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ULTRASTRUCTURE OF SOME PERMIAN AND TRIASSIC SPIRIFERIDA AND ATHYRIDIDA (BRACHIOPODA)

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Key-words: Ultrastructure, Brachiopoda, Spiriferida, Athyridida, Permian, Triassic.

Riassunto. In questo lavoro viene analizzata l'ultrastruttura del guscio di dodici specie di Brachiopodi permo-triassici appartenenti agli ordini Athyridida e Spiriferida, provenienti da diverse località e formazioni. Lo scopo del lavoro è di presentare nuovi dati sull'ultrastruttura del guscio di questi Brachiopodi e di verificare se gli elementi ultrastrutturali che li caratterizzano sono strumenti diagnostici per la loro determinazione tassonomica.

L'analisi ultrastrutturale di *Tetractinella trigonella* e *T. hexagonalis* ha messo in evidenza alcuni elementi (lo spessore dello strato secondario, la forma del profilo trasversale delle fibre dello strato secondario stesso ed il loro spessore) che permettono di distinguere le due specie. Inoltre elementi ultrastrutturali quali la forma e le dimensioni delle fibre dello strato secondario hanno permesso di differenziare tre specie appartenenti al genere *Trigonotreta* (*Trigonotreta stokesi, T. lyonsensis, Trigonotreta* sp.).

Infine è stata analizzata per la prima volta l'ultrastruttura di *Clavigera bisulcata, Elivina tibetana, Spiriferella rajah, Spirelytha petaliformis, Martinia tschernyschewi* e *Mentzelia mentzeli*. Per quanto riguarda l'ultrastruttura di "*Retzia*" *beneckei*, si sono confrontati i dati ottenuti con quelli già pubblicati da diversi Autori.

Abstract. Twelve species of Permian and Triassic Spiriferida and Athyridida from various localities and formations have been analysed in order to provide new data on the ultrastructure of these brachiopods.

Ultrastructural analysis of the genus *Tetractinella* has provided new elements (e.g. the thickness of the secondary layer, the transverse profile of the secondary layer fibres and their thickness) that enable distinction between the species *T. trigonella* and *T. hexagonalis*. Ultrastructural features, such as the shape and the dimensions of the secondary layer fibres, have also led to the ultrastructural differentiation of three species of the genus *Trigonotreta* (*Trigonotreta* sp., *T. stokesi* and *T. lyonsensis*).

Furthermore the ultrastructure of *Clavigera bisulcata, Elivina tibetana, Spiriferella rajah, Spirelytha petaliformis, Martinia tschernyschewi* and *Mentzelia mentzeli* has been investigated for the first time and new data on "*Retzia*" *beneckei* are provided.

Introduction.

The pioneering studies of Carpenter (1853) and King (1870) and the more comprehensive analyses of Williams (1968) and MacKinnon (1974) revealed that the articu-

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late brachiopod shell consists basically of two calcareous layers: an outer primary layer (finely granular) and an inner secondary layer (fibrous); in some taxa an innermost tertiary layer (prismatic) may occur.

Since the contributions of Williams (1968) and MacKinnon (1974), shell ultrastructure has been utilised as a taxonomic discriminant in articulate brachiopods. Williams (1968) undertook a comparative study of the shell ultrastructure of living Terebratulida and Rhynchonellida and various orders of fossil brachiopods including Spiriferida. MacKinnon (1974) published very important and new data concerning the ultrastructure of *Spiriferina walcotti* (Sowerby) and in general that of all the superfamilies of the Order Spiriferida (*sensu* Boucot et al. in Treatise, 1965), analysing representative species of each superfamily. In addition he showed the evolution in time of the shell structure of the Spiriferida and pointed out some diagnostic ultrastructural features. In 1981 Taddei Ruggero published further data on the ultrastructure of some Triassic Spiriferida (*sensu* Boucot et al. in Treatise, 1965) (*Anisactinella maurensis* Taddei Ruggero, *Pentactinella scandonei* Taddei Ruggero, "*Spiriferina fragilis*" (Schlotheim) and "*Retzia*" sp.). Benigni & Ferliga (1990, 1991) analysed the shell ultrastructure of the Carnian *Diplospirella* from the San Cassiano Fm. (Northern Italy) and that of the genus *Anisactinella*.

In the course of a PhD study of Permian brachiopods from Karakorum (L. Angiolini, in progress), in which species of Spiriferida and Athyridida were firstly determined on the basis of external and internal morphological characters, the shell ultrastructure was tentatively employed as a further discriminant feature. In the present study five species from Karakorum, are investigated along with seven spiriferid species of Permian and Triassic age from other regions. The number of the species analysed is not exhaustive and the selection of these twelve species can appear somewhat haphazard to attempt a taxonomic discrimination based only on ultrastructural features. In fact the aim of this study is only to present some new information on shell structure of brachiopods never investigated up till now. As far as known in literature, the data concerning the ultrastructure of brachiopods are still few, so that each new information is a contribution towards a major comprehension of the ultrastructural features.

The synonymy and gross morphology of the analysed species are not considered in this paper. The Treatise classification, as erected by Boucot et al. (1965), has been followed for the spiriferids, except for the genera *Spirelytha*, *Elivina*, *Spiriferella* and *Trigonotreta* for which respectively the keys of Archbold & Thomas (1984), Archbold & Thomas (1985) and that of Archbold & Thomas (1986) have been followed. The classification of the athyridids is based on the scheme of Dagys (1974) and on the work of Grunt (1986).

The analysed specimens are Permian and Triassic Athyridida (*Clavigera bisulcata* Hector, 1913; *Tetractinella trigonella* von Schlotheim, 1820 and *Tetractinella hexagonalis* Loretz, 1874), and Permian and Triassic *Spiriferida* ["*Retzia*" *beneckei* Bittner, 1890; *Trigonotreta stokesi* Koenig, 1825; *Trigonotreta lyonsensis* Archbold & Thomas, 1986;

Trigonotreta sp.; *Elivina tibetana* (Diener, 1897); *Spiriferella rajah* (Salter, 1865); *Spirelytha petaliformis* (Pavlova, 1973); *Martinia tschernyschewi* Grunt, 1973 and *Mentzelia mentzeli* (Dunker, 1851)] all coming from different localities and formations.

Of the nine genera investigated in the present study, only the genus "*Retzia*" has previously been the subject of exhaustive study (MacKinnon, 1974; Taddei Ruggero, 1981).

Material.

The material was collected by L. Angiolini, M. Gaetani and A. Tintori and is housed in the Museo di Paleontologia of the Department of Earth Sciences, University of Milano.

The examined species come from different localities and formations:

Clavigera bisulcata Hector was collected from the Rhaetian *Clavigera* Shellbed, in Roaring Bay, South Island, New Zealand (sample MPUM6907).

Tetractinella trigonella von Schlotheim was collected from the "Banco a Brachiopodi", at the top of the Angolo Formation (Middle Anisian), in Grigna Mountains (Lecco, Lombardy) (sample MPUM6908).

Tetractinella hexagonalis Loretz came from the Middle Anisian Dont Formation, from the locality of M. Rite, Northern Italy (samples MPUM6909, MPUM6910, MPUM6911).

"*Retzia*" *beneckei* Bittner was collected from the Middle Anisian Dont Formation (Section Prà della Vacca, Braies), Northern Italy (samples MPUM6912, MPUM6913).

Trigonotreta stokesi Koenig and *T. lyonsensis* Archbold & Thomas were collected near Spinji, in the Chapursan Valley (Upper Hunza Valley, Karakorum, Pakistan), in the Asselian-Lower Sakmarian Gircha Formation (samples MPUM6914, MPUM6915, MPUM6916, MPUM6917).

Trigonotreta sp. was found in the first member of the Panjshah Formation (Sakmarian) in the Lupghar Valley and near Khudabad (Chapursan Valley, Karakorum, Pakistan) (samples MPUM6918, MPUM6919). The age is Sakmarian.

Elivina tibetana (Diener) came from the first member of the Panjshah Formation cropping out in Chapursan Valley (Karakorum) and from the first member of the Lashkargaz Formation at Baroghil Pass (E Hindu Kush) (samples MPUM6920, MPUM6921, MPUM6922, MPUM6923). The age is Sakmarian.

Spiriferella rajah (Salter) was sampled in the Upper Permian of Dolpo, Himalaya (samples MPUM6924, MPUM6925, MPUM6926).

