (same shell as in Phot. 153). × 3900. 155. Section of shell of *P. obtusale* (peatbog near Ostrów, 1954), leg. et det. L. Berger. × 3200. 156. Inner shell surface of *P. obtusale* (peatbog near Ostrów, 1954), leg. et det. L. Berger, × 400. 157. A portion of Phot, 156. Inner shell surface of *P. obtusale*. × 2000. 158. A portion of Phot. 157. A pore in endostracum of *P. obtusale*. × 6000. 159. Inner shell surface of *P. obtusale* (Toporowy Staw, 1978), × 2000. 160. A portion of Phot. 159. Inner shell surface. × 6000. 161. Inner shell surface of *P. obtusale* (Toporowy Staw, 1978). × 430. 162. A portion of Phot. 161. Pores in endostracum of *P. obtusale*. × 2000

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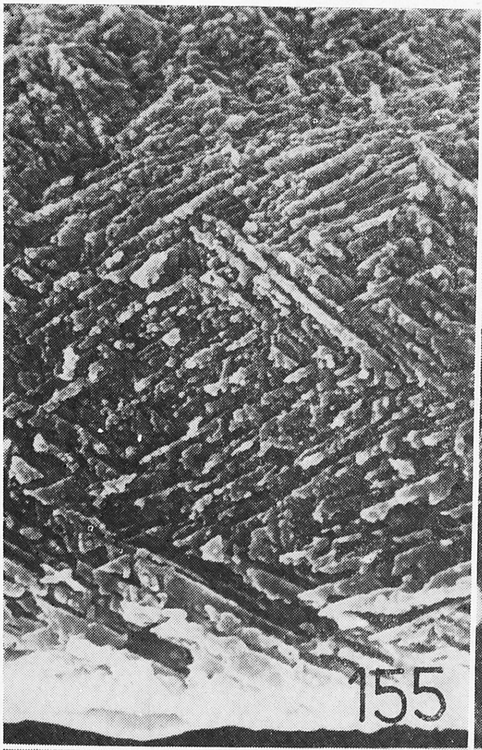
154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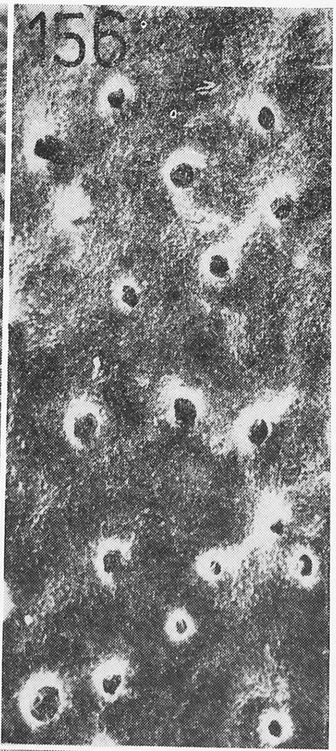
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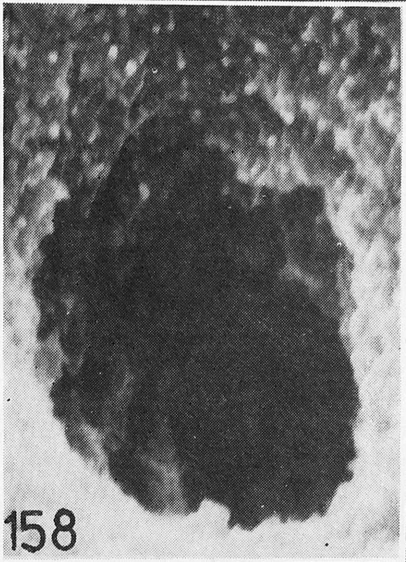
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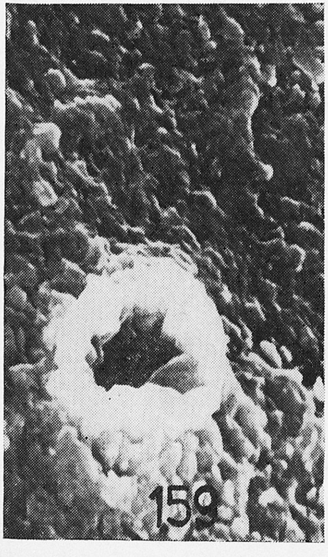
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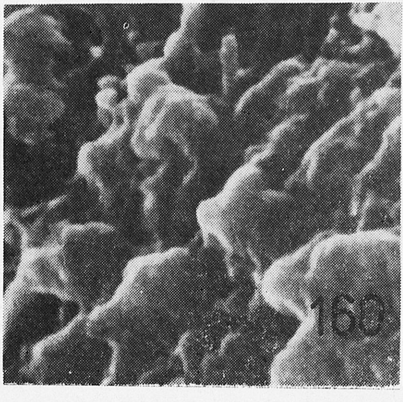
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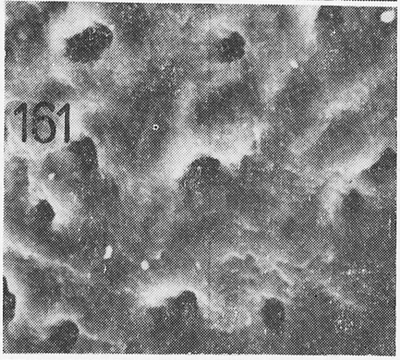
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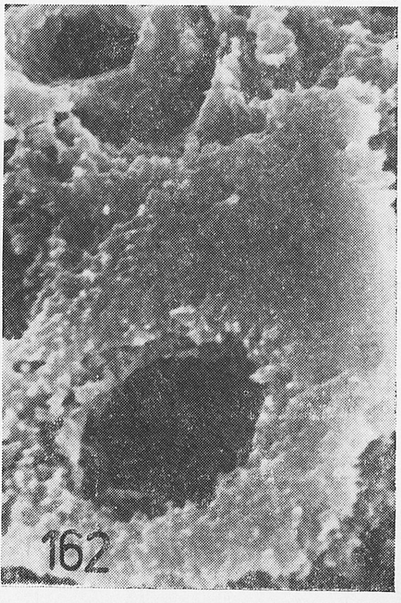
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Plate XXIX

163. Inner shell surface of *P. obtusale* (peatbog near Ostrów, 1954), leg. et det. L. Berger. × 430. 164. A portion of Phot. 163. A pore in inner shell surface of *P. obtusale.* × 6000. 165. Pores and first segment of canals in endostracum of *P. obtusale* (forest marsh near Makruty in Mazuria, 1977). × 1600. 166. Inner shell surface and pores in *P. obtusale* (forest marsh near Makruty in Mazuria, 1977) × 430. 167. Inner surface and pores of shell of *P. obtusale.* A portion of Phot. 166. × 2000. 168. Outer surface of embryo of *P. casertanum* (Zielona Góra, 1976), streaks perpendicular to lines of growth. × 780. 169. Outer shell surface of *P. casertanum* (Zielona Góra, 1976). × 2000. 170. Section through hinge plate of *P. casertanum* (Zielona Góra, 1976), perpendicular to lines of growth. × 1300

