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CONCLUSIONS

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Pp. 253–294; 15 *Plates*, 33 *Text-figures*, 22 *Tables*

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THE BULLETIN OF THE BRITISH MUSEUM (NATURAL HISTORY), *instituted in* 1949, *is issued in five series corresponding to the Departments of the Museum, and an Historical series.*

Parts will appear at irregular intervals as they become ready. Volumes will contain about three or four hundred pages, and will not necessarily be completed within one calendar year.

In 1965 *a separate supplementary series of longer papers was instituted, numbered serially for each Department.*

This paper is Vol. 22, *No.* 9 *of the Zoological series. The abbreviated titles of periodicals cited follow those of the World List of Scientific Periodicals.*

World List abbreviation
Bull. Br. Mus. nat. Hist. (Zool.).

TRUSTEES OF
THE BRITISH MUSEUM (NATURAL HISTORY)

Issued 16 *March,* 1973 *Price* £4·50

THE SHELL STRUCTURE AND MINERALOGY OF THE BIVALVIA

II. LUCINACEA — CLAVAGELLACEA CONCLUSIONS

By J. D. TAYLOR, W. J. KENNEDY & A. HALL

ABSTRACT

THE shell microstructure of twenty six remaining bivalve superfamilies is described with the aid of acetate peels and electronmicroscopy. In the order Heterodonta most shells consist of outer crossed-lamellar and an inner complex crossed-lamellar layers. Three superfamilies, the Lucinacea, Tellinacea and Veneracea have all, or some members, with an additional outer layer of composite prismatic structure. Minor variations consist of the occurrence of homogeneous structure in many families, resulting from a reduction in grain size and loss of crystal form in each structure. The order Myoida is more varied with crossed-lamellar and complex crossed-lamellar shells in the Corbulidae, Gastrochaenacea and some Pholadacea. The Hiatellacea are mainly all homogeneous but *Panopea* has a three layered shell consisting of an outer simple aragonite prismatic layer and middle and inner homogeneous layers. A very similar outer prismatic layer is found in some Pholadacea. In the Anomalodesmata two shell structure conditions are found, either a three layered shell, consisting of an outer layer of simple aragonite prisms and two nacreous layers or two homogeneous layers.

Twelve shell structure characters can be used as an aid to superfamilial classification; but they must be used in conjunction with other characters and geological history. The shell structure characters have been superimposed upon a phylogenetic tree derived from many characters; the points of variance and similarity of shell structure with this phylogeny are discussed in turn. It is suggested that the Arcoida may be more closely related to the Heterodonta than the Pteriomorphia. A 'pholadomyacean' stock has been in existence since the Ordovician and it is probable that both the Myoida and Anomalodesmata may be derived from this stock.

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INTRODUCTION

This is the continuation to Taylor, Kennedy & Hall (1969) in which we reviewed Bivalve shell structure, mineralogy and shell formation, and documented these features in the superfamilies Nuculacea to Trigonacea. Here we describe the distribution of structures in the remaining superfamilies and discuss the importance of shell structures in the classification of the Class.

SYSTEMATIC DESCRIPTIONS

Since the publication of the first part of this work was published the Treatise of Invertebrate Palaeontology, Part N Bivalvia has appeared, which uses a system of classification slightly modified from that of Newell (1965) which we used previously. As the 'Treatise' classification will stand for some time we have used it for the arrangement of superfamilies described below.

Sub Class *HETERODONTA*

Order VENEROIDA

LUCINACEA

(Plate 1, figs 1, 2 & 5; Text-figs 1 & 2)

Fifteen species of this family have been examined mineralogically and ten structurally. The shell is aragonitic throughout.

Three main shell layers are present in all the species examined. There is an outer composite prismatic layer, a middle crossed-lamellar layer, which forms much of the hinge plate and an inner complex crossed-lamellar layer which is bounded by the

TABLE I

LUCINACEA

Species	Locality	Mineralogy	Outer layer	Middle layer	Inner layer	Myostraca		Observations
						Pallial	Adductor	
Codakia punctata (Linnaeus)	Indo-Pacific	Aragonite	Composite prismatic	Crossed-lamellar	Complex crossed-lamellar	Thin, prismatic	Not seen	Thin bands of myostracal-type prisms and scattered large tubules in the inner layer
Codakia tigerina (Linnaeus)	Seychelles	Aragonite	Composite prismatic	Crossed-lamellar	Complex crossed-lamellar	Thick prismatic	Prismatic	Myostracal-type prisms build the bulk of the inner layer

Species Locality Mineralogy Outer layer Middle layer Inner layer Myostraca Pallial Adductor Observations

TABLE I

LUCINACEA

Species	Locality	Mineralogy	Outer layer	Middle layer	Inner layer	Myostraca		Observations
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Codakia punctata (Linnaeus)	Indo-Pacific	Aragonite	Composite prismatic	Crossed-lamellar	Complex crossed-lamellar	Thin, prismatic	Not seen	Thin bands of myostracal-type prisms and scattered large tubules in the inner layer
Codakia tigerina (Linnaeus)	Seychelles	Aragonite	Composite prismatic	Crossed-lamellar	Complex crossed-lamellar	Thick prismatic	Prismatic	Myostracal-type prisms build the bulk of the inner layer, complex-crossed lamellar structure is best developed below the umbonal regionds, where it contains fine ban of myostracal-type prisms and scattered tubules
Divaricella quadrisulcata (d'Orbigny)	W. Indies	Aragonite	Composite prismatic	Crossed-lamellar	Complex crossed-lamellar	Thin, prismatic	Not seen	Extensive layers of myostracal-type prisms in the inner layer. Tubules may be present
Fimbria lamellosa (Lamarck)	Eocene, Calcaire Grossier, France	Aragonite	Composite prismatic	Crossed-lamellar	Complex crossed-lamellar	Thin, prismatic	Not seen	Fine bands of myostracal-type prisms in the inner layer
Lucina columbella (Link)	Cape Verde	Aragonite	Composite prismatic	Crossed-lamellar	Complex crossed-lamellar	Thick, prismatic	Not seen	Prominent layers of myostracal-type prisms in the inner layer
Lucina fijiensis Smith	Sarawak Borneo	Aragonite	Composite prismatic	Crossed-lamellar	Complex crossed-lamellar	Thin, prismatic	Not seen	Layers of myostracal-type prisms beneath umbo
Lucina pila Reeve	Oshima Japan	Aragonite	Composite prismatic	Crossed-lamellar	Complex crossed-lamellar	Well-developed prismatic	Not seen	Extensive development of myostracal-type prisms in the inner layer
Lucina borealis (Linnaeus)	Galway	Aragonite	Composite prismatic	Crossed-lamellar	Complex crossed-lamellar	Thin, prismatic	Not seen	Extensive layer of myostracal-type prisms in the inner layer form the bulk of the marginal parts of this layer
Lucinopsis undata Forbes & Hanley	Tor Bay, England	Aragonite	Composite prismatic	Crossed-lamellar	Complex crossed-lamellar	Well-developed, prismatic	Not seen	Extensive development of myostracal pillars in the inner layer
Corbis fimbriata Cuvier	East Indies	Aragonite	Composite prismatic	Crossed-lamellar	Complex crossed-lamellar	Thin, prismatic	—	
Ctena divergens (Reeve)	Seychelles	Aragonite	Composite prismatic	Crossed-lamellar	Complex crossed-lamellar	Thin, prismatic	—	
Divaricella eburnea (Reeve)	Ecuador	Aragonite	Composite prismatic	Crossed-lamellar	Complex crossed-lamellar	Thin, prismatic	—	
Loripes lucinalis (Link)	Malta	Aragonite	Composite prismatic	Crossed-lamellar	Complex crossed-lamellar	Thin, prismatic	—	
Lucinisca liana (Pilsbry)	Ecuador	Aragonite	Composite prismatic	Crossed-lamellar	Complex crossed-lamellar	Thin, prismatic	—	
Thyasira sp.		Aragonite	Composite prismatic	Crossed-lamellar	Complex crossed-lamellar	Thin, prismatic	—	

Species	Locality	Mineralogy	Outer layer	Middle layer	Inner layer	Myostraca		Observations
						Pallial	Adductor	

trace of the pallial line. The outer composite prismatic layer is usually very thin but forms the ribs when present. The first order prisms lie with their long axes arranged radially to the umbo (Plate 1, fig. 1). In the middle crossed-lamellar layer the first order lamels are arranged with their long axes concentric to the shell margin. The lamels are often very fine when compared with some groups such as the Arcacea or Limopsacea but similar to those in the Carditacea and Astartacea. A prismatic pallial myostracum is present in all species examined, although variable in thickness. The inner shell layer is the most variable; complex crossed-lamellar structure is present in all species (Plate 1, figs 2 & 5) but varies in extent. The rest of the inner layer is made up of myostracal prisms which may occur as sheets, which alternate with the complex crossed-lamellar structure (*Lucina fijiensis*) or as large blocks (*Codakia tigerina*). These sheets of myostracal prisms may represent periods of temporary mantle attachment.

Scattered large tubules are present in the inner layer of *Codakia punctata*; tubules are also present in *Divaricella quadrisulcata* and *Codakia tigerina*.

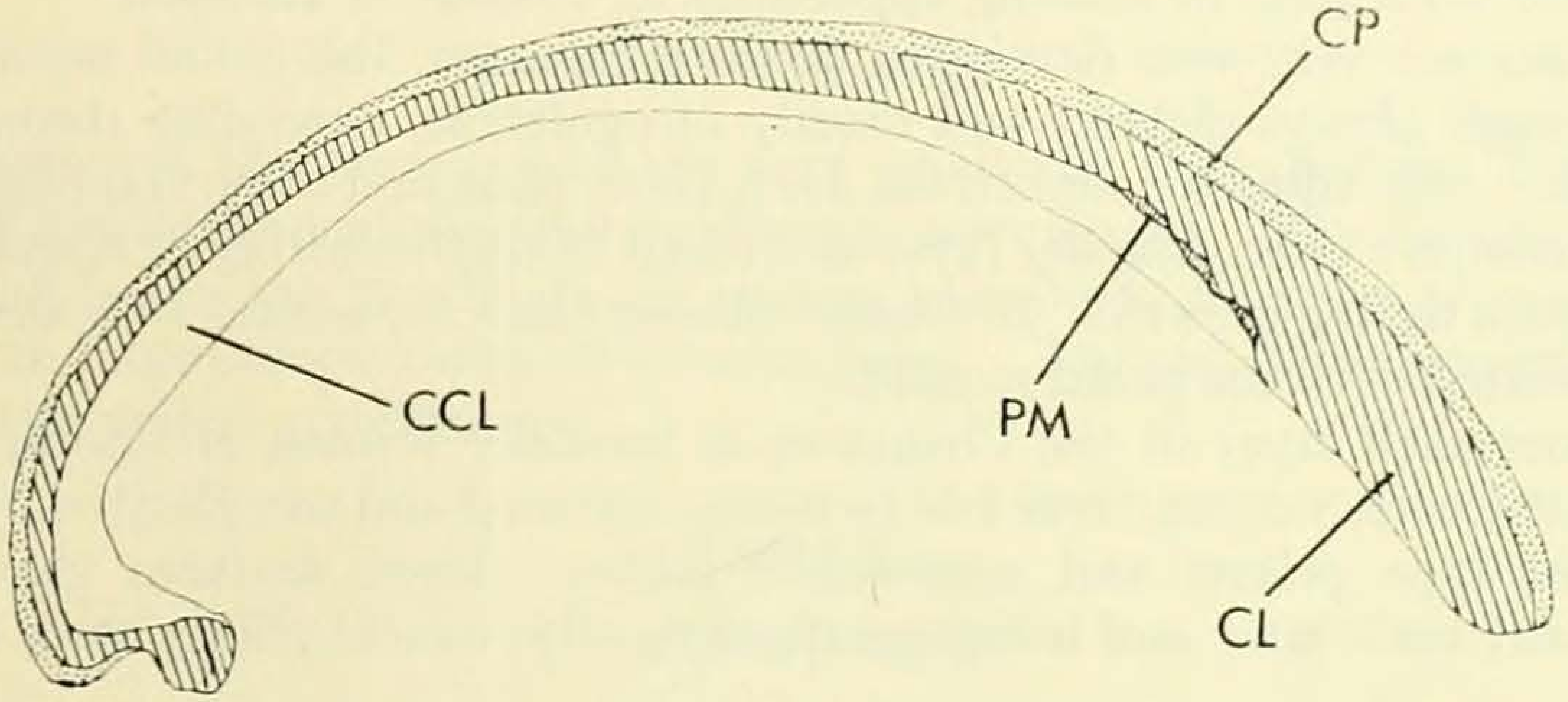

FIG. 1. Radial section of *Lucina columbella*. CP = composite prismatic, CL = crossed-lamellar, CCL = complex crossed-lamellar, PM = pallial myostracum.

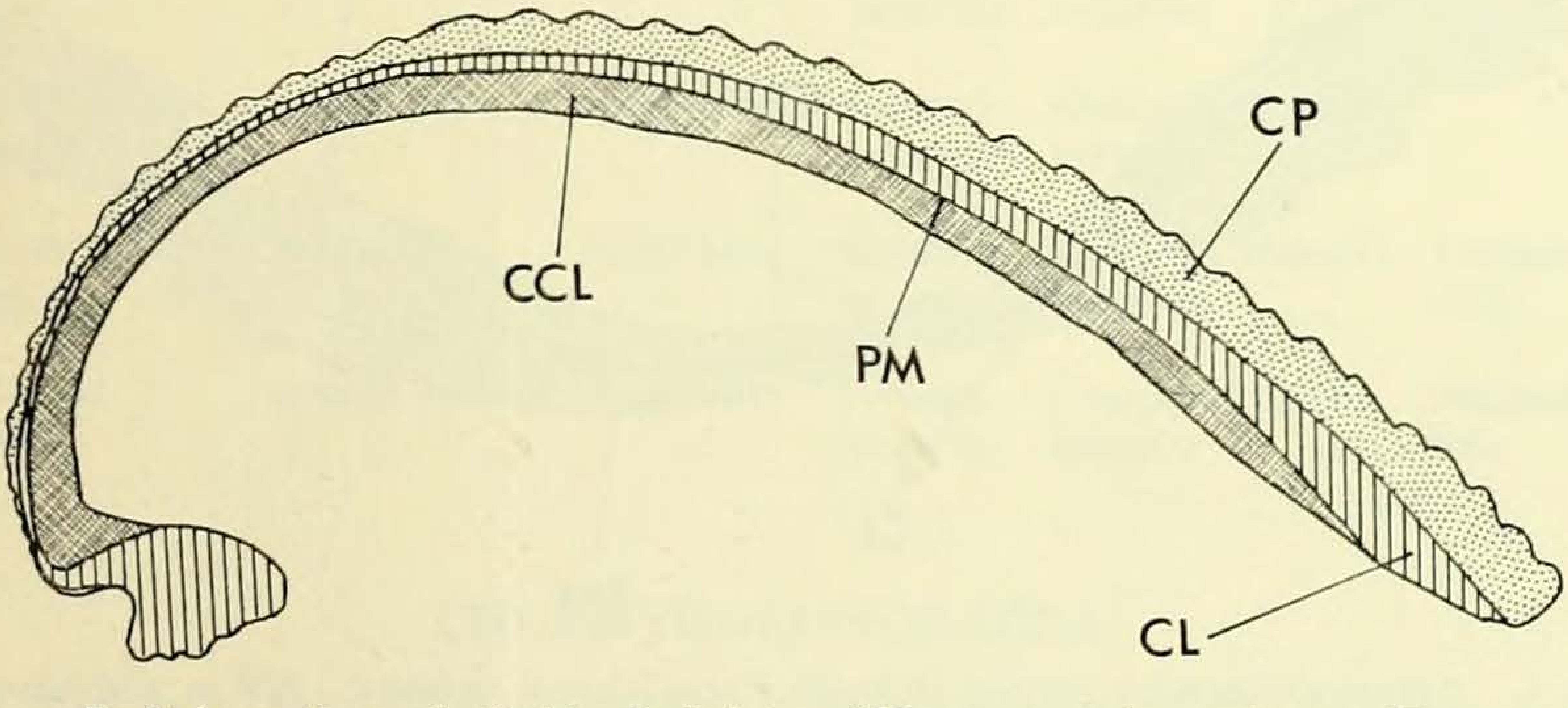

FIG. 2. Radial section of *Corbis fimbriata*. CP = composite prisms, CL = crossed-lamellar, CCL = complex crossed-lamellar, P = pallial myostracum.

CHAMACEA

(Text-fig. 3)

The shell structure, anatomy, and evolution of the Chamacea have been discussed in some detail elsewhere (Kennedy, Morris & Taylor, 1970), as has the shell structure and mineralogy of the anomalous species *Chama pellucida* (Taylor & Kennedy, 1969).

Amongst Recent species the shell is aragonitic throughout, with the exceptions of *Chama pellucida* and *C. exogyra*, which contain substantial amounts of calcite in a distinct outer layer. Two fossil species *Chama gryphina* (Miocene) and *Chama haueri* (Turonian) show traces of calcite but there is no evidence that this was an original feature of the shell.

In all wholly aragonitic species examined, two main shell layers are present (text-fig. 3). There is an outer, crossed-lamellar layer and an inner complex crossed-lamellar layer bounded by the trace of the pallial line. In the outer layer the first order lamels are arranged concentrically to the shell margin; in many specimens part of the outer layer may be missing apparently as a result of abrasion.

Myostraca are very well developed in the Chamacea, the pallial myostracum is thin, although always distinct and readily recognizable, extending throughout the hinge area. The adductor myostraca form thick pads and often interdigitate with the inner complex cross-lamellar layer as a result of slight shifting of attachment and body position during growth. In *Chama iostoma* other myostraca were seen presumably associated with the pedal muscles.

The inner shell layer of the Chamacea is basically formed of complex crossed-lamellar structure, varying from fine to coarse textured and complicated by sheets of myostracal type prisms and myostracal pillars. These features show varying development both inter and intra specifically. Myostracal pillars often arise from

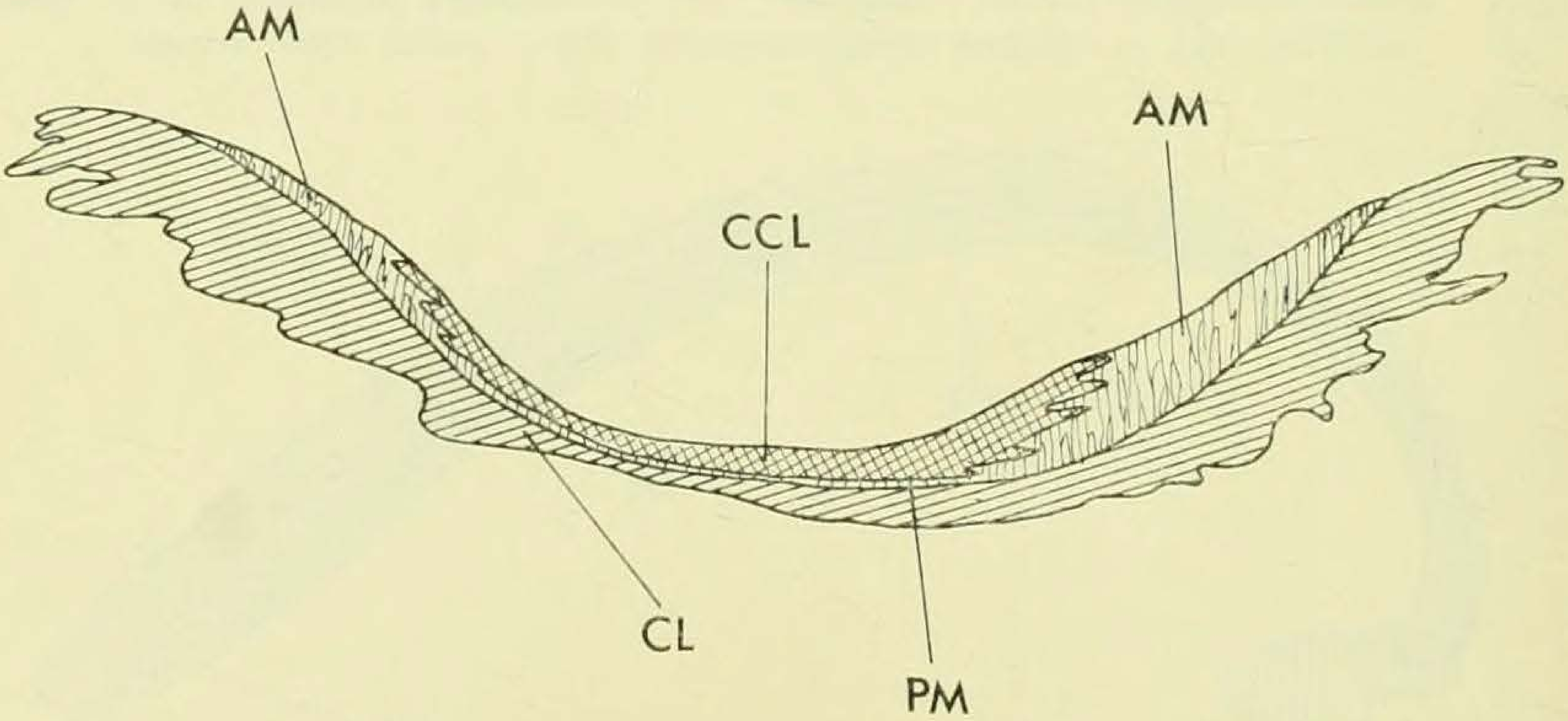

FIG. 3. Anterior-posterior section through *Pseudochama radians*. AM = adductor myostracum, PM = pallial myostracum, CL = crossed-lamellar, CCL = complex crossed-lamellar.

pallial and adductor myostraca. In *Chama spondyliodes* myostracal pillars are also present in parts of the outer crossed-lamellar layer. Seen on inner shell surface myostracal prisms are often arranged in rows radial from the umbo.

The Chamacea are markedly tubulate but there is much variation in the abundance and distribution of these structures which are usually confined to the inner layer.

Chama pellucida and *C. exogyra* differ from wholly aragonitic forms in possessing an outer prismatic calcite layer of unusual structure described by Taylor & Kennedy (1969). The remarkable occurrence of calcite was first noticed by Lowenstam (1954) but he considered (1964) that the outer crossed-lamellar layer of tropical species had changed to calcite prisms in the temperate *C. pellucida*. He used this example as evidence in the general temperature/mineralogy trends he demonstrated for invertebrate skeleta. However other temperate species of *Chama* seem to be wholly aragonitic.

A table of the shell structure characters of the thirty species of *Chama* examined will be found in Kennedy *et al* (1970, p. 390).

LEPTONACEA

Most species of this superfamily are very small and thin shelled. Four species were examined mineralogically and by electron-microscopy. The shell is aragonitic.

Two shell layers are present in all species examined; an outer crossed-lamellar layer and an inner complex crossed-lamellar layer. The two layers are separated by the prismatic pallial myostracum.

TABLE 2

LEPTONACEA

Species	Locality	Mineralogy	Outer layer	Inner layer	Pallial myostracum
Kellia suborbicularis Montagu	Britain	Aragonite	Crossed-lamellar	Complex crossed-lamellar	Prismatic, thin
Kellia pustula Deshayes	Indian Ocean	Aragonite	Crossed-lamellar	Complex crossed-lamellar	
Scintilli oweni Deshayes	Karachi	Aragonite	Crossed-lamellar	Complex crossed-lamellar	Prismatic, thin
Scintilla rosea Deshayes	Indian Ocean	Aragonite	Crossed-lamellar	Complex crossed-lamellar	Prismatic, thin

CHLAMYDOCONCHACEA

Lack of material prevented examination of specimens of this peculiar monogeneric superfamily which have internal shells contained within mantle sacs.

CYAMIACEA

Three species of this small superfamily were examined structurally and mineralogically. In all three species the shell is aragonitic and consists of two layers both of them of fine granular homogeneous structure. The layers are separated by a thin prismatic pallial myostracum.

TABLE 3

CYAMIACEA

Species	Locality	Mineralogy	Outer layer	Inner layer	Pallial myostracum
Cyamium antarcticum (Philippi)	Falkland Islands	Aragonite	Homogeneous	Homogeneous	Prismatic
Cyamium laminiferum (Lamy)	Antarctic	Aragonite	Homogeneous	Homogeneous	Prismatic
Neodavisia cobbi (Cooper & Preston)	Falkland Islands	Aragonite	Homogeneous	Homogeneous	

CARDITACEA

(Plate 2, figs 4, 5 & 6; text-figs 4 & 5)

Fifteen species have been examined mineralogically and eleven structurally. The shell is aragonitic throughout.

Two main shell layers are present, an outer crossed-lamellar layer which forms the bulk of the hinge and teeth, and an inner complex crossed-lamellar layer which is bounded by the trace of the pallial myostracum. The first order lamels of the outer layer are very fine and are mostly arranged concentrically, but in some species a reflected shell margin causes the lamels to appear to have a radial alignment (Plate

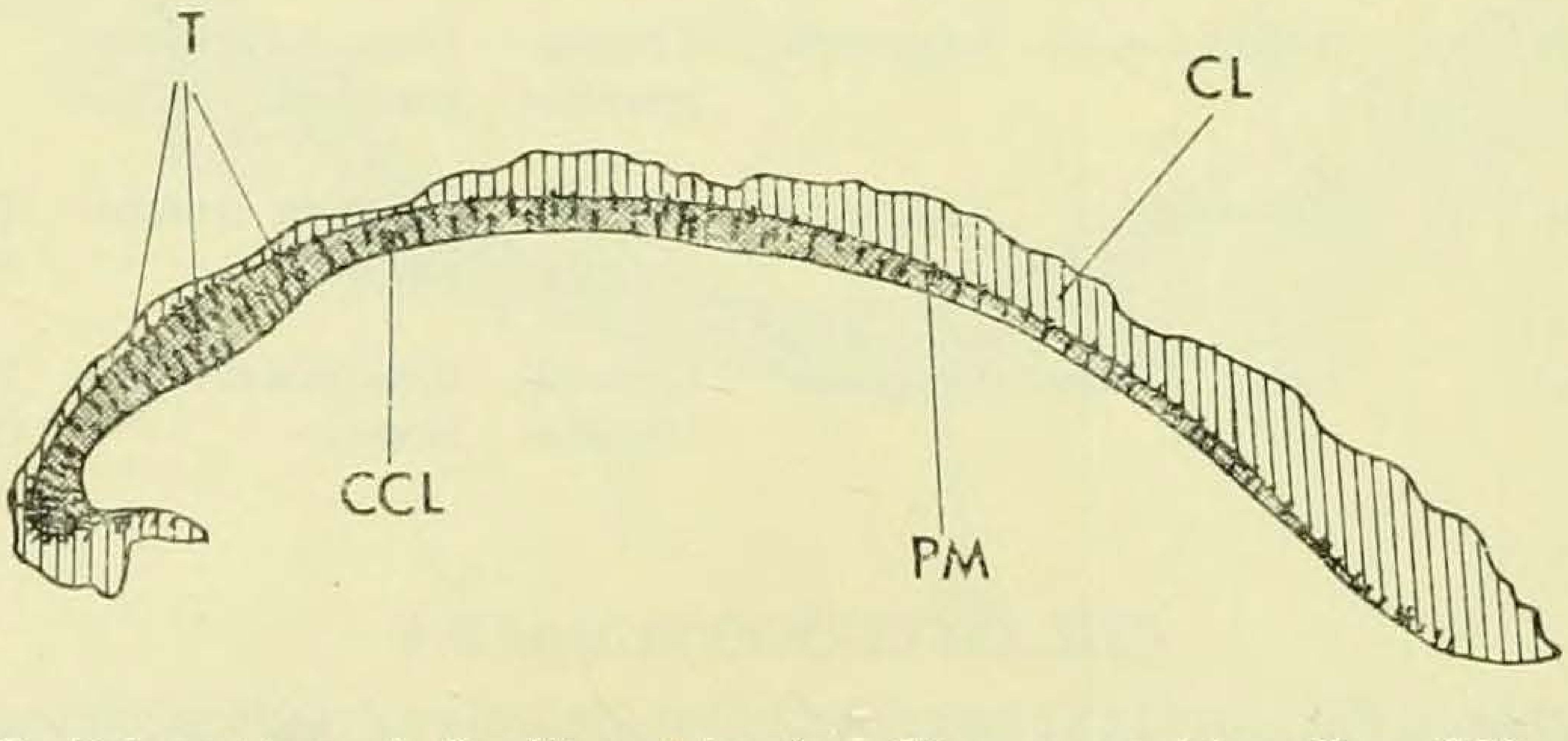

FIG. 4. Radial section of *Cardita variegata*. CL = crossed-lamellar, CCL = complex crossed-lamellar, PM = pallial myostracum, T = tubules.

TABLE 4

CARDITACEA

Species	Locality	Mineralogy	Outer layer	Inner layer	Myostraca		Observations
					Pallial	Adductor	
Cardita australis Lamarck	Auckland, New Zealand	Aragonite	Crossed-lamellar	Complex crossed-lamellar	Not seen	Not seen	The crossed-lamellar layer is very fine. Fine tubules and prominent banding are present in the inner layer.
Cardita borealis	New England France	Aragonite	Crossed-lamellar	Complex crossed-	Thin,	Not seen	The crossed-lamellar layer is banded, with abundant fine myostracal pillars, fine prismatic bands and fine tubules
Cardita aculeata Eichwald		Argonite	Crossed-lamellar	Complex crossed-lamellar	Thin, prismatic	Not seen	
Cardita sulcata Sowerby	Eocene, Britain	Aragonite	Crossed-lamellar	Complex crossed-lamellar	Thin, prismatic	Not seen	
Thecalia concamerata (de Blainville)	S. Africa	Aragonite	Crossed-lamellar	Complex crossed-lamellar	Thin, prismatic	Not seen	
Venericor planicostata (de Blainville)	Britain	Aragonite	Crossed-lamellar	Complex crossed-lamellar	Thin, prismatic	Not seen	

TABLE 4

CARDITACEA

Species	Locality	Mineralogy	Outer layer	Inner layer	Myostraca		Observations
					Pallial	Adductor	
Cardita australis Lamarck	Auckland, New Zealand	Aragonite	Crossed-lamellar	Complex crossed-lamellar	Not seen	Not seen	The crossed-lamellar layer is very fine. Fine tubules and prominent banding are present in the inner layer.
Cardita borealis Conrad	New England	Aragonite	Crossed-lamellar	Complex crossed-lamellar	Thin, prismatic	Not seen	The crossed-lamellar layer is very fine, as is the complex crossed-lamellar layer. Fine tubules are present in the inner layer
Cardita calyculata Bruguière	Indian Ocean	Aragonite	Crossed-lamellar	Complex crossed-lamellar with myostracal pillars and bands of myostracal-type prisms	Thin, prismatic	Not seen	The crossed-lamellar layer is very fine, the complex-crossed lamellar layer has prominent banding, scattered, rather fine, myostracal layers and fine tubules
Cardita floridana Conrad	Florida	Aragonite	Crossed-lamellar	Crossed complex-lamellar	Thin, prismatic	Not seen	The structure of both layers is rather fine. There are abundant tubules in the inner layer
Cardita incrassata Sowerby	Queensland	Aragonite	Crossed-lamellar	Complex crossed-lamellar	Not seen	Not seen	The structure of both layers is rather fine. There are fine tubules in the inner layer
Cardita marmorea Dunker	Queensland	Aragonite	Crossed-lamellar	Complex crossed-lamellar	Not seen	Not seen	The structure of the crossed lamellar layer is rather fine. There are traces of fine prism layers and fine tubules in the inner layer
Cardita sowerbyi Deshayes		Aragonite	Crossed-lamellar	Complex crossed-lamellar	Thin, prismatic?	Not seen	The structure of the crossed-lamellar layer is rather fine. There are abundant myostracal pillars in the inner layer and a few in the marginal parts of the outer layer. Fine tubules are present in the inner layer
Cardita variegata (Bruguière)	Kenya	Aragonite	Crossed-lamellar	Complex crossed-lamellar	Thin, prismatic	Not seen	There are abundant myostracal pillars in the inner layer, and in the inner part of the outer layer where this lies below the inner layer. These pillars are also present throughout most of the outer layer outside the pallial line. Fine tubules in both layers
Carditamera affinis (Reeve)	Ecuador	Aragonite	Crossed-lamellar	Complex crossed-lamellar	Thin, prismatic	Not seen	The structure of the crossed-lamellar layer is rather fine. The inner layer is strikingly banded, with abundant fine tubules
Venericardia imbricata Lamarck	Calcaire Grossier, Lutetian, Dameray, France	Argaonite	Crossed-lamellar	Complex crossed-lamellar	Thin, prismatic	Not seen	The structure of the crossed-lameller layer is rather fine. The inner layer is distinctly banded, with abundant fine myostracal pillars, fine prismatic bands and fine tubules
Cardita aculeata Eichwald		Argonite	Crossed-lamellar	Complex crossed-lamellar	Thin, prismatic	Not seen	
Cardita sulcata Sowerby	Eocene, Britain	Aragonite	Crossed-lamellar	Complex crossed-lamellar	Thin, prismatic	Not seen	
Thecalia concamerata (de Blainville)	S. Africa	Aragonite	Crossed-lamellar	Complex crossed-lamellar	Thin, prismatic	Not seen	
Venericor planicostata (de Blainville)	Britain	Aragonite	Crossed-lamellar	Complex crossed-lamellar	Thin, prismatic	Not seen	

TABLE 5

CRASSATELLACEA

Species	Locality	Mineralogy	Outer layer	Inner layer	Myostraca		Observations
					Pallial	Adductor	
Crassatella antillarum Reeve	W. Indies	Aragonite	Crossed-lamellar	Homogeneous	Indistinct, thin, prismatic?	Not seen	Outer layer very finely crossed-lamellar, inner layer with conspicuous banding
Crassatella decipiens Reeve	W. Australia	Aragonite	Crossed-lamellar	Homogeneous	Indistinct, thin,	Not seen	Outer layer very finely crossed-lamellar, inner layer

Conrad		
Astarte ellipta Macgillivray	Greenland	Aragonite
Astarte quexii (d'Orbigny)	L. Lias, Blockley, Gloucs.	Aragonite

Species	Locality	Mineralogy	Outer layer	Inner layer	Myostraca		Observations
					Pallial	Adductor	

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Species	Locality	Mineralogy	Outer layer	Inner layer	Myostraca		Observations
					Pallial	Adductor	
Crassatella antillarum Reeve	W. Indies	Aragonite	Crossed-lamellar	Homogeneous	Indistinct, thin, prismatic?	Not seen	Outer layer very finely crossed-lamellar, inner layer with conspicuous banding
Crassatella decipiens Reeve	W. Australia	Aragonite	Crossed-lamellar	Homogeneous	Indistinct, thin, prismatic?	Not seen	Outer layer very finely crossed-lamellar, inner layer with conspicuous banding
Crassatella lamellosa Lamarck	Lutetian, Dameray, France	Aragonite	Crossed-lamellar	Homogeneous	Not seen	Not seen	Prominent banding in the inner layer
Crassatella radiata (Sowerby)		Aragonite	Crossed-lamellar	Homogeneous	Not seen	Not seen	
Eucrassatella gibbosa (Sowerby)	Ecuador	Aragonite	Crossed-lamellar	Homogeneous	Thin, prismatic	Thin, prismatic	Outer layer very finely crossed-lamellar, becoming homogeneous when traced inwards
Astarte borealis (Schumacher)	Greenland	Aragonite	Crossed-lamellar	Homogeneous with myostracal prisms	Thin, prismatic	—	Inner layer largely built/of myostracal-type prisms; homogeneous structure present beneath umbones only
Astarte incrassata Deshayes	Pliocene, Italy	Aragonite	Crossed-lamellar	Complex crossed lamellar with myostracal prisms	Indistinct, thin, prismatic?	Not seen	Complex crossed-lamellar structure present only beneath umbones
Astarte obliqua Sowerby	Pliocene, Britain	Aragonite	Crossed-lamellar	Homogeneous with myostracal prisms	Thin, prismatic	Not seen	Myostracal-type prisms form most of the inner layer
Astarte omalii (Jonkiere)	Pliocene, Britain	Argonite	Crossed-lamellar	Complex crossed-lamellar with myostracal prisms	Indistinct, thin, prismatic	Not seen	Inner layer mostly built of myostracal-type prisms, inter-fingering with complex-crossed lamellar structure in umbonal region
Astarte striata Sowerby	Greenland	Aragonite	Crossed-lamellar	Homogeneous with myostracal prisms	thin prismatic	—	Inner layer almost entirely built of myostracal-type prisms
Astarte sulcata (da Costa)	Pilocene, Italy	Aragonite	Crossed-lamellar	Complex crossed-lamellar with myostracal prisms	Thin, prismatic	—	Inner layer almost entirely built of myostracal-type prisms
Astarte sulcata (da Costa)	Millport	Aragonite	Crossed-lamellar	Complex crossed-lamellar with myostracal prisms	Thin, prismatic	—	Inner layer almost entirely built of myostracal-type prisms
Crassatella dilatata Deshayes	Lutetian, Dameray, France	Aragonite					
Crassatella trigonata Lamarck	Lutetian, Dameray, France	Aragonite					
Crassinella lunatula Conrad	Florida	Aragonite					
Astarte ellipta Macgillivray	Greenland	Aragonite					
Astarte quexii (d'Orbigny)	L. Lias, Blockley, Gloucs.	Aragonite					

Species Locality Mineralogy Outer layer Inner layer Myostraca Pallial Adductor Observations

2, fig. 4). The outer layer is frequently very thin or worn off in the umbonal area.