Spirelytha petaliformis (Pavlova) was found in the Gircha Formation (Asselian-Lower Sakmarian) near Spinji and on the left side of the Yashkuk Glacier, in the Chapursan Valley (Upper Hunza Valley, Karakorum, Pakistan) (samples MPUM6929, MPUM6930).

Martinia tschernyschewi Grunt was sampled in the fourth member of the Panjshah Formation (Upper Permian), at Panjshah (Chapursan Valley) (MPUM6931).

Mentzelia mentzeli (Dunker) came from the Middle Anisian Dont Formation, from the locality of M. Rite, Northern Italy (MPUM6932, MPUM6933).

Technique of specimens preparation.

Small specimens were embedded in araldite to facilitate their subsequent sectioning and polishing. All specimens were sectioned both longitudinally and transversally. Acetate peels were executed along the sections of the shell in order to obtain a natural and undeformed pattern of the shell fibres.

Scanning electron microscope (S.E.M., Cambridge Instruments) analyses were carried out on both longitudinal and transverse sections of the specimens. S.E.M. analyses were carried out both in the Department of Earth Science of Milan and in the University of Cosenza. All observations were photographically recorded.

Diagnostic features.

According to MacKinnon (1974), Taddei Ruggero (1981), Benigni & Ferliga (1990, 1991), the main diagnostic ultrastructural element taken into account for taxonomical determination are:

- the thickness of the primary layer and of the secondary layer;
- the possible occurrence of a tertiary layer;
- the dimensions of the crystallites which comprise the primary layer;
- the shape and the dimensions of the terminal facies of secondary layer fibres;
- the profile and the dimensions of secondary fibres in cross sections;
- the periodicity of depositional banding in the two layers;
- the presence of punctae, their dimensions and their diameter;
- the dimensions and the disposition of fibres in the spiralia.

In the present study, in general, only secondary layer parameters were noted; remnants of a primary layer were preserved in only two species.

Ultrastructure

Phylum **Brachiopoda** Dumeril, 1806

Class **Articulata** Huxley, 1869

Order **Athyridida** Boucot, Johnson & Staton, 1964

Suborder **Athyrididina** Boucot, Johnson & Staton, 1964

Superfamily *Athyridacea* M'Coy, 1844

Family *Diplospirellidae* Schuchert, 1894

Genus *Clavigera* Hector, 1879

Clavigera bisulcata Hector, 1913

Pl. 1, fig. 1, 2

Material. One complete specimen (MPUM6907) has been analysed along a longitudinal section.

Description. The primary layer has not been observed. The secondary layer varies in thickness from 850 μm near the umbo to 120 μm at the anterior margin. It consists of short, compact, orthodoxly stacked fibres, wedging to the shell exterior. In cross section the fibres show rounded diamond-shaped outlines (Pl. 1, fig. 2). The thickness of the fibres is about 10 μm and the width in cross section is about 20-30 μm.

Genus *Tetractinella* Bittner, 1890

Tetractinella trigonella von Schlotheim, 1820

Pl. 1, fig. 3, 4

Material. One complete specimen (MPUM6908) has been examined along a transverse section.

Description. The primary layer has not been observed. The secondary layer is thin, being only 200 μm thick. It consists of orthodoxly stacked fibres, subparallel to the surface of the valve, which show flattened keel and saddle shape in transverse section. Keels and saddles are very well developed, as can be seen in Pl. 1, fig. 3, 4. The width of the fibres is about 14-17 μm and their thickness is 2-3 μm.

Tetractinella hexagonalis Loretz, 1874

Pl. 1, fig. 5-8

Material. Three complete specimens (MPUM6909, MPUM6910, MPUM6911) have been analysed along transverse sections.

Description. Only the secondary layer has been detected. Its thickness varies from 630 μm along the ribs to 300 μm in the sulci. Thickness decreases to 200 μm towards the anterior margin.

The secondary layer consists of short stacked fibres, inclined to the external surface of the valve, with rhomboidal terminal faces which give a characteristic diamond-shaped outline in transverse section. The thickness of the fibres is 3-8 μm and the diagonal of the diamond-shaped profile is about 13-25 μm.

Fragments of the spiralia have been analysed but constituent fibres are affected by recrystallization and dissolution. They consist of two lamellae situated 300-340 μm apart. The distance between individual whorls of the paired lamellae is about 440 μm.

Discussion. Analysis of the ultrastructure of the two species of *Tetractinella* indicates certain diagnostic elements by which they may be discriminated.

As shown in Tab. 1, the main differences between *T. trigonella* and *T. hexagonalis* consist of the thickness of the secondary layer, which is greater in *T. hexagonalis,* the shape of the secondary fibres in transverse section (keel & saddle in the former and diamond-shaped in the latter), the width of the fibres in transverse section and their thickness, both greater in *T. hexagonalis.*

No data on the ultrastructure of the genus *Tetractinella* have previously been published. MacKinnon (1974) analysed other genera of the Family Diplospirellidae (*Diplospirella* and *Anisactinella*), observing two calcareous shell layers. In particular he pointed out that secondary layer consisted of large fibres (width about 60 μm) showing spatulate terminal faces.

Taddei Ruggero (1981) analysed *Anisactinella* and *Pentactinella*. Both genera, like *Tetractinella*, belong to the Family Diplospirellidae. She did not observe the occurrence of a tertiary layer in either genus; sub-rhomboidal secondary layer fibres were detected in *Anisactinella maurensis* Taddei Ruggero. Furthermore Taddei Ruggero (1981) observed that the brachidium of *A. maurensis* consists of two lamellae with secondary layer fibres 5 μm thick.

The ultrastructural features of *Tetractinella* are in agreement with those of the Family Diplospirellidae, which can be summed up as follow (MacKinnon, 1974; Taddei Ruggero, 1981; this work):

- primary layer with fine lineation normal to the outer shell surface and transverse growth bands only sporadically developed;
- secondary layer consisting of keel & saddle to diamond shaped, thick, large fibres, which can be up to 60 μm in width. The secondary layer is thicker along the ribs than along the sulci;
- muscle scars with very irregular shaped long fibres, posteriorly surrounded by small fibres;
- spiralia consisting of two intercoiled spiral lamellae, with small secondary layer fibres.

Order **Spiriferida** Waagen, 1883

Suborder **Retziidina** Boucot, Johnson & Staton, 1964

Family *Retziidae* Waagen, 1883

Genus *Retzia* King, 1850

"Retzia" beneckei Bittner, 1890

Pl. 2, fig. 1-8; Pl. 3, fig. 1, 2

Material. One complete specimen (MPUM6912) and one ventral valve (MPUM6913) of the same species were analysed. The former was analysed along a longitudinal and an oblique section, the latter along a transverse section.

Description. The primary layer is very thin and consists of small crystallites oriented normal to the shell layers. Its maximum thickness is 30 μm. The primary layer is discontinuous probably due to diagenesis.

The secondary layer is very well preserved, its thickness ranging from 100 μm at the anterior margin to 690 μm near the umbo. Furthermore, in transverse section the thickness of the secondary layer is greater along the ribs (400 μm) than along the sulci (200 μm). The secondary layer is built up from compact stacked fibres, inclined at very low angles to the external surface. Transverse sections reveal the characteristic keel and saddle profile of the secondary layer fibres. The maximum width of the secondary fibres in transverse section is 14.3 μm; the thickness of the fibres is about 2-6 μm.

The secondary layer fibres are strongly deflected outwards (towards the shell exterior) around punctae, which are very dense. The diameter of punctae varies from 11 to 20 μm. The punctae seem to be randomly disposed, their spacing being very variable (24-40 μm). Punctae are generally unbranched, but below the ribs they can coalesce into one central canal (Pl. 2, fig. 1) towards the shell interior, due to the continuing deposition of calcite below the crests of the ribs. Commonly punctae are infilled by small irregular calcitic crystals.

Along the anterior and lateral margin of the shell prominent convolutions of the secondary layer fibres have been observed together with a cyclic arrangement of punctae in discrete levels (Pl. 3, fig. 1, 2). This is interpreted as growth stages during the secretion of the shell. During the normal course of deposition of the secondary layer, fibres are orthodoxly stacked and punctae can develop; instead, during periodic breaks in deposition of calcite with retraction of the mantle edge, backwards convolutions of the fibres occur.

Furthermore near the edge of the shell the punctae appear circular, notwithstanding the fact that the section is longitudinal (Fig. 1). This is very unusual and may be related to a random orientation of the punctae at the anterior margin of the shell.