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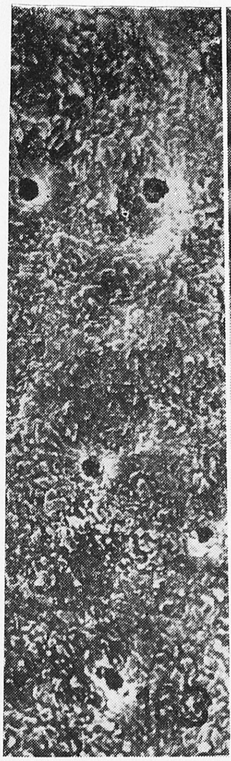
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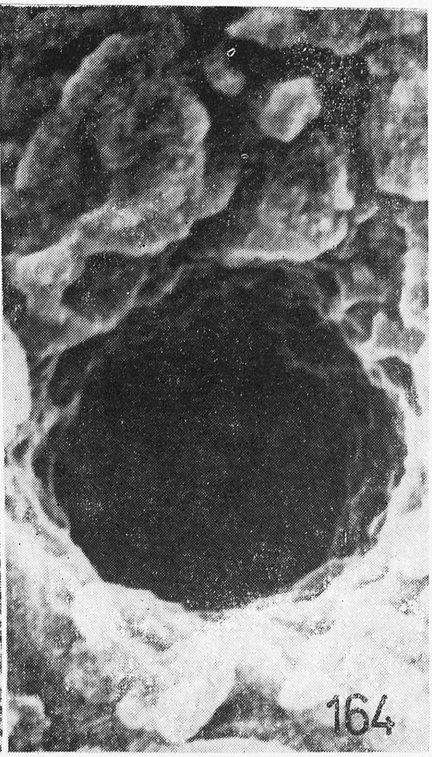
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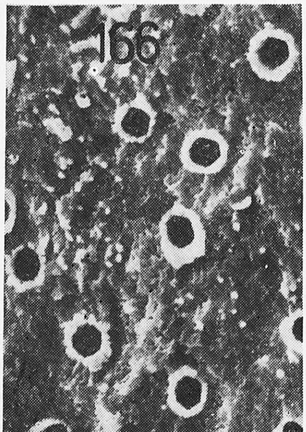
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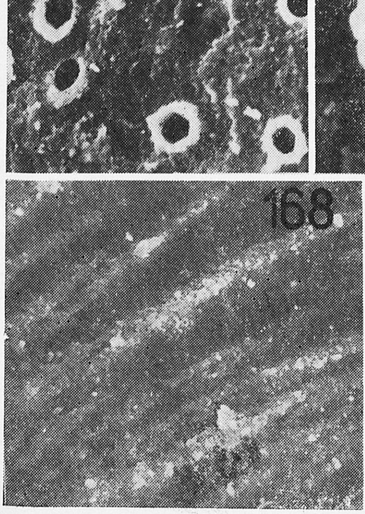
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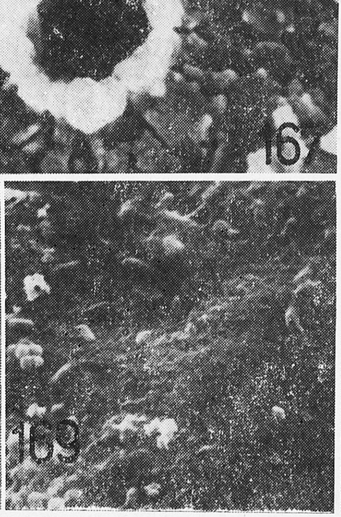
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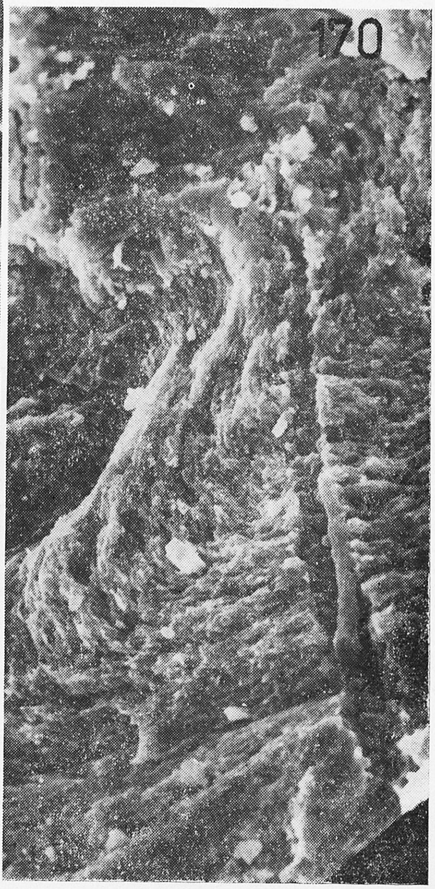
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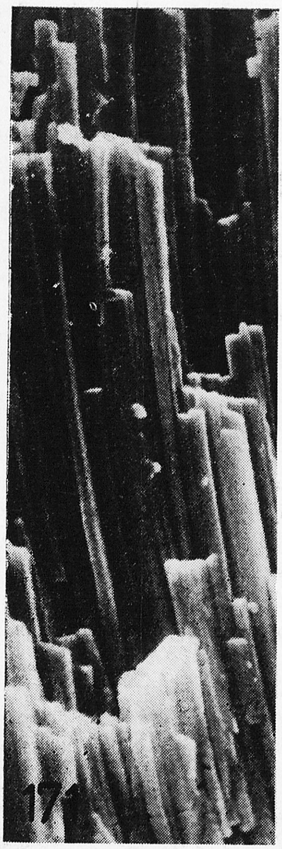
Plate XXX

171. A portion of Phot. 170. Section through hinge plate, perpendicular to lines of growth. × 6600. 172. Section of shell of *P. casertanum* (Zielona Góra, 1976), parallel to lines of growth. × 1800, undigested. 173. Section of shell of *P. casertanum* (Zielona Góra, 1976), parallel to lines of growth. × 2000, undigested. 174. A portion of Phot. 173. Section of shell of *P. casertanum*, parallel to lines of growth, showing transition between diagonal and palisade structures. × 6600, undigested. 175. Section of shell of *P. casertanum* (Zielona Góra, 1976), parallel to lines of growth. × 1800, undigested. 176. Section of shell of *P. casertanum* (Riv. Prądnik at Sułoszowa, 1978), parallel to lines of growth. × 2000. 177. Section of shell of *P. casertanum* f. *ponderosum* (stream at Węgorzewo, 1950), parallel to lines of growth. × 1600, leg. et det. L. BERGER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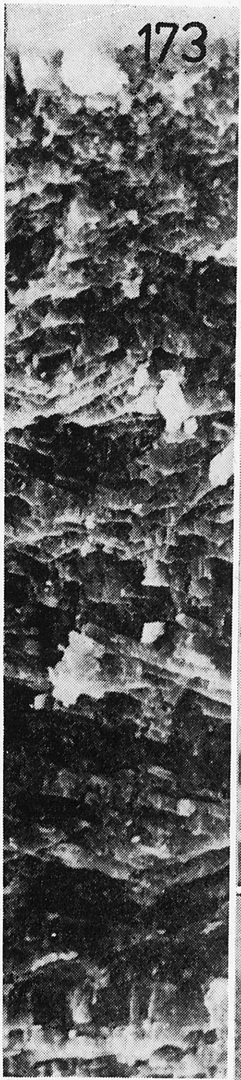
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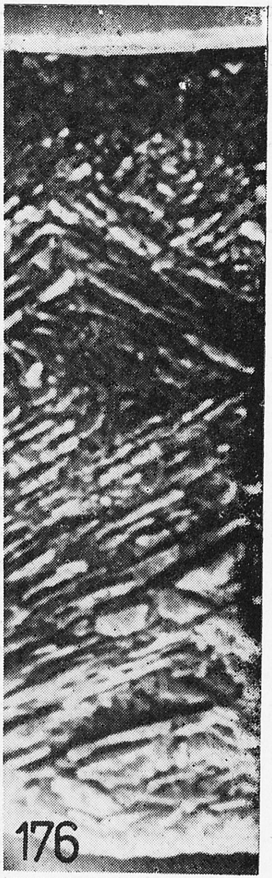
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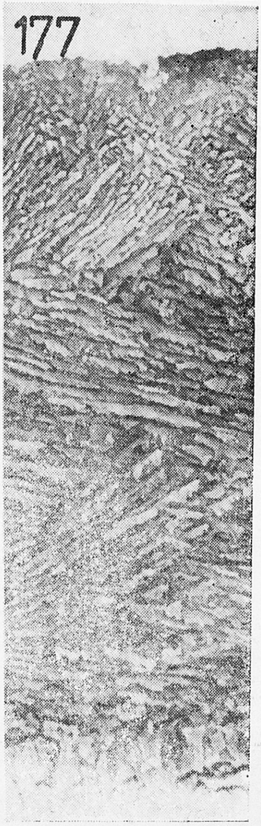
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Plate XXXI