A thin discontinuous prismatic pallial myostracum was seen in most species. In *Cardita calyculata* the prisms were seen in the umbonal area only.

The inner layer is somewhat variable; the complex crossed-lamellar structure is rather fine and prominent banding is seen in most species (Plate 2, fig. 6). Myostracal pillars are developed in several of the species examined: in *Cardita calyculata* and *Venericardia imbricata* they are restricted to the inner layer. In *C. sowerbyi* & *C. marmorea* there are abundant pillars in the inner layer and a few in the marginal parts of the outer layer (Plate 2, fig. 5). However in *C. variegata* there are abundant pillars in both inner and outer layers. Sheets of myostracal prisms are also present in the inner layer of *C. calyculata*, *C. marmorea* and *V. imbricata*.

Tubules are present in all the Carditacea examined and occur in the inner layer of all species and in both layers of *Cardita variegata*.

CRASSATELLACEA

(Plate 1, figs 3, 4, 6 & 8; Plate 2, figs 3 & 4; text-figs 6 & 7)

The superfamily Crassatellacea is represented by two living families, the Crassatellidae and the Astartidae Sixteen species have been examined mineralogically and twelve optically; the shell is aragonitic throughout.

In both families the shell consists of two layers; both have an outer crossed-lamellar layer but the inner layers differ. The inner layer of the Crassatellidae is homogeneous, whereas that of the Astartidae is largely built up of myostracal-type prisms, with only traces of complex crossed-lamellar or homogeneous structures. The outer crossed-lamellar layer of all the species examined is built up from very fine primary lamels, arranged concentrically with the shell margin (Plate 1, figs 3 & 4). The lamels are obvious in the outer parts of the layer but traced inwards they

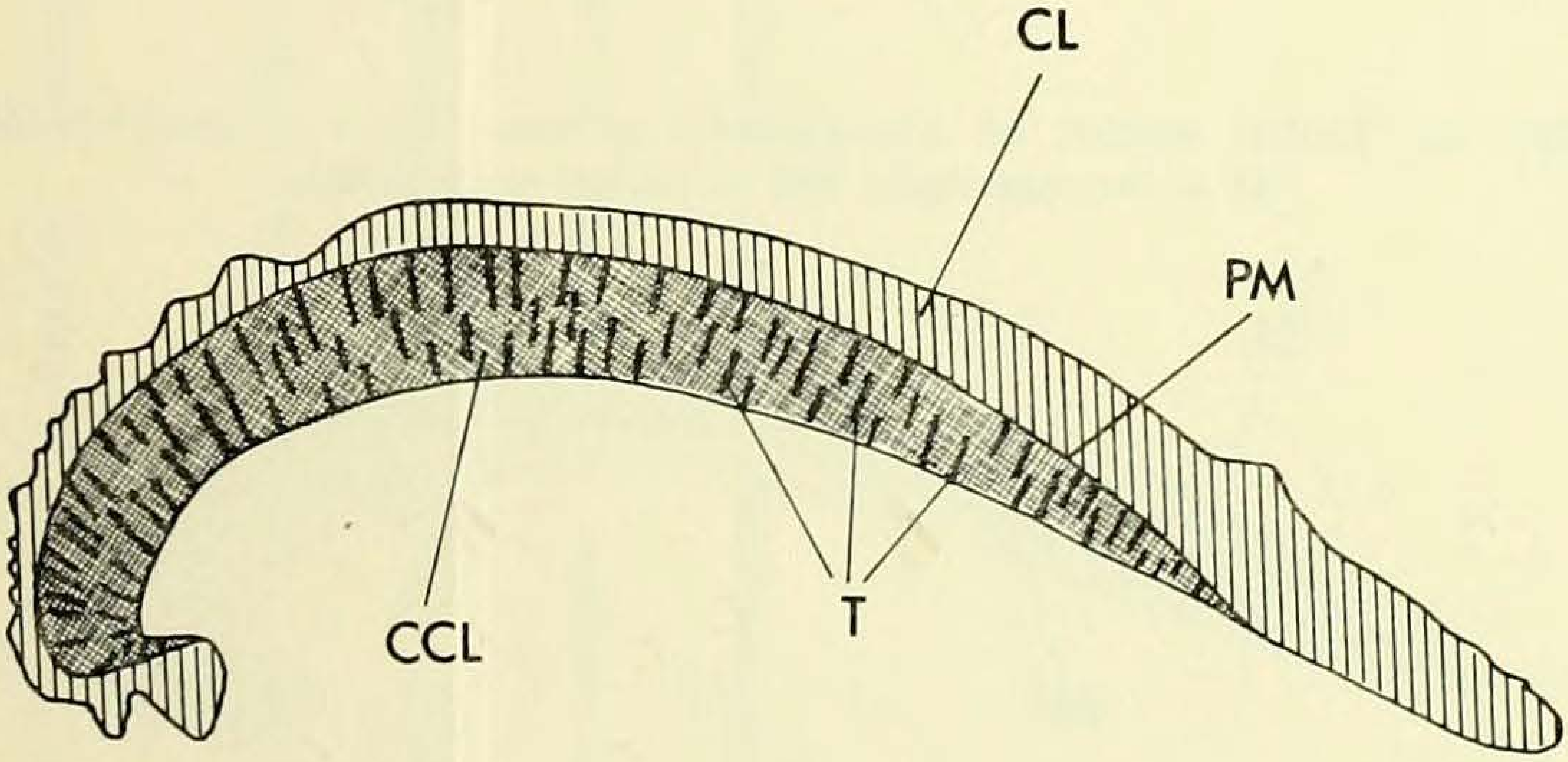


FIG. 5. Radial section of *Venericardia imbricata*. CL = crossed-lamellar, CCL = complex crossed-lamellar, PM = pallial myostracum, T = tubules.

become increasingly difficult to resolve and the layer appears homogeneous. Most of the hinge area is formed from crossed-lamellar structure.

The inner layer of the Crassatellidae shows no obvious macro-features other than conspicuous banding; electron-microscopy shows the structure to consist of irregular granular structure. In the Astartidae the inner layer is largely built up of myostracal prisms (Plate 1, figs 7 & 8; Plate 2, figs 2 & 3). In *Astarte borealis* scanning microscopy shows the outcropping prisms (Plate 2, fig. 3) revealed as distinct bosses; these show surface features of parallel ridges and striae. In *A. borealis* and *A. incrassata* there is a narrow homogeneous sheet on the inside of the pallial myostracum separating the myostracum from the main prismatic part of the inner layer. In other species the prisms arise directly from the pallial trace. There is considerable geometric selection of the prisms of the inner layer; those closest to the pallial myostracum are small and numerous but traced towards the inside of the shell there is a reduction in numbers and a resultant increase in size of the prisms.

The two shell layers are separated by the trace of the pallial myostracum. In the Crassatellidae this is marked by a distinct unconformity of growth lines but actual myostracal prisms have been detected in only one species. *Eucrassatella gibbosa* which is also the only species examined with a distinct prismatic layer associated with the adductor muscles. In the Astartidae all the species possess a prismatic myo-

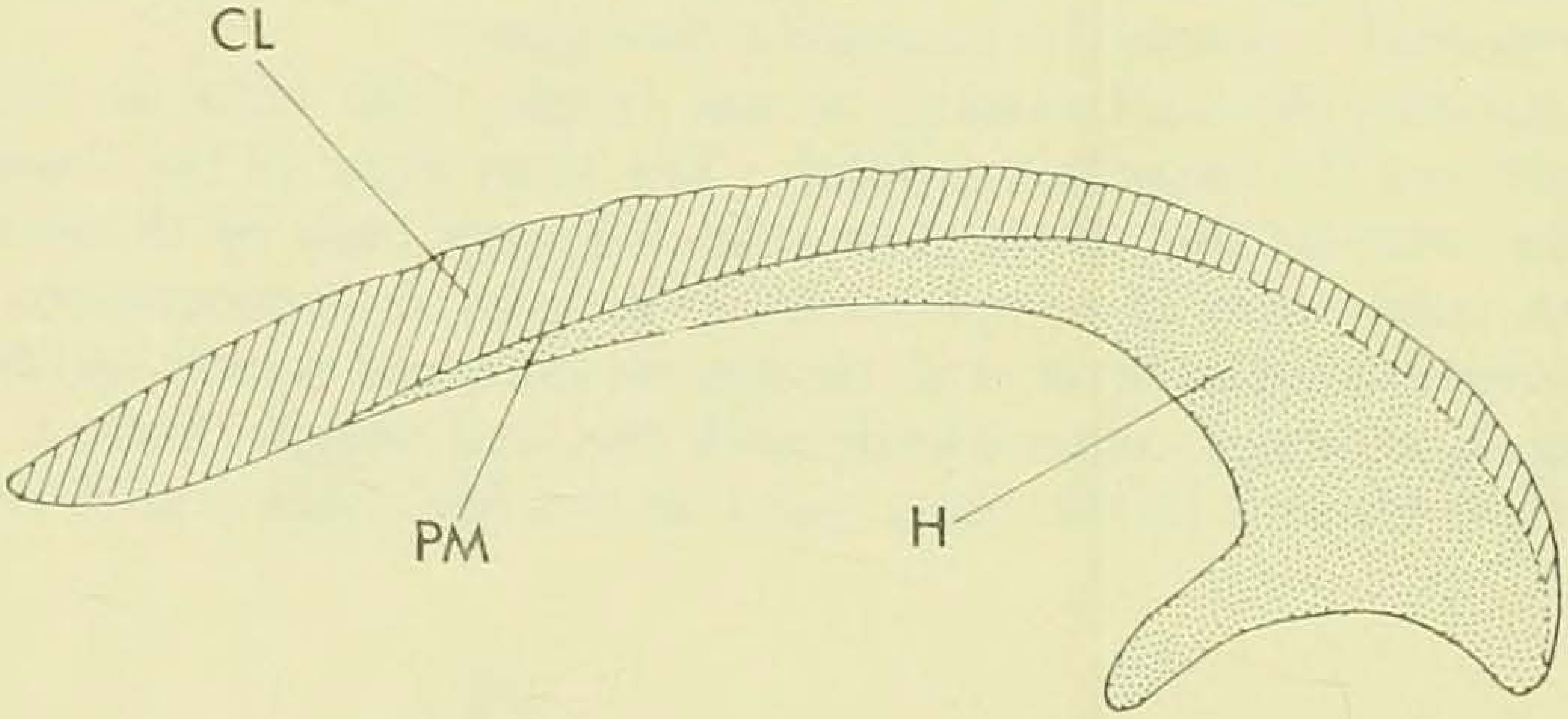


FIG. 6. Radial section of *Eucrassatella gibbosa*. CL = crossed-lamellar, H = homogeneous, PM = pallial myostracum.

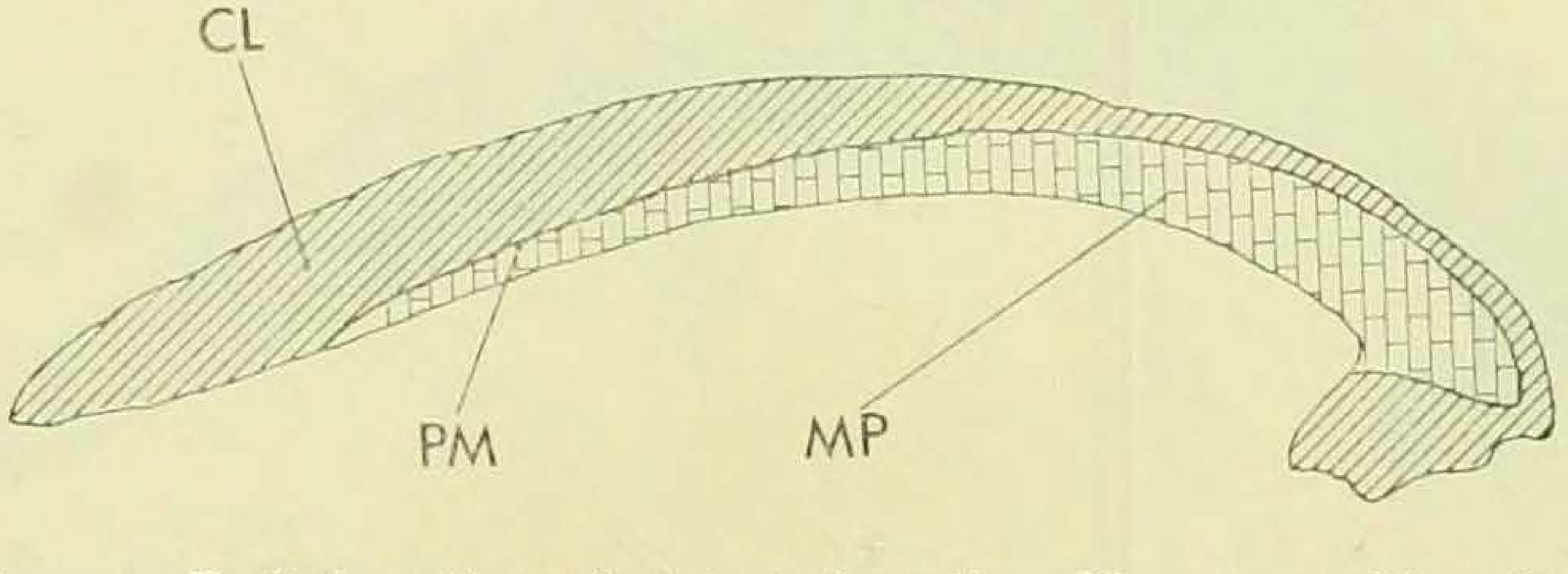


FIG. 7. Radial section of *Astarte borealis*. CL = crossed-lamellar, PM = pallial myo-stracum, MP = myostracal prisms.

TABLE 6

CARDIACEA

Species	Locality	Mineralogy	Outer layer	Inner layer	Myostraca		Observations
					Pallial	Adductor	
Acanthocardia aculeata	Britain France	Aragonite	Crossed-lamellar	Complex crossed-	Indistinct	Prismatic	
Parvicardium sueziense (Issel)	Seychelles	Aragonite					
Trachycardium senticosum (Sowerby)	Ecuador	Aragonite					

Species Locality Mineralogy Outer layer Inner layer Myostraca Pallial Adductor Observations

TABLE 6

CARDIACEA

Species	Locality	Mineralogy	Outer layer	Inner layer	Myostraca		Observations
					Pallial	Adductor	

Species Locality Mineralogy Outer layer Inner layer Myostraca Pallial Adductor Observations

Species	Locality	Mineralogy	Outer layer	Inner layer	Myostraca		Observations
					Pallial	Adductor	
Acanthocardia aculeata (Linnaeus)	Britain	Aragonite	Crossed-lamellar	Complex crossed-lamellar	Indistinct	Prismatic	
Acanthocardia echinata (Linnaeus)	Britain	Aragonite	Crossed-lamellar	Complex crossed-lamellar	Thin, prismatic	Prismatic	
Cerastoderma edule (Linnaeus)	Britain	Aragonite	Crossed-lamellar	Complex crossed-lamellar	Thin, prismatic	—	
Fragum unedo (Linnaeus)	China	Aragonite	Crossed-lamellar	Complex crossed-lamellar	Thin, prismatic	—	
Hemicardia hemicardia (Linnaeus)	China	Aragonite	Crossed-lamellar	Complex crossed-lamellar	Indistinct	—	
Laevicardium alternatum (Sowerby)		Aragonite	Crossed-lamellar	Complex crossed-lamellar	Prismatic	—	Parts of the complex crossed-lamellar layer are in continuity with the first-order lamels of the outer layer
Laevicardium australe (Sowerby)	Seychelles	Aragonite	Crossed-lamellar	Complex crossed-lamellar	Indistinct	—	
Laevicardium crassum (Gmelin)	Dublin Bay	Aragonite	Crossed-lamellar	Complex crossed-lamellar	Thin, prismatic	—	
Laevicardium serratum (Linnaeus)	Jamaica	Aragonite	Crossed-lamellar	Complex crossed-lamellar	Thin, prismatic		
Papyridea ringicula (Sowerby)	Antilles	Aragonite	Crossed-lamellar	Complex crossed-lamellar	Thin, prismatic	—	
Serripes groenlandicus (Möller)	Disco. Is. Greenland	Aragonite	Crossed-lamellar	Complex crossed-lamellar	Prismatic	—	A thin-shelled form, fine crossed-lamellar structure forms the hinge
Trachycardium consors (Sowerby)	Ecuador	Aragonite	Crossed-lamellar	Complex crossed-lamellar	Tin, prismatic	—	Thin myostracal bands beneath umbo
Trachycardium maculosum (Wood)	Seychelles	Aragonite	Crossed-lamellar	Complex crossed-lamellar	Indistinct	—	
Trigonocardia guanocostense (Hertlein & Strong)	Ecuador	Aragonite	Crossed-lamellar	Complex crossed lamellar	Prismatic	Prismatic	
Vasticardium incarnatum (Reeve)	Manilla	Aragonite	Crossed-lamellar	Complex crossed-lamellar	Thin, prismatic		
Acanthocardia parkinsoni (Sowerby)	Pleistocene, Britain	Aragonite					
'Cardium' ciliatum Fabricus	Greenland	Aragonite					
Loxocardium obliquum (Lamarck)	Lutetian, Dameray, France	Aragonite					
Parvicardium sueziense (Issel)	Seychelles	Aragonite					
Trachycardium senticosum (Sowerby)	Ecuador	Aragonite					

stracum beneath the pallial attachment, but no adductor myostracum was detected.

In a recent review of the Crassatellacea (Boyd & Newell 1968) a diphyletic origin for the superfamily was suggested. Our observations on the differences between the Crassatellidae and the Astartidae would tend to support this suggestion. The features of the Permian *Oriocrassatella elongata* described as "crater-like blisters in umbonal cavity" (Boyd & Newell, 1968) appear to be cavities left by the solution of myostracal prisms in the inner layer.

CARDIACEA

(Plate 3, figs 1–4; text-fig. 8)

Fifteen species of this group have been examined structurally and twenty mineralogically. The shell is aragonitic throughout.

Two main shell layers are present, an outer crossed-lamellar layer which forms the hinge and an inner complex crossed-lamellar layer which is bounded by the trace of the pallial line. In the outer layer the first order lamels are quite large and are aligned concentrically everywhere except for the hinge (Plate 3, figs 1, 2 & 3). Transverse sections show that the strong ribbing of most species of this superfamily produces complex patterns of first order lamels in the outermost part of the outer layer. This layer becomes very thin in the umbonal area and is frequently eroded and lost. There is a prismatic pallial myostracum in most Cardiacea, (indistinct in some species) which separates the inner complex crossed-lamellar layer. In *Laevicardium alternatum* the inner and outer layers are in direct local contact and the blocks of laths in each layer show structural continuity. Sections cut through the adductor muscle scars of some species show lenses of myostracal prisms. Bands of myostracal prisms associated with pedal muscles were seen in the umbonal area of *Trachycardium consors*.

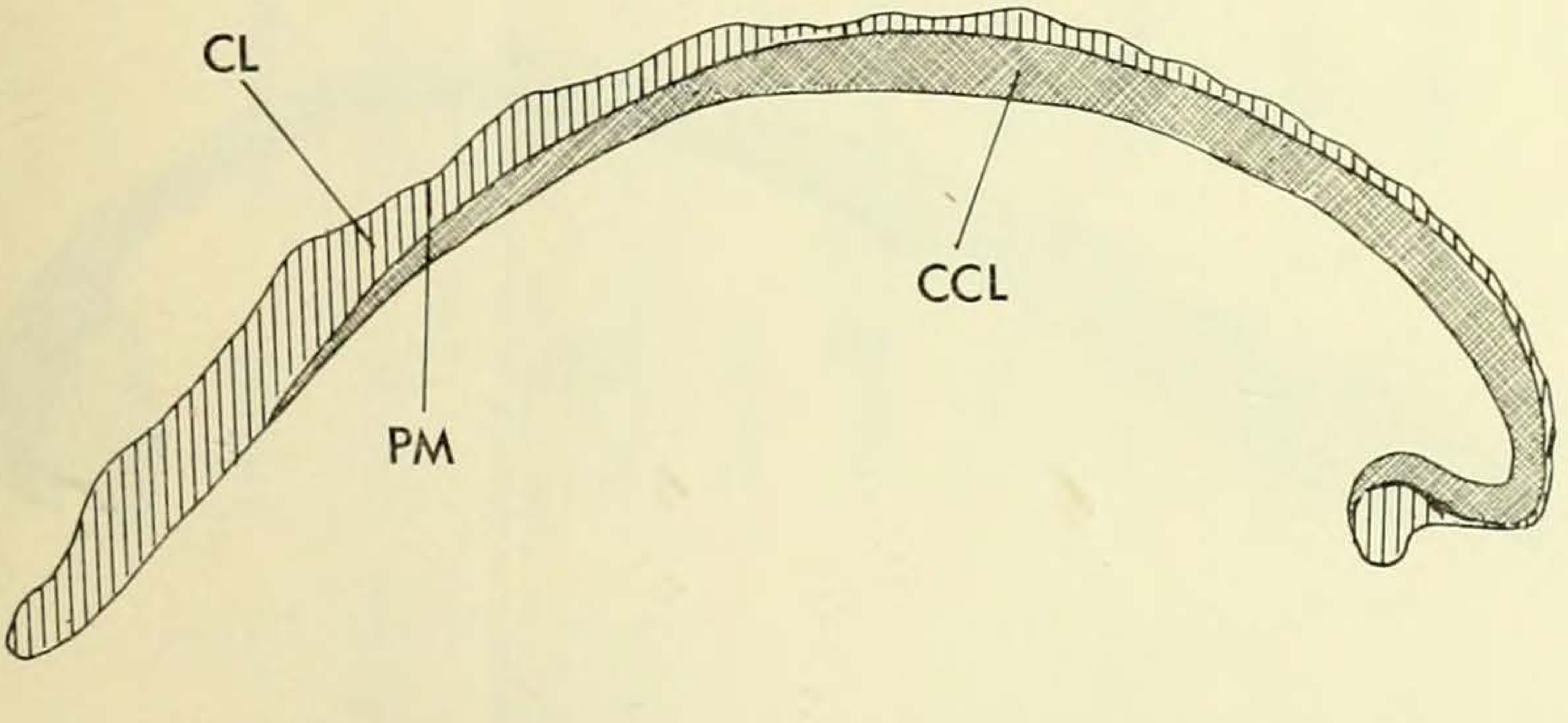


FIG. 8. Radial section of *Cerastoderma edule*. CL = crossed-lamellar, PM = pallial myostracum, CCL = complex crossed-lamellar.

TRIDACNACEA

(Plate 3, figs 5–8; text-fig. 9)

This is a small superfamily closely related to the Cardiacea (Stasek, 1962); included genera are *Tridacna* and *Hippopus*. Four species have been examined structurally and mineralogically. The shell is wholly aragonitic.

The shell is very thick, with two shell layers, an outer crossed-lamellar layer and an inner complex crossed-lamellar layer which is bounded in extent by the trace of the pallial line. In the outer layer the first order lamels are large (Plate 3, fig. 6) and arranged concentrically in all but the hinge area. The strong ribbing however causes an apparent complex pattern of first order lamels (Plate 3, fig. 4). There is a thin prismatic pallial myostracum in all the species examined. The inner complex crossed-lamellar layer is somewhat variable in character; in the three species of *Tridacna* studied the structural elements are fairly coarse and interleaved with thin sheets of myostracal-prisms. In *Hippopus* however the structure is very fine with an almost homogeneous appearance and with many fine prismatic sheets (Plate 3, figs 7 & 8). Higher magnifications (Plate 3, fig. 7) show that the structure consists of sheets of fine needles.

All species show very strong daily growth bands in both layers and show prismatic pedal and adductor myostraca.

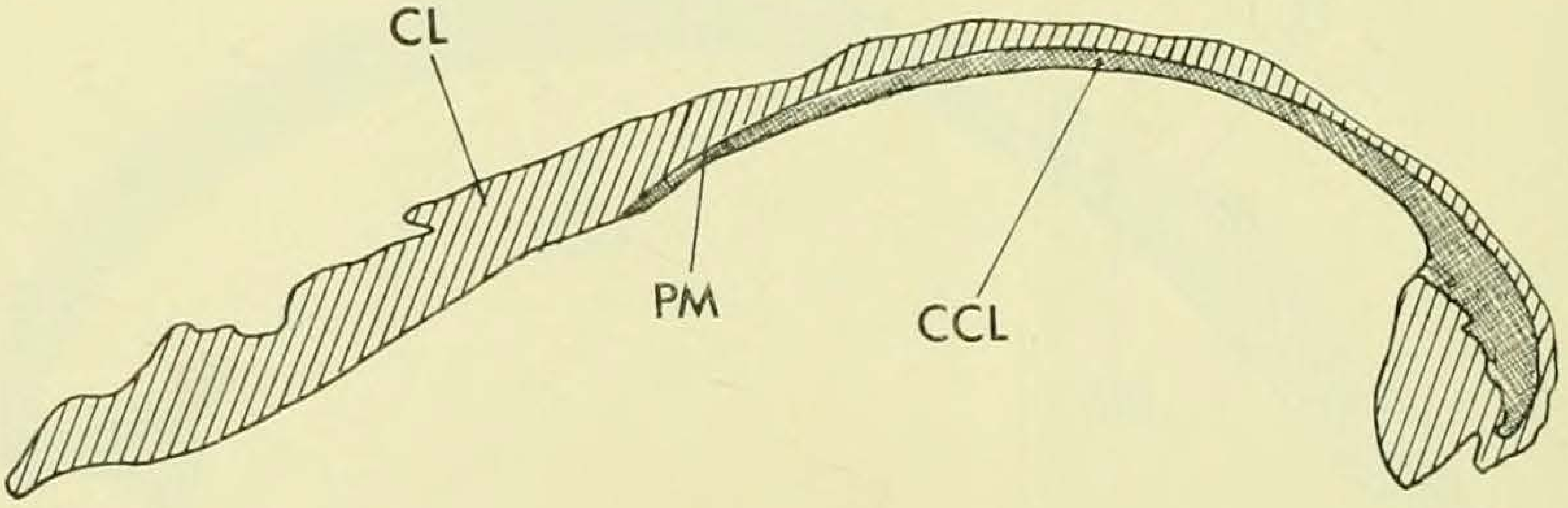


FIG. 9. Radial section of *Tridacna maxima*. CL = crossed-lamellar, CCL complex crossed-lamellar, PM = pallial myostracum.

TABLE 7

TRIDACNACEA

Species	Locality	Mineralogy	Outer layer	Inner layer	Myostraca		Observations
					Pallial	Adductor	
Hippopus hippopus Linnaeus	Australia	Aragonite	Crossed-lamellar	Complex crossed-lamellar	Thin, prismatic	Thin, prismatic	Prism bands in inner layer
Tridacna crocea Lamarck	East Indies	Aragonite	Crossed-lamellar	Complex crossed-lamellar	Thin, prismatic	Thin, prismatic	Prism bands in inner layer, pedal myostraca
Tridacna maxima Röding	Indian Ocean	Aragonite	Crossed-lamellar	Complex crossed-lamellar	Thin, prismatic	Thin, prismatic	Prism bands in inner layer, pedal myostraca

Name	Locality	Mineralogy	Outer layer	Inner layer	Myostraca		Observations
					Pallial	Adductor	
Ensis ensis (Linnaeus)	Britain	Aragonite	Finely crossed-lamellar	Homogeneous, lamellate	Thin, prismatic	—	
Ensis siliqua (Linnaens)	Britain	Aragonite	Finely crossed-lamellar	Homogeneous, lamellate	Thin, prismatic	—	
Cultellus lactuosus (Spengler)	India	Aragonite	Finely crossed-lamellar to homogeneous	Homogeneous, lamellate	Thin, prismatic	—	
Siliqua sp.	Ecuador	Aragonite	Finely crossed-lamellar	Complex crossed-lamellar	Thin, prismatic	—	
Solen truncata (Wood)	Ceylon	Aragonite					

TABLE 7

TRIDACNACEA

Species	Locality	Mineralogy	Outer layer	Inner layer	Myostraca		Observations
					Pallial	Adductor	
Hippopus hippopus Linnaeus	Australia	Aragonite	Crossed-lamellar	Complex crossed-lamellar	Thin, prismatic	Thin, prismatic	Prism bands in inner layer
Tridacna crocea Lamarck	East Indies	Aragonite	Crossed-lamellar	Complex crossed-lamellar	Thin, prismatic	Thin, prismatic	Prism bands in inner layer, pedal myostraca
Tridacna maxima Röding	Indian Ocean	Aragonite	Crossed-lamellar	Complex crossed-lamellar	Thin, prismatic	Thin, prismatic	Prism bands in inner layer, pedal myostraca
Tridacna squamosa Lamarck	Indian Ocean	Aragonite	Crossed-lamellar	Complex crossed-lamellar	Thin, prismatic	Thin, prismatic	Prism bands in inner layer, pedal myostraca

TABLE 8

MACTRACEA

Name	Locality	Mineralogy	Outer layer	Inner layer	Myostraca		Observations
					Pallial	Adductor	
Atactodea glabrata (Gmelin)	Seychelles	Aragonite	Crossed-lamellar	Complex crossed-lamellar	Thin, prismatic	Not seen	
Mactra corallina (Linnaeus)	Britain	Aragonite	Crossed-lamellar	Complex crossed-lamellar	Not seen	Not seen	
Mactra leucozonica Philippi	Philippines	Aragonite	Crossed-lamellar	Complex crossed-lamellar	Not seen	Not seen	
Mactra producta Angas	Port Jackson	Aragonite	Crossed-lamellar	Complex crossed-lamellar	Indistinct, prismatic	Indistinct, prismatic	
Mactra violacea Solander	Tranquebar	Aragonite	Crossed-lamellar	Complex crossed-lamellar	Thin, prismatic	Thin, prismatic	
Matronella clisea Dall	Ecuador	Aragonite	Crossed-lamellar	Complex crossed-lamellar	Thin, prismatic	Not seen	
Mactronella exoleta (Gray)	W. America	Aragonite	Crossed-lamellar	Complex crossed-lamellar	Thin, prismatic	Not seen	
Mulina pallida Broderip & Sowerby	Ecuador	Aragonite	Crossed-lamellar	Complex crossed-lamellar	Thin, prismatic	Not seen	Thin bands of myostracal-type prisms in the inner layer
Raeta undulata (Gould)	Ecuador	Aragonite	Crossed-lamellar	Complex crossed-lamellar	Thin, prismatic	Thin, prismatic	Thin bands of myostracal-type prisms in the inner layer
Spisula solida (Linnaeus)	Britain	Aragonite	Crossed-lamellar	Complex crossed-lamellar	Thin, prismatic	Not seen	Inner layer very fine, with sheets of myostracal-type prisms. Pedal myostraca visible beneath umbo
Cardilia martini (Deshayes)	Indian Ocean	Aragonite					
Mactroderma velata Philippi	Ecuador	Aragonite					

TABLE 9

SOLENACEA

Name	Locality	Mineralogy	Outer layer	Inner layer	Myostraca		Observations
					Pallial	Adductor	
Ensis ensis (Linnaeus)	Britain	Aragonite	Finely crossed-lamellar	Homogeneous, lamellate	Thin, prismatic	—	
Ensis siliqua (Linnaens)	Britain	Aragonite	Finely crossed-lamellar	Homogeneous, lamellate	Thin, prismatic	—	
Cultellus lactuosus (Spengler)	India	Aragonite	Finely crossed-lamellar to homogeneous	Homogeneous, lamellate	Thin, prismatic	—	
Siliqua sp.	Ecuador	Aragonite	Finely crossed-lamellar	Complex crossed-lamellar	Thin, prismatic	—	
Solen truncata (Wood)	Ceylon	Aragonite					

MACTRACEA

(Plate 4, figs 1 & 2; text-fig. 10)

Thirteen species have been examined mineralogically and ten structurally. The shell is entirely aragonite.

There are two shell layers in all species examined, an outer crossed-lamellar layer and an inner complex crossed-lamellar layer bounded by the pallial myostracum. In the outer layer, the first order lamels are arranged concentrically and in this superfamily are characteristically very fine (Plate 4, fig. 2). The layer is usually very thin and worn in the umbonal region but forms most of the hinge. In *Spisula solida* the crossed-lamellae are finer than in most other species and appear homogeneous in the inner parts of the layer. The inner layer of this species also has a very fine structure and sheets of myostracal prisms are present. These sheets also occur in *Raeta undulata*. The separation of the two layers is sharp (Plate 4, fig. 1) but the pallial myostracum is thin and indistinct in most species. The adductor myostraca are also poorly defined.