Discussion. A comparison between this observations on the ultrastructure of "*R.*" *beneckei* and the data provided by MacKinnon (1974) for "*Retzia*" sp. show similarity in the shape of secondary layer fibres and in the coalescing of punctae into one central canal below the ribs. However small differences concern the width of the fibres which do not exceed 10 μm in MacKinnon (1974) compared with punctal diameter which measure up to 25 μm in his study. Furthermore no evidence of the convolutions of the secondary layer fibres at the margins of the shell was observed by MacKinnon (1974) together with the circular sections of the punctae at the anterior margin of the shell.

The greater thickness of the shell of "*Retzia*" along the ribs with respect to the sulci is in agreement with that previously observed by Taddei Ruggero (1981). In fact she measured a thickness of 150 μm along the sulci and 550 μm below the ribs. Furthermore Taddei Ruggero (1981) observed that the secondary fibres of the spiralia of "*Retzia*" sp. have the same dimensions as those of the shell.

Suborder Spiriferidina Waagen, 1883

Superfamily *Spiriferacea* King, 1846

Family *Spiriferidae* King, 1846

Subfamily *Trigonotretinae* Schuchert, 1893

Genus *Trigonotreta* Koenig, 1825

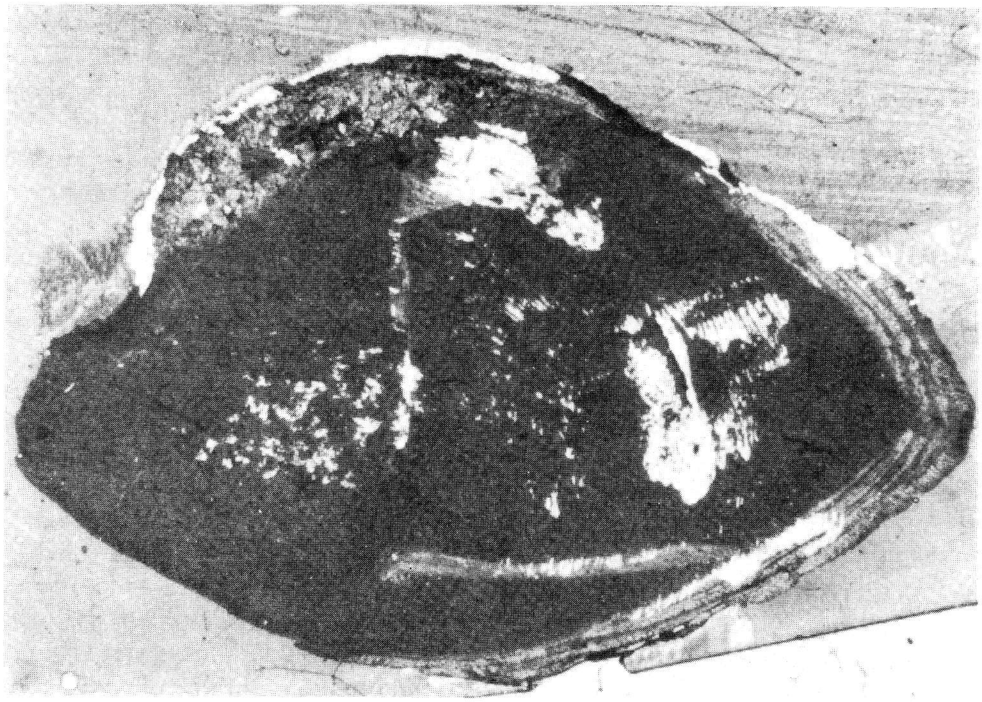

Fig. 1 - Longitudinal section of a complete specimen (MPUM6912) of "*R.*" *beneckei*. Photo under binocular microscope. 9 X.

Trigonotreta stokesi Koenig, 1825

Pl. 3, fig. 3-7

Material. One complete specimen (MPUM6914) has been analysed along longitudinal and transverse sections and one ventral valve (MPUM6915) along longitudinal section.

Description. The secondary layer is very thick near the umbo, being 1900 μm. Its thickness decreases anteriorly, reaching 236 μm at the margin and it is greater along the fold than along the sulcus. The fibres of the secondary layer are close-packed and are rather irregular in profile, probably due to diagenesis. In fact sometimes they show smooth keel and saddle shape in transverse section. The width of the fibres is 13-20 μm and their thickness is 4-5 μm.

In transverse section fragments of the spiralia have been observed (Pl. 3, fig. 6, 7). They consist of flattened secondary layer fibres, whose width is 9 μm and thickness is 4 μm.

Trigonotreta lyonsensis Archbold & Thomas, 1986

Pl. 3, fig. 8; Pl. 4, fig. 1-4

Material. One ventral valve (MPUM6917) along longitudinal section and another ventral valve (MPUM6916) along marginal transverse section have been analysed.

Description. The primary layer has been observed along the transverse section. It consists of crystallites oriented with their long axes normal to the boundary with the secondary layer (Pl. 3, fig. 8). Its thickness is about 18 μm. The width of the crystallites is about 3 μm.

The secondary layer consists of long, orthodoxly stacked fibres, aligned subparallel to the external surface of the valve. Its thickness is 150-450 μm. In transverse section the fibres of the secondary layer show an irregular, platy profile; sometimes they show two keels both on the inner and outer surfaces (Pl. 4, fig. 1-2). The width of the secondary layer fibres is about 8-10 μm. The thickness of the fibres is 4-6 μm.

Convolutions of the secondary fibres have been observed away from the margins of the shell (Pl. 4, fig. 3). They are probably related to the re-orientation of the secondary layer fibres parallel or oblique to the commissure, after the initial (peripheral) stage of growth occurring normally to the commissure (Williams, 1968, p. 9).

The occurrence of the tertiary layer can be inferred by the local presence of an inner irregular layer (Pl. 4, fig. 4). This tertiary layer is 40-56 μm thick.

Trigonotreta sp.

Pl. 4, fig. 5-8

Material. Two ventral valves along longitudinal and marginal transverse sections have been analysed (samples respectively MPUM6918 and MPUM6919).

Description. The primary layer has not been observed. The secondary layer consists of orthodoxly stacked fibres subparallel to the external surface of the valve. Its thickness varies from 600 μm at the margins to 1400 μm towards the umbo. The fibres show a sub-rhomboidal profile in transverse section. The width of the fibres is 13-15 μm, their thickness is about 6-10 μm.

Discussion. As pointed out for the two species of *Tetractinella*, the three species of *Trigonotreta* may also be differentiated on the basis of shell ultrastructure. The ultrastructural features considered diagnostic for the taxonomic discrimination of the three species of *Trigonotreta* are the shape and width of secondary layer fibres in transverse section, their thickness and the possible occurrence of a tertiary layer (Tab. 1).

The profile of the secondary fibres is keel and saddle in *T. stokesi*, sub-rhomboidal in *Trigonotreta* sp. and platy, sometimes with two keels on the inner and outer surfaces of the fibres in *T. lyonsensis*. The width of the transverse profile of the secondary fibres is greater in *T. stokesi* and smallest in *T. lyonsensis*, whereas the thickness of the fibres is greatest in *Trigonotreta* sp. than in the other two species. Finally, the tertiary layer has been tentatively observed only in *T. lyonsensis*.

On the contrary, the thickness of the secondary layer is not considered a valid criterion, showing great variation along the shell of the single specimen. In any case the shell is thicker in *T. stokesi* and in *Trigonotreta* sp. than in *T. lyonsensis*.

	Primary layer thickness	Secondary layer thickness	Tertiary layer thickness	Shape of fibres	Width of fibres	Thickness of fibres	Diameter of punctae
C. bisulcata	not preserved	120-850	absent	diamond	20-30	10	
T. trigonella	not preserved	200	absent	keel & saddle	14-17	2-3	
T. hexagonalis	not preserved	200-630	absent	diamond	13-25	3-8	
"*R.*" *beneckei*	30	100-690	absent	keel & saddle	14.3	2-6	11-20
T. stokesi	not preserved	236-1900	absent	keel & saddle	13-20	4-5	
T. lyonsensis	18	150-450	40-56	platy two keels	8-10	4-6	
Trigonotreta sp.	not preserved	600-1400	absent	sub-rhomboidal	13-15	6-10	
E. tibetana	not preserved	300	absent	sub-rectangular	13-16	2-3	
S. rajah	not preserved	180-200	absent	rhomboidal	12.5-16	2.5-3	
S. petaliformis	not preserved	350	50-60	irregular	8-11	4-7	
M. tschernyschewi	not preserved	300	absent	sub-rhomboidal	16-24		
M. mentzeli	not preserved	200-500	60	keel & saddle	8-14	2-4	

Tab. 1 - A tabulation of the main diagnostic ultrastructural features in the twelve analysed species. All measurements are in microns (μm).