178. A portion of Phot. 177. Section of shell of *P. casertanum* f. *ponderosum*, parallel to lines of growth, showing homogeneo-granular structure (H). × 4800. 179. A portion of Phot. 177. Section through endostracum of *P. casertanum* f. *ponderosum*, parallel to lines of growth. × 7800. 180. Section of shell of *P. casertanum* typ. (stream at Węgorzewo, 1950), parallel to lines of growth. × 1500, leg. et det. L. Berger. 181. A portion of Phot. 180. Section of shell of *P. casertanum* typ., parallel to lines of growth, showing homogeneo-granular layer (H). × 8600. 182. A portion of Phot. 180. Section of endostracum of *P. casertanum* typ., parallel to lines of growth. × 6600. 183. Inner shell surface of *P. casertanum* f. *ponderosum* (stream at Węgorzewo, 1950), leg. et det. L. Berger. × 6000

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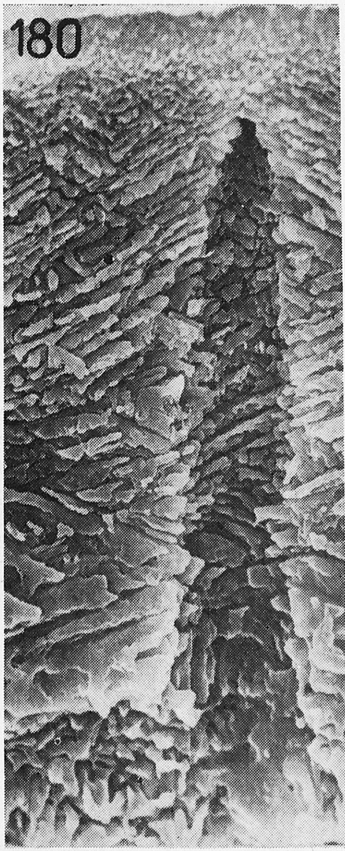
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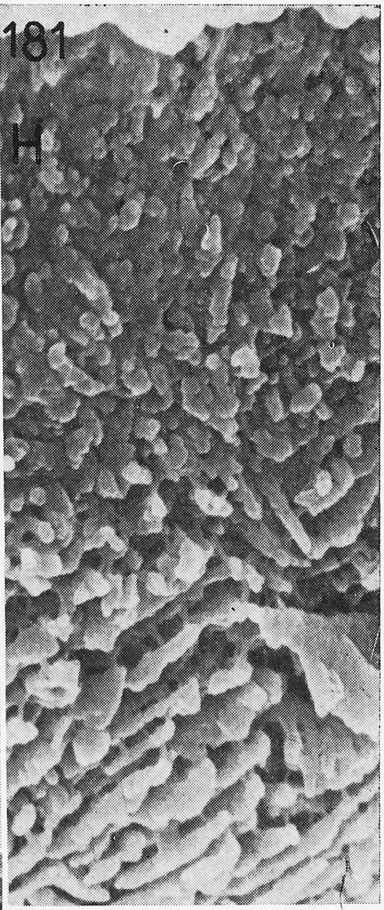
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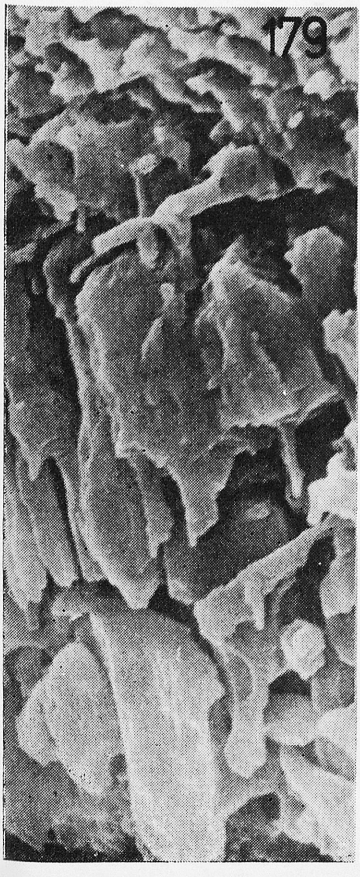
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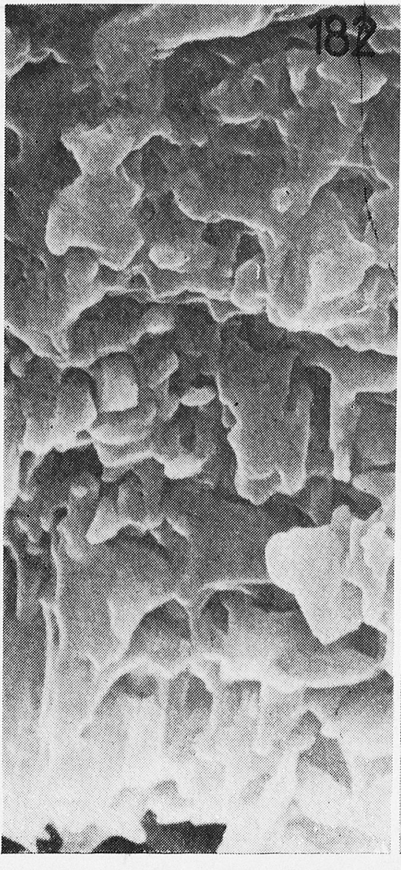
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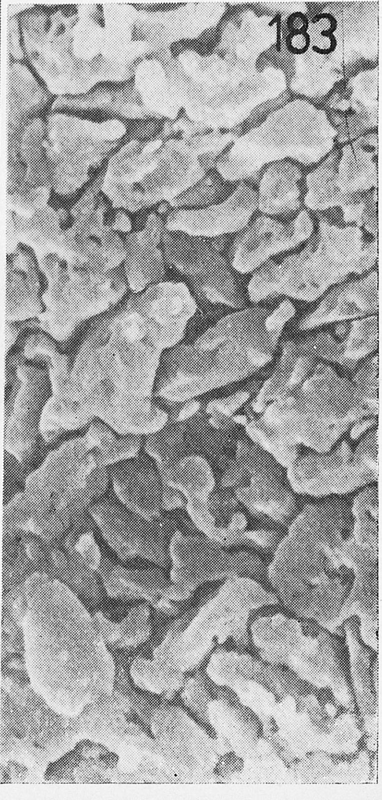
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Plate XXXII