SOLENACEA

(Plate 4, fig. 3)

Seven species have been examined mineralogically and four structurally. The shell is aragonitic throughout. Two main shell layers are present, an outer crossed-lamellar layer which forms the hinge and an inner homogeneous layer bounded by the trace of the pallial line. In the outer crossed-lamellar layer the first order lamels are very fine and arranged concentrically to the shell margin over most of the shell. Locally this layer may appear homogeneous. A very thin prismatic pallial myostracum, best developed below the umbo is present in all species. The inner layer of all the examples appears homogeneous with a striking lamellate appearance. Electron-microscopy of the inner layer of *Ensis siliqua* shows that the apparent homogeneous layer is in fact built up from layers of very fine complex crossed-lamellar structure (Plate 4, fig. 3) which alternate with bands of fibrous appearance which may be organic matrix. Etching reveals the presence of a reticulum of organic matrix sandwiched between carbonate laths.

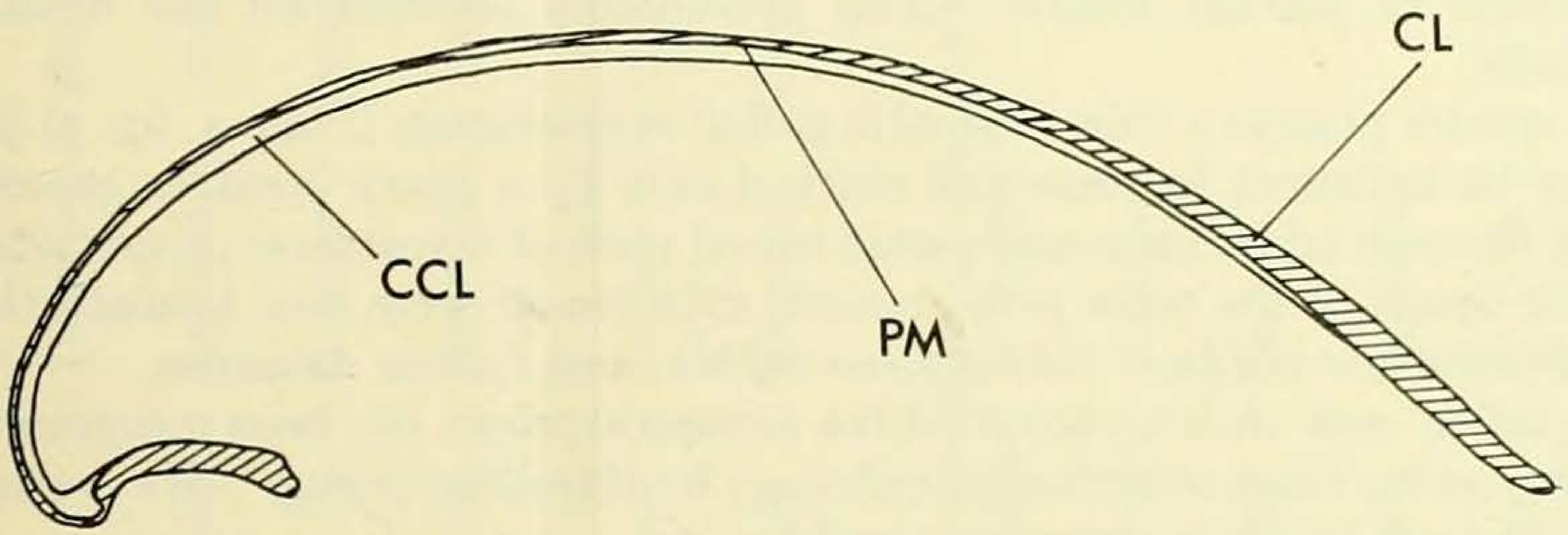


FIG. 10. Radial section of *Mactronella exoleta*. CL = crossed-lamellar, CCL = complex crossed-lamellar, PM = pallial myostracum.

TELLINACEA

(Plate 4, figs 4, 5 & 6; Plate 5, figs 1–7; Text-figs 11–15)

Thirty-one species have been examined mineralogically and twenty-four optically. The shell is totally aragonite.

Most of the species we have examined have three layered shells (Plate 4, fig. 4), with an outer composite prismatic layer, a middle crossed-lamellar layer and an inner layer which may be made of complex crossed-lamellar or homogeneous structures. The inner layer is, as usual, bounded by the pallial trace. In *Egeria radiata, Florimetis corrugata, Psammotea radiata, Macoma balthica, Tellidora burneti* and two species of *Solenotellina*, there are however only two shell layers, an outer crossed-lamellar layer and an inner, complex crossed-lamellar layer which is bounded by the trace of the pallial line. Trueman (1942) described a three layered shell in *Tellina tenuis*.

The outer composite prismatic layer of three layered species is usually very thin and is frequently worn away from the umbonal area. It consists of horizontal first order prisms, arranged radially from the umbo. Each prism is built up of fine needle-like second order prisms (Plate 4, figs 5 & 6) which are arranged in the characteristic divergent feathery pattern seen in longitudinal section. This layer is at its thickest development in the Donacidae and Semelidae, where the arrangement of first and second order prisms is very clear. The Donacidae develop strong internal marginal denticles with a resultant thickening of the outer shell layer (as in the Nuculidae).

The middle layer of three layered shells and the outer layer of two layered shells is built of crossed-lamellar structure with rather fine concentrically arranged first order lamels (Plate 4, fig. 4; Plate 5, fig. 3). This layer forms the hinge in all species examined.

The inner layer of most species examined is built of complex crossed-lamellar structure (Plate 5, figs 5 & 6) although as in the Solenacea the fabric is so fine as to appear homogeneous under light microscopy (Plate 5, fig. 7). Electron-microscopy reveals that this is very fine complex crossed-lamellar structure. In some species *Quidnipagus palatam, Asaphis deflorata,* and *Psammotea radiata* thin prismatic sheets are developed. In *Semele tortuosa* these occupy most of the inner layer (Plate 5, figs 1 & 2). The inner layer is also often markedly lamellate caused by the presence of thick sheets of protein matrix which presumably account for the flexibility of these shells.

Most species possess a thin prismatic pallial myostracum (Plate 5, fig. 2) although this may be indistinct in some and marked only by a sharp break in growth lines. Sections through adductor muscle scars reveal pads of myostracal prisms whilst thin prismatic bands of the trace pedal muscle attachment were seen beneath the hinge line in *Psammotea occidens, Solenotellina diphos,* and *Tellina calcarina*.

A 'so called' new shell layer called the mosaicostracum has been recognized in the Tellinacea on the basis of surface morphology by Hamilton (1969). We are uncertain how this relates to the layers recognized herein.

We have examined the fine structure of *Semele tortuosa, Donax faba, hecuba scortum, Tellina radiata, Quidnipagus palatam, Asaphis deflorata* and *Scutarcopagia scobinata*.

TABLE 10

TELLINACEA

Name	Locality	Mineralogy	Outer layer	Middle layer	Inner layer	Myostraca		Observations
						Pallial	Adductor	
Asaphis deflorata (Linnaeus)	Seychelles	Aragonite	Composite prismatic	Crossed-lamellar	Complex crossed-lamellar	Prismatic	Prismatic	Inner layer fine, banded
Donax asper Hanley	Ecuador	Aragonite	Composite prismatic	Crossed-lamellar	Complex crossed-lamellar	Prismatic	—	
Donax epidermia Lamarck	Brisbane	Aragonite	Composite prismatic	Crossed-lamellar	Homogeneous/ complex crossed-lamellar	Prismatic	—	Inner layer lamellate
Tellinella virgata Linnaeus	Indian Ocean	Aragonite	Composite prismatic	Crossed-lamellar	Complex crossed-lamellar	Prismatic	—	Inner layer lamellate
Tellidora burneti (Broderip & Sowerby)	Mazaltan	Aragonite	Crossed-		Homogeneous	—	—	Inner layer lamellate

The following species are all aragonitic:—

Donax denticulatus Linnaeus	W. Indies
Donax transversus Sowerby	Ecuador
Gastrana fragilis (Linnaeus)	Italy
Scissulina dispar (Conrad)	Seychelles
Solecurtus broggi Pilsbry & Olsson	Ecuador
Strigilla carinaria (Linnaeus)	Ecuador

TABLE 10

TELLINACEA

Name	Locality	Mineralogy	Outer layer	Middle layer	Inner layer	Myostraca		Observations
						Pallial	Adductor	
Asaphis deflorata (Linnaeus)	Seychelles	Aragonite	Composite prismatic	Crossed-lamellar	Complex crossed-lamellar	Prismatic	Prismatic	Inner layer fine, banded
Donax asper Hanley	Ecuador	Aragonite	Composite prismatic	Crossed-lamellar	Complex crossed-lamellar	Prismatic	—	
Donax epidermia Lamarck	Brisbane	Aragonite	Composite prismatic	Crossed-lamellar	Homogeneous/ complex crossed-lamellar	Prismatic	—	Inner layer lamellate
Donax faba Gmelin	Swan River, Australia	Aragonite	Composite prismatic	Crossed-lamellar	Complex crossed-lamellar	Prismatic	—	
Donax vittatus (da Costa)	Britain	Aragonite	Composite prismatic	Crossed-lamellar	Homogeneous/ complex crossed-lamellar	Prismatic	—	Inner layer lamellate
Egeria radiata (Lamarck)	S. Nigeria	Aragonite	Crossed-lamellar	—	Complex crossed-lamellar	Prismatic	—	
Florimetis corrugata (Sowerby)	Ecuador	Aragonite	Crossed-lamellar	—	Complex crossed-lamellar	Prismatic	—	Tubules? in inner layer
Hecuba scortum (Linnaeus)	S. Africa	Aragonite	Composite prismatic	Crossed-lamellar	Homogeneous	—	—	Lamellate inner layer
Macoma balthica (Linnaeus)	Britain	Aragonite	Crossed-lamellar	—	Complex crossed-lamellar	Prismatic	—	
Psammotea occidens Deshayes	Philippines	Aragonite	Composite prismatic	Crossed-lamellar	Homogeneous	Prismatic	—	Inner layer lamellate
Psammotea radiata (Philippi)	Seychelles	Aragonite	Crossed-lamellar	—	Complex crossed-lamellar	Prismatic	—	Prism bands in inner layer
Quidnipagas palatam Iredale	Seychelles	Aragonite	Composite prismatic	Crossed-lamellar	Complex crossed-lamellar	Prismatic	—	
Scrobicularia magna (Spengler)	Ecuador	Aragonite	Composite prismatic	Crossed-lamellar	Complex crossed-lamellar	Prismatic	—	
Scutarcopagia linguafelis (Linnaeus)	Antilles	Aragonite	Composite prismatic	Crossed-	Homogeneous	—	—	Inner layer lamellate
Scutarcopagia scobinata (Linnaeus)	Queensland	Aragonite	Composite prismatic	Crossed-lamellar	Homogeneous	—	—	Inner layer lamellate
Semele tortuosa (C. B. Adams)	Ecuador	Aragonite	Composite prismatic	Crossed-lamellar	Complex crossed-lamellar	Prismatic	—	Very thick pallial myostracum
Semele sp	Ecuador	Aragonite	Composite prismatic	Crossed-lanellar	Homogeneous	—	—	Lamellate inner layer
Solecurtus strigillatus Blainville	Mediterranean	Composite	Composite prismatic	Crossed-lamellar	Complex crossed-lamellar	—	—	Inner layer lamellate
Solenotellina diphos (Sowerby)	India	Aragonite	Crossed-lamellar		Complex crossed-lamellar	Prismatic	—	Thin prism bands in inner layer; pedal myostraca beneath umbo
Solenotellina biradiata (Wood)	Swan River, Australia	Aragonite	Crossed-lamellar		Complex crossed-lamellar	Prismatic	Prismatic	Inner layer lamellate
Macoma calcarea (Gmelin)	Greenland	Aragonite	Composite prismatic	Crossed-lamellar	Complex crossed-lamellar	Prismatic	—	Prism bands present in inner layer beneath hinge
Tellina radiata Linnaeus	W. Indies	Aragonite	Composite prismatic	Crossed-lamellar	Homogeneous	—	—	Inner layer lamellate
Tellinella virgata Linnaeus	Indian Ocean	Aragonite	Composite prismatic	Crossed-lamellar	Complex crossed-lamellar	Prismatic	—	Inner layer lamellate
Tellidora burneti (Broderip & Sowerby)	Mazaltan	Aragonite	Crossed-		Homogeneous	—	—	Inner layer lamellate

The following species are all aragonitic:—

Donax denticulatus Linnaeus	W. Indies
Donax transversus Sowerby	Ecuador
Gastrana fragilis (Linnaeus)	Italy
Scissulina dispar (Conrad)	Seychelles
Solecurtus broggi Pilsbry & Olsson	Ecuador
Strigilla carinaria (Linnaeus)	Ecuador

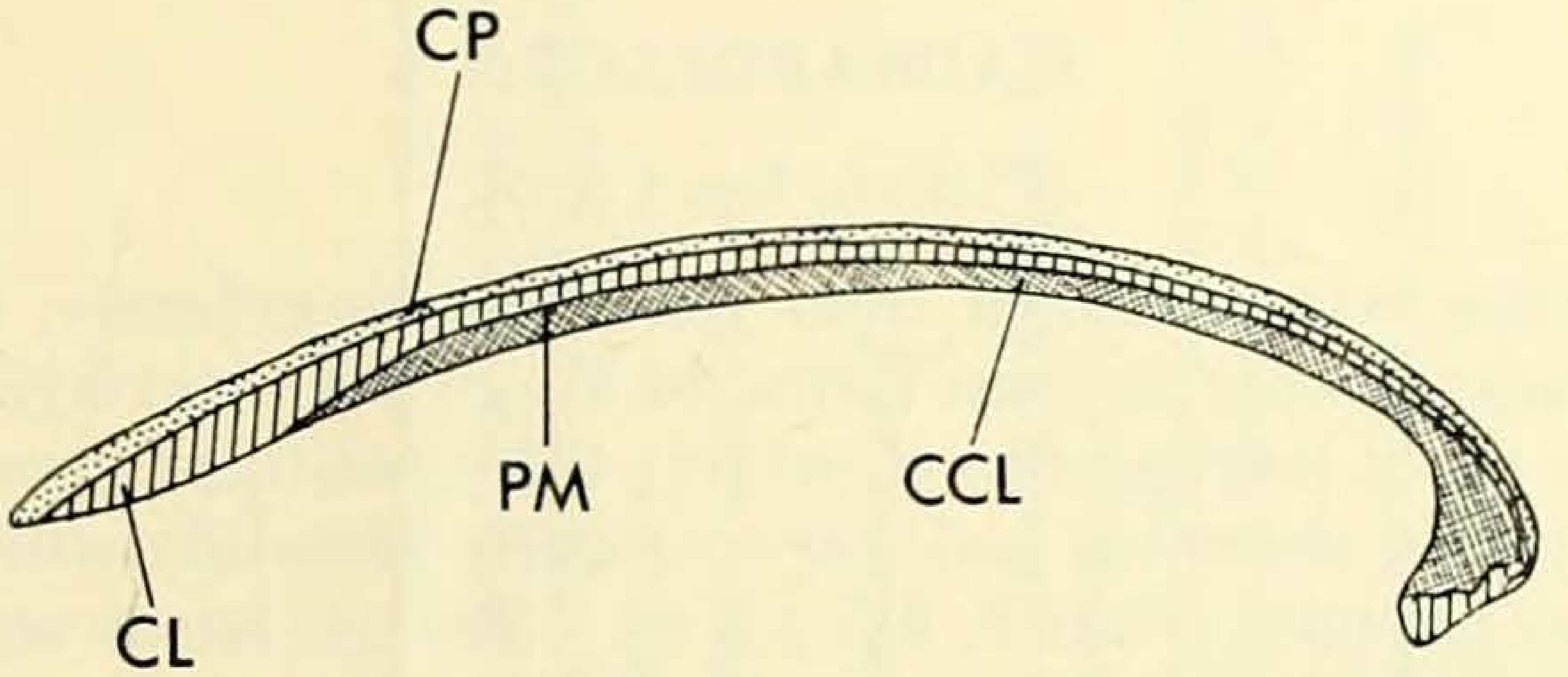


FIG. 11. Radial section of *Donax faba.* CP = composite prismatic, CL = crossed-lamellar, CCL = complex crossed-lamellar, PM = pallial myostracum.

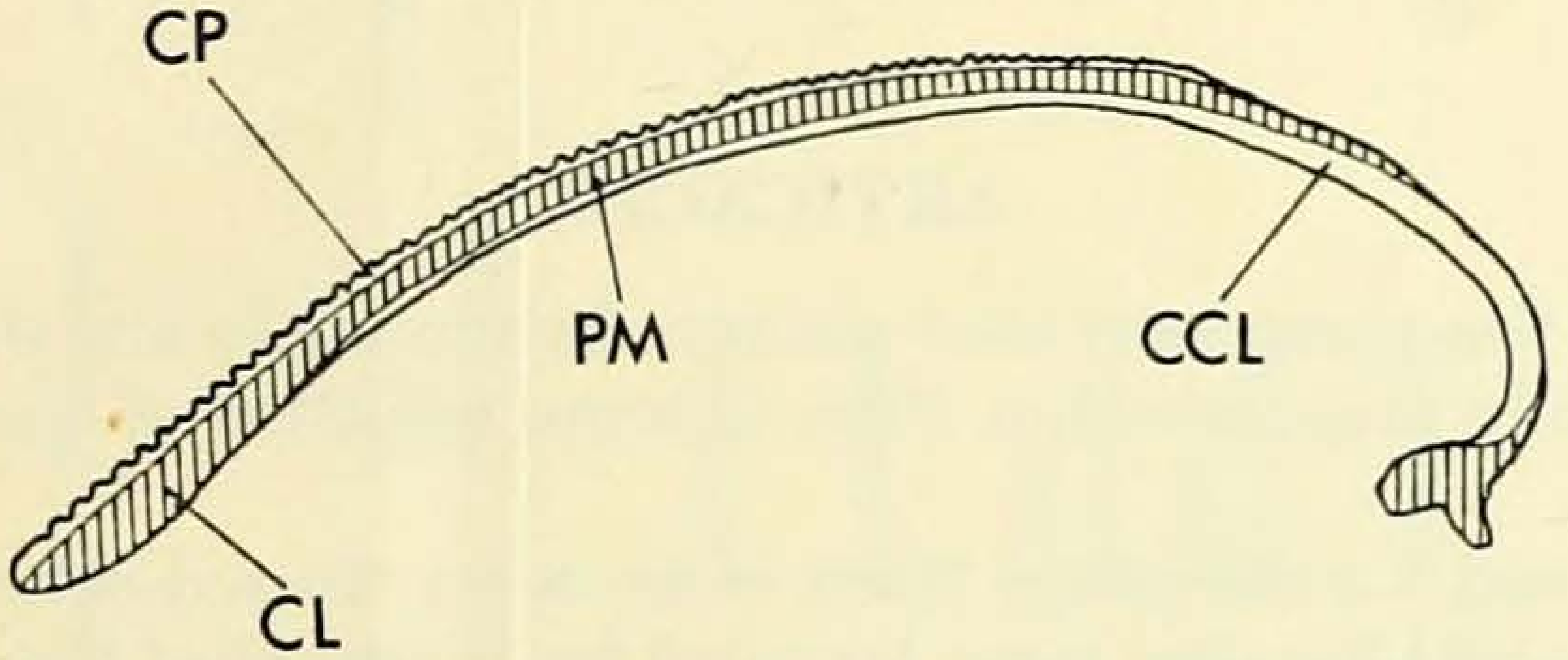
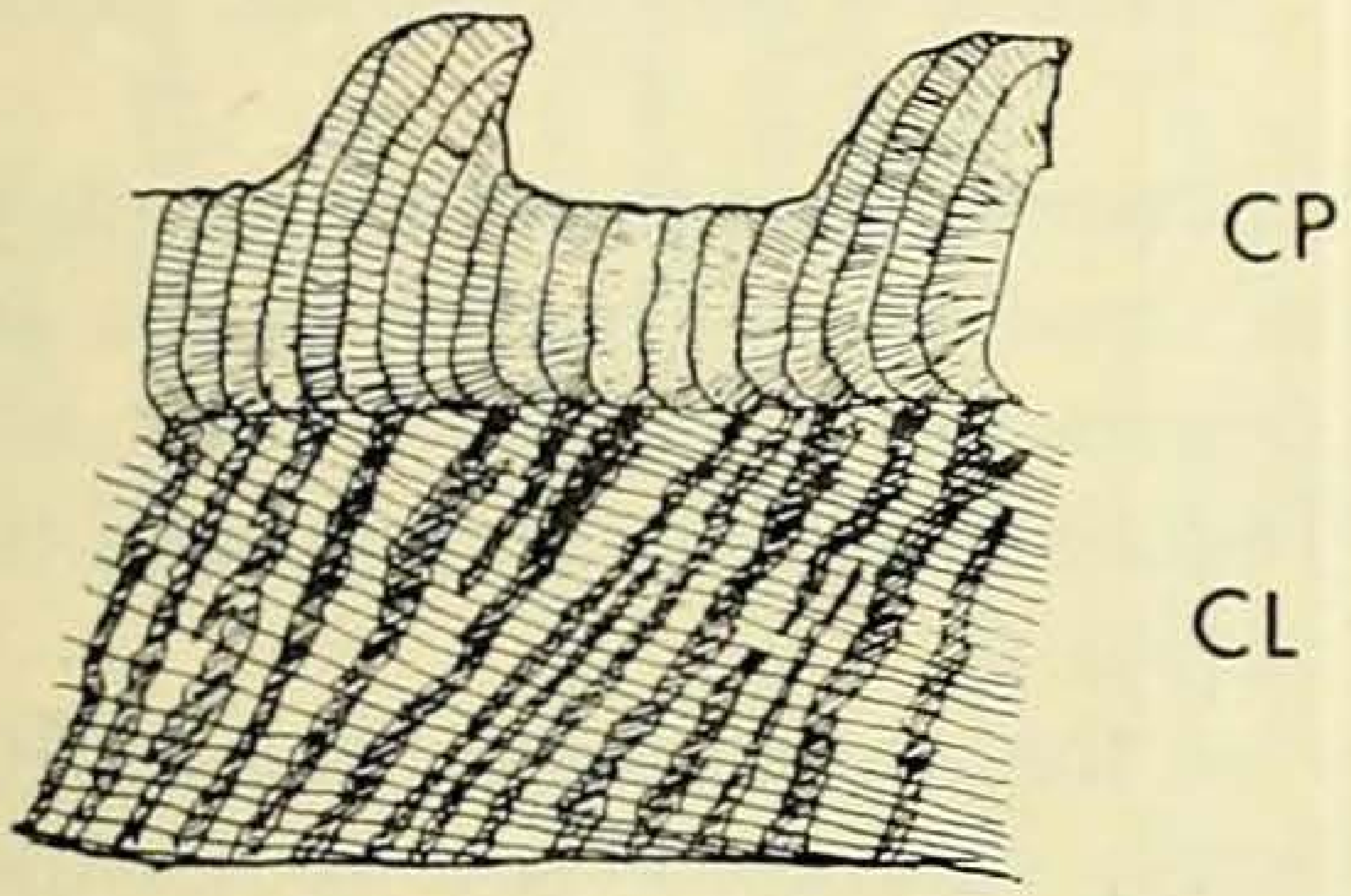


FIG. 12. Radial section of *Hecuba scortum.* CP = composite prismatic, CL = crossed-lamellar, PM = pallial myostracum, CCL = complex crossed- lamellar.



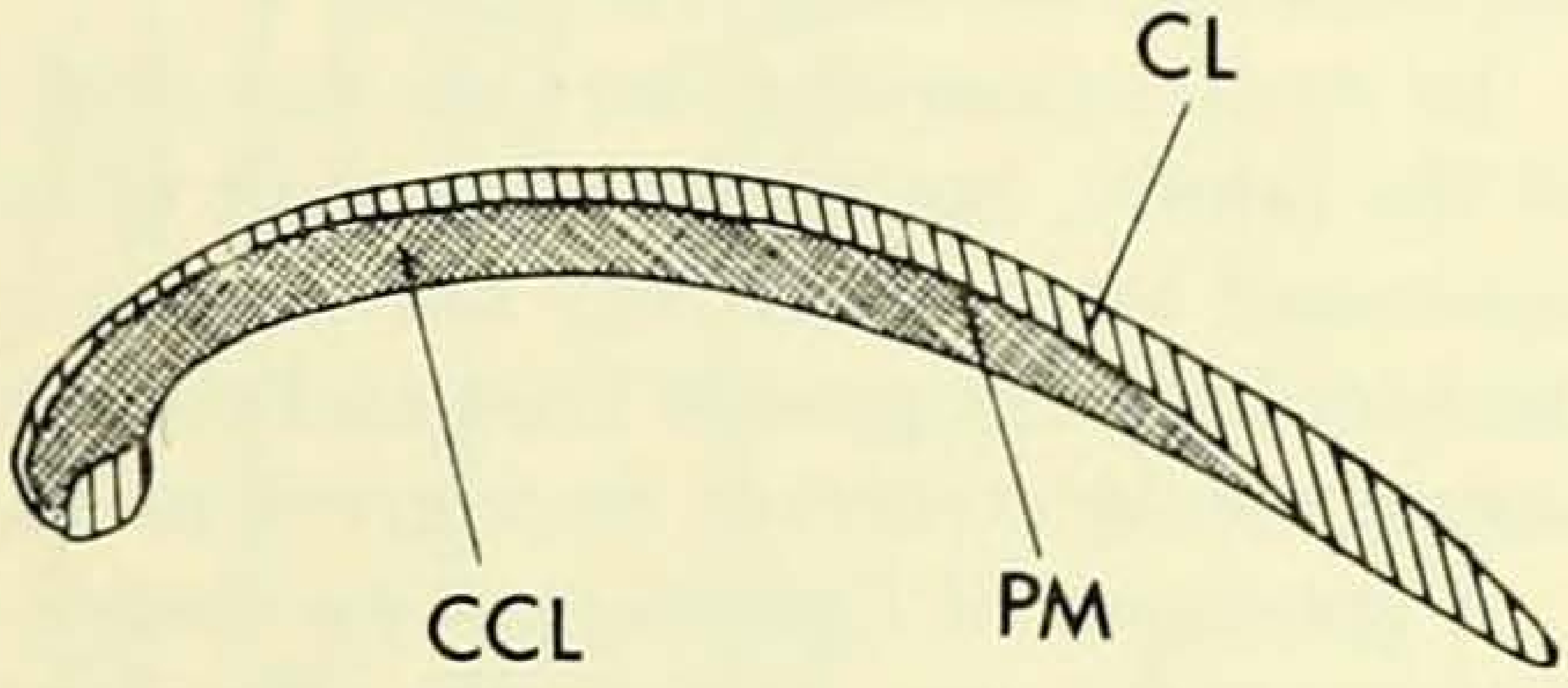


FIG. 13. Detail of a radial section of *Hecuba scortum* showing alignment of crystallites in the outer composite prismatic layer (CP), and of lamellae in the middle crossed-lamellar layer (CL).

FIG. 14. Radial section of *Macoma balthica.* CL = crossed-lamellar, CCL = complex crossed-lamellar, PM = pallial myostracum.

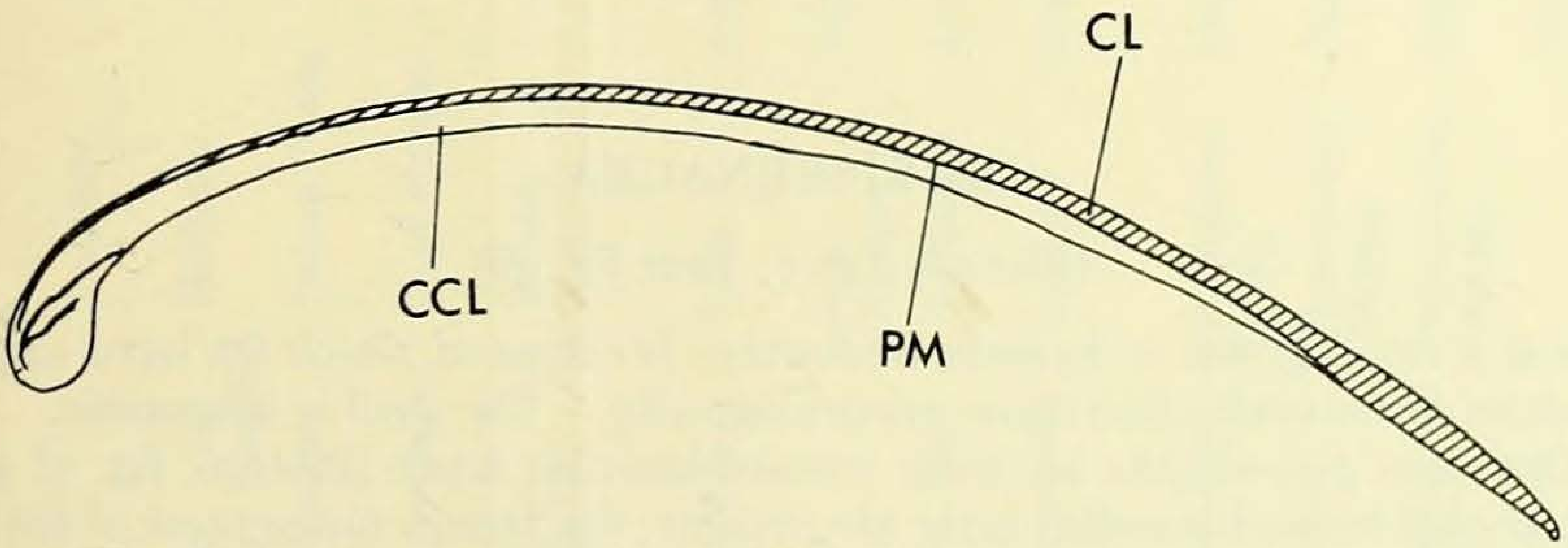


FIG. 15. Radial section of *Solenotellina sipho.* CL = crossed-lamellar, CCL = complex crossed-lamellar, PM = pallial myostracum.

GAIMARDIACEA

(Plate 6, figs 5 & 6)

Only one species was examined from this small superfamily, it is aragonitic. *Gaimardia trapezina* (Lamarck) from Tierra del Fuego has a two layered shell. Both layers are made up of homogenous structure; the constituent crystallites are very small about 0·5 μ in diameter and have irregular rounded outlines so that the structure appears granular (Plate 6, figs 5 & 6). The two layers are separated by a thin prismatic pallial myostracum.

ARTICACEA

Four species of this group have been examined structurally and six mineralogically. The shell is entirely aragonitic but there is some variation of structure within the superfamily.

In *Trapezium* and *Coralliophaga* there is an outer crossed-lamellar layer and an inner complex crossed-lamellar layer bounded by the trace of the pallial line. The primary lamels of the outer layer are very coarse and are arranged concentrically to the shell margin; this layer also forms the hinge. There is a thin prismatic pallial myostracum dividing the layers.

In *Arctica islandica* there are two shell layers, but in contrast to the other members of the family, both layers are built of homogeneous structure. The two layers are separated by an extremely fine prismatic pallial myostracum along which there is a distinct break in growth lines and shell layering. Details of the fine structure of the homogeneous structure were given in Taylor *et al* (1969).

A specimen of *Calyptogena ponderosa,* a member of the problematical family the Vesicomyidae was examined. Members of this family exhibit certain similarities with both the Veneracea and the Arcticacea, Boss (1968). The shell structure consists of two homogeneous layers and in this respect resembles the Arcticacea more than any other superfamily and is thus placed here for convenience. A similar conclusion was reached by Oberling & Boss (1970).

DREISSENACEA

(Plate 6, fig. 3; Text-fig. 16)

This is a small group of byssate freshwater bivalves of which we have examined one species structurally and three mineralogically. The shell is aragonitic.

In *Dreissena polymorpha* an outer crossed-lamellar layer (Plate 6, fig. 3) and an inner complex crossed-lamellar layer are present; the former forms most of the hinge. The layers are separated by a thin prismatic pallial myostracum. The primary lamels of the outer layer are arranged concentrically.