Subfamily *S p i r i f e r e l l i n a e* Waterhouse, 1968

Genus *Elivina* Fredericks, 1919

Elivina tibetana (Diener, 1897)

Pl. 5, fig. 1-3

Material. One complete specimen (MPUM6920) and three ventral valves (MPUM6921, MPUM6922, MPUM6923) were analysed along longitudinal and transverse sections. The complete specimen and one of the ventral valves were partially recrystallized.

Description. The primary layer is not preserved. The secondary layer is about 300 μm thick and it consists of thin, platy, orthodoxly stacked fibres, sub-parallel to the external surface of the valve. The secondary layer fibres show a platy, sub-rectangular profile in cross and oblique section. No keel has been observed on the fibres. The thickness of the fibres is 2-3 μm and their width in transverse section is 13-16 μm, when not affected by recrystallization. Partial fusion of adjacent fibres in some parts of the shell is attributed to recrystallization.

Towards the interior and away from the lateral margins a coarse, prismatic calcite layer has been detected. It is more probably related to recrystallisation of secondary fibres than to the occurrence of a tertiary layer.

Genus *Spiriferella* Tschernyschew, 1902

Spiriferella rajah (Salter, 1865)

Pl. 5, fig. 4-6

Material. Three ventral valves (MPUM6924, MPUM6925, MPUM6926) have been analysed along longitudinal and transverse sections. One valve (MPUM6925) was completely recrystallized.

Description. The primary layer has not been observed. The preserved secondary layer is about 180-200 μm thick and consists of orthodoxly stacked thin fibres, wedging out to the external surface of the valve. The long secondary fibres are characterized by a sharp carina (Pl. 5, fig. 5) running along the upper and lower surfaces. The secondary fibres thus show a characteristic rhomboidal profile in transverse section. The secondary layer fibres are 2.5-3 μm thick and 12.5-16 μm wide.

Towards the interior secondary recrystallization seems to affect the secondary layer and to obliterate the shell structure. Thus data is lacking on the thickness of the secondary layer and on the possible presence of a tertiary layer.

Discussion. *E. tibetana* and *S. rajah*, both representatives of the subfamily *Spiriferellinae*, may be readily distinguished from one another on the basis of the shell ultrastructure. The main differences consist of the shape of fibres in transverse section, which are rhomboidal with carina in *S. rajah* and platy in *E. tibetana*. Also the orientation of the fibres seems to be different: inclined to the external surface of the valve in the former, but subparallel in the latter.

Superfamily *Reticulariacea* Waagen, 1883

Family *Elythidae* Fredericks, 1924

Genus *Spirelytha* Fredericks, 1919

Spirelytha petaliformis (Pavlova, 1973)

Pl. 5, fig. 7, 8; Pl. 6, fig. 1, 2

Material. One dorsal valve (MPUM6929) along oblique transverse section and one ventral valve (MPUM6930) along longitudinal section have been analysed.

Description. The primary layer has not been observed. The secondary layer is 350 μm thick. It consists of long fibres subparallel to the external surface of the valve which show a very irregular shape in transverse section. In fact the secondary fibres can show a platy profile or a subrhomboidal shape. The width of fibres is 8-11 μm and their thickness is 4-7 μm. The secondary layer fibres are thicker towards the interior.

The scars of attachment of the double-barrelled spines, which constitute the micro-ornamentation of the shell, consist of thin secondary layer fibres. Towards the interior the fibres of the secondary layer pass to irregular, poorly defined crystals inferred to represent a tertiary layer. This layer is 50-60 μm thick. It can possibly be myotest.

Discussion. The only published data on the ultrastructure of the Family Elythidae concern *Phricodothyris* sp. of the Pennsylvanian Finis Shale of Texas (MacKinnon, 1974). The dimensions of the secondary fibres of this genus are greater than those of *Spirelytha petaliformis* but in both of them a tertiary layer occurs.

MacKinnon (1974) observed that the spines of *Phricodothyris* sp. consist entirely of primary layer, whereas in the examined specimens the spines are not preserved.

Family *Martiniidae* Waagen, 1883

Genus *Martinia* M'Coy, 1844

Martinia tschernyschewi Grunt, 1973

Pl. 6, fig. 3-5

Material. One ventral valve (MPUM6931) has been analysed along longitudinal section.

Description. The primary layer is not preserved. The secondary layer consists of fibres inclined at large angle to the external surface of the valve; fibres show a subrhomboidal outline in cross section and are 16-24 μm wide. In addition secondary layer fibres show a prominent depositional banding (Pl. 6, fig. 4, 5). The periodicity of the depositional banding is about 3-4 μm.

Discussion. A badly altered *Martinia* was analysed by MacKinnon (1974) who recognized a secondary layer and a thick tertiary layer. No clear evidence of a tertiary layer was found in the specimen of *M. tschernyschewi* under study.

Genus *Mentzelia* Quenstedt, 1871

Mentzelia mentzeli (Dunker, 1851)

Pl. 6, fig. 6-8

Material. Two complete specimens (MPUM6932, MPUM6933) have been analysed: one (MPUM6933) was found to be completely recrystallized, the other was studied along longitudinal section.

Description. The primary layer has not been observed. The secondary layer is 200-500 μm thick, with maximum thickness near the umbo. This layer consists of short, flattened fibres aligned parallel to the external surface of the valve, with spatulate terminal faces. In cross section the secondary fibres show a flattened keel and saddle profile. The thickness of the fibres is 2-4 μm and their width is about 8-14 μm.

The tertiary layer is probably present in the ventral valve in a restricted area near the anterior margin. Its thickness is 60 μm.

Furthermore the ultrastructure of the spiralia has been observed. Fragments of the spiralia consist of secondary layer fibres, irregular in shape and 8 μm wide. The secondary layer is surrounded by an outer layer composed of crystallites orientated with their long axes normal to the inner boundary which are the result of diagenetic overgrowth.

Conclusions.

All significant data on the ultrastructure of the twelve species analysed are depicted in Tab. 1, which enables a comparison to be made between the ultrastructural elements of the various taxa.

As can be seen in Tab. 1, the primary layer has been detected in only two of the twelve species analysed. In fact the presence and also the thickness of the primary layer strictly depends on the state of preservation of the specimens. No periodic depositional banding and lineation normal to the shell layers, such as that observed by MacKinnon (1974), was detected in the analysed specimens, probably due to diagenesis. Furthermore the dimensions of the crystallites, which constitute this layer, are similar in the two analysed species (i.e. *"R." beneckei* and *T. lyonsensis*).

On the contrary the secondary layer is always present and well preserved. The diagnostic features which characterize the secondary layer are its thickness, the shape of the transverse profile of the fibres, the width and the thickness of the fibres. As can be seen in Tab. 1 the thickness of the secondary layer shows great variability, even between the anterior and posterior parts of the shell of a single specimen (e.g. *T. stokesi*). The two species of *Tetractinella* can be differentiated also on the base of the thickness of the secondary layer, which is greater in *T. hexagonalis.*

The shape of the secondary layer fibres can be keel and saddle, diamond, rhomboidal, sub-rhomboidal, platy with two keels, sub-rectangular and irregular. This is a character which seems to be diagnostic at generic and specific level; in fact the shape of the transverse profile of the fibres is different in the analysed species of the genus *Trigonotreta* and in those of the genus *Tetractinella*. The shape of the fibres in cross section is also a discriminating feature between *E. tibetana* and *S. rajah*.

With regard to the dimensions of the fibres, three categories of width (8-11 μm; 13-20 μm; 20-30 μm) and two of thickness (2-8 μm; 10 μm) can be established (Tab. 1). The first category of width is associated with the lower interval of thickness, whereas the third category of width corresponds to the greater thickness. The second category of width is in general associated with the lower category of thickness, but in *Trigonotreta* sp. the thickness of the fibres can reach 10 μm. *Clavigera bisulcata* is the species with the widest and thickest fibres (Tab. 1).

A tertiary layer occurs in two of the twelve analysed species and generally it consists of indistinct crystals. Its thickness is about 40-60 μm. Unfortunately the number of species analysed is not sufficient to point out the real diagnostic value of this ultrastructural feature.

The occurrence of the punctae, their diameter, their density and the amount of deflection of the secondary fibres around them can act as good diagnostic ultrastructural elements, as already observed by MacKinnon (1974) and Taddei Ruggero (1981).