184. A pore in endostracum of same shell of *P. casertanum* f. *ponderosum* as in Phot. 183. × 6000. 185. Inner shell surface of *P. casertanum* typ. (stream at Węgorzewo, 1950). × 10 000, leg. et det. L. Berger. 186. A pore in endostracum of same shell of *P. casertanum* typ. as in Phot. 185. × 6000 .187. A pore in inner shell surface of *P. casertanum* (Zielona Góra, 1976). × 6000. 188. Inner shell surface of *P. casertanum* typ. (Riv. Biała Przemsza, 1978) ×2000. 189. A portion of Phot. 188. Inner shell surface of *P. casertanum* typ. × 6000

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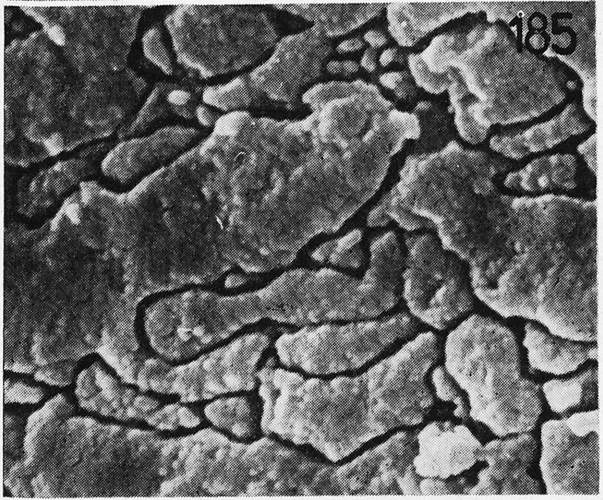
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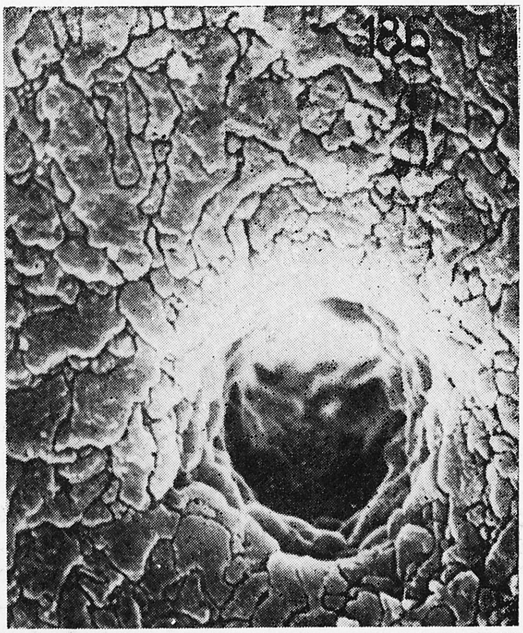
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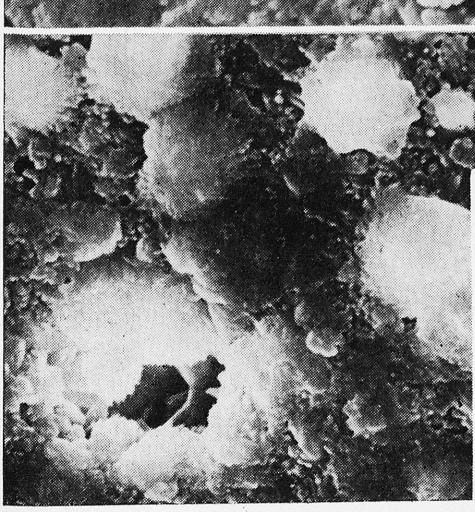
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Plate XXXIII

190. Outer portion of section through shell of *P. ponderosum* (L. Gardno, 1975), parallel to lines of growth. × 1300. 191. Inner portion of section through same shell of *P. ponderosum*, parallel to lines of growth. × 1300. 192. Inner shell surface of *P. ponderosum* (L. Gardno 1975). × 6000. 193. Section of shell of *P. hibernicum* (L. Gardno, 1975), parallel to lines of growth. × 4000. 194. A portion of Phot. 193. Section of shell of *P. hibernicum*, parallel to lines of growth, showing homogeneo-granular layer (H). × 13 000

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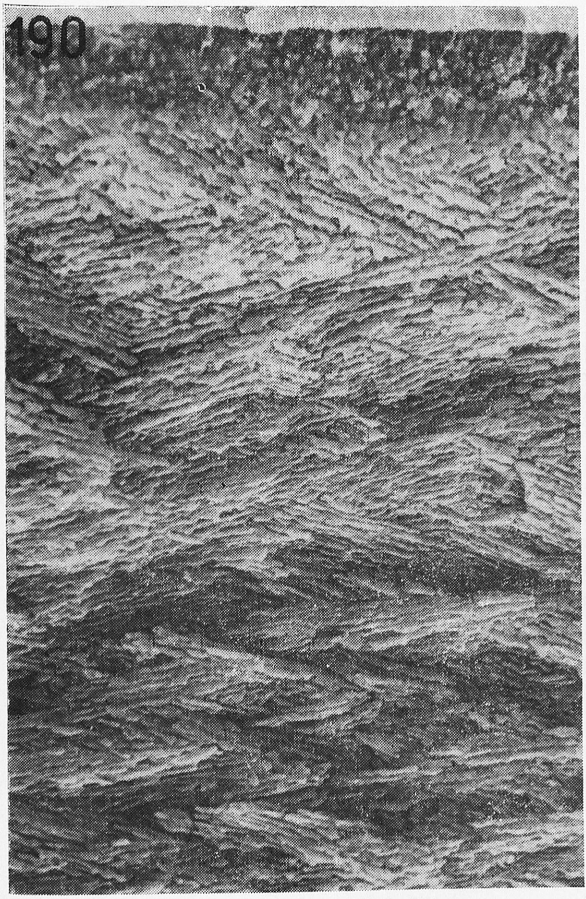

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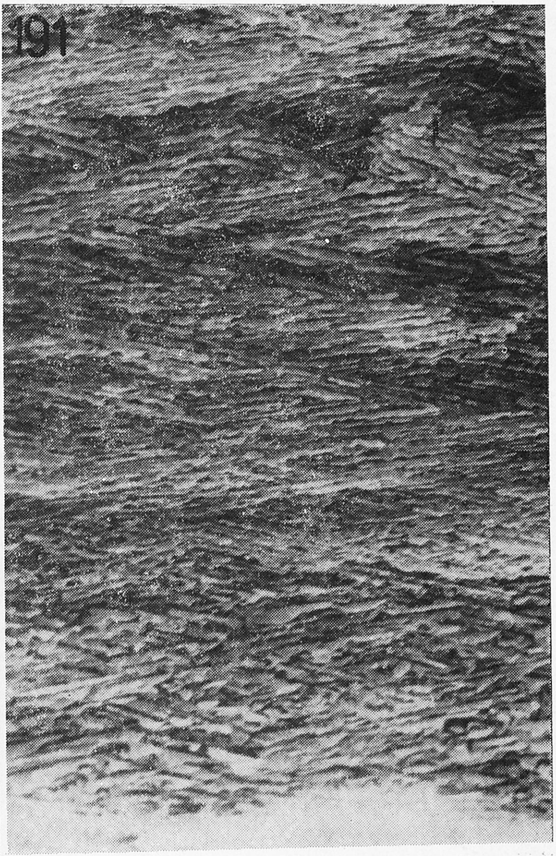