TABLE II

ARCTICACEA

Name	Locality	Mineralogy	Outer layer	Inner layer	Myostraca		Observations
					Pallial	Adductor	
Coralliophaga coralliophaga (Gmelin)	Mollucas	Aragonite	Crossed-lamellar	Complex crossed-lamellar	Prismatic	—	
Trapezium oblongum (Linnaeus)	Indian Ocean	Aragonite	Crossed-lamellar	Complex crossed-lamellar	Prismatic	—	
Calyptogena ponderosa Boss	G. of Mexico	Aragonite	Homogeneous	Homogeneous		—	
Arctica islandica (Linnaeus)	Britain	Aragonite	Homogeneous	Homogeneous	Thin, prismatic	Indistinct	Thin prismatic bands in inner layer. Prominently banded

							very regular columns, as in the Limopsacea
Corbicula occidens Deshayes	India	Aragonite	Finely crossed-lamellar	Complex-crossed-lamellar	Indistinct	—	Inner layer as above
Corbicula sp.	Lake Nyanza	Aragonite	Finely crossed-lamellar	Complex crossed-lamellar	Indistinct	—	Inner layer as above
Cyrena inflata Say	Nicaragua	Aragonite	Finely crossed-lamellar	Complex crossed-lamellar	Thin, prismatic	—	The pallial myostracum is discontinuous
Polymesoda anomala (Deshayes)	Ecuador	Aragonite	Finely crossed-lamellar	Complex crossed-lamellar	Thin, prismatic	—	Thin sheets of myostracal-type prisms are present in the inner layer
Velorita cyprinoides (Gray)	Mangalore, India	Aragonite	Finely crossed-lamellar	Complex crossed-lamellar	Indistinct	—	Inner layer as in *C. fluminea*
Corbicula cordata (Morris)	Sparnacian, Britain	Aragonite					
Corbicula cuneiformis (Sowerby)	Sparnacian, Britain	Argonite					
Cyrena consobrina (Cailliaud)		Aragonite					
Pisidium amnicum Müller	Notts., England	Aragonite					

Table 11

ARCTICACEA

Name	Locality	Mineralogy	Outer layer	Inner layer	Myostraca		Observations
					Pallial	Adductor	
Coralliophaga coralliophaga (Gmelin)	Mollucas	Aragonite	Crossed-lamellar	Complex crossed-lamellar	Prismatic	—	
Trapezium oblongum (Linnaeus)	Indian Ocean	Aragonite	Crossed-lamellar	Complex crossed-lamellar	Prismatic	—	
Calyptogena ponderosa Boss	G. of Mexico	Aragonite	Homogeneous	Homogeneous		—	
Arctica islandica (Linnaeus)	Britain	Aragonite	Homogeneous	Homogeneous	Thin, prismatic	Indistinct	Thin prismatic bands in inner layer. Prominently banded
Arctica plana (Sowerby)	Tertiary, Thanetian, Britain	Aragonite					
Arctica cordiformis (Sowerby)	Cretaceous, Albian, Britain	Argonite					

Table 12

DREISSENACEA

Species	Locality	Mineralogy	Outer layer	Inner layer	Myostraca		Observations
					Pallial	Adductor	
Dreissena polymorpha (Pallas)	Notts., England	Aragonite	Crossed-lamellar	Complex crossed-lamellar	Thin prismatic	—	Outer layer forms hinge
Dreissena polymorpha (Pallas)	Bessarabia	Aragonite					
Dreissena africana van Beneden	Nigeria	Aragonite					
Dreissena brandii	Eocene, Britain	Aragonite					

Table 13

GLOSSACEA

Species	Locality	Mineralogy	Outer layer	Inner layer	Myostraca		Observations
					Pallial	Adductor	
Glossus humanus (Linnaeus)	Isle of Man	Aragonite	Homogeneous	Complex crossed-lamellar with bands of myostracal-type prisms	Thin, prismatic	Thin, prismatic	Many prism bands in inner layer
Glossus humanus (Linnaeus)	Pleistocene Italy	Aragonite	Homogeneous	Complex crossed-lamellar with bands of myostracal-type prisms	Thin, prismatic	Thin, prismatic	Prism bands in inner layer
Meiocardia lamarckii (Reeve)	Japan	Aragonite	Crossed-lamellar	Complex crossed-lamellar structure	Thin, prismatic	—	

Table 14

CORBICULACEA

Species	Locality	Mineralogy	Outer layer	Inner layer	Myostraca		Observations
					Pallial	Adductor	
Corbicula fluminea (Lamarck)	Japan	Aragonite	Finely crossed-lamellar	Complex-crossed-lamellar	Indistinct	—	The complex-crossed lamellar layer shows laths arranged in very regular columns, as in the Limopsacea
Corbicula occidens Deshayes	India	Aragonite	Finely crossed-lamellar	Complex-crossed-lamellar	Indistinct	—	Inner layer as above
Corbicula sp.	Lake Nyanza	Aragonite	Finely crossed-lamellar	Complex crossed-lamellar	Indistinct	—	Inner layer as above
Cyrena inflata Say	Nicaragua	Aragonite	Finely crossed-lamellar	Complex crossed-lamellar	Thin, prismatic	—	The pallial myostracum is discontinuous
Polymesoda anomala (Deshayes)	Ecuador	Aragonite	Finely crossed-lamellar	Complex crossed-lamellar	Thin, prismatic	—	Thin sheets of myostracal-type prisms are present in the inner layer
Velorita cyprinoides (Gray)	Mangalore, India	Aragonite	Finely crossed-lamellar	Complex crossed-lamellar	Indistinct	—	Inner layer as in *C. fluminea*
Corbicula cordata (Morris)	Sparnacian, Britain	Aragonite					
Corbicula cuneiformis (Sowerby)	Sparnacian, Britain	Argonite					
Cyrena consobrina (Cailliaud)		Aragonite					
Pisidium amnicum Müller	Notts., England	Aragonite					

GLOSSACEA

(Plate 6, fig. 1)

Two species of this very small superfamily have been examined structurally and mineralogically. The shell consists of aragonite.

In *Glossus humanus* there is an outer layer which is largely homogeneous and an inner complex crossed-lamellar layer which is bounded by the trace of the pallial line. In some specimens and in some parts of the shell there is a faint vertical structure similar to crossed-lamellar structure (Plate 6, fig. 1). The inner layer is built of rather fine lamels and in all specimens there are many thin sheets of myostracal prisms. In very old individuals where the inner layer is thick these prism sheets become abundant and closely spaced; in some irregularities develop and spherulite patterns appear in some sections. This is probably due to the development of corrugations upon the accretionary surface.

In *Meiocardia lamarckii* there is an outer crossed-lamellar layer in which the lamels are distinct and arranged concentrically; within this there is an inner complex crossed-lamellar layer bounded by a thin prismatic pallial myostracum.

CORBICULACEA

(Plate 6, figs 2 & 4)

Six species of this superfamily have been examined structurally and ten mineralogically. The shell is totally aragonite.

Again two shell layers are present, an outer crossed-lamellar layer which forms the hinge and teeth and an inner complex crossed-lamellar layer bounded by the trace of the pallial line. In the outer layer the lamels are rather fine and arranged concentrically (Plate 6, fig. 4). In most forms no prismatic pallial myostracum is visible only a dense granular zone separating the layers. Prisms are however detectable in *Polymesoda* and *Velorita cyprinoides*. The inner complex crossed-lamellar layer is always built of rather coarse laths, and in all species of *Corbicula* examined and in *Velorita* these are arranged in columns as in the Limopascea (Taylor *et al*, 1969). Tubules were seen in *Pisidium amnicum*.

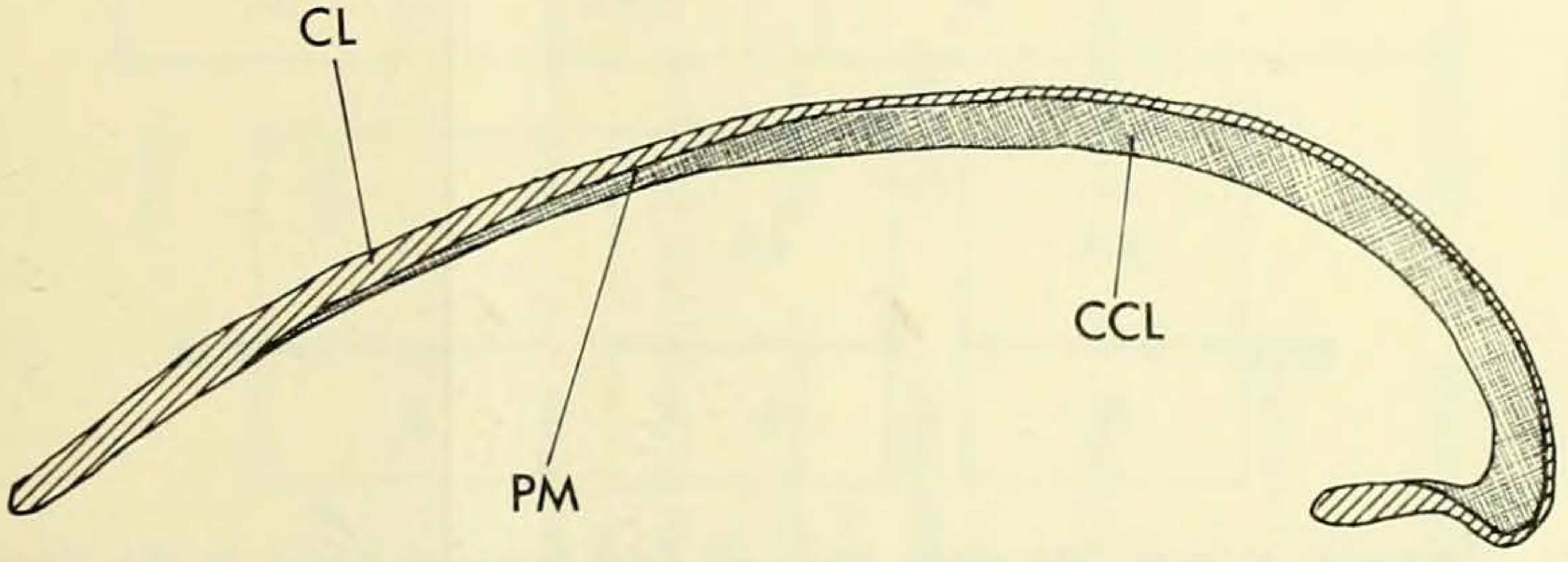


FIG. 16. Radial section of *Dreissena polymorpha*. CL = crossed-lamellar, CCL = complex crossed-lamellar, PM = pallial myostracum.

VENERACEA

(Plate 7, figs 1–5; Plate 8, figs 1–5; Text-figs 17–22)

This superfamily includes a large number of extant genera and species, consequently we have examined over fifty species structurally and mineralogically. The shell is aragonitic in all species. Both Bøggild (1930) and Oberling (1964) stated that the distribution of shell structure types is highly variable, thus in order to ascertain if there is any systematic variation we have listed and discussed the species examined at family and sub-family level. (Table 15).

The shell structural variations found are indeed more variable than any other superfamily. The various combinations are shown diagrammatically in Text-fig. 17. The apparently most important structural distinction is that between species having an outer composite prismatic layer and those without. The other variations exhibited between crossed-lamellar, complex crossed-lamellar and homogeneous structures almost always show transitions and all gradations between these structures may be found.

There is thus in many species a basically three layered shell consisting of an outer composite prismatic layer, a middle crossed-lamellar/homogeneous layer and an inner complex crossed-lamellar/homogeneous layer. In most other species the shell is basically two layered with an outer crossed-lamellar/homogenous layer and an inner complex crossed-lamellar/homogeneous layer.

The composite prismatic layer consists of radially aligned primary units made up of smaller crystallites radiating from a central axis (Plate 7, figs 1–5). Each of these smaller crystallites may be several mm. in length and 40 μ in diameter, but the size varies greatly from species to species. Each of these crystallites is surrounded by a sheath of organic matrix. Closer examination shows that each of the larger crystallites

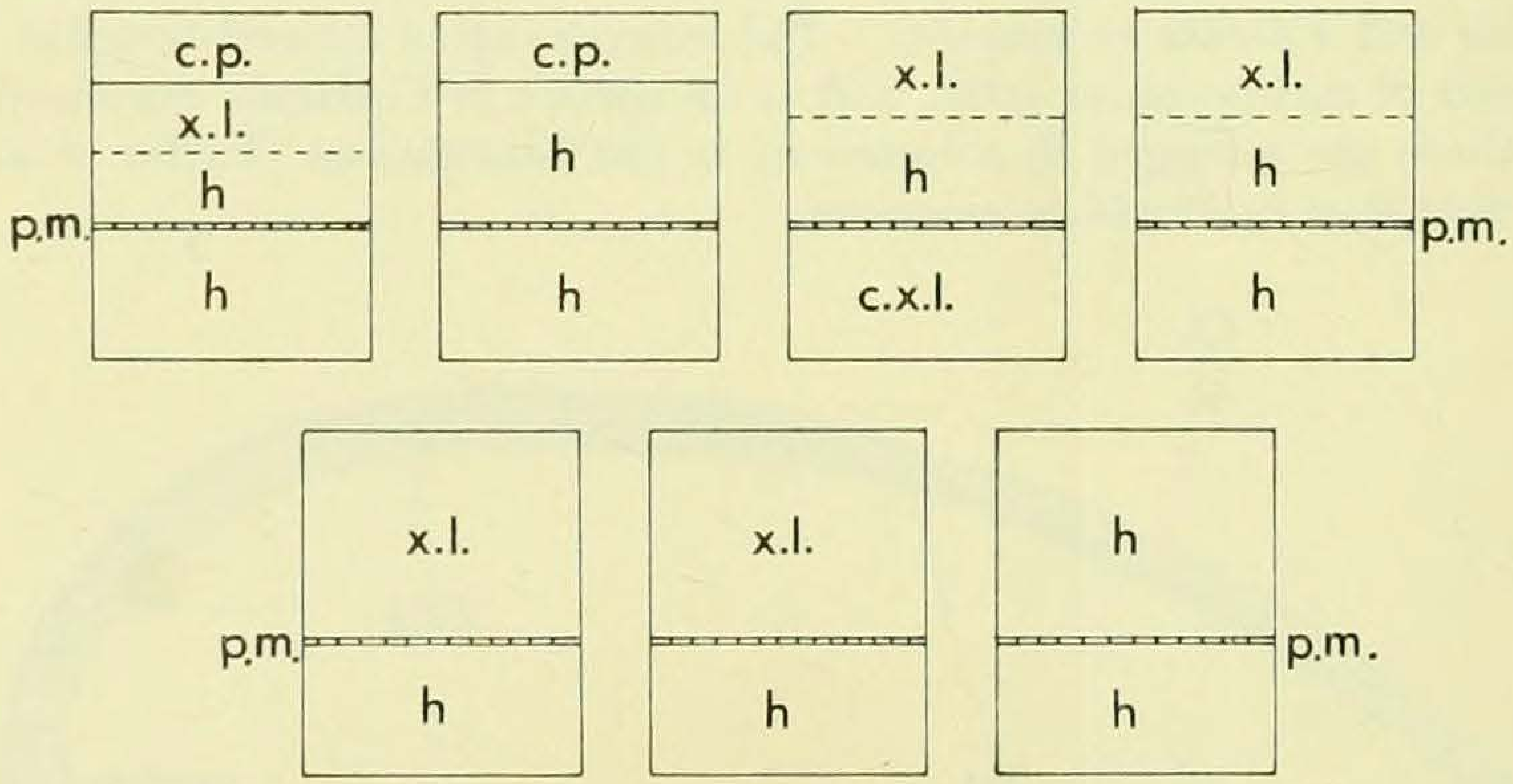


FIG. 17. Diagram showing the main types of shell layering found in the Veneracea. CP = composite prisms, CL = crossed-lamellar, CCL = complex crossed-lamellar, H = homogeneous, PM = pallial myostracum.

TABLE 15

VENERACEA

Species	Locality	Mineralogy	Outer layer	Middle layer	Inner layer	Pallial myostracum
Venerinae:						
Venus alata (Reeve)	Italy	Aragonite	Composite prismatic	Crossed-lamellar becoming homogeneous inwards	Homogeneous	Thin, prismatic
Venus striatula (da Costa)	Italy	Aragonite	Composite prismatic	Crossed-lamellar thin, becoming homogeneous inwards	Homogeneous	Thin, prismatic
Hysteroconcha dione (Linnaeus)	West Indies	Aragonite	Crossed-lamellar homogeneous inwards	—	Homogeneous	Prismatic
Hysteroconcha multispinosa (Sowerby)	Ecuador	Aragonite	Crossed-lamellar	—	Complex crossed-lamellar/homogeneous	
Lamelliconcha paytensis (d'Orbigny)	Ecuador	Aragonite	Crossed-lamellar	—	Complex crossed-lamellar	Thin, prismatic
Lioconcha asperrima (Sowerby)	Ecuador	Aragonite	Composite prismatic	Crossed-lamellar	Homogeneous/ complex crossed-lamellar	Thin, prismatic
Lioconcha castrensis (Linnaeus)	Queensland	Aragonite	Crossed-lamellar/ becoming homogeneous inwards	—	Complex crossed-lamellar	Thin, prismatic
Macrocallista squalida (Sowerby)		Aragonite	Crossed-lamellar, becoming homogeneous inwards	—	Homogeneous	
Pitar affinis (Gmelin)	Indian Ocean	Aragonite	Crossed-lamellar	—	Homogeneous	Thin, prismatic
Pitar sp.	Ecuador	Aragonite	Crossed-lamellar	—	Homogeneous	Thin, prismatic

Table 15

VENERACEA

Species	Locality	Mineralogy	Outer layer	Middle layer	Inner layer	Pallial myostracum
Venerinae:						
Venus alata (Reeve)	Italy	Aragonite	Composite prismatic	Crossed-lamellar becoming homogeneous inwards	Homogeneous	Thin, prismatic
Venus striatula (da Costa)	Italy	Aragonite	Composite prismatic	Crossed-lamellar thin, becoming homogeneous inwards	Homogeneous	Thin, prismatic
Venus subimbricata Sowerby	Central America	Aragonite	Crossed-lamellar, becoming homogeneous inwards	—	Homogeneous	Thin, prismatic
Venus verrucosa Linnaeus	Naples & Britain	Aragonite	Composite prismatic	Crossed-lamellar, becoming homogeneous inwards	Homogeneous	Thin, prismatic
Circomphalus plicata (Gmelin)	West Africa	Aragonite	Finely crossed-lamellar becoming homogeneous inwards	—	Homogeneous	Indistinct
Periglypta reticulata (Linnaeus)	Torres Str.	Aragonite	Composite prismatic	Crossed-lamellar, becoming homogeneous inwards	Complex crossed-lamellar with lenses of myostracal prisms	Prismatic
Circinae:						
Circe crocea Gray	Red Sea	Aragonite	Crossed-lamellar/ homogeneous inwards	—	Homogeneous	Indistinct
Circe intermedia (Reeve)	Aden	Aragonite	Crossed-lamellar/ homogeneous inwards	—	Homogeneous	Thin, prismatic
Circe scripta (Linnaeus)	Indo-Pacific	Aragonite	Crossed-lamellar/ homogeneous inwards	—	Complex crossed-lamellar, prism sheets	Prismatic
Gafrarium divaricatum (Gmelin)	East Indies	Aragonite	Crossed-lamellar/ homogeneous inwards	—	Complex crossed-lamellar with myostracal prisms	Prismatic
Gafrarium pectinatam (Linnaeus)	Indian Ocean	Aragonite	Crossed-lamellar/ homogeneous inwards	—	Complex crossed-lamellar with myostracal prisms	Prismatic
Gafrarium tumidum Bolten	Seychelles	Aragonite	Crossed-lamellar/ homogeneous inwards	—	Complex crossed-lamellar with myostracal prisms	Prismatic
Gouldia australis Angas	Australia	Aragonite	Finely crossed-lamellar	—	Homogeneous	
Gouldia cerina Gray	Bermuda	Aragonite	Finely crossed-lamellar	—	Homogeneous	
Sunnetinae:						
Sunetta solanderi (Gray)	Indian Ocean	Aragonite	Radial crossed-lamellar/ passing into homogeneous inwards	—	Homogeneous	Prismatic
Meretricinae:						
Meretrix dillwyni Reeve	Indian Ocean	Aragonite	Finely crossed-lamellar homogeneous inwards	—	Homogeneous	Prismatic
Tivela hians (Phillips)	Ecuador	Aragonite	Composite prismatic	Homogeneous	Homogeneous	Prismatic, indistinct
Tivela ponderosa Koch	Aden	Aragonite	Corossed-lamellar homogeneous inwards	—	Homogeneous	
Pitarinae:						
Agriopoma catharia Dall	Ecuador	Aragonite	Finely crossed-lamellar becoming homogeneous inwards	—	Homogeneous/ complex crossed-lamellar	Indistinct, prismatic
Amiantis erycina (Linnaeus)	Indian Ocean	Aragonite	Finely-crossed lamellar homogeneous inwards	—	Homogeneous	
Hysteroconcha dione (Linnaeus)	West Indies	Aragonite	Crossed-lamellar homogeneous inwards	—	Homogeneous	Prismatic
Hysteroconcha multispinosa (Sowerby)	Ecuador	Aragonite	Crossed-lamellar	—	Complex crossed-lamellar/homogeneous	
Lamelliconcha paytensis (d'Orbigny)	Ecuador	Aragonite	Crossed-lamellar	—	Complex crossed-lamellar	Thin, prismatic
Lioconcha asperrima (Sowerby)	Ecuador	Aragonite	Composite prismatic	Crossed-lamellar	Homogeneous/ complex crossed-lamellar	Thin, prismatic
Lioconcha castrensis (Linnaeus)	Queensland	Aragonite	Crossed-lamellar/ becoming homogeneous inwards	—	Complex crossed-lamellar	Thin, prismatic
Macrocallista squalida (Sowerby)		Aragonite	Crossed-lamellar, becoming homogeneous inwards	—	Homogeneous	
Pitar affinis (Gmelin)	Indian Ocean	Aragonite	Crossed-lamellar	—	Homogeneous	Thin, prismatic
Pitar sp.	Ecuador	Aragonite	Crossed-lamellar	—	Homogeneous	Thin, prismatic

TABLE 15 *Continued*

Species	Locality	Mineralogy	Outer layer	Middle layer	Inner layer	Pallial myostracum
Dosiniinae:						
Dosinia sp.	S. Carolina	Aragonite	Composite prisms	Crossed-lamellar becoming homogeneous inwards	Complex crossed-lamellar	Thin, prismatic
Dosinia annae Carpenter	Ecuador	Aragonite	Composite prismatic	Crossed-lamellar, homogeneous inwards	Complex crossed-lamellar	Thin, prismatic
Dosinia ponderosa (Gray)	Ecuador	Aragonite	Composite prismatic	Crossed-lamellar, homogeneous inwards	Complex crossed-lamellar	Thin, prismatic
Mercenaria mercenaria (Linnaeus)	England	Aragonite	Composite prismatic	Crossed-lamellar, becoming homogeneous inwards	Homogeneous	Thin, prismatic
Petricolidae:						
Petricola denticulata Sowerby	Ecuador	Aragonite	Crossed-lamellar	—	Complex crossed-lamellar	Thin, prismatic
Petricola pholadiformis Lamarck	Britain	Aragonite	Crossed-lamellar	—	Complex crossed-lamellar	Thin, prismatic
Petricola lithophaga (Retzius)	Mediterranean	Aragonite	Crossed-lamellar	—	Complex crossed-lamellar	
Cooperellidae:						
Cooperella subdiaphana Carpenter	California	Aragonite	Homogeneous	—	Homogeneous	

Species Locality Mineralogy Outer layer Middle layer Inner layer Pallial myostracum

TABLE 15 *Continued*

Species	Locality	Mineralogy	Outer layer	Middle layer	Inner layer	Pallial myostracum
Dosiniinae:						
Dosinia sp.	S. Carolina	Aragonite	Composite prisms	Crossed-lamellar becoming homogeneous inwards	Complex crossed-lamellar	Thin, prismatic
Dosinia annae Carpenter	Ecuador	Aragonite	Composite prismatic	Crossed-lamellar, homogeneous inwards	Complex crossed-lamellar	Thin, prismatic
Dosinia ponderosa (Gray)	Ecuador	Aragonite	Composite prismatic	Crossed-lamellar, homogeneous inwards	Complex crossed-lamellar	Thin, prismatic
Cyclininae:						
Cyclina chinensis (Bolten)		Aragonite	Crossed-lamellar, radial on outside, concentric inwards	—	Complex crossed-lamellar	Thin, prismatic
Gemminae:						
Gemma gemma (Totten)	U.S.A.	Aragonite	Crossed-lamellar, becoming homogeneous inwards	—	Homogeneous	
Tapetinae:						
Paphia textilis (Linnaeus)	China	Aragonite	Finely crossed-lamellar	—	Complex crossed-lamellar	Prismatic
Tapes litterata (Linnaeus)	Indian Ocean	Aragonite	Composite prismatic	—	Homogeneous	Thin, prismatic
Venerupis crenata (Lamarck)	Port Jackson	Aragonite	Composite prismatic	Crossed-lamellar becoming homogeneous inwards	Homogeneous	Thin, prismatic
Chioninae:						
Anomalocardia braziliana (Gmelin)	Brazil	Aragonite	Composite prismatic	Crossed-lamellar, becoming homogeneous inwards	Homogeneous	Thin, prismatic
Chione stutchburyi (Gray)	New Zealand	Aragonite	Crossed-lamellar/ homogeneous inwards	—	Complex crossed-lamellar/homogeneous	Prismatic
Chione granulata (Gmelin)	West Indies	Aragonite	Composite prismatic	Crossed-lamellar, becoming homogeneous	Homogeneous	Thin, prismatic
Chione paphia (Linnaeus)	West Indies	Aragonite	Composite prismatic	Crossed-lamellar, becoming homogeneous inwards	Homogeneous	Prismatic
Chione undatella Sowerby	California	Aragonite	Crossed-lamellar/ becoming homogeneous inwards	—	Homogeneous	Thin, prismatic
Chione subrugosa Sowerby	Ecuador	Aragonite	Composite prismatic	Crossed-lamellar/ becoming homogeneous inwards	Homogeneous	Thin, prismatic
Chionopsis guida (Sowerby & Broderip)	Ecuador	Aragonite	Composite prismatic	Crossed-lamellar/ becoming homogeneous inwards	Homogeneous	Thin, prismatic
Lirophora effosa (Bivona)	Madeira	Aragonite	Crossed-lamellar becoming homogeneous inwards	—	Homogeneous	Thin, prismatic
Lirophora peruviana (Sowerby)	Peru	Aragonite	Crossed-lamellar, becoming homogeneous inwards	—	Homogeneous/ complex-crossed-lamellar	Thin, prismatic
Perothaca jedoensis (Lischke)	Japan	Aragonite	Composite prismatic	Crossed-lamellar, homogeneous inwards	Homogeneous	Thin, prismatic
Mercenaria mercenaria (Linnaeus)	England	Aragonite	Composite prismatic	Crossed-lamellar, becoming homogeneous inwards	Homogeneous	Thin, prismatic
Petricolidae:						
Petricola denticulata Sowerby	Ecuador	Aragonite	Crossed-lamellar	—	Complex crossed-lamellar	Thin, prismatic
Petricola pholadiformis Lamarck	Britain	Aragonite	Crossed-lamellar	—	Complex crossed-lamellar	Thin, prismatic
Petricola lithophaga (Retzius)	Mediterranean	Aragonite	Crossed-lamellar	—	Complex crossed-lamellar	
Cooperellidae:						
Cooperella subdiaphana Carpenter	California	Aragonite	Homogeneous	—	Homogeneous	

Species Locality Mineralogy Outer layer Middle layer Inner layer Pallial myostracum

is made up of further smaller units about $0 \cdot 5\ \mu$ in diameter and diverging in a feathery manner from the central axis of the larger crystallites (Plate 7, fig. 4).

The outer layer is separated by various degrees of distinctiveness from the underlying crossed-lamellar layer which has concentrically aligned primary lamels (Plate 7, fig. 1). This middle layer changes to homogeneous structure when traced towards the shell interior. In some species the distinctly crossed-lamellar portion of the layer is almost entirely suppressed (Plate 7, fig. 2). The crossed-lamellar and homogeneous portions of the shell cannot be designated as separate layers for they vary in extent both between and within a species.

In two layered Veneracea the outer part of the outer layer consists of crossed-lamellar structure (Plate 8, figs 2 & 4) which passes transitionally inwards into homogeneous structure (Plate 8, fig. 3). The orientation of the lamels in the outer layer is controlled by the type of shell margin present in each species. In the Veneracea the marginal areas are variable with margins which are reflected, inflected, shelf-like or combinations of these. A further complication to the shape of the shape of the margin may be ribbing and strong concentric sculpture. With a reflected shell margin the first order lamels in the outer region of the outer shell layer lie

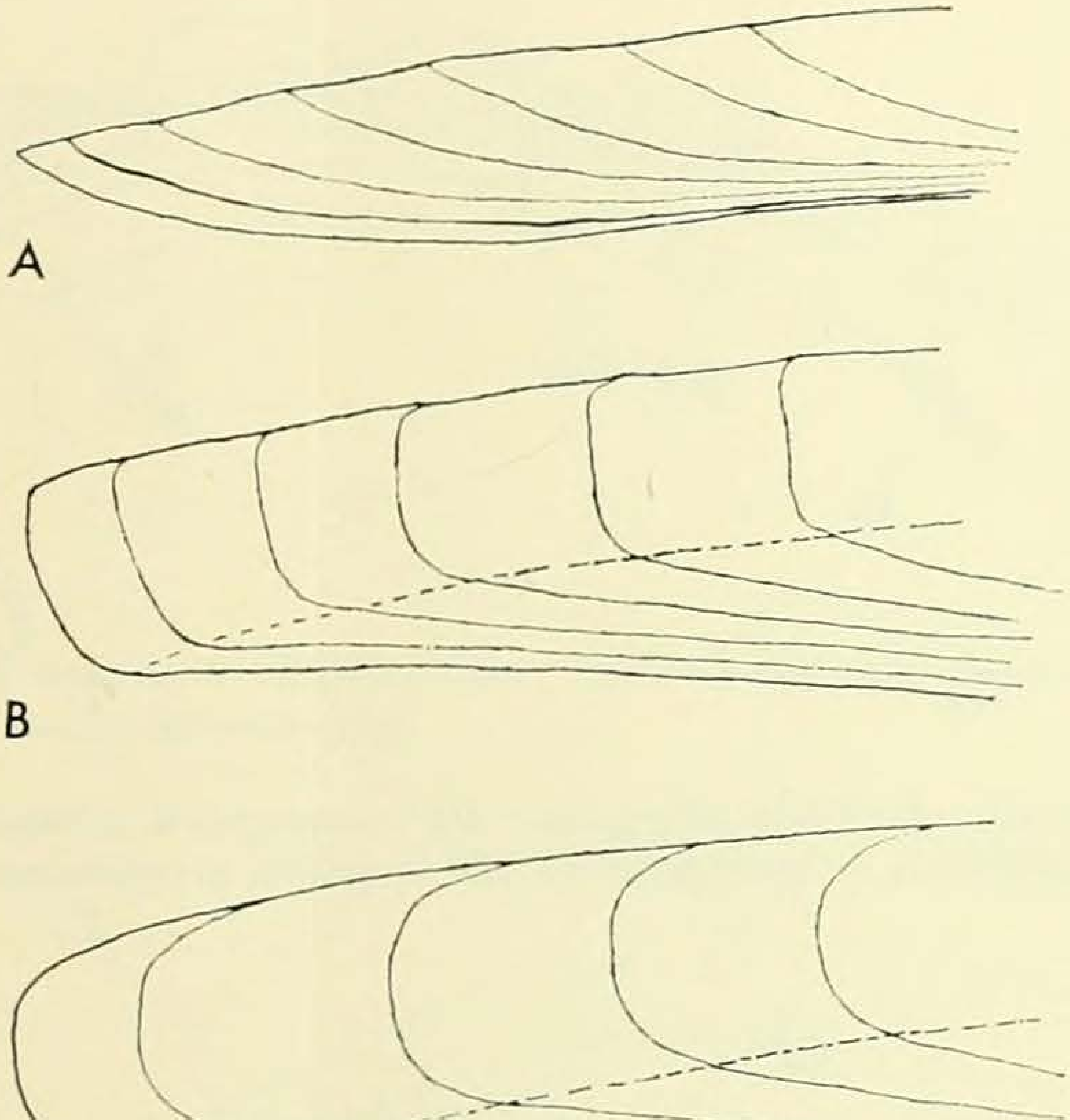


Fig. 18. Diagram showing radial sections of three types of shell margin found in the Veneracea. A. Here the margin is slightly reflected; there will be a gradual change from crossed-lamellar structure on the outside to homogeneous structure inwards. B. In this case the margin is strongly reflected and in the position marked by the dotted line there will be a sharp structural change. C. The margin is even more strongly reflected than in B and similarly there will be a sharp change in structure along the dotted line.

subparallel to the outer shell surface, although at the time of secretion, they were aligned normal to the secreting surface. With an inflected shell margin (Text-fig. 18) the first order lamels retain more of a concentric alignment. Again, when traced towards the shell interior the crossed-lamellae pass into homogeneous structure. The point at which the change takes place is usually where the reflection or inflection of growth lines changes rapidly. Further inwards from these points the growth increment lines are much more closely bunched suggesting a slower growth rate. The change from crossed-lamellar structure to homogeneous can thus be interpreted as a result of differential growth rates imposed by geometrical constraints caused by the shape of the shell margin.

In all cases the inner shell layer consists of complex crossed-lamellar or homogeneous structures or combinations of the two. Sheets of myostracal prisms are also common.

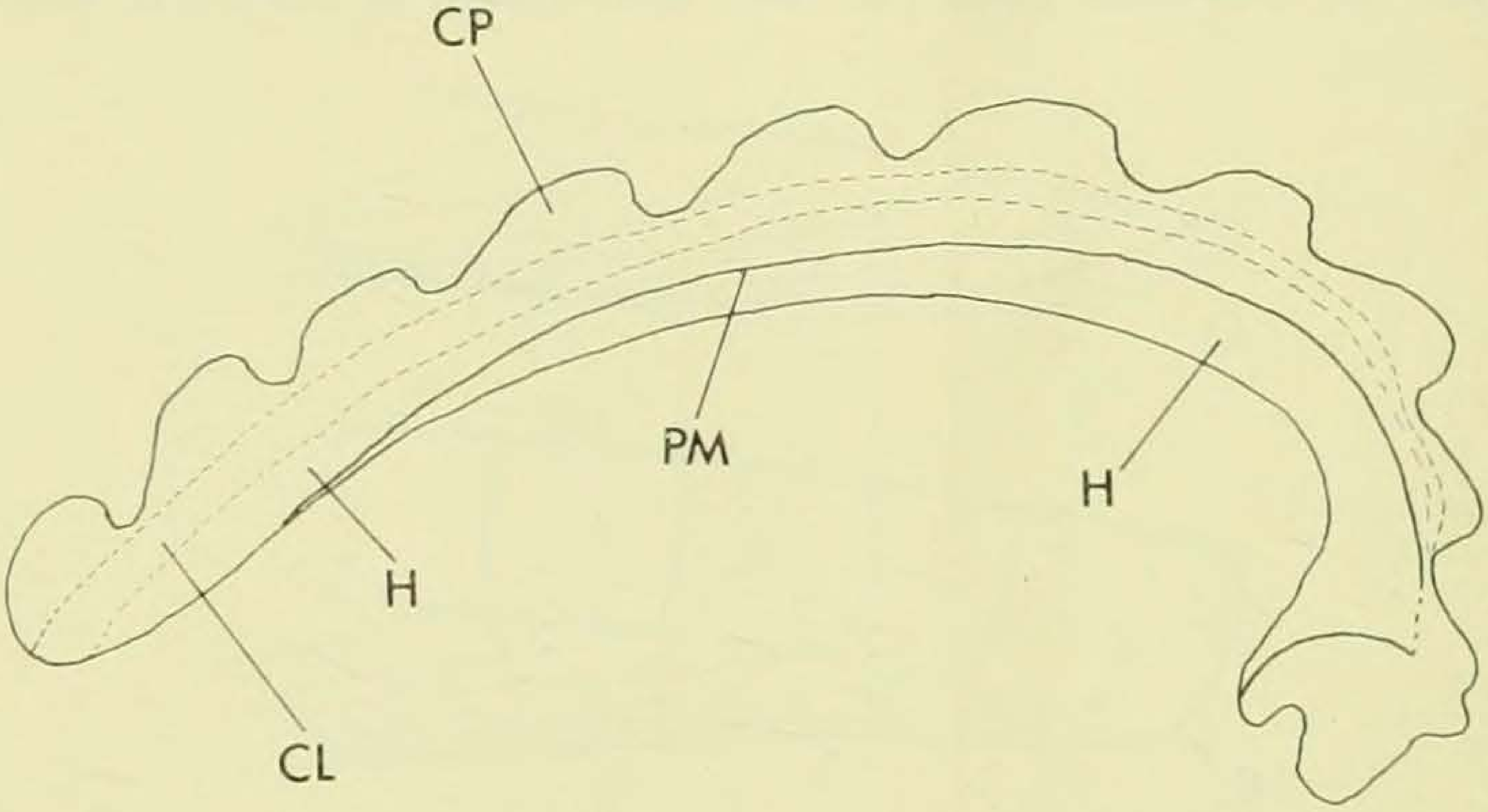


FIG. 19. Radial section of *Chione subrugosa*. CP = composite prismatic, CL = crossed-lamellar, h = homogeneous, PM = pallial myostracum.