Also the analysis of the ultrastructure of the spiralia can provide further diagnostic data. The spiralia of *T. stokesi* consist of secondary layer fibres less wide but with about the same thickness as fibres which constitute the shell.

In conclusion the variability of the analysed ultrastructural features is too low and the number and the choice of the examined species not exaustive to establish the real diagnostic value of the ultrastructure. Nevertheless the ultrastructure of some of the analysed genera seems to agree with the data published in literature for other genera of the same family. In fact the ultrastructure of *T. stokesi, T. lyonsensis, T.* sp., *E. tibetana* and *S. rajah* is in general agreement with that previously observed for the Family Spiriferidae by MacKinnon (1974) and the ultrastructure of the examined specimens of the genus *Tetractinella* is similar to that described for the Family Diplospirellidae by MacKinnon (1974) and Taddei Ruggero (1981). Furthermore in this work ultrastructure seems to play a role in the differentiation and determination of the species. As pointed out above the three analysed species of the genus *Trigonotreta* and the two of the genus *Tetractinella* can be differentiated also on the basis of shell ultrastructure.

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PLATE 1

Fig. 1 - *Clavigera bisulcata* Hector. Longitudinal section of a complete specimen (MPUM6907) showing short secondary layer fibres wedging to the shell exterior.

Fig. 2 - *Clavigera bisulcata* Hector. Longitudinal section of a complete specimen (MPUM6907) showing rhomboidal profile of the secondary layer fibres.

Fig. 3 - *Tetractinella trigonella* von Schlotheim. Transverse section of a complete specimen (MPUM6908) showing characteristic keel & saddle profiles of secondary layer fibres. The shell exterior is toward bottom left of micrograph.

Fig. 4 - *Tetractinella trigonella* von Schlotheim. Transverse section of a complete specimen (MPUM6908) showing a panoramic view of the organization of the secondary layer fibres with keel & saddle transverse profiles. The shell exterior is at the top.

Fig. 5 - *Tetractinella hexagonalis* Loretz. Transverse section of a complete specimen (MPUM6910) showing rhomboidal profile of the fibres of the secondary layer.

Fig. 6 - *Tetractinella hexagonalis* Loretz. Transverse section of a complete specimen (MPUM6910) showing oblique sections of the secondary layer fibres.

Fig. 7 - *Tetractinella hexagonalis* Loretz. Transverse section of a complete specimen (MPUM6909) showing diamond-shaped terminal faces of the fibres of the secondary layer.

Fig. 8 - *Tetractinella hexagonalis* Loretz. Transverse section of a complete specimen (MPUM6909) showing the diamond-shaped terminations of the secondary layer fibres at higher magnification.

PLATE 2

Fig. 1 - "*Retzia*" *beneckei* Bittner. Transverse section of a ventral valve (MPUM6913) showing primary and secondary layer along a fold. The secondary layer fibres are deflected around punctae, which coalesce towards the interior. The external surface of the shell is at the top of the micrograph.

Fig. 2 - "*Retzia*" *beneckei* Bittner. Transverse section of a ventral valve (MPUM6913) showing primary layer (below) and secondary layer (above) in detail, along a sulcus. The primary layer consists of crystallites aligned normal to the isotopic boundary with the secondary layer.

Fig. 3 - "*Retzia*" *beneckei* Bittner. Longitudinal section of a complete specimen (MPUM6912) showing outward deflection of secondary layer fibres around punctae. (Exterior of the shell toward bottom right of micrograph).

Fig. 4 - "*Retzia*" *beneckei* Bittner. Transverse section of a ventral valve (MPUM6913) showing roughly keel & saddle profile of the fibres of the secondary layer.

Fig. 5 - "*Retzia*" *beneckei* Bittner. Longitudinal section of a complete specimen (MPUM6912) showing closely spaced disposition of the punctae and deflection of the secondary layer fibres around them.

Fig. 6 - "*Retzia*" *beneckei* Bittner. Transverse section of a ventral valve (MPUM6913) showing the orientation of secondary layer fibres along a fold, sub-parallel to the shell exterior. An unusual cluster of fibres can be observed at bottom right.

Fig. 7 - "*Retzia*" *beneckei* Bittner. Longitudinal section of a complete specimen (MPUM6912) showing oblique-transverse sections of the punctae.

Fig. 8 - "*Retzia*" *beneckei* Bittner. Longitudinal section of a complete specimen (MPUM6912) (margin of the ventral valve) showing backwards convolutions of the secondary layer fibres at the anterior margin of the shell, due to periodic phases of retraction of the mantle edge. The external surface of the shell is bottom right.

PLATE 3

Fig. 1 - "*Retzia*" *beneckei* Bittner. Longitudinal section of a complete specimen (MPUM6912) (margin of the ventral valve) showing convolutions of the secondary layer fibres at the anterior margin in detail.

Fig. 2 - "*Retzia*" *beneckei* Bittner. Longitudinal section of a complete specimen (MPUM6912) (margin of the ventral valve) showing cyclicity and arrangement of the secondary layer fibres and of the

punctae at the margins of the shell, due to alternating phases of growth and of pause during the secretion of the shell. The circular sections of punctae along a longitudinal section of the shell testify for an unusual orientation of punctae at the anterior margin.

Fig. 3 - *Trigonotreta stokesi* Koenig. Longitudinal section of a ventral valve (MPUM6915) showing longitudinal sections of secondary layer fibres.

Fig. 4 - *Trigonotreta stokesi* Koenig. Longitudinal section of a ventral valve (MPUM6915) showing spatulate terminal faces of the fibres of the secondary layer.

Fig. 5 - *Trigonotreta stokesi* Koenig. Transverse section of a complete specimen (MPUM6914) showing smooth keel & saddle profile of the secondary layer fibres.

Fig. 6 - *Trigonotreta stokesi* Koenig. Transverse section of a complete specimen (MPUM6914) showing fragments of the spiralia.

Fig. 7 - *Trigonotreta stokesi* Koenig. Transverse section of a complete specimen (MPUM6914) showing secondary layer fibres of the spiralia.

Fig. 8 - *Trigonotreta lyonsensis* Archbold & Thomas. Transverse section of a ventral valve (MPUM6916) showing primary and secondary layers below a sulcus. The primary layer consists of crystallites normal to the isopic boundary with the secondary layer. The fibres of the secondary layer are oriented sub-parallel to the shell exterior.

PLATE 4

Fig. 1 - *Trigonotreta lyonsensis* Archbold & Thomas. Transverse section of a ventral valve (MPUM6916) showing profile of the secondary layer fibres, sometimes with two keels, along a rib. A diagenetic effect may be present.

Fig. 2 - *Trigonotreta lyonsensis* Archbold & Thomas. Micrograph taken along the external surface of a ventral valve (MPUM6916) showing fibres of the secondary layer with two keels.

Fig. 3 - *Trigonotreta lyonsensis* Archbold & Thomas. Transverse section of a ventral valve (MPUM6916) showing convolutions of the secondary layer fibres due to re-orientation of the fibres away from the margins.

Fig. 4 - *Trigonotreta lyonsensis* Archbold & Thomas. Transverse section of a ventral valve (MPUM6916) showing secondary and tertiary layers. The shell interior is at the bottom.

Fig. 5 - *Trigonotreta* sp. Longitudinal section of a ventral valve (MPUM6918) showing secondary layer fibres orthodoxly stacked sub-parallel to the valve exterior.

Fig. 6 - *Trigonotreta* sp. Fracture surface of the shell of a ventral valve (MPUM6918) showing secondary layer fibres with sub-rhomboidal profile.

Fig. 7 - *Trigonotreta* sp. Transverse section of a ventral valve (MPUM6919) showing sub-rhomboidal profile of the secondary layer fibres.

Fig. 8 - *Trigonotreta* sp. Transverse section of a ventral valve (MPUM6919) showing a detail of the sub-rhomboidal-shaped secondary layer fibres.

PLATE 5

Fig. 1 - *Elivina tibetana* (Diener). Longitudinal section of a ventral valve (MPUM6921) showing long and thin fibres of the secondary layer, partially recrystallised. The interior of the valve is on the left side of the micrograph.

Fig. 2 - *Elivina tibetana* (Diener). Longitudinal section of a ventral valve (MPUM6921) showing secondary layer fibres sub-parallel to the external surface of the valve.

Fig. 3 - *Elivina tibetana* (Diener). Longitudinal section of a ventral valve (MPUM6921) showing secondary layer fibres in cross section. They show an irregular profile due to partial fusion of adjacent fibres and recrystallisation.