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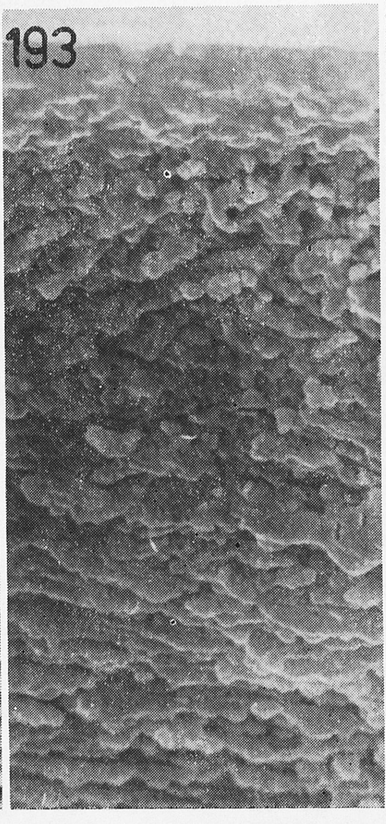

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Plate XXXIV

195. Inner shell surface of *P. hibernicum* (L. Gardno, 1975). × 2000. 196. Section of shell of *P. moitessierianum* (L. Gardno, 1975), rectangular to lines of growth. × 1000. 197. Section of shell of *P. moitessierianum* (L. Gardno, 1975), parallel to lines of growth. × 1800. 198. A portion of Phot. 197. Section of shell of *P. moitessierianum*, parallel to lines of growth, showing homogeneo-granular layer (H) and transition into diagonal layer. × 6000. 199. Inner portion of section in Phot. 197. Section of shell of *P. moitessierianum*, parallel to lines of growth. × 3000. 200. Section of shell of *P. moitessierianum*, (L. Gardno, 1975) parallel to lines of growth. × 1100

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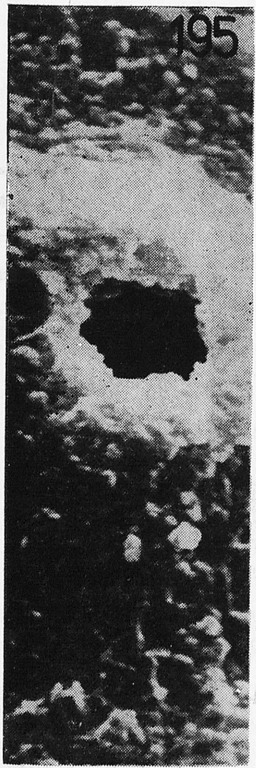

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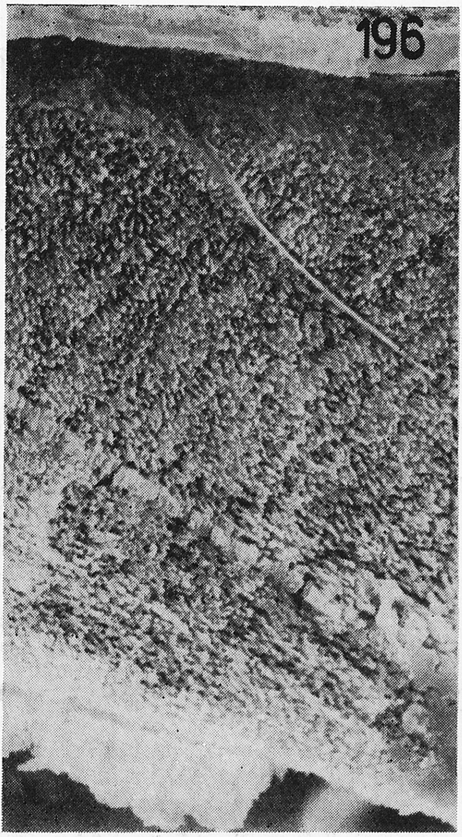

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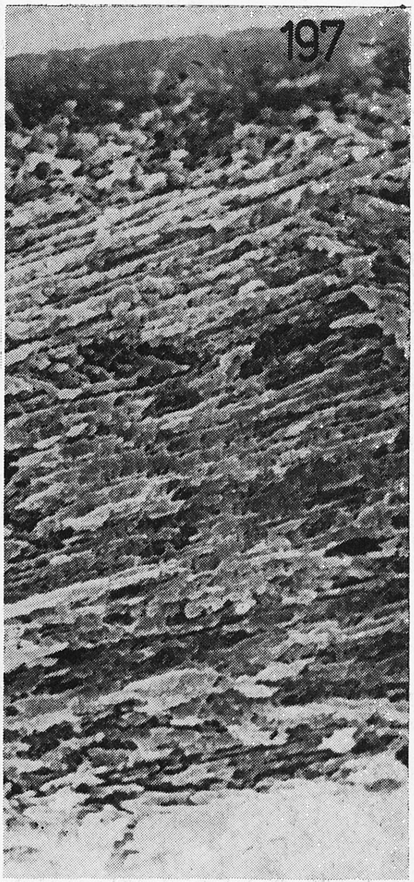

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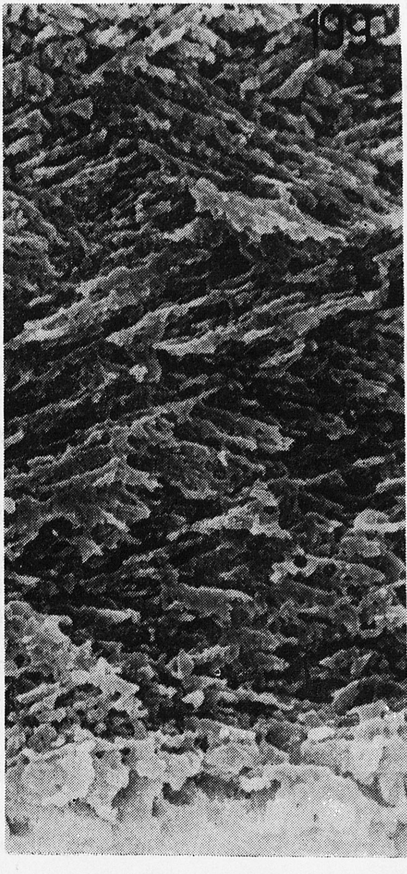

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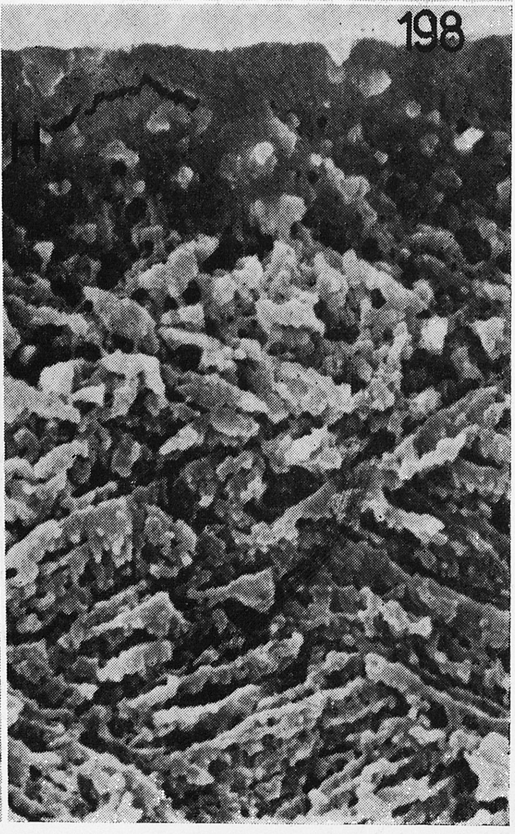