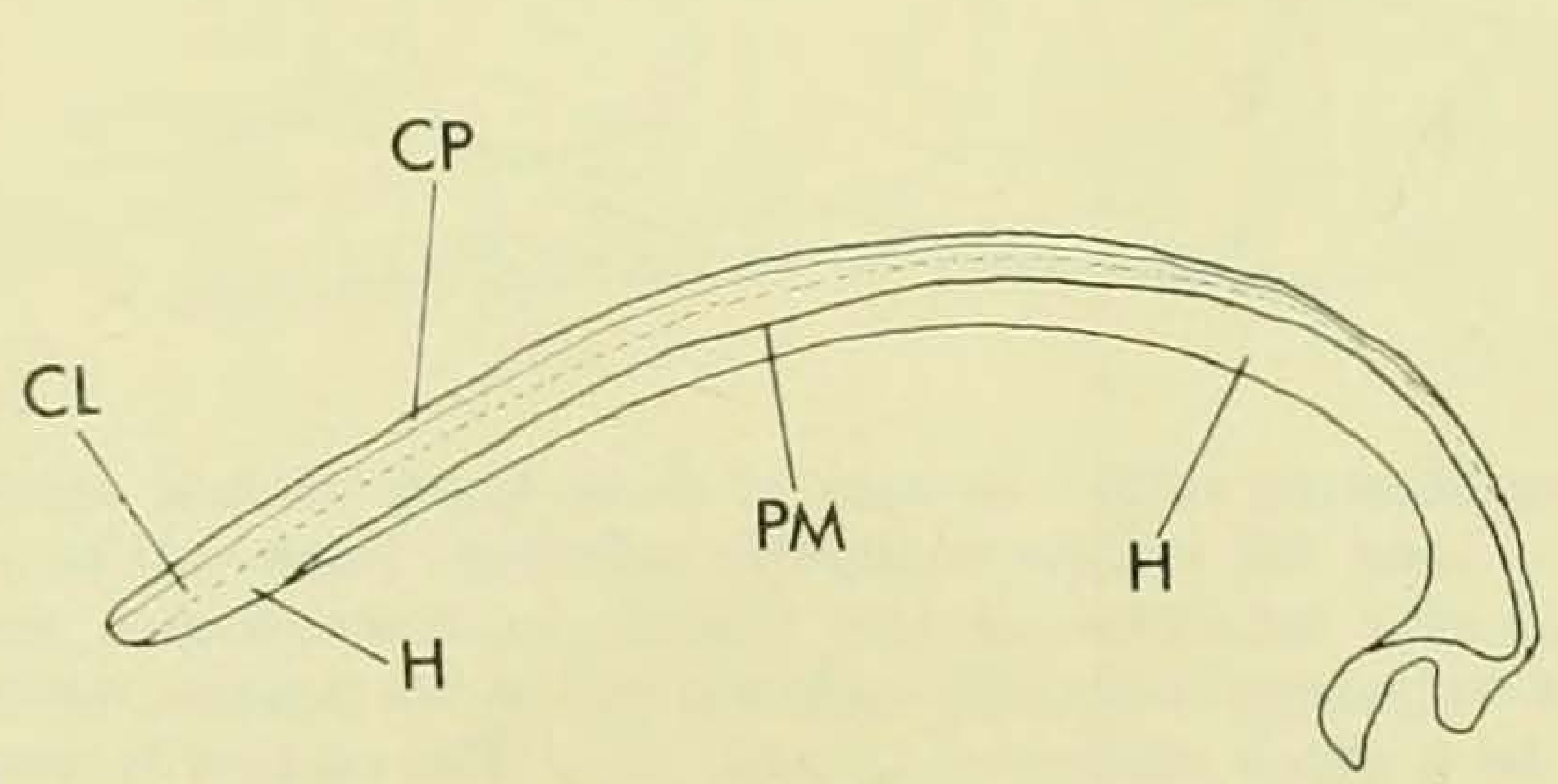


FIG. 20. Radial section of *Chamalea striatula*. CP = composite prisms, CL = crossed-lamellar, H = homogeneous, PM = pallial myostracum.

Subfamily **VENERINAE**

Most species in this group possess the three layered shell; composite prisms, crossed-lamellar/homogeneous and with one exception an inner homogeneous layer. Two species have only two layered shells. In *Periglypta puerpera* the inner layer is largely constructed of myostracal prisms with small areas of complex crossed-lamellar structure.

Subfamily **CIRCINAE**

All species in this group have the basic two layered shell. In most species there is a well defined prismatic pallial myostracum. The inner layer is variable; in the species of *Gafrarium* examined it is largely made up of myostracal prisms with small amounts of complex crossed-lamellar structure. In most other species it is homogeneous.

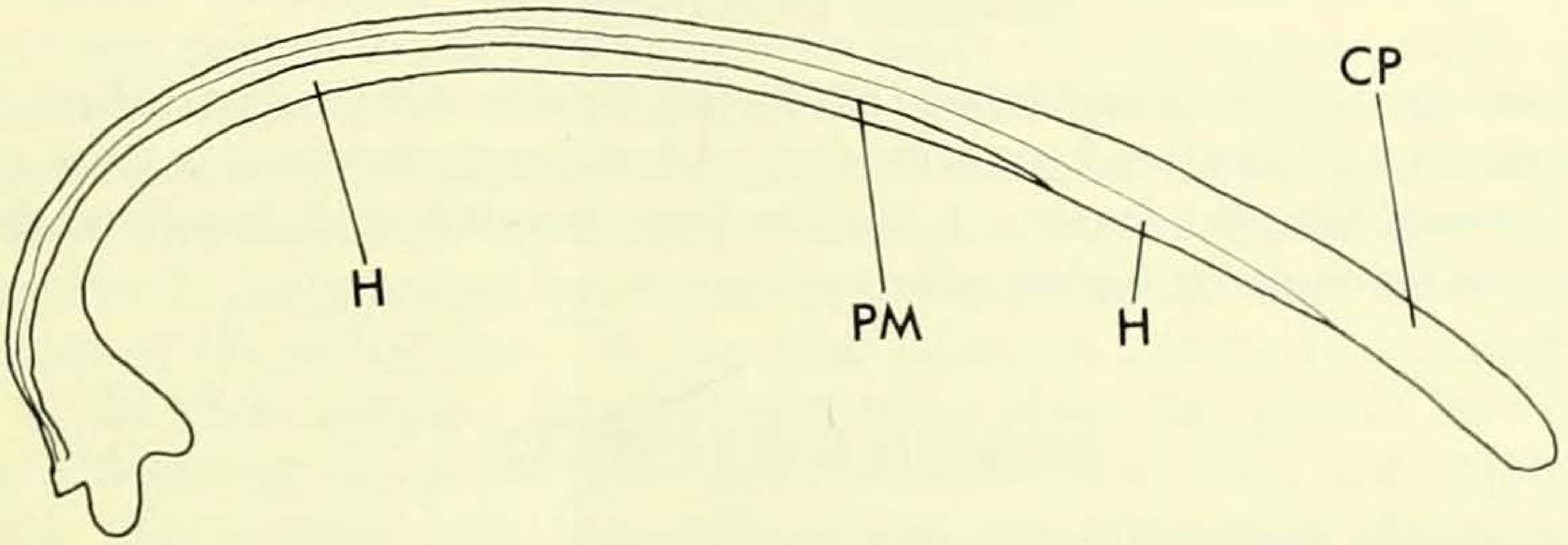


FIG. 21. Radial section of *Tivela hians*. CP = composite prisms, H = homogeneous, PM = pallial myostracum.

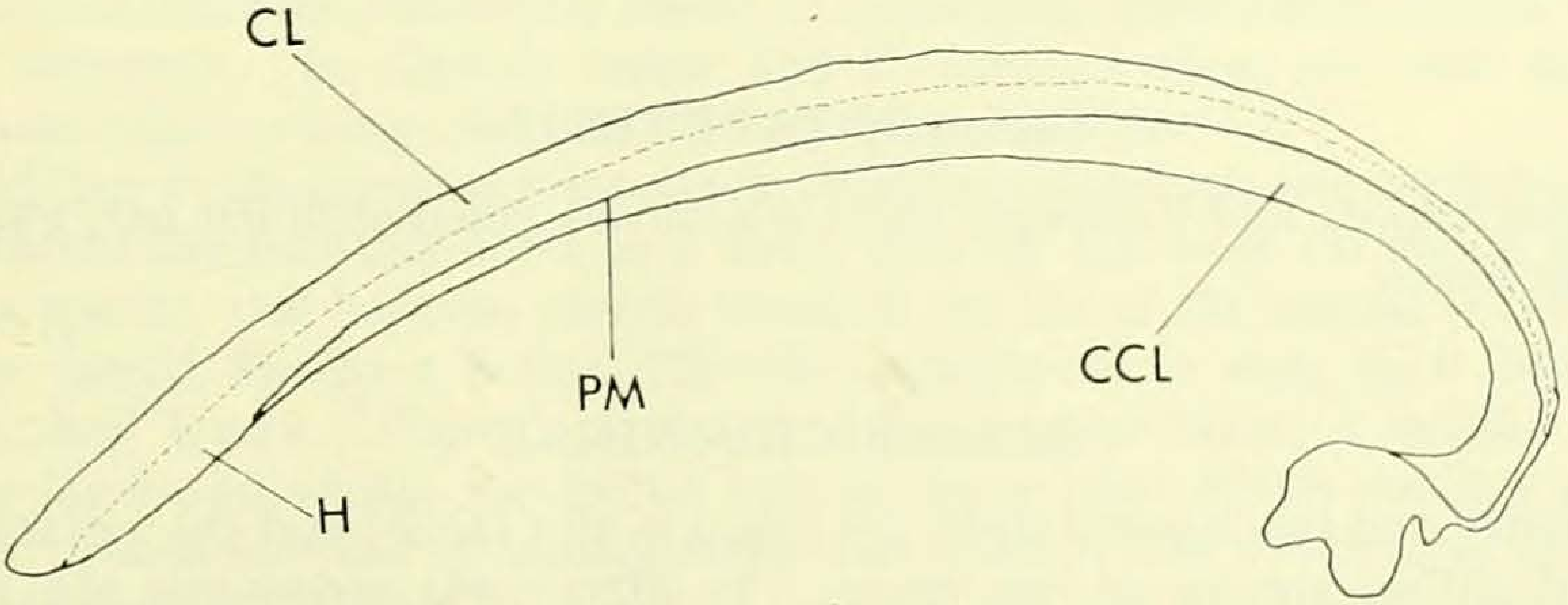


FIG. 22. Radial section of *Lioconcha castrensis*. CL = crossed-lamellar, H = homogeneous, PM = pallial myostracum, CCL = complex crossed-lamellar.

Subfamily SUNNETINAE

In *Sunetta solanderi* the margin is strongly reflected and the structure consists of outer crossed-lamellar structure, with the lamels radially aligned, which pass inwards into homogeneous structure. The inner layer is homogeneous with thin sheets of myostracal prisms.

Subfamily MERETRICINAE

In *Tivela hians* there is a three layered shell with the middle layer consisting entirely of homogeneous structure and also a homogeneous inner layer. *Tivela ponderosa* and *Meretrix* have a two layered shell.

Subfamily PITARINAE

Most of this family have a two layered shell but in *Lioconcha asperrima* there is an outer composite prismatic layer.

Subfamily DOSININAE

The three species examined in this group, all have a three layered shell, with an outer composite prismatic, a middle crossed-lamellar/homogeneous and an inner complex crossed-lamellar layer. A similar three layered shell has been described from *Dosinia japonica* by Kobayashi (1966).

Subfamily CYCLININAE

The one species examined has a two layered shell.

Subfamily GEMMINAE

Both species examined have a two layered shell.

Subfamily TAPETINAE

In *Tapes litterata* and *Venerupis* there is a three layered shell but only two layers in *Paphia textilis*.

Subfamily CHIONINAE

Both three and two layered shells are found in this family and the variation may be found within species of one genus. In *Mercenaria mercenaria* the crossed-lamellar portion of the middle layer is often indistinct but the structure is revealed by electron microscopy. Most species have an inner homogeneous layer.

Subfamily **PETRICOLIDAE**

This group has two layered shells; in the outer layer the crossed-lamellar structure does not grade inwards into homogeneous structure, as in most other Veneracea.

Subfamily **COOPERELLIDAE**

In the one species examined both layers consisted of homogeneous structure.

Order MYOIDA

MYACEA

(Plate 11, fig. 4; Text-figs 23–25)

Six species have been examined structurally and twelve mineralogically. The shell is aragonitic. The superfamily divides naturally into two groups the Corbulidae and the Myidae, these are discussed in turn.

In the family Corbulidae the shell is inaequivalve, the left valve being the smaller. The outermost part of the left valve consists solely of periostracum which fits like a flap against the right valve when the shell is closed (Yonge, 1946). In both valves, the periostracum may line the inner margin of the shell for some distance in preserved specimens. Two main shell layers are present, an outer crossed-lamellar layer which forms most of the hinge and an inner complex crossed-lamellar layer which is bounded by the trace of the pallial line. In the outer layer the lamels are arranged concentrically to the shell margin. In adult specimens where the growth rate is slower, marginal thickening has taken place and the periostracal flaps and extensions are frequently incorporated into the shell proper, by subsequent deposition. The periostracal flap of the left valve may even become incorporated into the shell of the right valve.

In most species there is a well developed pallial myostracum and within this there is the inner shell layer of complex crossed-lamellar structure which is fairly coarse. In all species there are commonly sheets of myostracal prisms interbedded with the normal structure. In *Corbula crassa* and *C. tunicata* there are well developed myostracal pillars arising from the trace of the pallial line.

In addition to the marginal periostracal flaps the animal appears capable of laying periostracum-like material down as a sheet, over all the inner surface of the shell. In some species, this happens several times in the life of the animal (Text-fig. 25).

In the family Myidae a rather different arrangement is seen, there being three distinct shell layers. There is an outer homogeneous layer, a middle crossed-lamellar layer and within the pallial line an inner layer which consists of either complex crossed-lamellar or homogeneous structures. The outer layer consists of granular crystals (Plate 11, fig. 4) about 5 μ in length and 2·5 μ in diameter with no obvious crystal form but with a slight elongation towards the shell margin. Although this layer is called homogeneous it differs from all other homogeneous

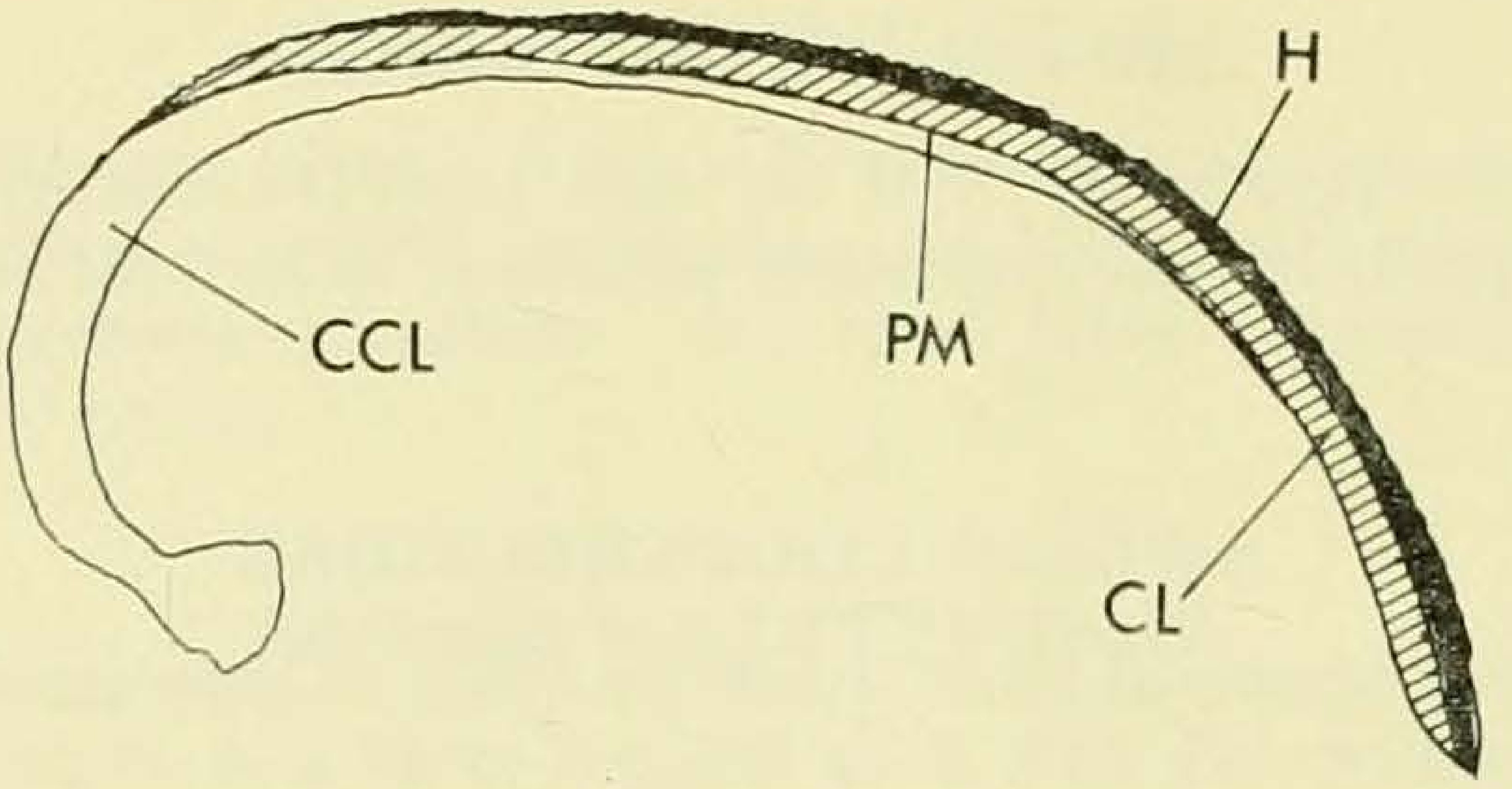


FIG. 23. Radial section of *Platydon cancellata*. H = homogeneous, CL = crossed-lamellar, PM = pallial myostracum, CCL = complex crossed-lamellar.

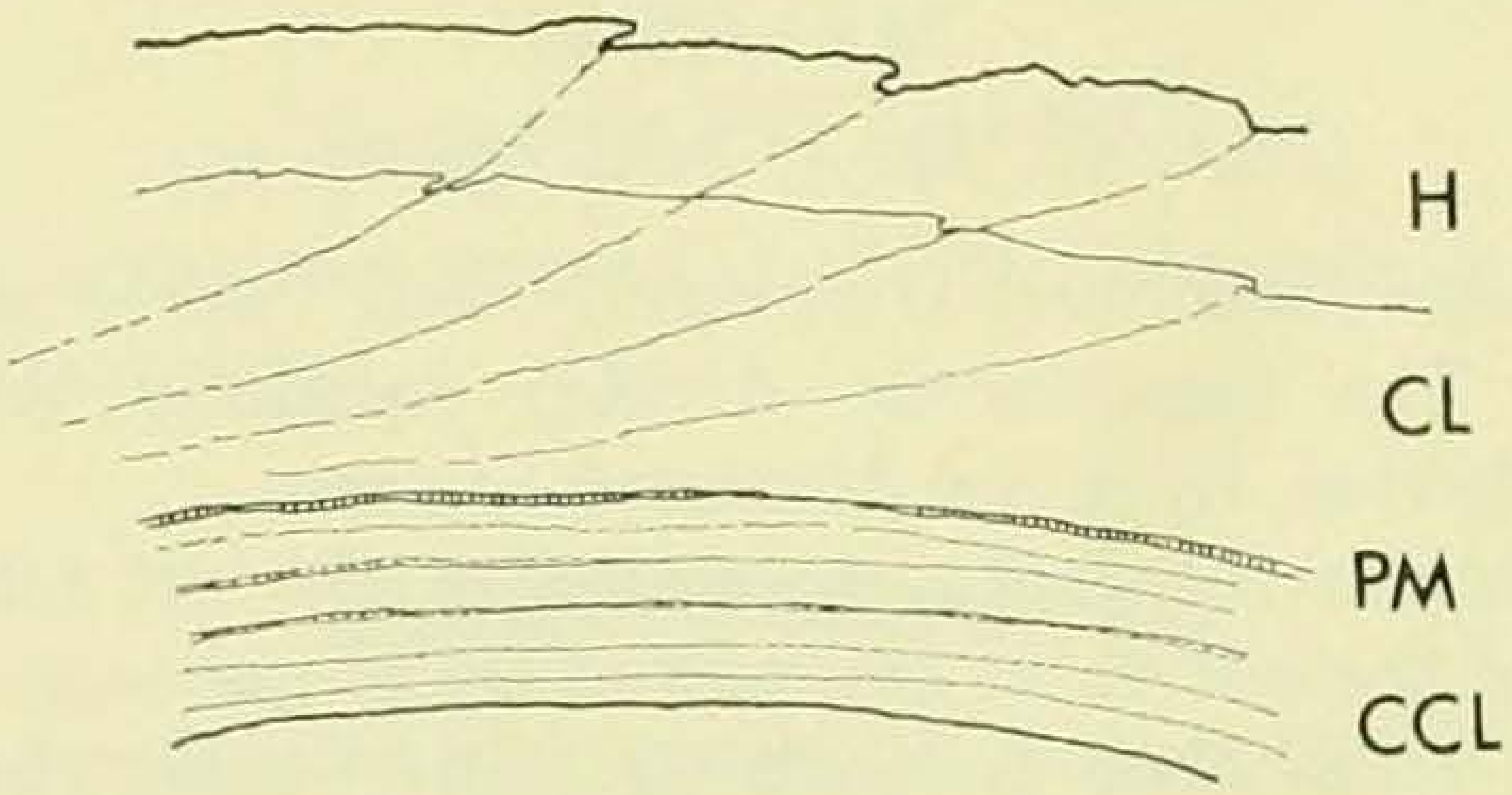


FIG. 24. Detail of shell layers in radial section of *Platydon cancellata*. H homogeneous, CL = crossed-lamellar, PM = pallial myostracum, CCL = complex crossed-lamellar.

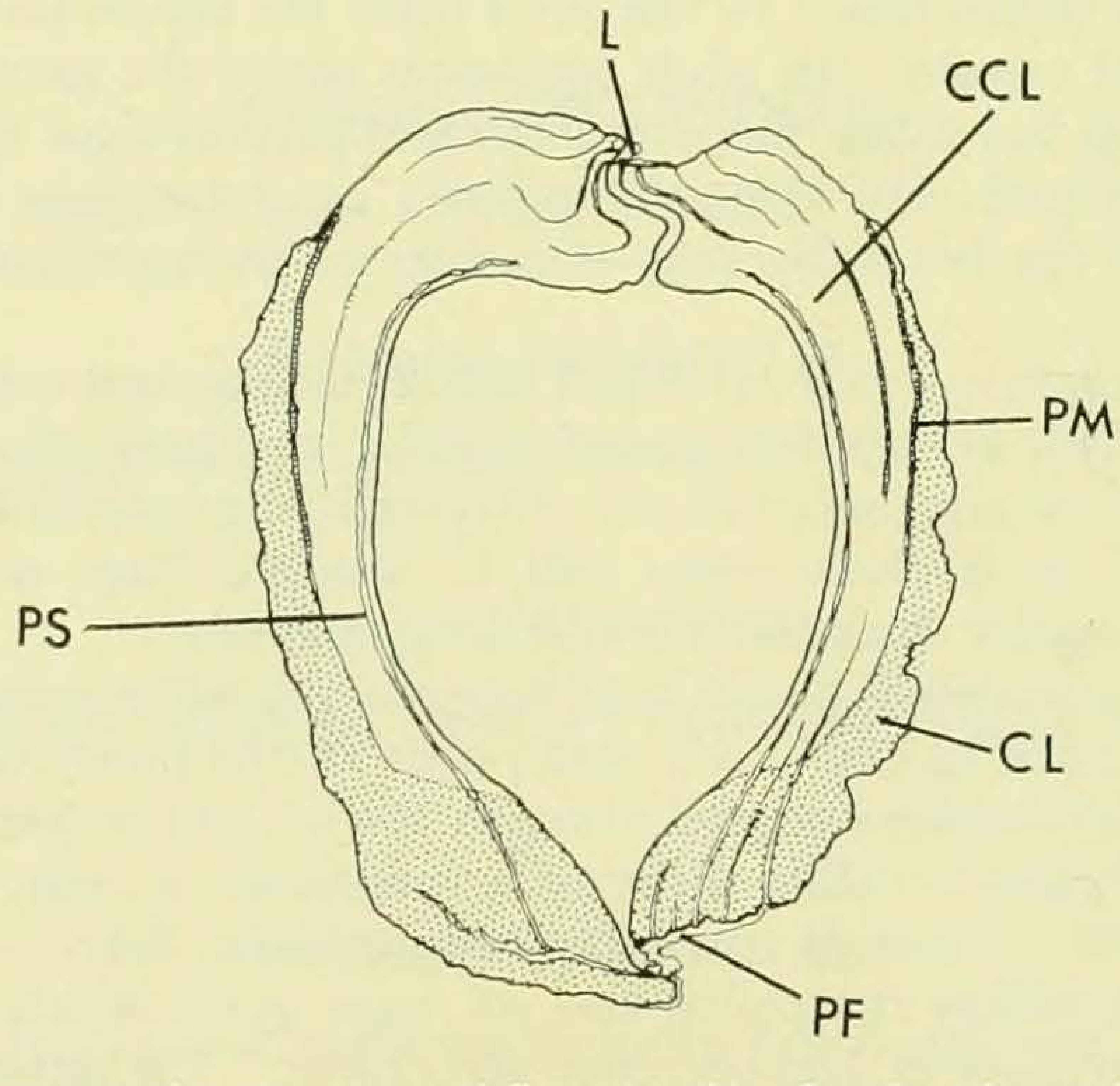


FIG. 25. Radial section of both valves of *Corbula gibba* showing the periostracal flaps (PF) and sheets (PS) incorporated into the shell a characteristic of this family. Other lettering; CL = crossed-lamellar, CCL = complex crossed-lamellar, PM = pallial myostracum, L = ligament.

structures we have recognized by appearing grey instead of brown in thin section. It is probable that the outer layer may have been derived by the degeneration of a phylogenetically earlier prismatic layer. The middle layer consists of very fine primary lamels, arranged concentrically. There is a thin, prismatic pallial myostracum in *Platydon cancellata* but only a sharp change in shell banding in *Mya arenaria*. Distinct sheets of myostracal prisms are often found in the inner layer.

GASTROCHAENACEA

Three species of this small superfamily of rock borers have been examined structurally and mineralogically. The shell is aragonitic.

The shell consists of two layers, an outer crossed-lamellar layer and an inner layer which may be complex crossed-lamellar or homogeneous. In all three species the outer layer has concentrically arranged lamels which pass transitionally inwards into homogeneous structure. The inner layer of *Gastrochaena gigantea* is complex crossed-lamellar but that of *G. ovata* and *G. truncata* is homogeneous, the former being distinctly lamellate. A thin prismatic pallial myostracum is present in all three species.

HIATELLACEA

(Plate 9, figs 1–4; Text-fig. 26)

This is a very small superfamily consisting of four extant genera, one of which *Panopea*, is divided into two subgenera *Panopea* and *Panomya*. Five species have been examined structurally and mineralogically, all are aragonitic.

In *Panopea* s.s. the shell consists of three layers, an outer simple prismatic layer which may be very thin, a middle homogeneous layer and an inner layer which may be homogeneous or complex crossed-lamellar. The simple prisms of the outer layer have rather irregular boundaries and orientations (Plate 9, fig. 1). They vary in width between 30–50 μ and are made up of smaller platy crystallites between 0·5–1·5 μ in width, which radiate from the central prism axis (Plate 9, fig. 3). The rate

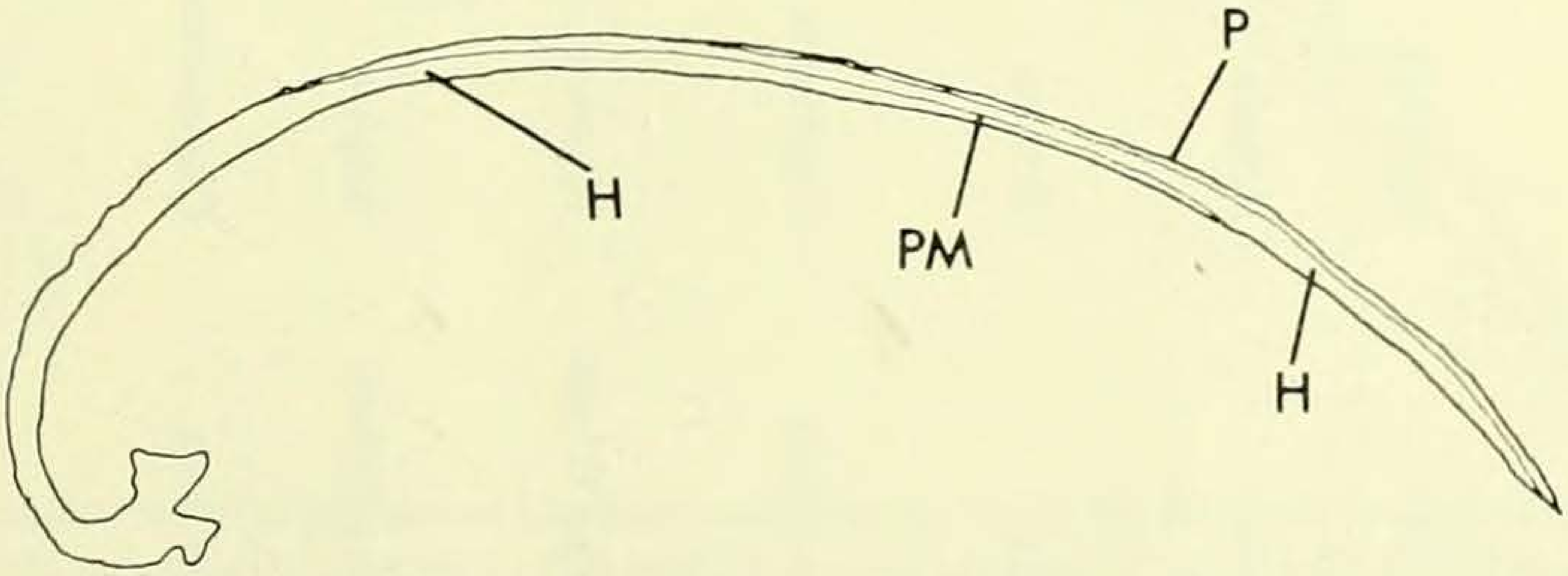


FIG. 26. Radial section of *Panopea zeylandica*. P = prisms, H = homogeneous, PM = pallial myostracum.

TABLE 16

MYACEA

Species	Locality	Mineralogy	Outer layer	Middle layer	Inner layer	Myostraca	
						Pallial	Adductor
Mya arenaria Linnaeus	Britain	Aragonite	Grey, granular homogeneous	Crossed-lamellar, fine	Finely complex crossed-lamellar with myostracal sheets	Prismatic	
Mya truncata Linnaeus	Britain	Aragonite	Grey, granular, homogeneous	Crossed-lamellar	Finely complex crossed-lamellar with myostracal sheets	Prismatic	
Platydon cancellata Conrad	California	Aragonite	Grey, granular, homogeneous	Crossed-lamellar	Complex crossed-lamellar with myostracal sheets	Prismatic, thin	
Corbula crassa Hinds	Japan	Aragonite	Crossed-lamellar	—	Complex crossed-lamellar with myostracal bands and pillars	Prismatic	Prismatic
Corbula gibba (Olivi)	Naples	Aragonite	Crossed-lamellar	—	Complex crossed-lamellar	Prismatic	
Corbula hydropica Iredale	Queensland	Aragonite	Crossed-lamellar	—	Complex crossed-lamellar with myostracal sheets and pillars	Prismatic	Prismatic
Caryocorbula amethystina Olsson	Ecuador	Aragonite	Crossed-lamellar	—	Complex crossed-lamellar with myostracal sheets and pillars	Prismatic	Prismatic

of divergence from the axis is high, so that the crystallites appear almost horizontal in relation to the axis (Plate 9, fig. 2). The middle homogeneous layer at high magnifications is seen to consist of short crystallites aligned in two directions (Plate 9, fig. 4) suggesting perhaps a transition to crossed-lamellar structure. The outer shell surface of *Panopea* is ornamented by granules arranged into rows radiating from the umbo.

In *Hiatella, Cyrtodaria* and *Panomya* there are only two layers. In all cases, the outer layer is homogeneous and excepting *Panomya* the inner layer is also homogeneous. In *Panomya* the inner layer may be homogeneous with thin prismatic sheets or it may consist of complex crossed-lamellar structure. In a specimen of *Hiatella arctica* from Spitzbergen the inner layer consisted almost entirely of myostracal prism sheets. Prismatic adductor myostraca were seen in *Panomya norvegica* and *Hiatella arctica*.

The presence of the outer simple prismatic layer in *Panopea* may be of considerable phylogenetic significance and this is discussed further in the conclusions.

PHOLADACEA

(Plate 10, figs 1–4; Plate 11, figs 1–3; Text-figs 27–29)

Two families constitute this superfamily the Pholadidae and the Teredinidae; these are discussed separately.