Fig. 4 - *Spiriferella rajah* (Salter). Longitudinal section of a ventral valve (MPUM6924) showing thin orthodoxly stacked fibres of the secondary layer.

Fig. 5 - *Spiriferella rajah* (Salter). Micrograph taken along the external surface of a ventral valve (MPUM6924). Secondary layer fibres showing a sharp and pointed carina.

Fig. 6 - *Spiriferella rajah* (Salter). Longitudinal section of the ventral valve (MPUM6924). Transverse section of the secondary layer fibres showing a rhomboidal profile.

Fig. 7 - *Spirelytha petaliformis* (Pavlova). Oblique-transverse section of a dorsal valve (MPUM6929) showing fibres of the secondary layer with an irregular, sometimes platy profile.

Fig. 8 - *Spirelytha petaliformis* (Pavlova). Oblique-longitudinal section of a ventral valve (MPUM6930) showing long fibres of the secondary layer.

PLATE 6

Fig. 1 - *Spirelytha petaliformis* (Pavlova). Oblique-longitudinal section of a ventral valve (MPUM6930) showing secondary layer (left) and probable tertiary layer (right) with indistinct crystalls.

Fig. 2 - *Spirelytha petaliformis* (Pavlova). Oblique-longitudinal section of a ventral valve (MPUM6930) showing thin fibres of the secondary layer below the scar of attachment of a spine.

Fig. 3 - *Martinia tschernyschewi* Grunt. Longitudinal section of a ventral valve (MPUM6931) showing secondary layer fibres, stacked at high angle to the external surface of the valve (top left).

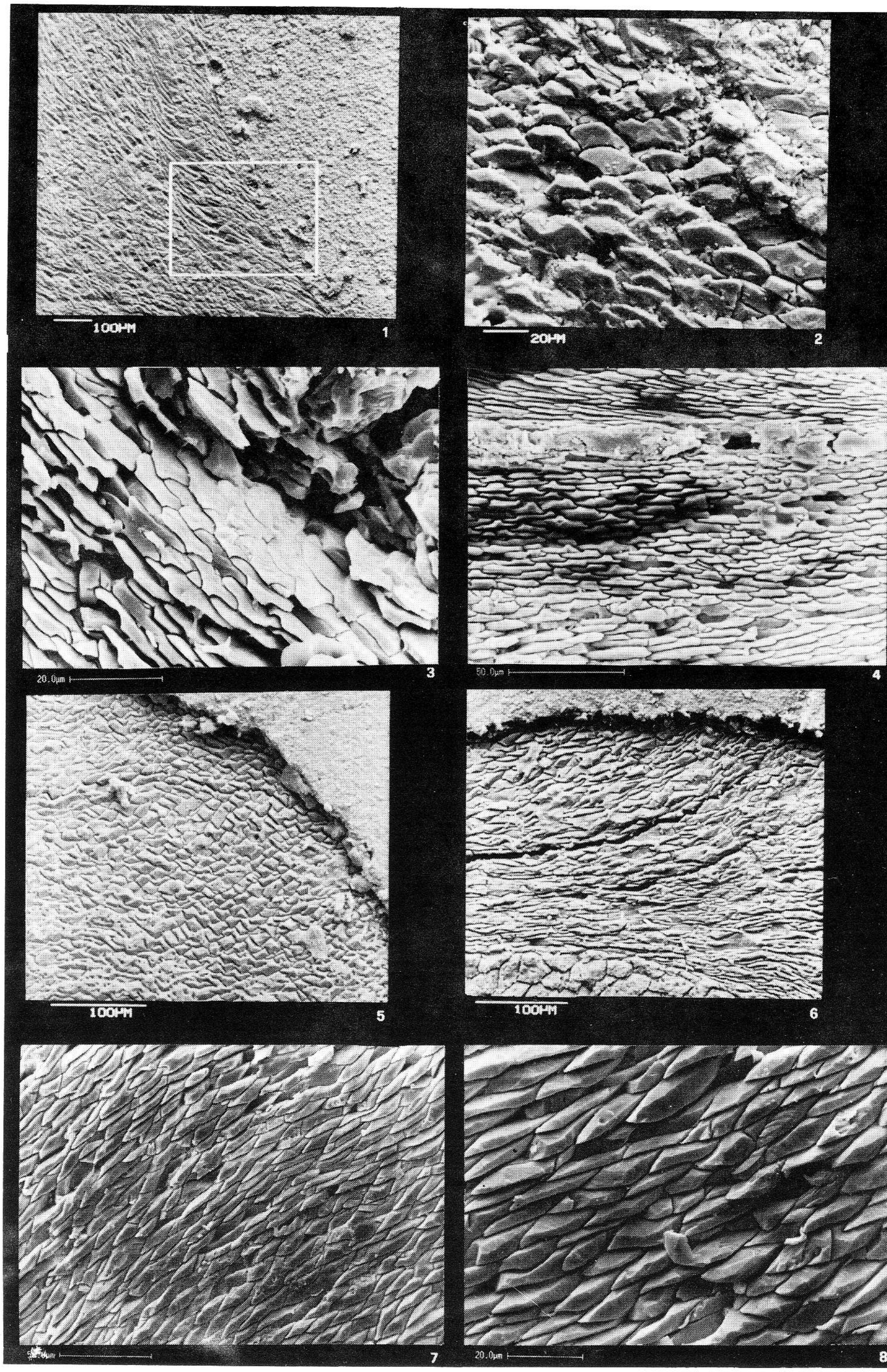
Fig. 4 - *Martinia tschernyschewi* Grunt. Longitudinal section of a ventral valve (MPUM6931) showing prominent depositional banding of the secondary layer fibres.

Fig. 5 - *Martinia tschernyschewi* Grunt. Longitudinal section of a ventral valve (MPUM6931) showing detail of the depositional banding.

Fig. 6 - *Mentzelia mentzeli* (Dunker). Longitudinal section of a complete specimen (MPUM6932) showing keel & saddle profile of the fibres of the secondary layer.

Fig. 7 - *Mentzelia mentzeli* (Dunker). Longitudinal section of a complete specimen (MPUM6932) showing secondary layer (left) and tertiary layer (right).