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Plate XXXV

201. Section of shell of *P. moitessierianum* (L. Gardno, 1975), parallel to lines of growth. × 1800. 202. A portion of Phot. 201. Section of shell of *P. moitessierianum*, parallel to lines of growth, showing transition between homogeneo-granular and diagonal layers. × 6600. 203. Section of shell of *P. moitessierianum*, (L. Gardno, 1975) parallel to lines of growth. × 2000. 204. Outer portion of section in Phot. 203. Section of shell of *P. moitessierianum*, parallel to lines of growth. × 6600. 205. Inner portion of section in Phot. 203. Section of shell of *P. moitessierianum*, parallel to lines of growth. × 6600

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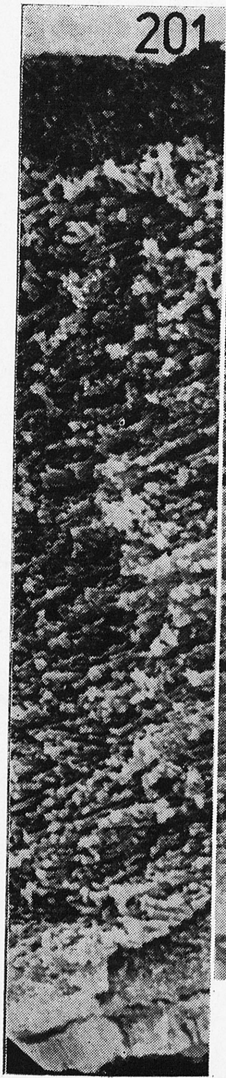
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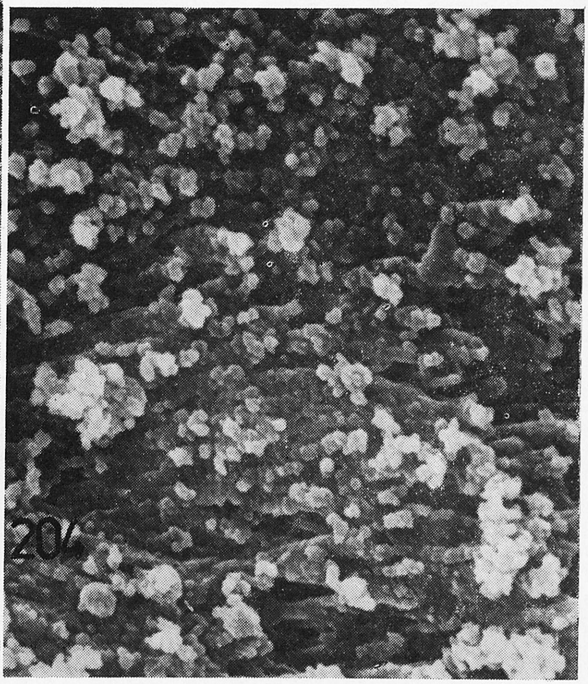
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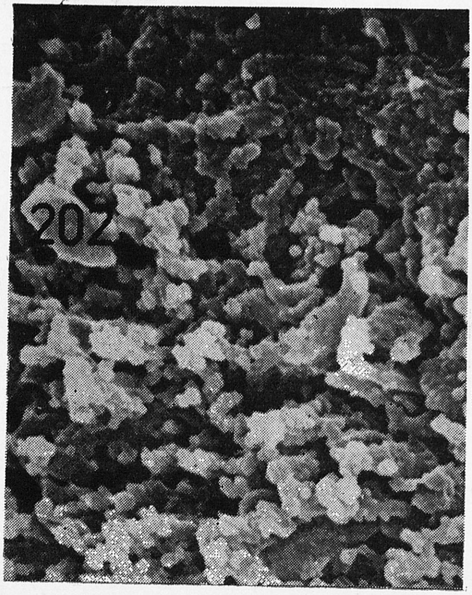
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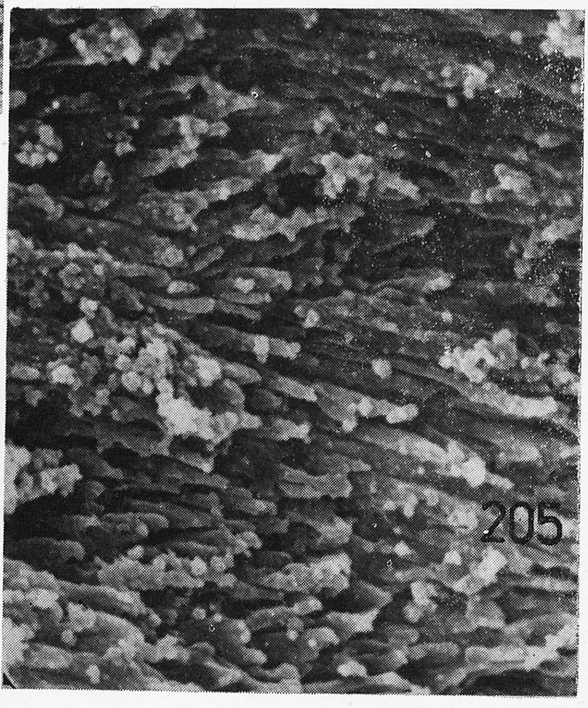
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Plate XXXVI

206. Section of shell of *P. moitessierianum*, (L. Gardno, 1975) parallel to lines of growth. × 1200. 207. A portion of Phot. 206. Section of shell of *P. moitessierianum*, parallel to lines of growth, showing homogeneo-granular structure (H). × 7200. 208. Inner shell surface of *P. moitessierianum* (L. Gardno, 1975). × 2000. 209. A portion of Phot. 208. Inner shell surface of *P. moitessierianum*. × 10 000. 210. Inner shell surface of *P. moitessierianum* (L. Gardno, 1975). × 6000

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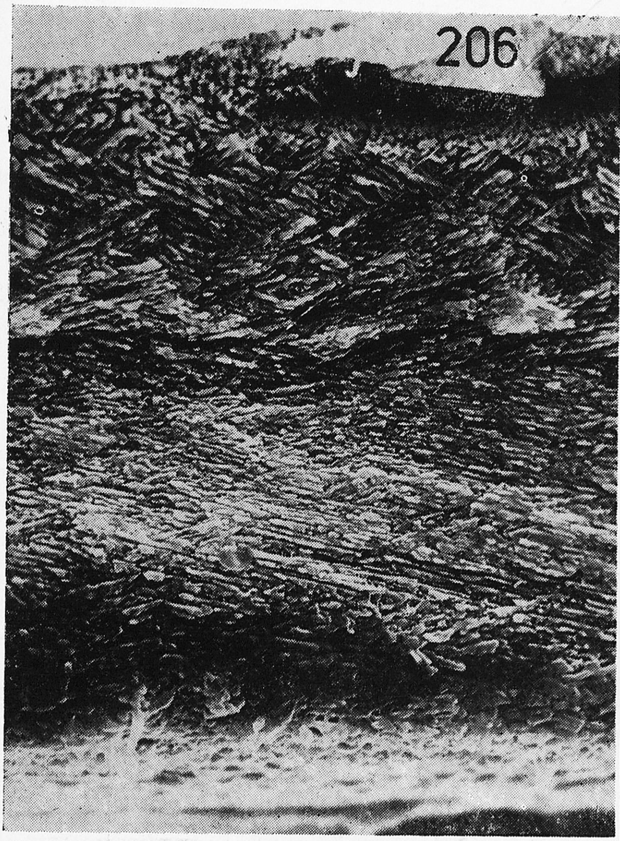