Eleven species of Pholadidae have been examined structurally and mineralogically; all species examined consisted of aragonite. Two main types of shell structure were found in this family. In three species examined there was a three layered shell consisting of an outer simple prismatic layer, a middle crossed-lamellar layer and an inner complex crossed-lamellar or homogeneous layer. The outer layer consists of prisms (Plate 11, fig. 3) very similar to those found in *Panopea* (Hiatellacea p. 34);

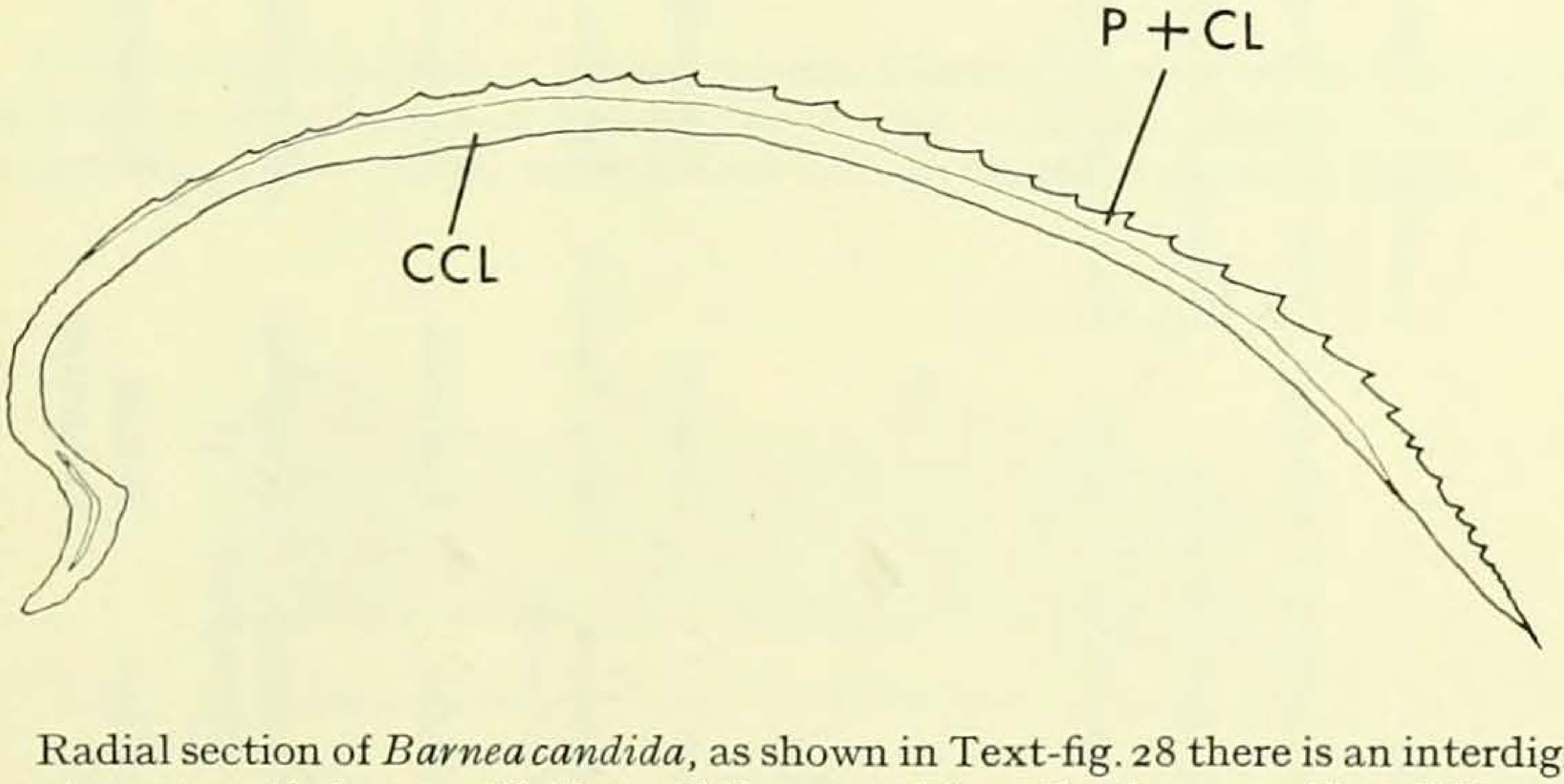


FIG. 27. Radial section of *Barnea candida*, as shown in Text-fig. 28 there is an interdigitation of the outer prismatic layer with the middle crossed-lamellar layer making differentiation at this magnification difficult. P = prisms, CL = crossed-lamellar, CCL = complex crossed-lamellar.

TABLE 17

GASTROCHAENACEA

Species	Locality	Mineralogy	Outer layer	Inner layer	Pallial myostracum
Gastrochaena gigantea Deshayes	India	Aragonite	Crossed-lamellar/homogeneous	Complex crossed-lamellar	Prismatic, thin
Gastrochaena ovata Sowerby	Panama	Aragonite	Crossed-lamellar/homogeneous	Complex crossed-lamellar	Prismatic, thin
Gastrochaena truncata Sowerby	Mazatlan	Aragonite	Crossed-lamellar/homogeneous	Homogeneous	Prismatic, thin

TABLE 18

HIATELLACEA

Species	Locality	Mineralogy	Outer layer	Middle layer	Inner layer	Pallial myostracum
Panopea zeylandica (Quoy & Gaimard)	New Zealand	Argonite	Simple prisms	Homogeneous	Homogeneous or complex crossed-lamellar	Prismatic
Panopea australis Sowerby	Australia	Argonite	Simple prisms	Homogeneous	Homogeneous or complex crossed lamellar	Prismatic
Panopea (*Panomya*) *norwegica* (Spengler)	North Sea	Aragonite	Homogeneous		Complex crossed-lamellar or homogeneous with prism sheets	Prismatic
Cyrtodaria siliqua (Spengler)	British Columbia	Aragonite	Homogeneous		Homogeneous	Prismatic
Hiatella arctica (Linnaeus)	Britain	Aragonite	Homogeneous		Homogeneous	Prismatic

the prisms are irregular in size, length, and orientation in contrast to the more regular arrangement found, for example, in the Unionacea. The prismatic layer is not deposited continuously, for as seen in Text-fig. 28, the imbricating concentric ornament of this family is formed by a cyclical deposition and non-deposition of the prismatic structure (Plate 11, figs 1–2). A ventral 'shoot' of crossed-lamellar structure corresponds with each period of non-deposition of prisms. The crossed-lamellar layer is usually thin and the first order lamels short and coarse. The inner layer within the pallial line may be homogeneous or complex crossed-lamellar and is frequently lamellate and may contain sheets of myostracal prisms.

In *Zirfaea crispata* there is also a three layered shell but the outer layer consists of grey homogeneous structure. The individual crystallites (Plate 10, figs 1 & 2) are approximately 5–10 μ long and 2–4 μ wide with a slightly elongate shape. In this species the concentric ornament consists entirely of homogeneous structure. The structure resembles that of the Myidae and is conceivably derived from the simple prisms described above for other pholads.

In all other species of Pholadidae examined there is a two layered shell, with the outer ribbing and ornament being formed from crossed-lamellar structure. The

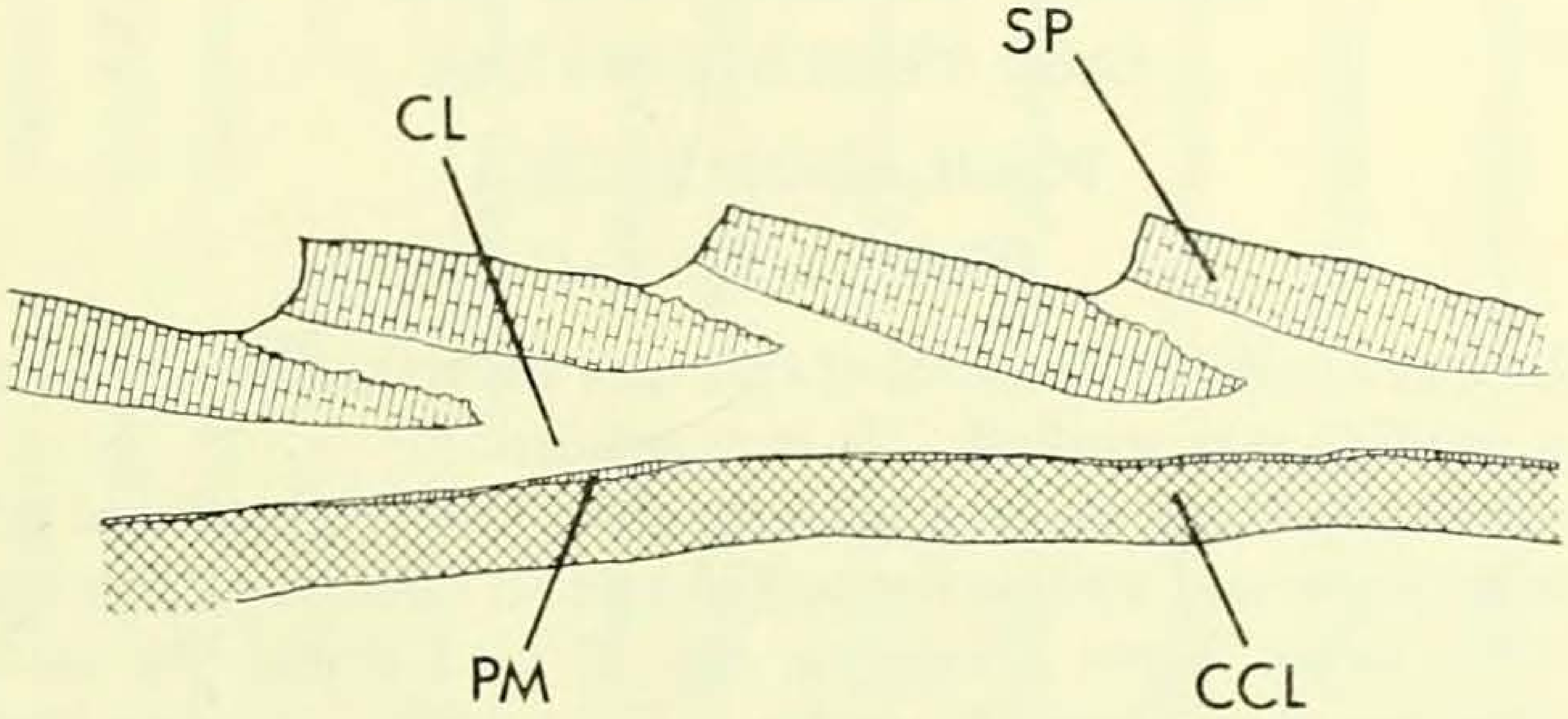


FIG. 28. Detail of radial section of *Barnea candida* showing the alternation of prismatic and crossed-lamellar structure in the outer layer. SP = simple aragonite prisms, CL = crossed-lamellar, PM = pallial myostracum, CCL = complex crossed-lamellar.

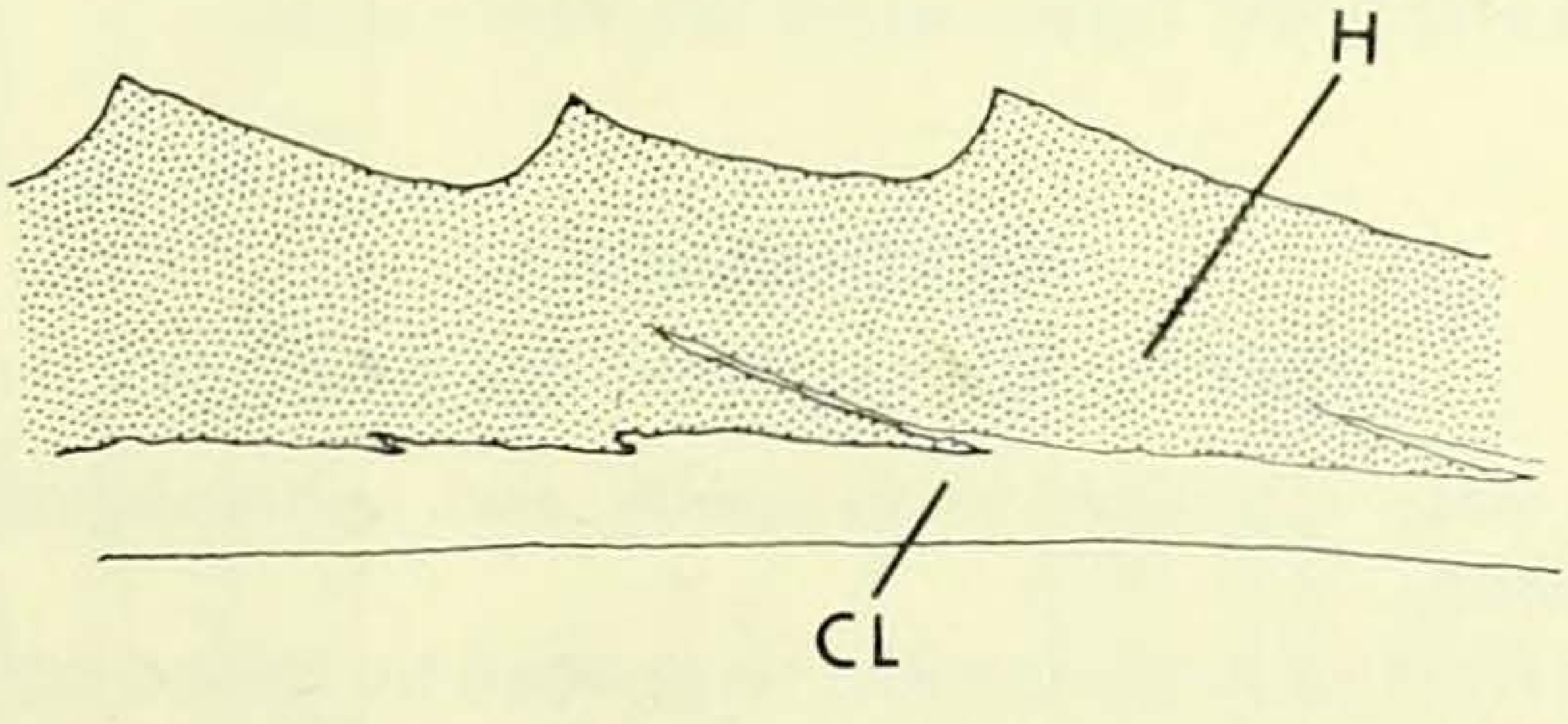


FIG. 29. Detail of a radial section of *Zirfaea crispata* showing outer homogeneous (H), and middle crossed-lamellar layer (CL).

strong umbonal reflections characteristic of the Pholadacea are formed from complex crossed-lamellar structure. Deposits of myostracal prisms occur beneath the adductor, pallial and other muscle attachment sites.

One species of Teredinae was examined structurally and mineralogically. The shell and tube are both aragonite.

The shell is nearly hemispherical in shape and complicated as in the Pholadidae by apophyses, shelves and condyles associated with the wood-boring habit (Turner, 1966). The shell is basically two layered, with an outer crossed-lamellar (Plate 10, figs 3 & 4) and an inner complex crossed-lamellar layer. The outermost part of the outer layer shows strongly reflected growth lines and the crossed-lamels are consequently radially aligned. In addition the lamels are very fine and present an almost homogeneous appearance. The complex crossed-lamellar layer is restricted to the umbonal ridge. Pads of myostracal prisms were seen beneath the large posterior adductor and beneath the anterior adductor which is situated on the umbonal reflection. The ventral condyle has homogeneous structure.

The calcareous tube which is secreted by the mantle surrounding the siphon tips consists of layers of irregular granular crystals about 5–10 μ in diameter.

Sub-Class *ANOMALODESMATA*

Order PHOLADOMYINA

PHOLADOMYACEA

(Plate 12, figs 1–4)

Because of lack of available material of this rare superfamily only a small fragment of *Pholadomya candida* was studied. It is aragonitic.

The shell is basically three layered with an outer very thin simple prismatic layer a middle nacreous layer and within the pallial line an inner nacreous inner (Plate 12, fig. 1). The thin outer layer (Plate 12, fig. 1) also forms the surface granules arranged in radiating rows from the umbo. The middle nacreous layer appears to be 'Treppen' structure of Wise (1970) (Plate 12, fig. 4) and the inner nacre to be sheet nacre. The inner part of the inner layer consists of alternations of thin sheets of nacre with layers of myostracal prisms which form the dominant component (Plate 12, figs 2 & 3). Because of the very limited sampling it is not certain how typical the myostracal prism layers are of the whole shell.

PANDORACEA

(Plate 13, figs 1–4; Text-figs 30 & 31)

Sixteen species were examined structurally and mineralogically. The shell is aragonitic throughout.

Representatives from all seven families recognized by Moore (1969) were examined and two distinct structural arrangements were found. One of these, with both layers consisting of homogeneous structure, is found in the Thracidae alone; all the

TABLE 19

PHOLADACEA

Species	Locality	Mineralogy	Outer layer	Middle layer	Inner layer	Myostraca	
						Pallial	Adductor
Barnea candida (Linnaeus)	Britain	Aragonite	Prismatic	Crossed-lamellar	Complex crossed-lamellar	Prismatic	
Pholas chiloensis Molina	Ecuador	Aragonite	Prismatic	Crossed-lamellar	Complex crossed-lamellar	Prismatic	
Pholas dactylus Linnaeus	Britain	Aragonite	Prismatic	Crossed-lamellar	Complex crossed-lamellar	Prismatic	
Parapholas acuminata (Sowerby)	Ecuador	Aragonite	Crossed-lamellar	—	Complex crossed-lamellar	Prismatic	

POROMYACEA

Species	Locality	Mineralogy	Outer layer	Middle layer	Inner layer	Pallial myostraca
Euciroa eburnea (Wood-Mason & Alcock)	Andamans	Aragonite	Simple prisms	Lenticular nacre	Sheet naclre	Prismatic, thin
Verticordia deshayesiana (Fischer)	Atlantic	Aragonite	Simple prisms	Lenticular nacre	Sheet nacre	Prismatic
Pecchiola argentea Savi & Meneghini	Italy	Aragonite	Simple prisms	Lenticular nacre	Sheet nacre	Prismatic
Poromya granulata (Nyst & Westendrop)	Britain	Aragonite	Homogeneous	Nacre	Sheet nacre	Prismatic
Cuspidaria arctica (Sars)	Norway	Aragonite	Homogeneous	—	Homogeneous	Indistinct
Cuspidaria chinensis (Griffith & Pidgeon)	Borneo	Aragonite	Homogeneous	—	Homogeneous	
Cuspidaria rostrata (Spengler)	Britain	Aragonite	Homogeneous	—	Homogeneous	Indistinct

TABLE 19

PHOLADACEA

Species	Locality	Mineralogy	Outer layer	Middle layer	Inner layer	Myostraca	
						Pallial	Adductor
Barnea candida (Linnaeus)	Britain	Aragonite	Prismatic	Crossed-lamellar	Complex crossed-lamellar	Prismatic	
Pholas chiloensis Molina	Ecuador	Aragonite	Prismatic	Crossed-lamellar	Complex crossed-lamellar	Prismatic	
Pholas dactylus Linnaeus	Britain	Aragonite	Prismatic	Crossed-lamellar	Complex crossed-lamellar	Prismatic	
Parapholas acuminata (Sowerby)	Ecuador	Aragonite	Crossed-lamellar	—	Complex crossed-lamellar	Prismatic	
Martesia striata (Linnaeus)	Trinidad	Aragonite	Crossed-lamellar	—	Complex crossed-lamellar	Prismatic	
Pholadidea loscombiana Turton	Britain	Aragonite	Crossed-lamellar	—	Complex crossed-lamellar	Prismatic	
Zirfaea crispata (Linnaeus)	Britain	Aragonite	Grey, granular, homogeneous	Crossed-lamellar	Complex crossed-lamellar	Prismatic	Prismatic
Teredo navalis (Linnaeus)	Britain	Aragonite	Crossed-lamellar	—	Complex crossed-lamellar	Prismatic	Prismatic

TABLE 20

PANDORACEA

Species	Locality	Mineralogy	Outer layer	Middle layer	Inner layer	Myostraca	
						Pallial	Adductor
Pandora arcuata Sowerby	Ecuador	Aragonite	Simple prisms	Lenticular nacre	Sheet nacre	Thin, prismatic	Prismatic
Pandora albida (Roding)	Naples	Aragonite	Simple prisms	Lenticular nacre	Sheet nacre		
Pandora trilineata Say	Eastern U.S.A.	Aragonite	Simple prisms	Lenticular nacre	Sheet nacre		
Periploma inaequivalvis Schumacher	Jamaica	Aragonite	Simple prisms	Lenticular nacre	Sheet nacre	Thin, prismatic	
Offadesma angasi (Crosse & Fischer)	Australia	Aragonite	Simple prisms	Nacre	Sheet nacre		
Laternula anatina (Linnaeus)		Aragonite	Simple prisms	Lenticular nacre	Sheet nacre		
Myadora brevis Sowerby		Aragonite	Simple prisms	Lenticular nacre	Sheet nacre and myostracal prisms	Prismatic	Prismatic
Myadora striata (Quoy & Gaimard)	Auckland	Aragonite	Simple prisms	Lenticular nacre	Sheet nacre and myostracal prisms	Prismatic	
Myadora tasmanica Wood	Tasmania	Aragonite	Simple prisms	Lenticular nacre	Sheet nacre and myostracal prisms	Prismatic	
Cleidothaerus albida Lamarck	N.S. Wales	Aragonite	Simple prisms	Lenticular nacre	Sheet nacre	Prismatic	Prismatic
Myochama amomoides (Stutchbury)	Australia	Aragonite	Simple prisms	Lenticular nacre	Sheet nacre	Prismatic	Prismatic
Kennerlya sp.	California	Aragonite	Simple prisms	Lenticular nacre	Sheet nacre	Prismatic	
Thracia convexa Wood	Britain	Aragonite	Homogeneous		Homogeneous	Trace	
Thracia phaseolina (Lamarck)	Britain	Aragonite	Homogeneous		Homogeneous	Trace	
Thracia villiosusulca (Macgillivray)	Britain	Aragonite	Homogeneous		Homogeneous		

TABLE 21

POROMYACEA

Species	Locality	Mineralogy	Outer layer	Middle layer	Inner layer	Pallial myostraca
Euciroa eburnea (Wood-Mason & Alcock)	Andamans	Aragonite	Simple prisms	Lenticular nacre	Sheet naclre	Prismatic, thin
Verticordia deshayesiana (Fischer)	Atlantic	Aragonite	Simple prisms	Lenticular nacre	Sheet nacre	Prismatic
Pecchiola argentea Savi & Meneghini	Italy	Aragonite	Simple prisms	Lenticular nacre	Sheet nacre	Prismatic
Poromya granulata (Nyst & Westendrop)	Britain	Aragonite	Homogeneous	Nacre	Sheet nacre	Prismatic
Cuspidaria arctica (Sars)	Norway	Aragonite	Homogeneous	—	Homogeneous	Indistinct
Cuspidaria chinensis (Griffith & Pidgeon)	Borneo	Aragonite	Homogeneous	—	Homogeneous	
Cuspidaria rostrata (Spengler)	Britain	Aragonite	Homogeneous	—	Homogeneous	Indistinct

other families have a three layered shell consisting of an outer simple prismatic layer a middle lenticular nacre layer and an inner sheet nacre layer. The outer simple prism layer is very thin and frequently worn off much of the shell. In most species examined a thin pallial myostracum separated the middle and inner nacreous layers. In *Myadora striata* most of the inner layer consists of myostracal prisms. Radial rows of granules are present on the outside of the shell in many species.

In the three species of *Thracia* examined, the two layered shell consists of homogeneous structure in both layers. Two species were examined at high magnifications and the inner surface of the shell appears granular with irregular crystals about 3 μ in diameter. In section these crystals are slightly flattened and have a slightly laminar arrangement. On the outside of the shell patterns of granules are seen (Tebble, 1966, fig. 103), when these are examined more closely they are seen to be isolated spherulitic structures (Plate 13, figs 1–4). These spherulites are made up of smaller crystallites (Plate 13, fig. 3) about 3 μ in length. The spherules form columnar growths intercalated with layers of periostracum (Plate 13, fig. 2). Eventually as growth proceeds these spherulites merge together and the crystal arrangement passes into a uniform homogeneous structure.

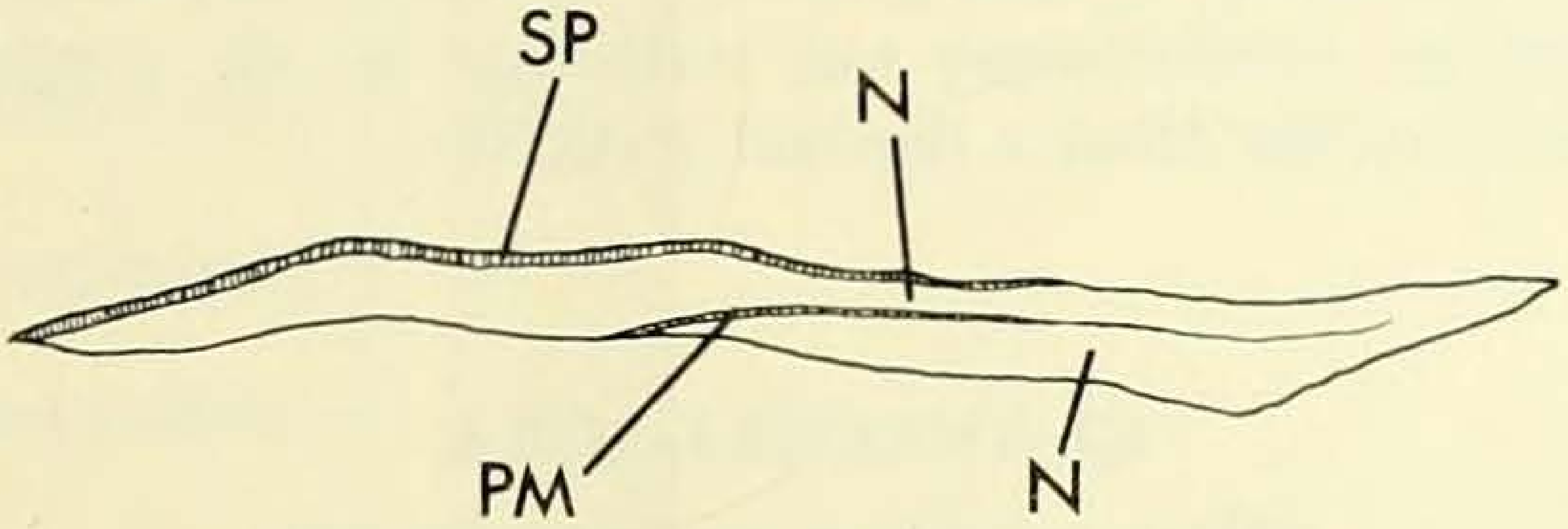


FIG. 30. Radial section of the flat right valve of *Pandora albida*. SP = aragonite simple prisms, N = nacre, PM = pallial myostracum.

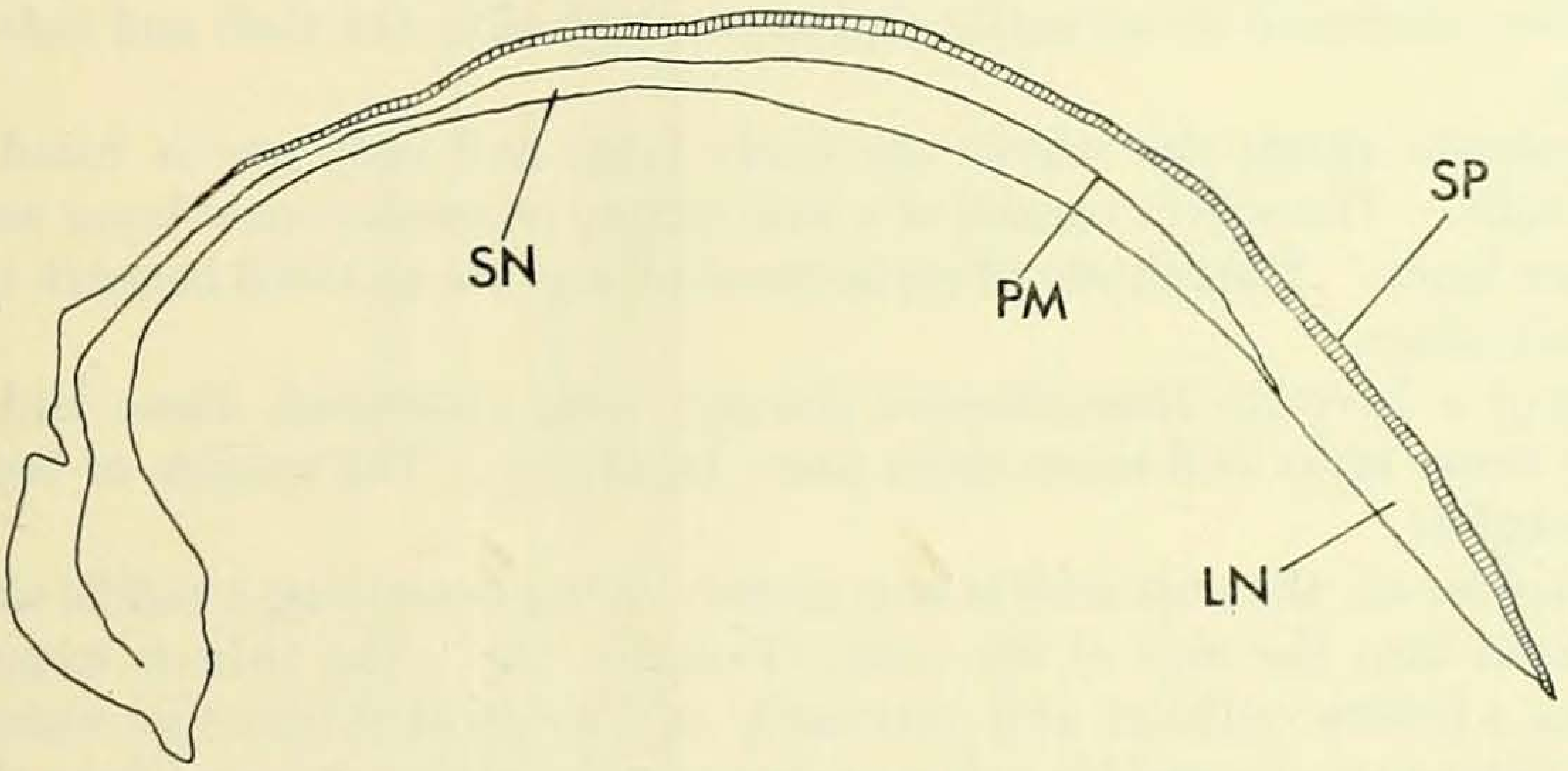


FIG. 31. Radial section of *Cleidothaerus albida*. SP = simple prisms, LN = lenticular nacre, PM = pallial myostracum, SN = sheet nacre.

Order POROMYOIDA

POROMYACEA

(Plate 13, figs 5; Plate 14, figs 1–5)

Seven species were examined structurally and mineralogically. The shell is aragonitic.

This superfamilyis represented by three families, the Poromyidae, the Cuspidaridae and the Verticordidae. The latter have a three layered shell consisting of an outer, simple prismatic layer, a lenticular nacre a middle layer and a sheet nacre inner layer. The middle and inner layers are separated by a thin sheet of pallial myostracal prisms. The shell structure is generally similar to that of most of the Pandoracea; in *Euciroa* the prisms are irregular (Plate 13, fig. 5) and resemble those of *Panopea* (Hiatellacea). In *Poromya granulata* there is a three layered shell as above but the outer layer consists of granular homogeneous structure probably phylogenetically derived from a structural breakdown of simple prismatic structure (Plate 14, figs 2 & 4).

The Cuspidaridae and some Poromyidae both have a two layered shell with homogeneous structure in both layers. The granules of the homogeneous layers are about 2 μ in size (Plate 14, fig. 5) and generally similar in appearance to those of the Thracidae. The pallial myostracum was indistinct in the species examined and shows a discontinuity rather than a distinct structure.

CLAVAGELLACEA

(Plate 15, figs 1–5; Text-fig. 32)

This is a small highly aberrant superfamily which consists of three extant genera *Clavagella, Humphreysia* and *Penicillus* which show a progressive fusion of the true shell with the calcareous tube. The valves are however free when young. Three species were examined structurally and mineralogically; the shell and tube are both aragonite.

In *Clavagella aperta* the valves are fairly large and only one is fused with the siphonal tube. The valves consist of a thin simple prismatic outer layer with a sheet nacre inner layer. Thin sheets of myostracal prisms are secreted beneath the muscle attachment scars.

Valves of a juvenile *Humphreysia strangei* were examined, these had a simple prismatic outer layer and inner sheet nacre layers (s). The outside of the valves is finely pustulate.

In *Penicillus* s.s. the true shell is seen as two valves occupying a saddle shaped area incorporated into the side of the tube (Text-fig. 32). The tube is extended posteriorly as a hollow cylinder and anteriorly as a perforated disc (the watering pot). The true valves are covered by a thin periostracum which is inserted from the outside of the shell to line the inside of the tube at the edge of the saddle shaped area. The valves consist of two layers, an outer extremely thin simple prismatic layer with an

TABLE 22

SUPERFAMILY	MINERALOGY	ARAGONITE SIMPLE PRISMS	CALCITE SIMPLE PRISMS	COMPOSITE PRISMS	LENTICULAR NACRE	SHEET NACRE	FOLIATED	CROSSED-LAMELLAR	COMPLEX CROSSED-LAMELLAR	HOMOGENEOUS	MYOSTRACAL PILLARS	TUBULES
Nuculacea	A	.	.	X	X	X	.	.	.	.	.	.
Nuculanacea	A	.	.	.	.	.	.	.	.	X	.	.

TABLE 22

SUPERFAMILY	MINERALOGY	ARAGONITE SIMPLE PRISMS	CALCITE SIMPLE PRISMS	COMPOSITE PRISMS	LENTICULAR NACRE	SHEET NACRE	FOLIATED	CROSSED-LAMELLAR	COMPLEX CROSSED-LAMELLAR	HOMOGENEOUS	MYOSTRACAL PILLARS	TUBULES
Nuculacea	A	.	.	X	X	X	.	.	.	.	.	.
Nuculanacea	A	.	.	.	.	.	.	.	.	X	.	.
Solemyacea	A	X	.	.	.	.	.	.	.	X	.	.
Arcacea	A	.	.	.	.	.	.	X	X	.	X	X
Limopsacea	A	.	.	.	.	.	.	X	X	.	X	X
Mytilacea	A + C	.	X	.	X	X	.	.	.	.	.	X
Pinnacea	A + C	.	X	.	X	X	.	.	.	.	.	.
Pteriacea	A + C	.	X	.	X	X	.	.	X	.	.	.
Pectinacea	A + C	.	X	.	.	.	X	X	X	.	.	X
Anomiacea	A + C	.	.	.	.	.	X	X	.	.	.	.
Limacea	A + C	.	.	.	.	.	X	X	.	.	.	.
Ostreacea	A + C	.	X	.	.	.	X	.	.	.	.	.
Unionacea	A	X	.	.	X	X	.	.	.	.	.	.
Trigonacea	A	X	.	.	X	X	.	.	.	.	.	.
Lucinacea	A	.	.	X	.	.	.	X	X	.	X	X
Chamacea	A*	.	.	.	.	.	.	X	X	.	X	X
Leptonacea	A	.	.	.	.	.	.	X	X	X	.	.
Chlamydoconchacea	.	.	.	.	.	.	.	.	.	.	.	.
Cyamiacea	A	.	.	.	.	.	.	.	.	X	.	.
Carditacea	A	.	.	.	.	.	.	X	X	.	X	X
Crassatellacea	A	.	.	.	.	.	.	X	X	X	X	X
Cardiacea	A	.	.	.	.	.	.	X	X	.	.	.
Tridacnacea	A	.	.	.	.	.	.	X	X	.	.	.
Mactracea	A	.	.	.	.	.	.	X	X	.	.	.
Solenacea	A	.	.	.	.	.	.	X	X	X	.	.
Tellinacea	A	.	.	X	.	.	.	X	X	X	.	.
Dreissenacea	A	.	.	.	.	.	.	X	X	.	.	.
Gaimardiacea	A	.	.	.	.	.	.	.	.	X	.	.
Arcticacea	A	.	.	.	.	.	.	X	X	X	.	.
Glossacea	A	.	.	.	.	.	.	X	X	X	.	.
Corbiculacea	A	.	.	.	.	.	.	X	X	.	.	occ
Veneracea	A	.	.	X	.	.	.	X	X	X	.	.
Myacea	A	X?	.	.	.	.	.	X	X	X	.	.
Gastrochaenacea	A	.	.	.	.	.	.	X	X	X	.	.
Hiatellacea	A	X	.	.	.	.	.	.	X	X	.	.
Pholadacea	A	X	.	.	.	.	.	X	X	X	.	.
Pholadomyacea	A	X	.	.	X	X	.	.	.	.	.	.
Pandoracea	A	X	.	.	X	X	.	.	.	X	.	.
Poromyacea	A	X	.	.	X	X	.	.	.	X	.	.
Clavagellacea	A	X	.	.	.	X	.	.	.	.	.	.

inner sheet nacreous layer about 500 μ thick (Plate 15, figs 1 & 2). The outer shell surface is ornamented with small granules radiating from the umbo (Plate 15, fig. 5). The outer more irregular part of the saddle shaped area consists of homogeneous structure and is lain down on the inside of the nacreous layer. On the inner surface of the homogeneous layer, is the attachment of the pallial muscles which secrete beneath them, myostracal prisms forming a conspicuous 'W' shaped scar. The tube and pot form the most conspicuous part of the animal. Optically the shell structure of these features appears homogeneous with conspicuous lamellate banding. Electronmicroscopy shows that both the tube and pot are made up of platy crystals 0·5–2 μ in diameter, 0·3–0·5 μ in width irregular in outline but aligned with the long axis parallel with the outside of the tube. (Plate 15, figs 2 & 4).