Fig. 8 - *Mentzelia mentzeli* (Dunker). Longitudinal section of a complete specimen (MPUM6932) showing fragments of the spiralia consisting of secondary layer fibres surrounded by perpendicular crystallites, which are probably diagenic overgrowth of sparry calcite.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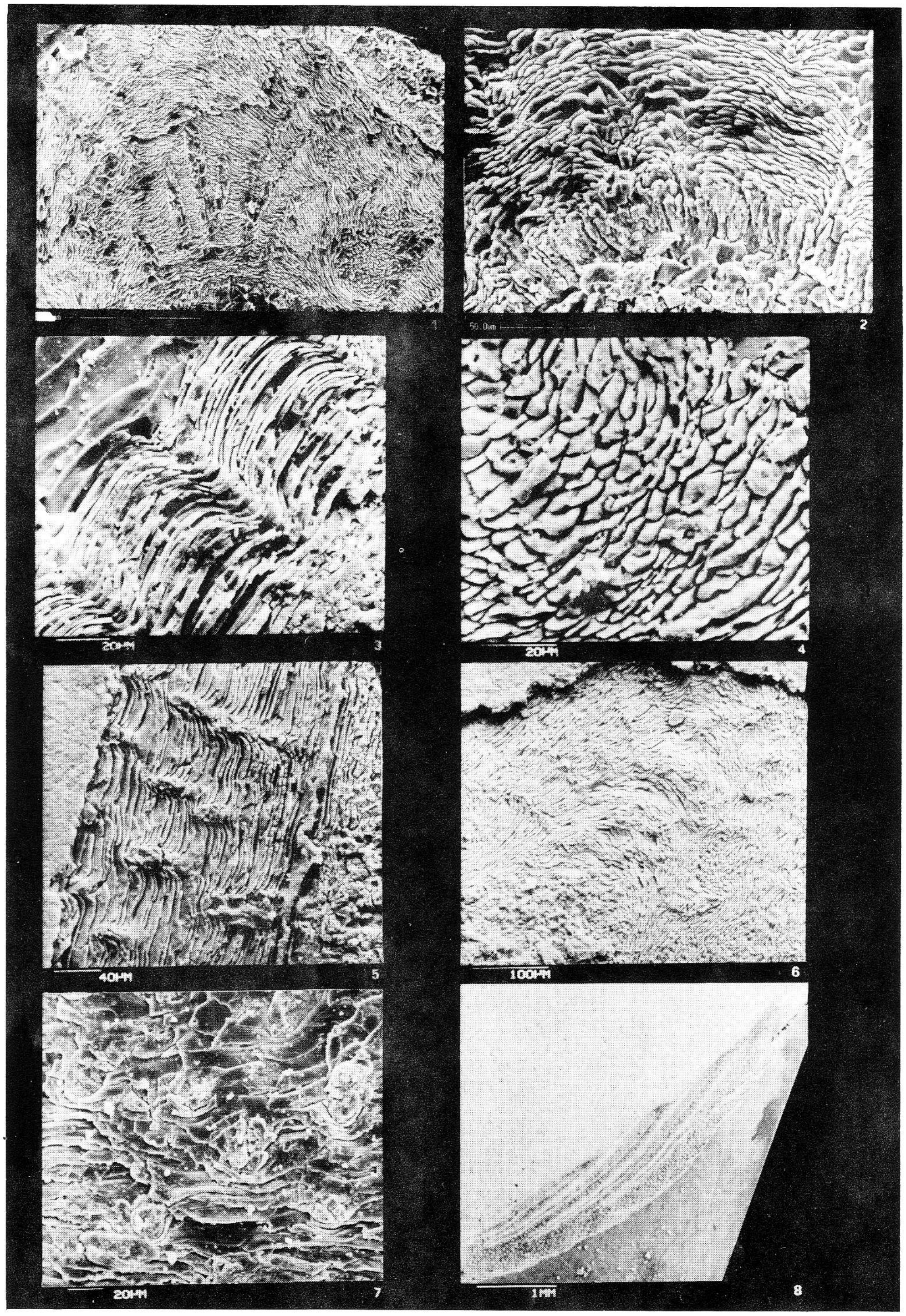