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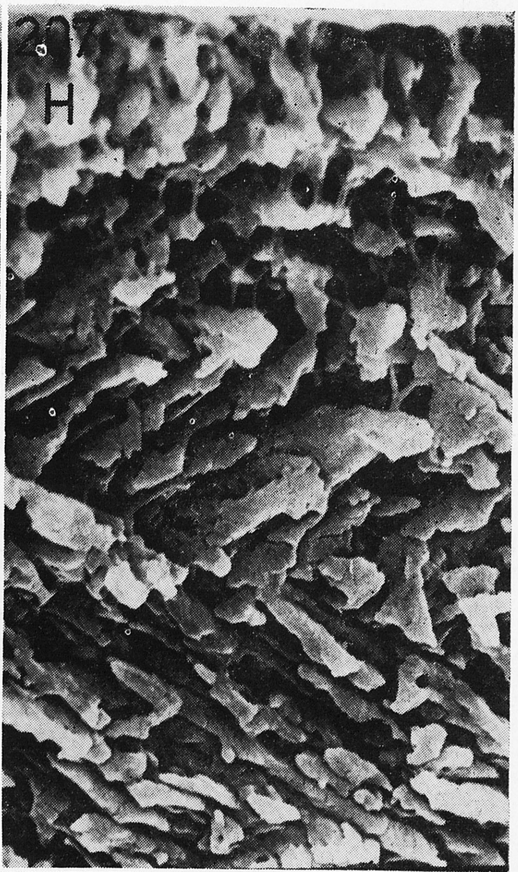

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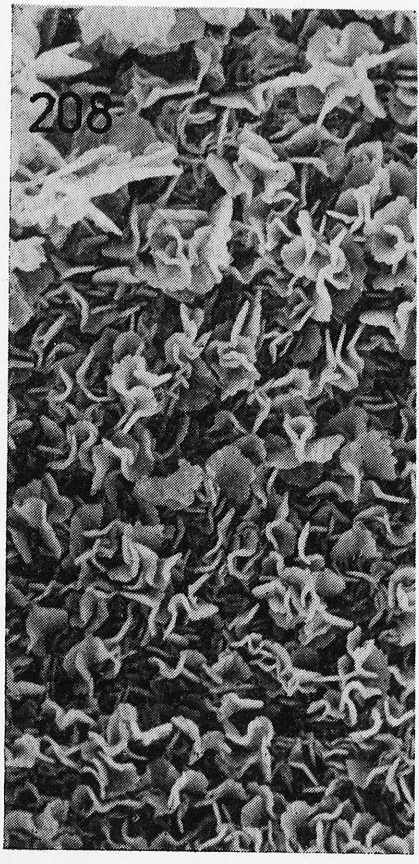

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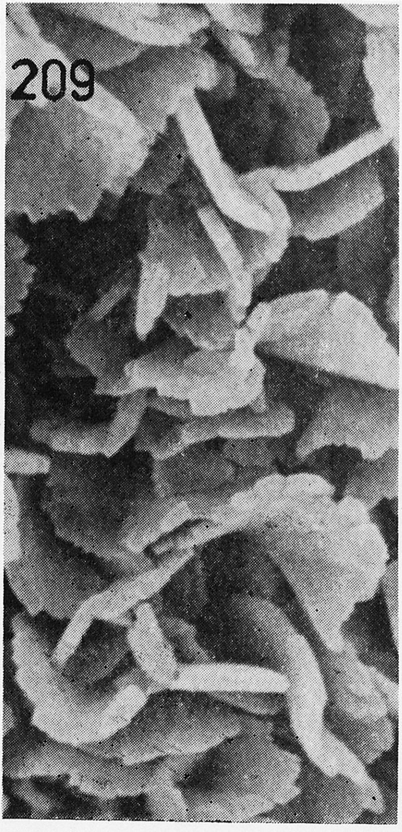

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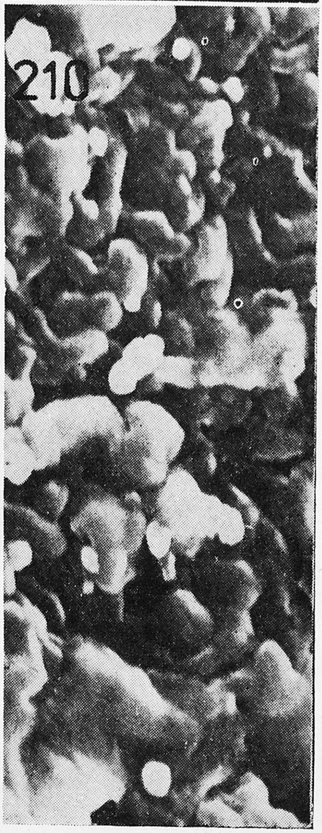

Plate XXXVII

211. Section of shell of *P. tenuilineatum* (stream at Grochowo near Poznań, 1956), parallel to lines of growth. × 3600, leg. et det. L. Berger. 212. Outer portion of section in Phot. 211, showing granular structure. × 10 000. 213. Inner portion of section in Phot. 211, showing palisade structure (Pa). × 10 000. 214. Section of shell of *P. tenuilineatum* (stream at Grochowo near Poznań, 1956), parallel to lines of growth. × 4000, leg. et det. L. Berger. 215. Inner shell surface of *P. tenuilineatum* (stream at Grochowo near Poznań, 1956). × 12 000, leg. et det. L. Berger

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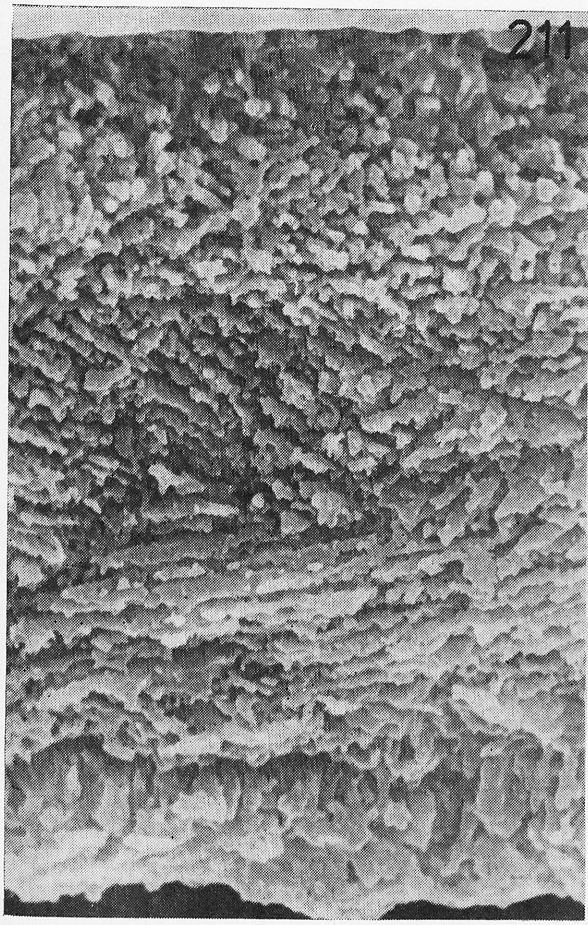