The mode of secretion of the pot and tube pose problems; both of these two structures lie external to the periostracum which is not in intimate contact with the tube but encases the long siphons (Purchon, 1956). On many specimens growth increments can be seen at the posterior end of the tube and this must be formed by

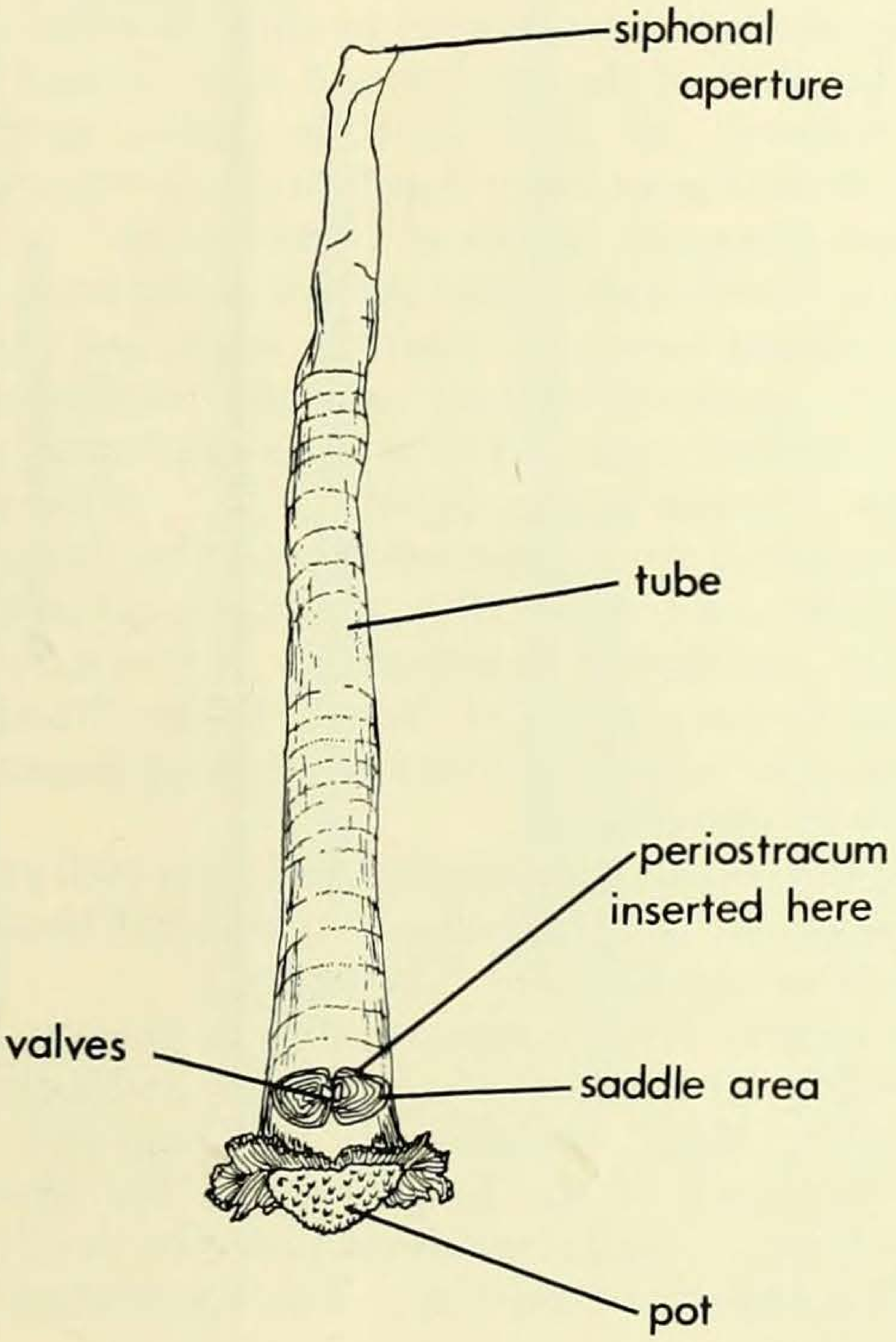


FIG. 32. Sketch showing the main features of the shell of *Penicillus* sp.

mantle at the tips of the siphons. However it is difficult to see how the pot could be formed as a continuous growth process without repeated resorbtion. It is possible that the tube and pot are secreted only when the animal is near fully grown. The common occurrence of sand, pebbles, shells and other debris incorporated into the pot and tube, together with the general lack of growth lines, is slight evidence in favour of a rapid secretion process. The posterior end of the tube, grows subsequently by the addition of material by the tips of the siphons; in this case we see clear growth increments and no debris incorporated into the shell. However, until more is known about the biology of *Penicillus*, we have no real evidence to support either alternative explanation of shell secretion.

CONCLUSIONS

It has become increasingly clear that the Bivalvia cannot be classified on single character systems (Cox, 1960; Newell, 1965) and that a total organism study involving shell characters, comparative anatomy, geological history and more recently biochemical characters must be employed or attempted (Ghiselin *et al*, 1967). Shell microstructure and mineralogy can therefore be only contributory evidence towards establishing the relationships of the bivalves and must be used in conjunction with other characters. However, our shell structure studies have established twelve characters which can be used as an aid to classification; in some cases these characters can be crucial evidence (Kennedy, Morris & Taylor, 1970).

The classifications of Newell (1956, 1969) and Cox (1960) are essentially similar and are compilations of existing knowledge from the single and multiorgan systems of previous neontologists, geological history and the relationships of fossil forms established on shell characters alone. This is in contrast to the single organ classifications of for example Purchon (1959), Atkins (1938). If the shell structure combinations we have recognized are superimposed upon these compilations of previous knowledge, it is possible to see where these characters support or are in apparent disagreement with the established classification. A summary of shell characters arranged in the classificatory order of Newell (1969, Treatise of Invertebrate Palaeontology) is shown in Table 22. There is a striking general agreement of shell structure characters with classification.

The relationship of the bivalve superfamilies and their shell structures is best seen in the form of a phylogenetic tree[1], showing the geological history possible ancestry and known shell structure combinations (Text-fig. 33).

It is apparent that many bivalve superfamilies or lineages have long and continuous records extending far back into the Palaeozoic and in many cases have been extremely conservative. Major evolutionary radiations are seen in the early Ordovician, Permo-Trias and of the heterodonts in the Mesozoic; the latter is discussed by Stanley (1967). Shell structure information at critical points of radiation in the Palaeozoic is almost non-existent. This information would be extremely

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[1] The construction of this tree has been carried out in close collaboration with Dr. N. J. Morris and draws heavily upon his wide knowledge of Palaeozoic and Mesozoic bivalves.

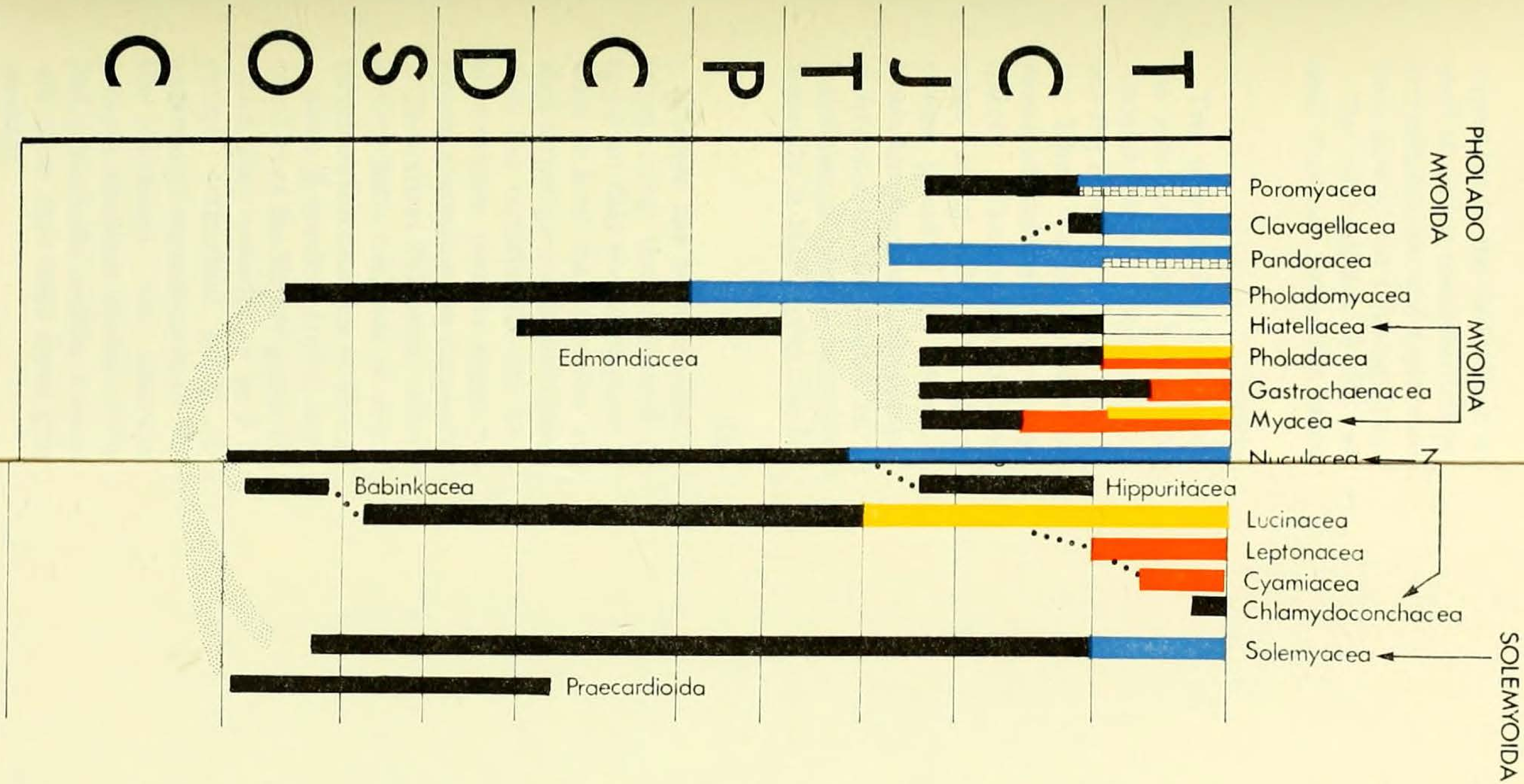
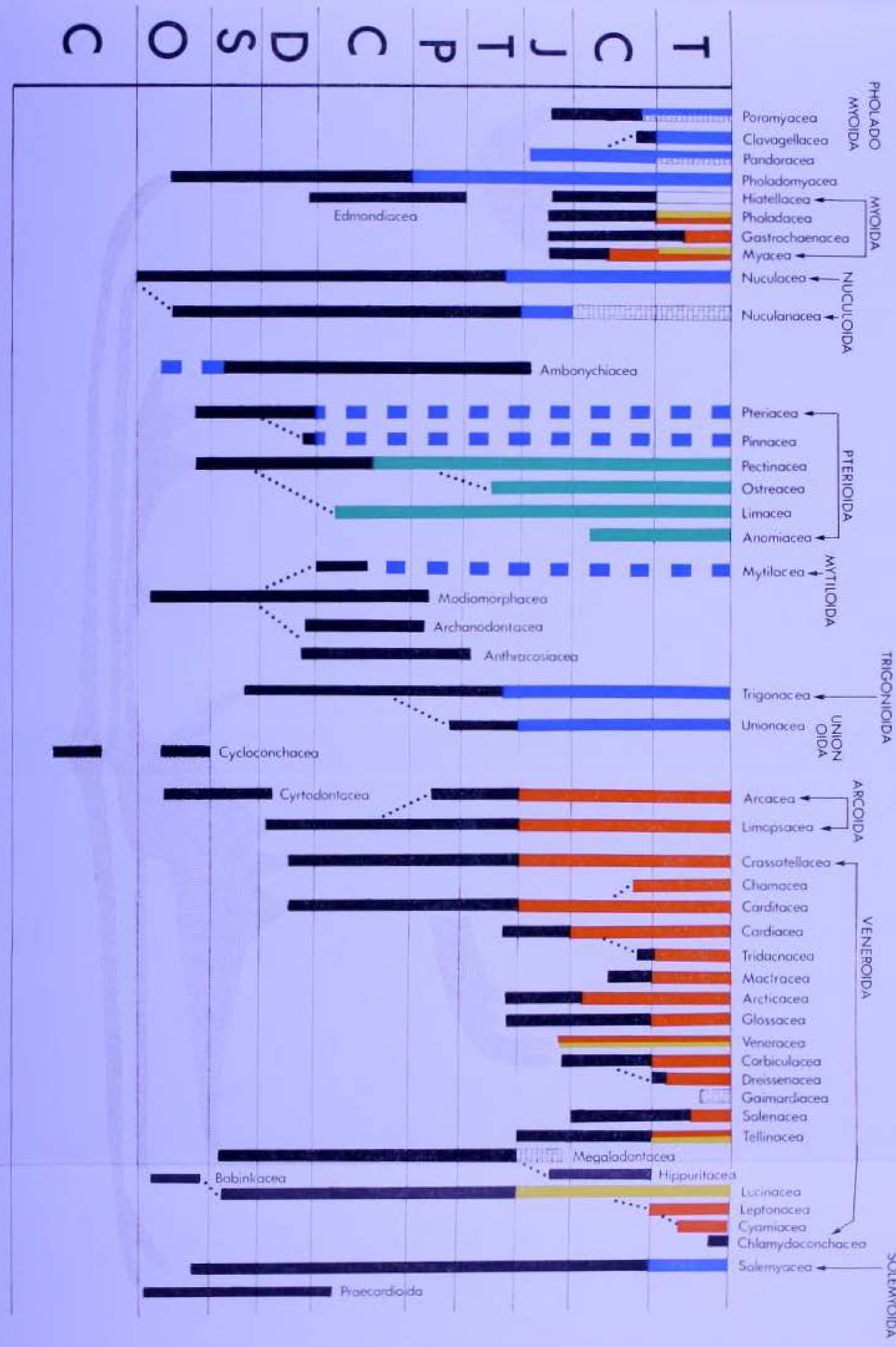


FIG. 33. Geological history and possible phylogeny of the Bivalvia. The main shell structure groupings (colours) have been superimposed on the superfamily lineages.

Orange = Crossed-lamellar/complex crossed-lamellar
Blue (continuous) = Aragonite simple prisms/nacre.
Green = Foliated structure.
Black = Unknown.
Yellow = Composite prisms/crossed-lamellar, complex crossed-lamellar.
Blue (broken) = Calcite prisms/nacre.
Brick pattern = Homogeneous.
Stippled = Areas of uncertain relationships.

The Hiatellacea are mainly homogeneous but *Panopea* has an outer simple aragonite prismatic layer. This layer is also present in some Pholadacea which have middle crossed-lamellar and inner complex crossed-lamellar layers. Calcite prism outer layers are found in the Ostreacea and some Pectinacea.



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important in the Ordovician where most of the radiation of the major lineages and shell structure combinations probably took place. However because of dissolution, recrystallisation and replacement the original shell fabrics have disappeared or have been altered out of recognition.

The relationships of the various bivalve superfamilies are discussed in terms of shell structure variations below.

Subclass *PALAEOTAXODONTA*

Two superfamilies belong in this group; the Nuculacea are generally regarded as the most primitive living bivalves (Yonge, 1959) but the other superfamily the Nuculanacea are considered to be as highly specialized as any similar group throughout the bivalves (Yonge, 1959). The origin of the Nuculacea can be traced back to the Upper Cambrian *Ctenodonta* (Cox, 1959) and the group appears to have remained relatively unchanged morphologically throughout their subsequent history. The nacreous and composite prismatic shell is different from that of any other family. However, we consider that the difference between simple aragonite prisms (possibly the ancestral condition) such as found in the Unionacea and Pholadomyacea and the composite prisms of the Nuculacea is slight and arises from differences in the degree of mantle reflection at the shell margin. The extant Nuculanacea have a homogeneous shell but as shown by Cox (1959) and Taylor, Kennedy & Hall (1969) this has not always been the case.

Subclass *CRYPTODONTA*

Solemya has been considered to be a protobranch (Palaeotaxodonta) by Yonge (1939, 1959) but as Newell (1965) has pointed out, it is becoming increasingly apparent that the Solemyacea have been separated from the rest of the protobranchs from at least the Devonian and are not obviously related to the Nuculacea. The shell structure and in particular the character of the outer prismatic layer, is distinctive, but nevertheless can be readily derived from simple aragonite prisms. Our observations tend to support Newell's opinion that the Solemyacea belong to a separate subclass the Cryptodonta.

The extinct Palaeozoic order Praecardioida is placed in the Cryptodonta, but there is very little evidence of any relationship to the Solemyacea. We have no shell structure information on this group.

Allen & Sanders (1969) have recently described the anatomy and discussed the affinities of the Recent genus (*Nucinella* classified in the Limopsacea, in the Treatise) which they consider to be a monomyarian 'solemyid' and possibly related to the extinct actinodont group (i.e. Cycloconchacea). Although there are several anatomical resemblances of *Nucinella* to *Solemya* other characters resemble those of the Nuculacea. Our observations of the shell structure show that it is homogeneous structure similar to that of *Nuculana* but unlike *Solemya* or the Nuculacea. But if *Nucinella* is either a nuculacean or a solemyacean then reference to Text-fig. 33 will show that both these groups were probably derived from a cycloconchacean ancestor.

Subclass *PTERIOMORPHIA*

The Arcacea are generally thought to be derived from the Cyrtodontacea of the lower Ordovician (Cox, 1959, 1960) but as pointed out by Morris (1967) the connection is not firmly established. Newell (1954) has considered that the 'cyrtodontids' are also the ancestors of the Pteriacea, Pectinacea and also possibly the Mytilacea. These latter groups probably became separate from the "cyrtodontid stock" rather earlier (Text-fig. 33). The Arcacea have a crossed-lamellar and complex crossed-lamellar shell structure with tubules and myostracal pillars. This structure is very different from that of the rest of the Pteriomorphia, but similar to that of some heterodonts such as the Carditacea. The only character which is common between the Arcacea and the rest of the Pteriomorphia is the filibranch gill and it seems to us that there is no close relationship between the groups and the Arcoida (Arcacea & Limopsacea) should possibly be considered as a separate subclass related to the Heterodonta. This does not of course deny a once common ancestry.

The Mytilacea have a very distinctive prismatic, calcitic, outer shell layer, sometimes called 'fibrillar' (Oberling, 1964). This particular structure is found in no other bivalve group. The work of Osborn (1970) on mammalian teeth has shown that all the different prism-like structures may not be very different from each other. The Mytilacea may have arisen directly from the lower Ordovician-Permian family the Modiomorphidae and have no apparent derivatives. Newell (1965) placed the Pinnacea in the order Mytiloida (implying relationship) but the simple calcite prisms, general shell form and anatomy suggest derivation from the Pteriacea.

As mentioned above the Pteriacea and the Pectinacea are both considered to have been derived from a cyrtodontid ancestor (Cox, 1960; Newell, 1938). Although they have different shell structures this does not rule out a common ancestor. The occurrence of an outer prismatic layer in oysters, the early post larval stages of some pectens (Jackson, 1890) and in some species of *Propeamussium* suggests that the foliated layer in these forms may have originally been derived from aragonite nacreous structure by a change in the calcium carbonate polymorph. The superfamily Ambonychiiacea which ranges from middle Ordovician to upper Devonian has been extensively discussed by Pojeta (1966); it includes many '*Pteria*'-like forms. Recently we have examined an *Ambonychia* from the upper Ordovician (Ashgill) from near Girvan, Scotland which has some shell structure preserved. As might be expected it showed nacreous inner layers, but unfortunately the outer layer was recrystallised, but was probably calcite prisms.

Newell & Boyd (1970) have recently described the earliest known members of the Anomiacea, from the Permian. This superfamily is probably derived from the Pectinacea. The same is probably true of the Limacea. The Ostreacea first appeared in the Permian and were probably derived from a Pectinacean ancestor the Pseudomonotidae (Newell, 1961; Newell & Boyd, 1970). The shell structure characters support this suggestion.

Subclass *PALAEOHETERODONTA*

The Unionacea and Trigonacea have a very similar shell structure of aragonite simple prisms and lenticular and sheet nacreous layers. There has long been debate as to the possible relationship of these two families (Cox, 1960). The anatomical evidence suggests that they may be distinct groups, whereas the palaeontological evidence is ambiguous and unsatisfactory. As well as the morphological and shell structure similarities, they have a character in common which is usually overlooked; this is the possession of calcareous gill spicules recorded for the Unionacea by Ridewood (1904) and for the Unionacea and Trigonacea (Atkins, 1938). They are the only bivalve superfamilies to possess these spicules.

Subclass *HETERODONTA*

The Lucinacea are known from the Silurian to Recent and can be traced through the Babinkacea back to the middle Ordovician (McAlester, 1965, 1966). McAlester has argued that the Lucinacea are a distinct bivalve group and should be considered as a separate subclass. Certainly the Lucinacea have been distinct for a long period of time and only the Leptonacea and Cyamiacea can be related to them. However Boss (1969) considers from anatomical and shell morphological evidence that the Lucinacea are closely connected to other bivalves of the heterodont subclass. The Lucinacea have a three layered shell of an outer composite prismatic layer, a middle crossed-lamellar layer and an inner complex crossed-lamellar layer. This combination is also found in the Tellinacea and some Veneracea. The shell structure evidence thus supports the opinion of Boss (1969) that the Lucinacea belong to the Heterodonta, but reference to Text-figure 33 will show that they have been distinct from the rest of the heterodont stock for a long time.

The Tellinacea are known from the Upper Triassic to Recent but their phylogenetic relationships are obscure. As noted above the three layered shell structure is found in the Lucinacea and Veneracea. The Solenacea may have arisen from the Tellinacea in the late Cretaceous or early Cainozoic (Davies, 1935; Morris, 1967). In the process they must have lost the outer composite prismatic layer, as indeed have some of the Tellinacea.

The Astartacea, Carditacea, Chamacea, Cardiacea, Tridacnacea, Mactracea, Arcticacea, Veneracea, Corbiculacea, Dreissenacea and the Glossacea all appear to be generally related (Text-fig. 33). The shell structure is generally similar in all these groups with only relatively small variations (Table 22). The most important variation is the three layered shell in some Veneracea. Most of these families arose in the Mesozoic and Cainozoic, and Stanley (1968) has discussed this spectacular radiation. The most striking trend is the appearance and extensive radiation of the infaunal siphonate feeders, which Stanley relates to the development of siphons and the closure of the mantle cavity by mantle fusion. Most of the families involved in this radiation have a two layered shell of crossed-lamellar structure and complex crossed-lamellar structures. In some families one or both layers may consist of homogeneous structure, but in these cases it is obviously derived from the structures mentioned.

The Mesozoic Veneroida were probably derived from either the Crassatellacea (Stanley, 1968), which first appeared in the Devonian, or from the Carditacea which also appeared in the Devonian (Morris, 1967). These two families probably have a common origin in the lower Palaeozoic from a cyrtodontacean stock (Text-fig. 33). Yonge, (1969) has recently stressed the similarities between the Crassatellacea and the Carditacea.

The Chamacea which first appeared in the upper Cretaceous are thought on the basis of shell structure and anatomical characters to have been derived from the Carditacea (Kennedy, Morris & Taylor, 1970).

The Cardiacea first appeared in the Trias, but no obvious ancestor can be cited from older rocks. The Tridacnacea can be readily derived from the Cardiacea in the Eocene or late Cretaceous (Stasek, 1962). The Mactracea appear similar to the Cardiacea in shell structure details but there is no real evidence of any relationship.

The Arcticacea, Veneracea and Corbiculacea may have been derived from the Jurassic forms *Pseudotrapezium* and *Pronella* (Casey, 1952; Morris, 1967). The Arcticacea and the Veneracea are probably very closely related. Although *Arctica* shows a homogeneous shell structure traces of crossed-lamellar structure may sometimes be seen. Other members of the Arcticacea show crossed-lamellar and complex crossed-lamellar structure. The Veneracea show two distinct types of shell structure; this may be a result of the loss of the outer composite layer in some forms or a polyphyletic origin for the Veneracea.

The Dreissenacea are a group of fresh water byssate anisomyarian bivalves which appeared in the Cainozoic. Because of their mytilid-like shell, their relations have remained obscure, but it has been realized for some time that they are unrelated to the Mytilacea (Yonge & Campbell, 1968). The shell structure shows great similarity in micro-details to that of the Corbiculacea and it is reasonable to suppose that the Dreissenacea arose from the fresh and brackish water Corbiculacea. Morton (1970) has made a study of the morphological changes seen in fossil forms, demonstrating a progression from the Corbiculacea to the Dreissenacea. However, the idea of some relationship to the Mytilacea has not entirely disappeared (Purchon & Brown, 1969).

Subclasses *MYOIDA* and *PHOLADOMYOIDA*

The Myoida and Pholadomyoida although classified in separate subclasses show obvious similarities and we consider that all the superfamilies in these subclasses can be derived from a "pholadomyacean" stock which has been in existence since the middle Ordovician. Other workers however, consider the resemblances to be the result of morphological convergence (Runnegar, 1966, 1967).

Pholadomya s.s. has a shell structure of simple aragonite prisms and middle and inner nacreous layers. *Panopea* of the Hiatellacea (Myoida) is anatomically and morphologically very similar to *Pholadomya* (even including surface granules) but has an outer prismatic layer, a middle homogeneous and an inner complex crossed-lamellar later. Other members of the Hiatellacea have shells consisting of homogeneous structure alone. It seems very probable that the Hiatellacea have been derived from the "pholadomyoid" stock. Some Pholadacea have a shell structure of simple prisms, crossed-lamellar and complex crossed-lamellar layers. The structure of the outer layer closely resembles that of *Panopea*. It seems that the Pholadacea may have arisen from the Pholadomyacea in the early Jurassic; the genera *Myopholas* and *Giradotia* would seem to be transitional forms (Morris, unpub.).

The Myacea consist of two families, the Myidae (Palaeocene-Recent) and the Corbulidae (L. Jurassic-Recent). It does not seem very likely on anatomical and shell morphological grounds that the Corbulidae gave rise to the Myidae. This is supported by the fact that the Corbulidae have a two layered and the Myidae a three layered shell. The origin of the Corbulidae might perhaps be found in the Permian pholadomyoid forms such as *Pyramus* amd *Megadesmus* (see figures in Runnegar, 1967). The Myidae would seem to have been independently derived from the "pholadomyoid" stock at a much later date.

Most Pandoracea have a shell structure of simple prisms and two nacreous layers, this and anatomical characters suggest a derivation from the Pholadomyacea in the Trias or lower Jurassic. The Thracidae (family of Pandoracea) have today a largely homogeneous shell, the outermost part of which retains a vestige of prismatic structure. However in the Cretaceous the Thracidae had a prismato-nacreous shell and apart from shell structure there is little to differentiate the Thracidae, from other Pandoracean families such as the Laternulidae.

The origins of the Poromyacea are obscure but certainly the Cuspidariidae can be traced back to the Trias (Cox, 1960; Morris, 1967) and have probably arisen from the Edmondiacean genus *Solenomorpha*. The Edmondiacea appear to be a heterogeneous Palaeozoic group closely related to the Pholadomyacea. Some of the Poromyacea have a prismato-nacreous shell and others are entirely homogeneous. Although the superfamily has a septibranch gill there are many anatomical resemblances to the Pandoracea.

The Clavagellacea are a highly aberrant group but anatomical characters, the nacreo-prismatic shell and the surface granules suggest a close affinity with the Pandoracea.

Evidence from the Monoplacophora (Erben, *et al*, 1968), Archaeogastropoda (Wise, 1970; Wise & Hay, 1968), *Nautilus* (Grégoire, 1962) and some of the oldest bivalve lineages strongly suggests that the "primitive" shell structure of the bivalves is a simple aragonite prism outer layer and middle and inner nacreous layers. Subsequent evolutionary radiation of the shell structures has been a result of the increased exploitation of different habitats and different modes of life. Taylor & Layman (1972) have stressed the functional significance of bivalve shell structures and present evidence correlating structure with mode of life. However we need much more information on the course of evolutionary change in shell structures and it is probable that in time sufficient well preserved Palaeozoic material will be discovered in order to document these changes.

ACKNOWLEDGEMENTS

We are very grateful for the constant interest, assistance and advice of Dr. Noel Morris, particularly in the preparation of the conclusions.

We should also like to thank Dr. R. P. S. Jefferies, Mr. R. J. Cleevely and Mr. C. P. Palmer for advice and assistance in various ways. We are especially grateful to the staff of the electron microscope unit at the British Museum (Natural History) under the direction of Mr. B. Martin for patient advice and assistance.

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PLATE 1

All figures on this plate are acetate peels

FIG. 1. Radial section of the outer composite prismatic layer of ***Codakia tigerina*** showing the fine needle-like crystallites aligned normal to the growth increments. × 160

FIG. 2. Radial section of ***Lucina fijiensis*** showing complex crossed-lamellar inner layer (bottom) with step-like blocks of pallial myostracum (upper). × 160

FIG. 3. Radial section of the outer crossed-lamellar layer of ***Astarte sulcata*** showing very fine first order lamels and growth increments. × 160

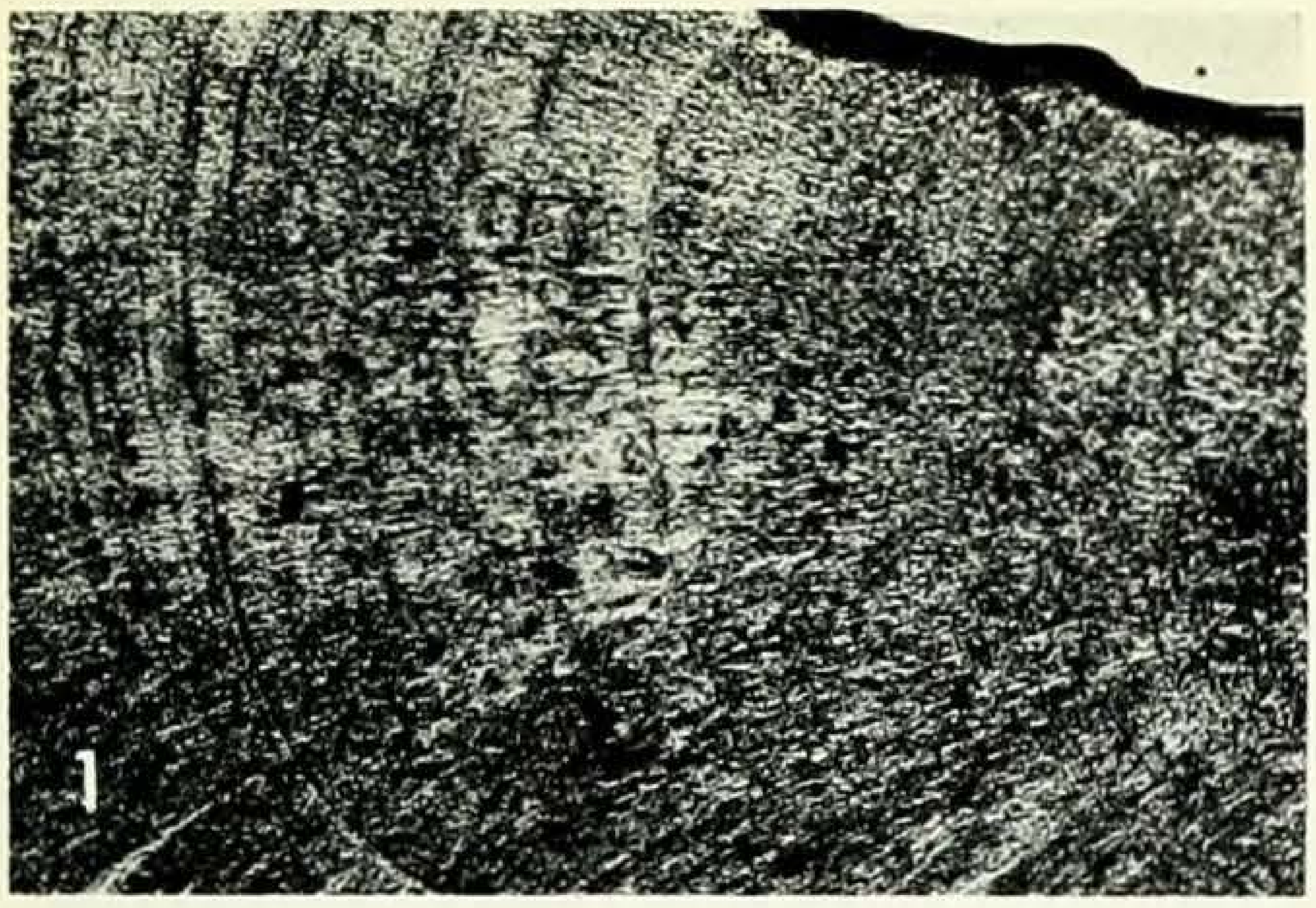
FIG. 4. Radial section of the outer layer of ***Astarte sulcata*** illustrating the change in orientation of the first order lamellae inwards from the outside of the shell (upper). × 100.

FIG. 5. Radial section of the inner complex crossed-lamellar layer of ***Lucina fijiensis.*** × 100.

FIG. 6. Radial section of ***Crassatella decipiens*** showing the outer crossed-lamellar layer (top), the pallial myostracum and the inner layer which begins as complex crossed-lamellar but grades into homogeneous structure. × 160.

FIG. 7. Radial section of the inner layer of ***Astarte incrassata*** showing both the myostracal prisms and homogeneous structures. × 160.