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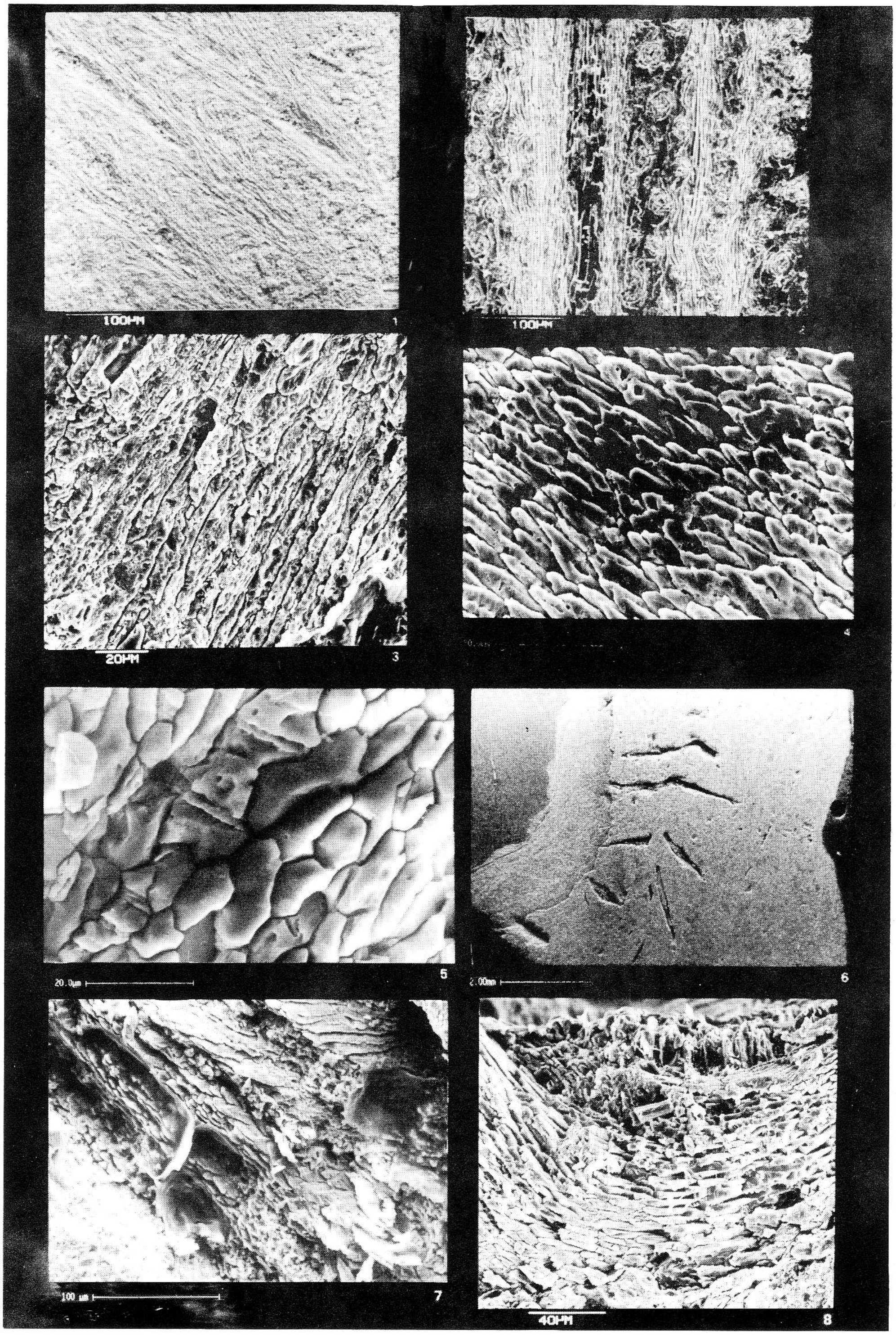
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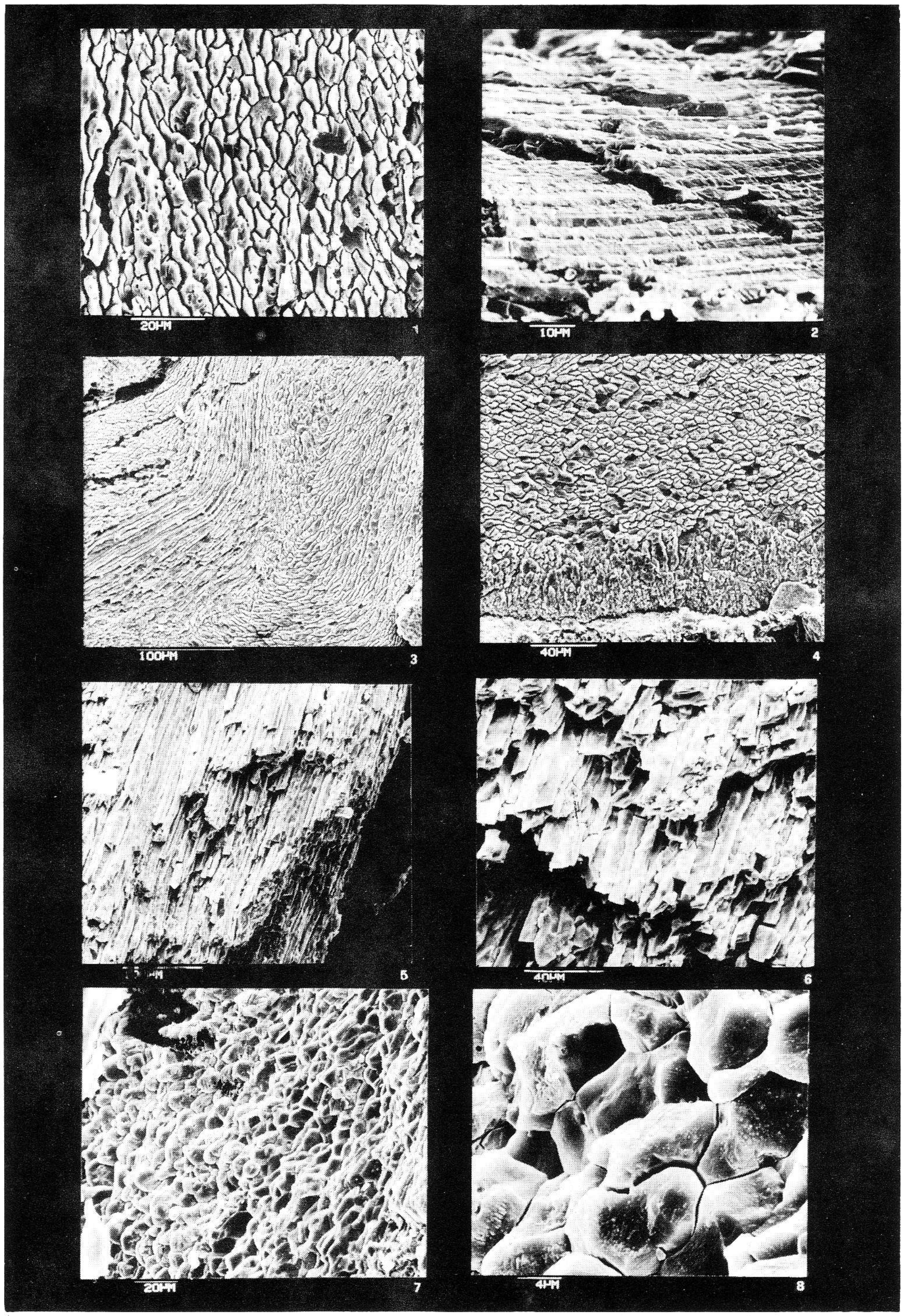
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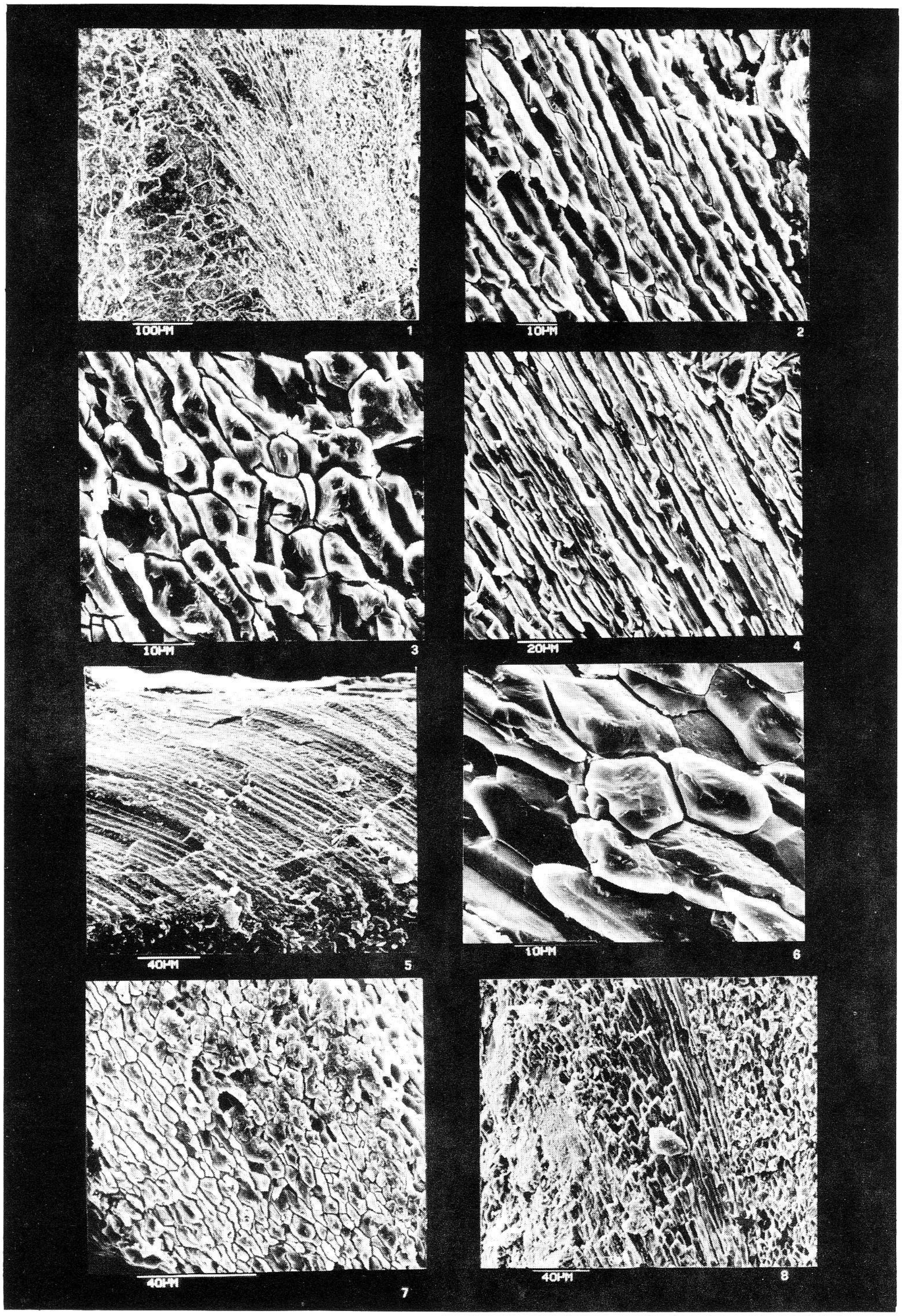
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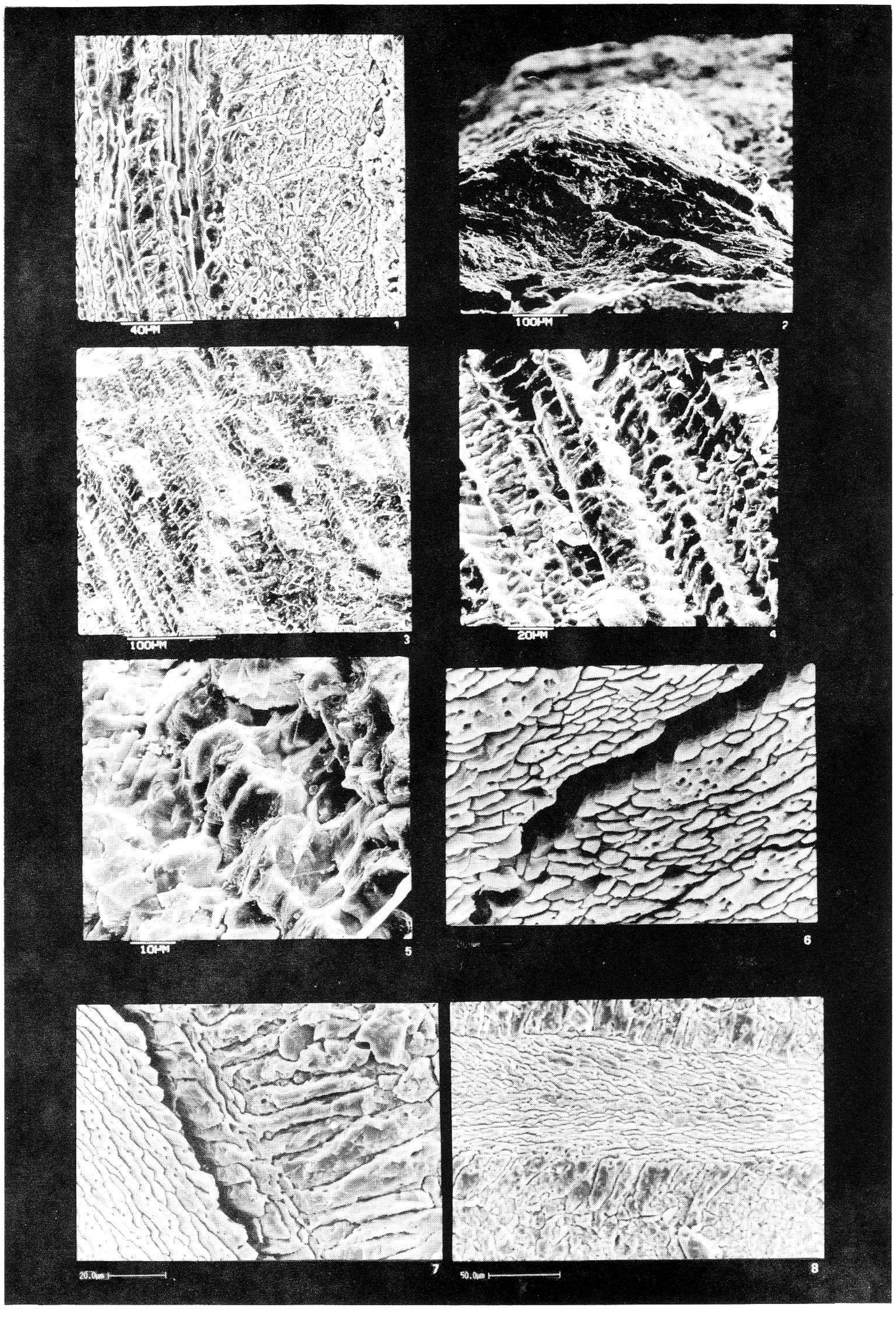
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