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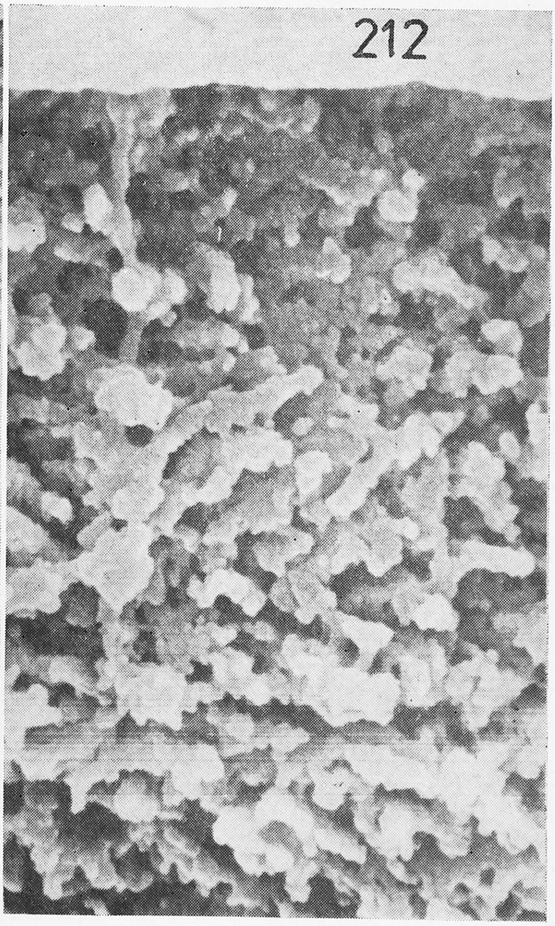

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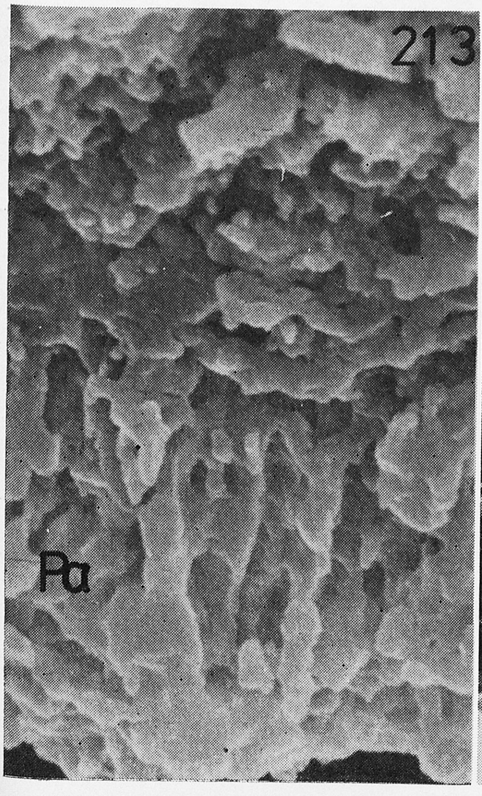

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Plate XXXVIII

216. *P. subtruncatum* (Stary Wisłok, collection of Museum of Natural History, P. A. Scs. in Cracow, undated). 217. *P. subtruncatum* (L. Sarąg, 1974). 218. *P. nitidum A* (L. Gardno, 1975). 219. *P. nitidum* f. *bohemica* (L. Gardno, 1975). 220. *P. nitidum* f. *crassa* (L. Sarąg, 1977). 221—223. *P. obtusale* (Mazuria, 1977). 224. *P. moitessierianum* (L. Gardno, 1975). SEM, × 48

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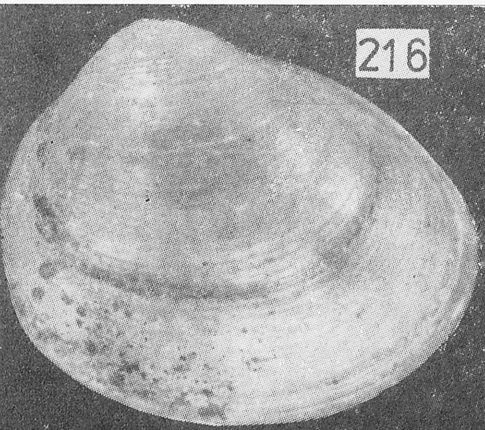

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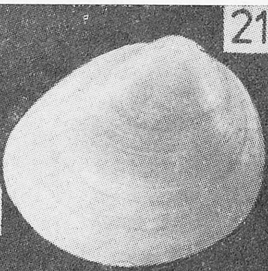

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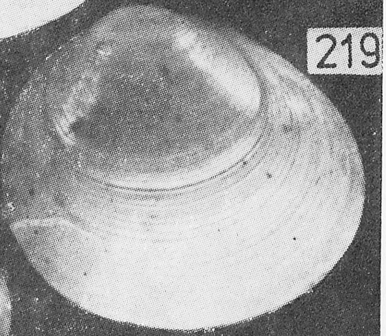

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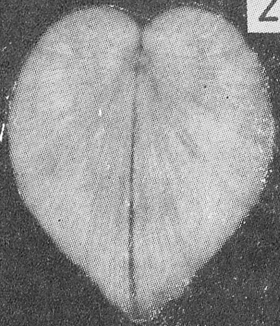

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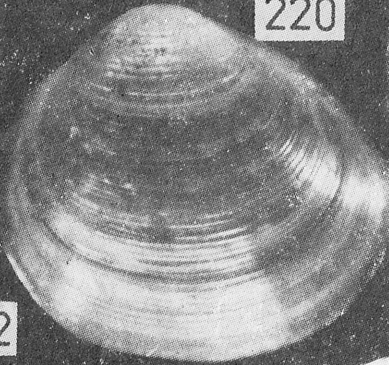

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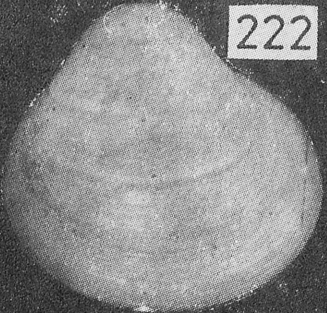

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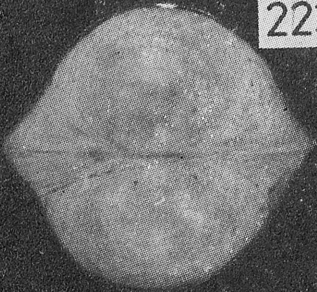

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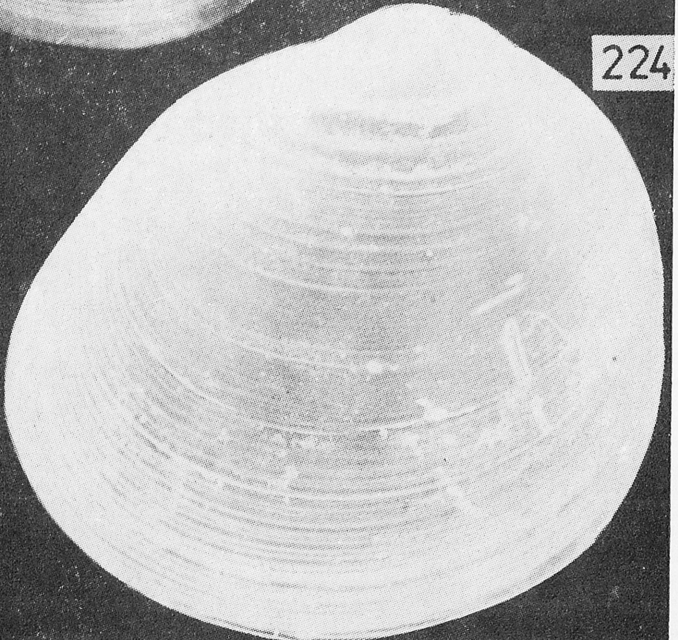

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