FIG. 8. Oblique section through the inner layer of ***Astarte incrassata*** in the umbonal area showing the individual myostracal prisms surrounded by homogeneous structure. × 80.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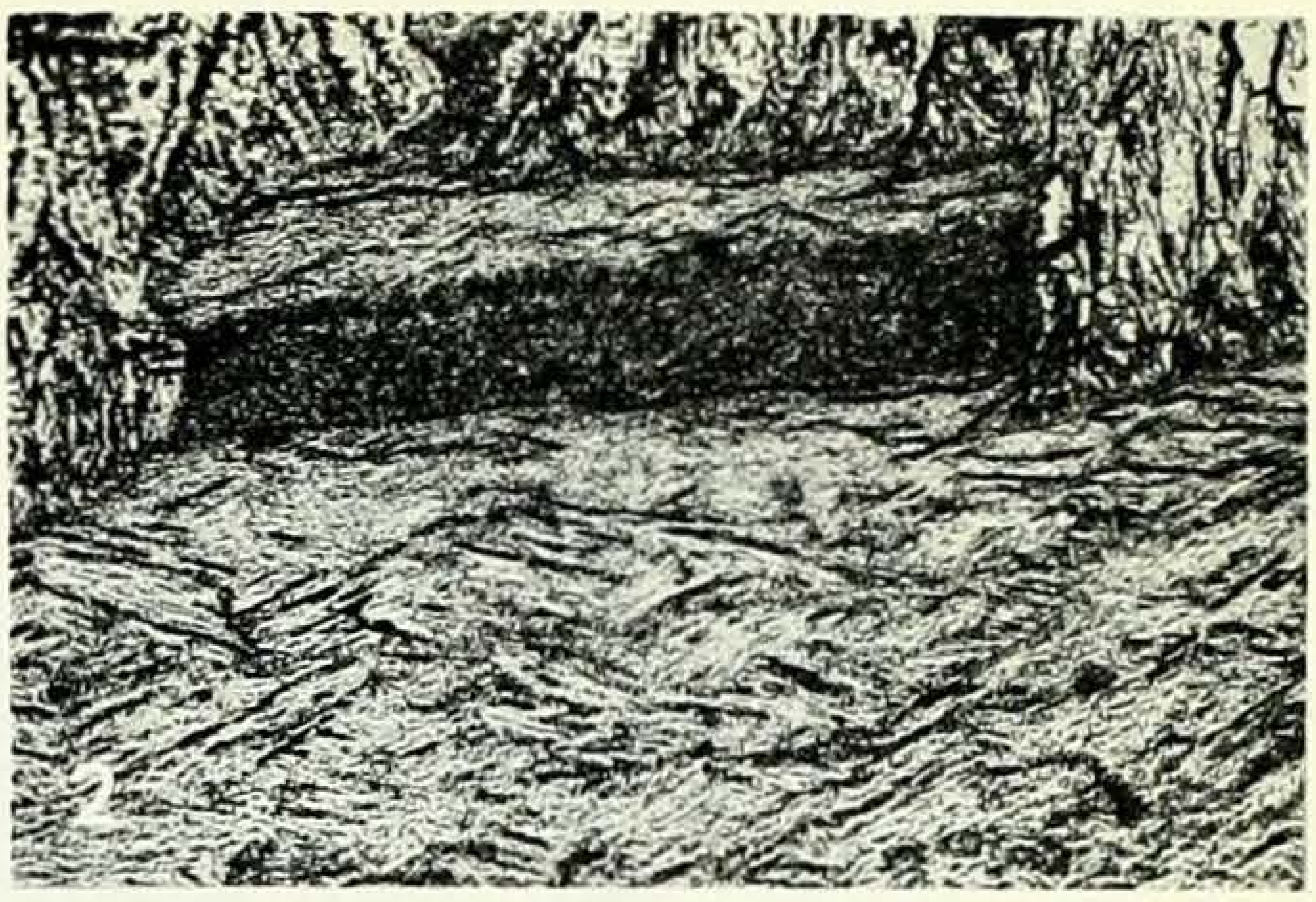
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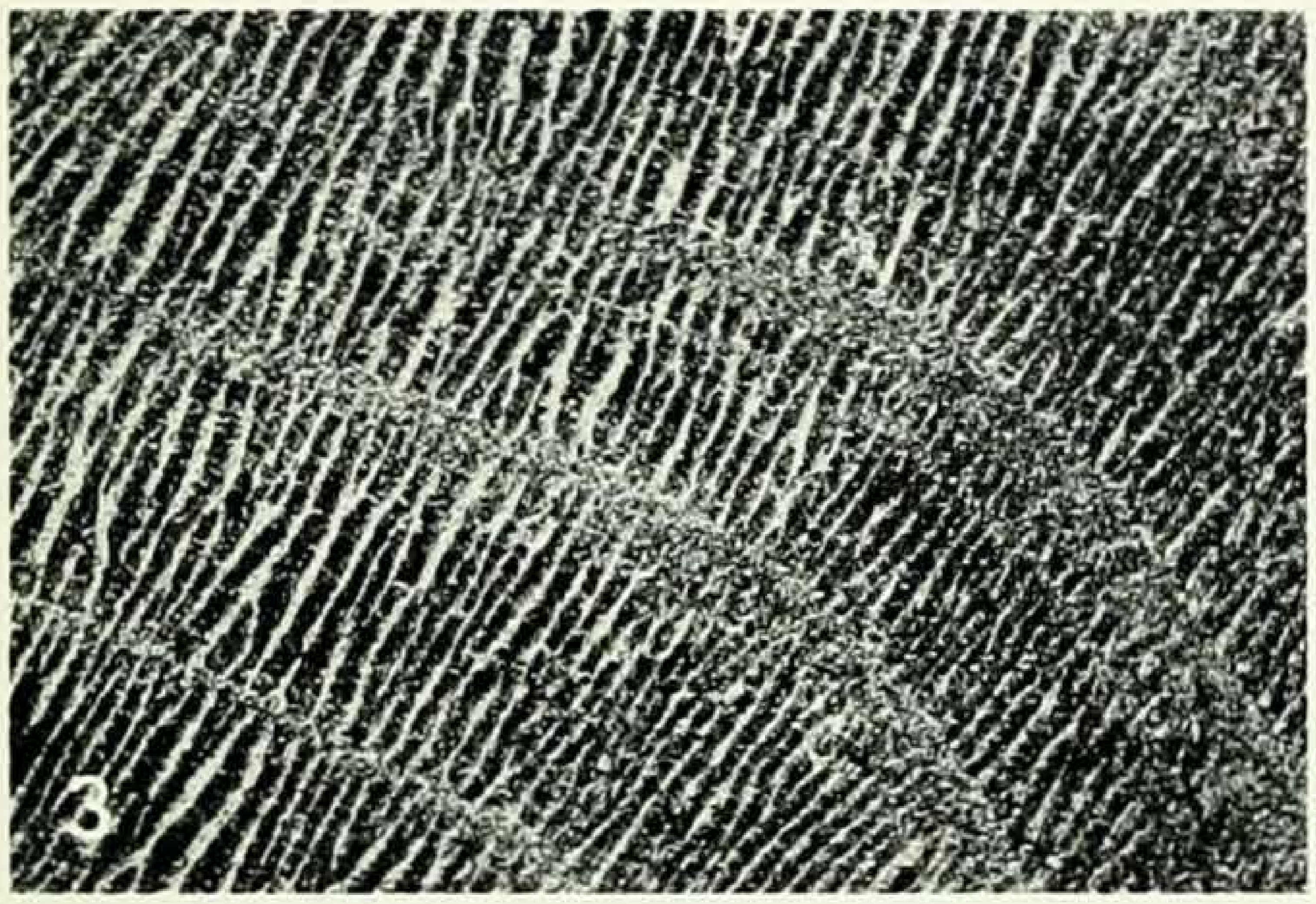
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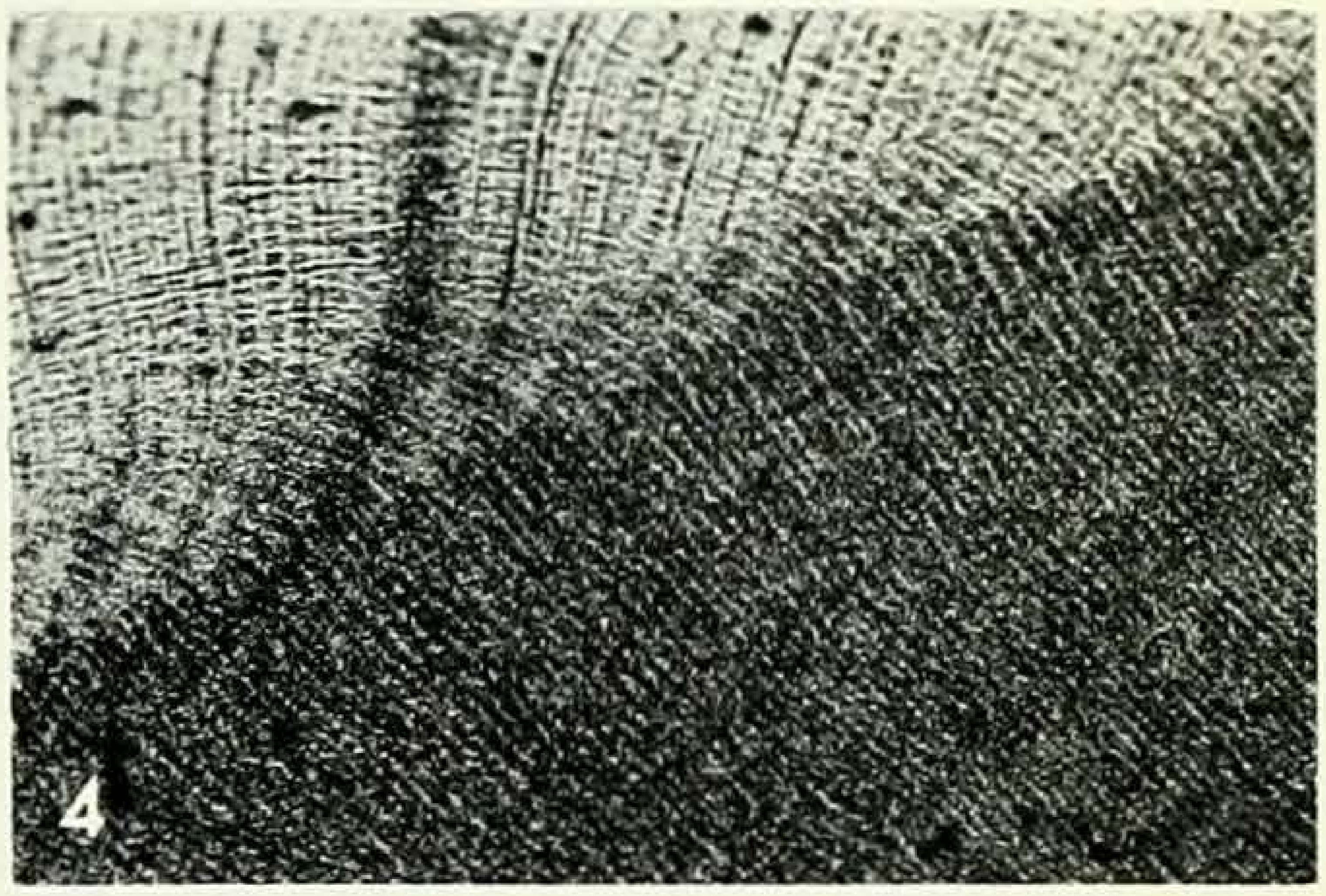
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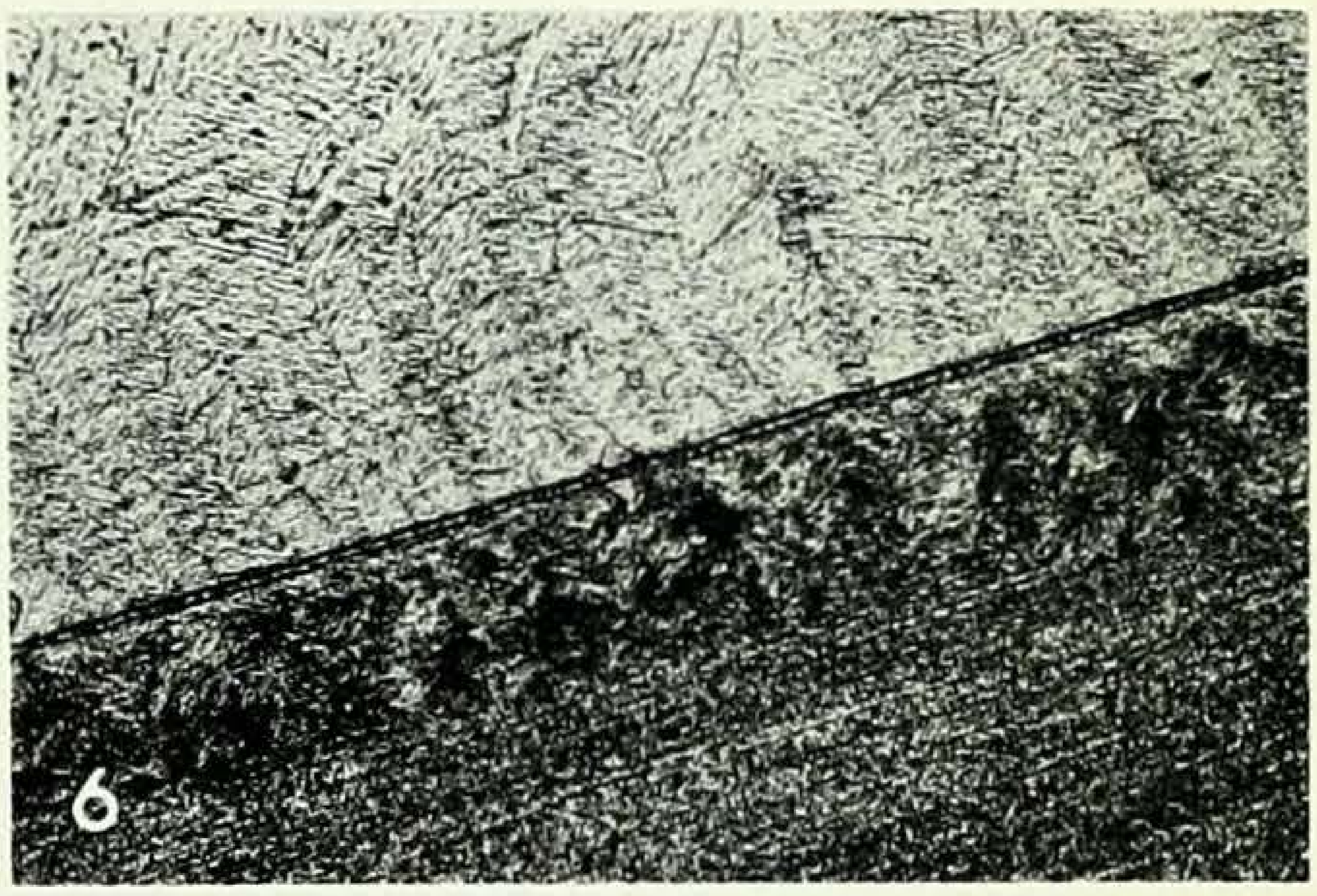
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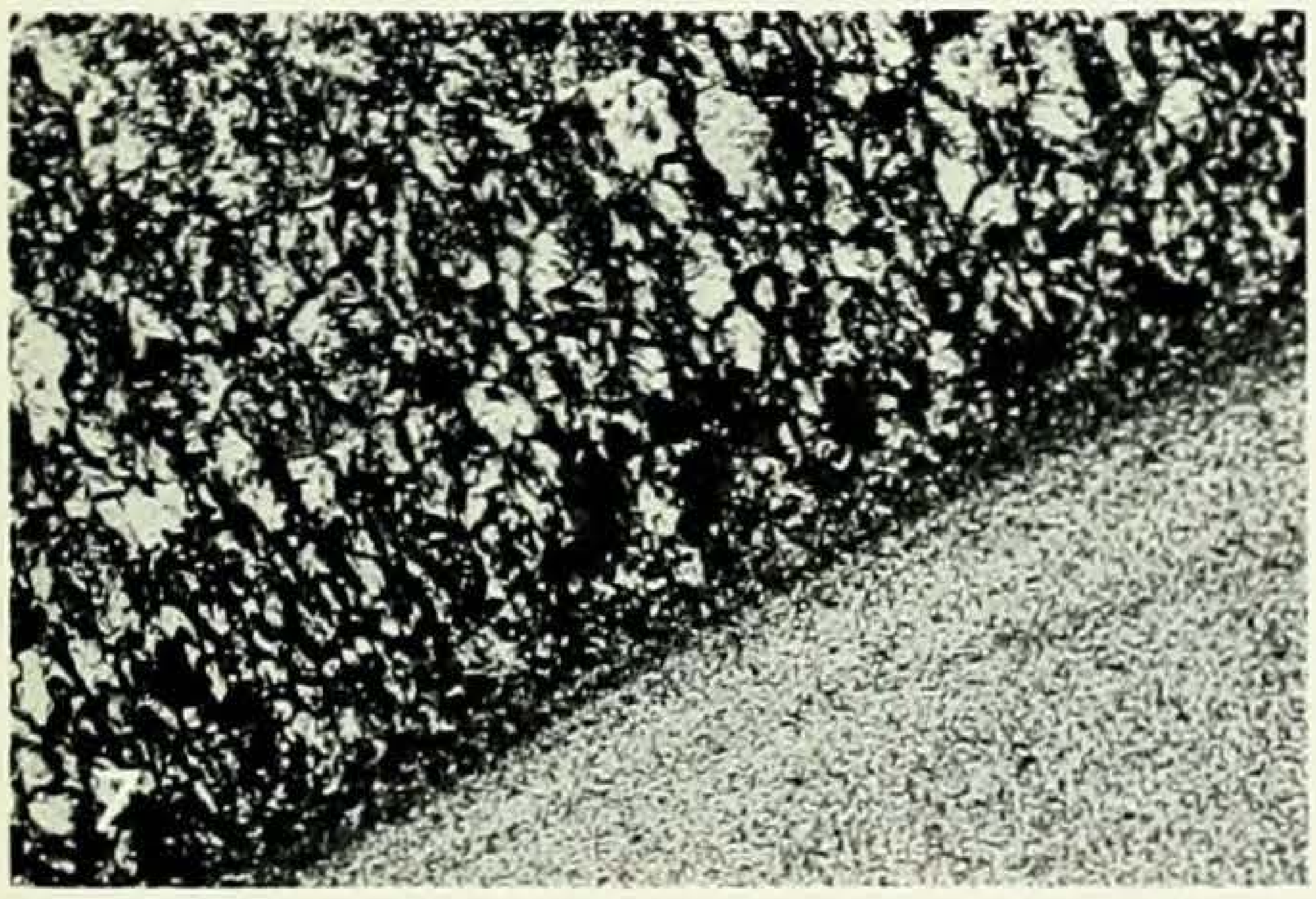
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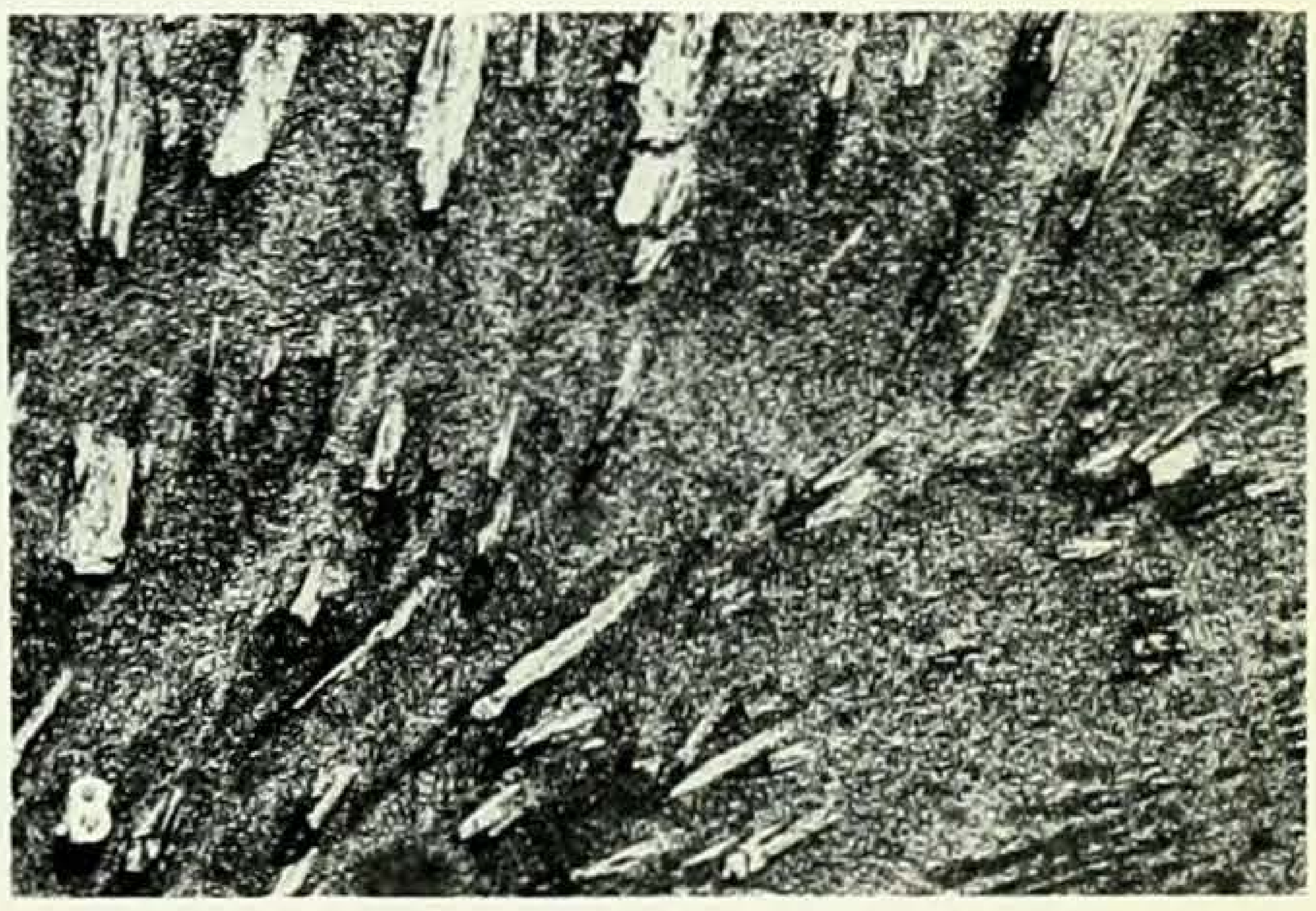
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PLATE 2

FIG. 1. ***Crassatella radiata***, radial section showing myostracal pillars in the inner complex crossed-lamellar layer. These terminate at the inner shell surface to produce boss-like structures as in fig. 2. Acetate peel, × 160.

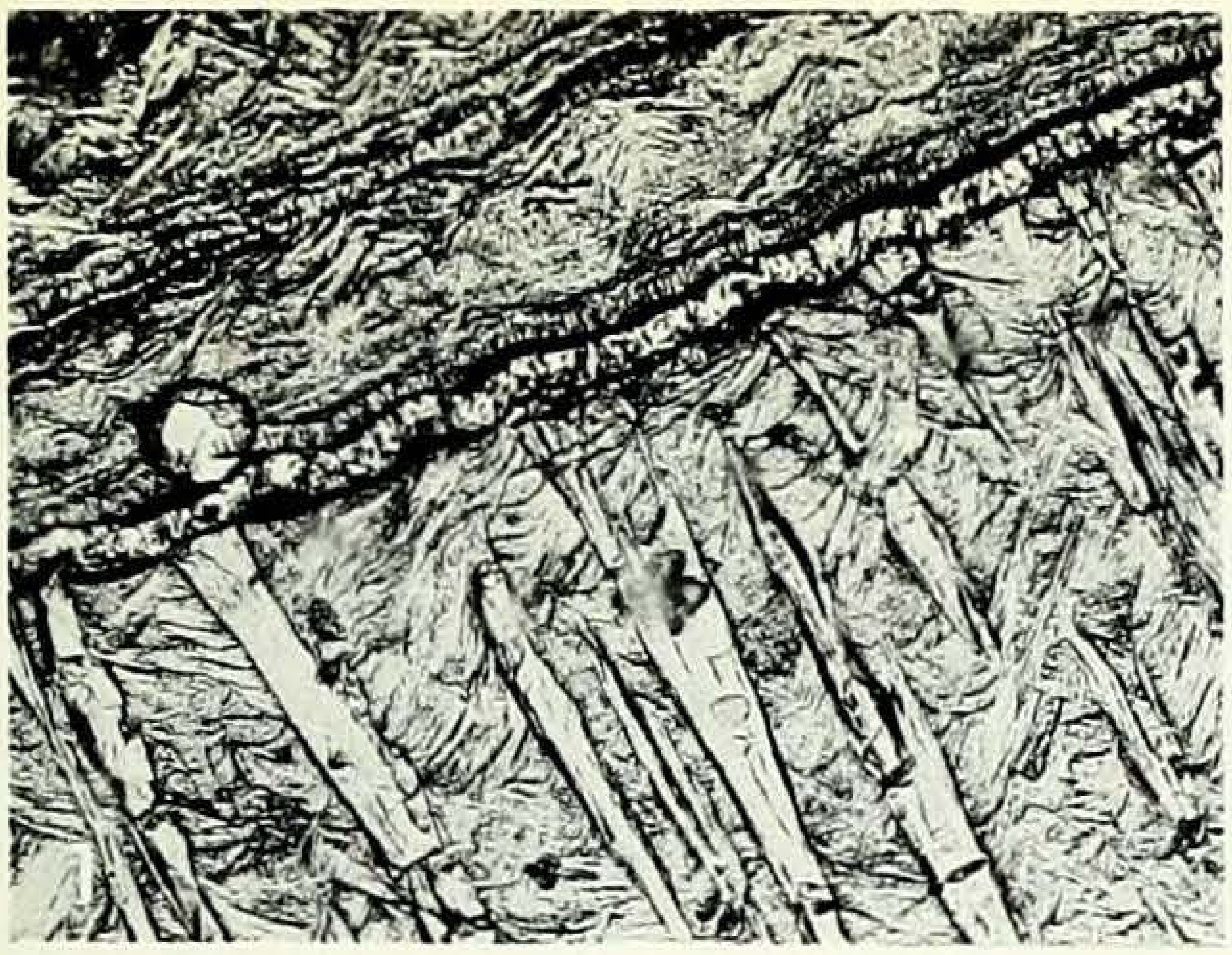
FIG. 2. Surface of the inner layer of ***Astarte borealis*** showing the high density of myostracal bosses, separated by homogeneous structure. Scanning electron-micrograph, × 50.

FIG. 3. Similar area to Fig. 2 but higher magnification. × 280.

FIG. 4. Radial section of the outer crossed-lamellar layer of ***Cardita sowerbyi*** showing how the primary lamels are arranged radially in the outer part of the shell (top) and become aligned concentrically inwards. Acetate peel, × 160.

FIG. 5. Radial section of ***Cardita marmorea*** showing the myostracal pillars cutting both the outer crossed-lamellar layer (bottom) and the inner complex crossed-lamellar layer. Acetate peel, × 160.

FIG. 6. Radial section of the inner complex crossed-lamellar layer of ***Cardita sowerbyi.*** Note the sheets of myostracal prisms and the continuity of the major structures through them. Acetate peel, × 160.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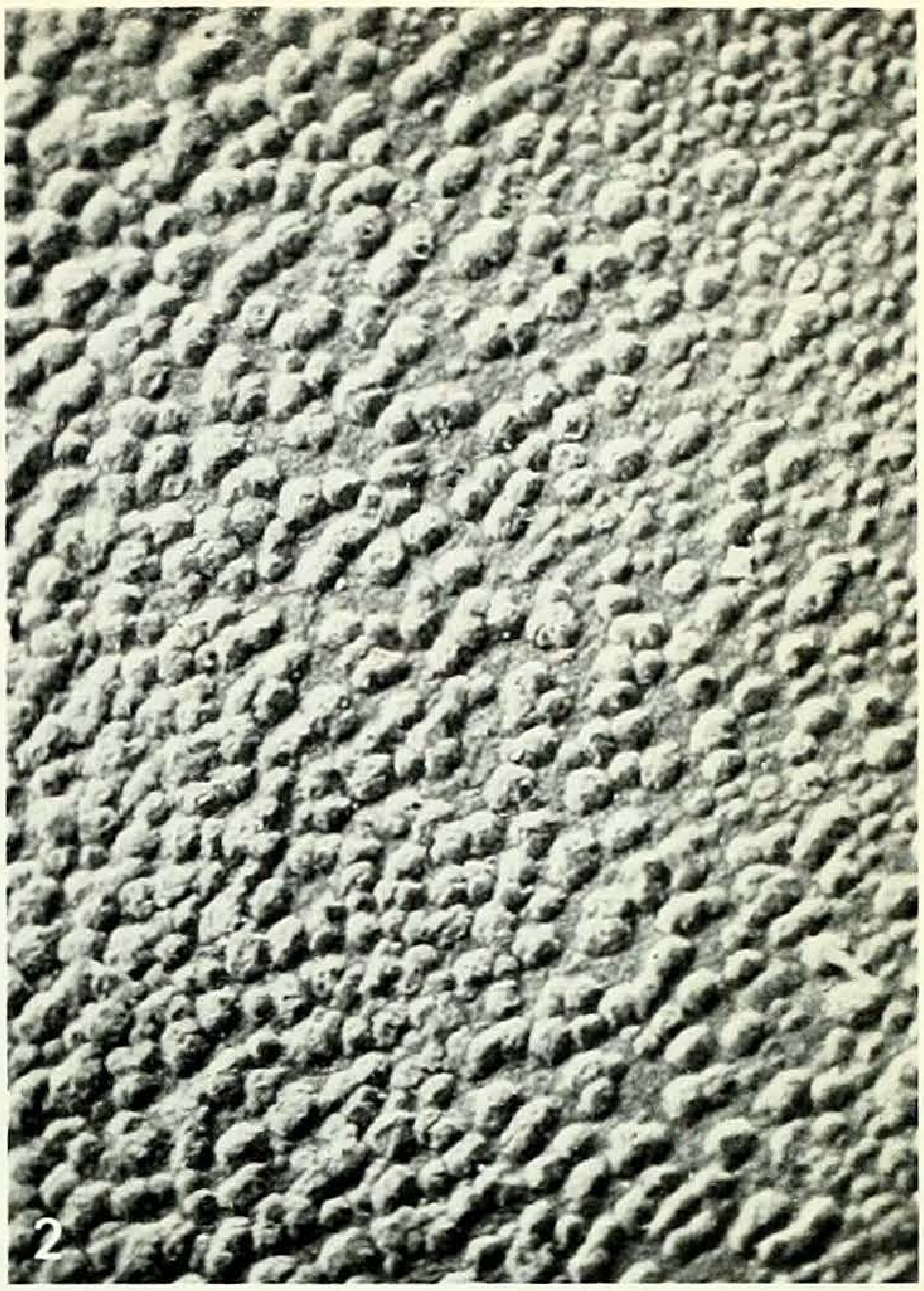
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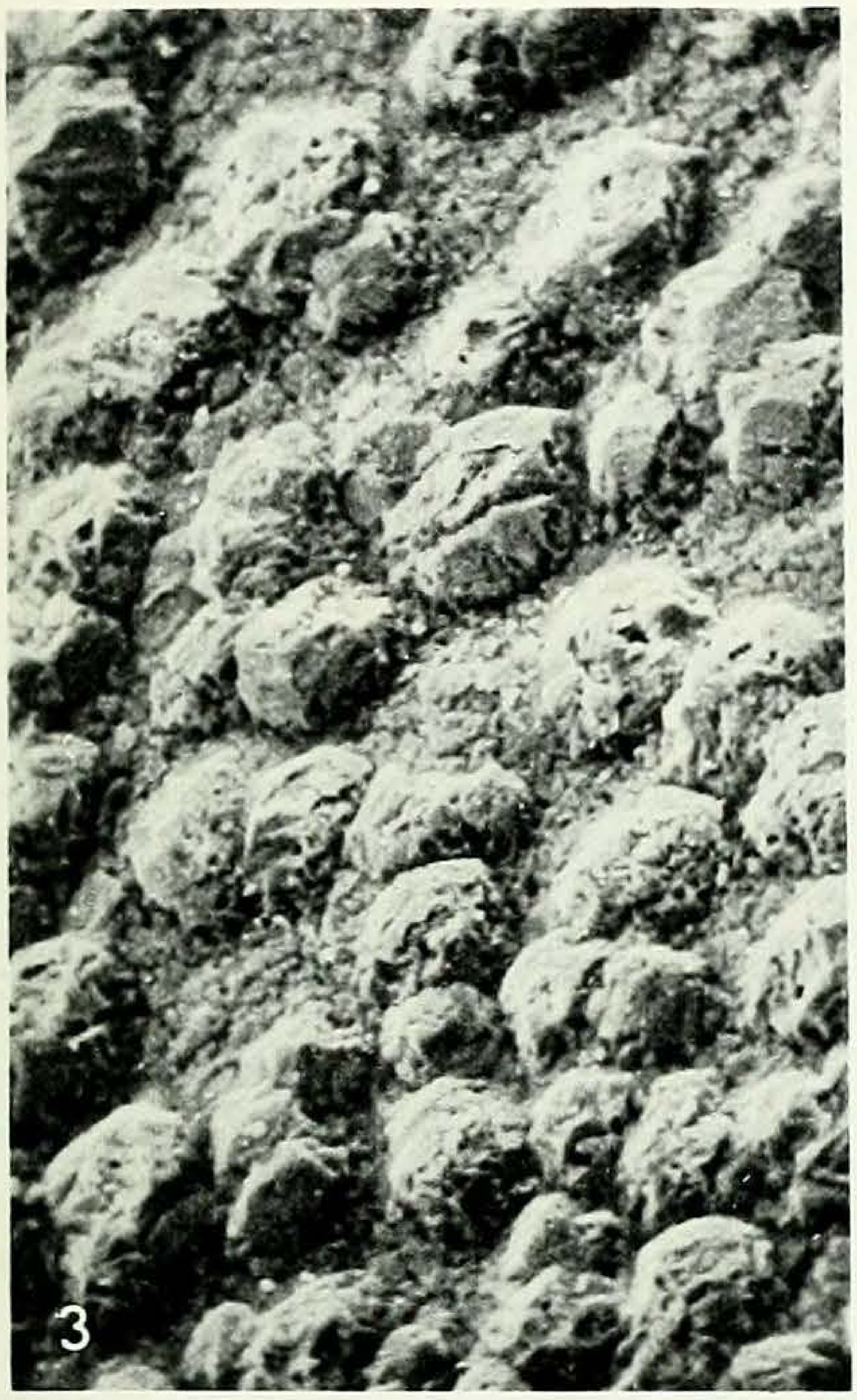
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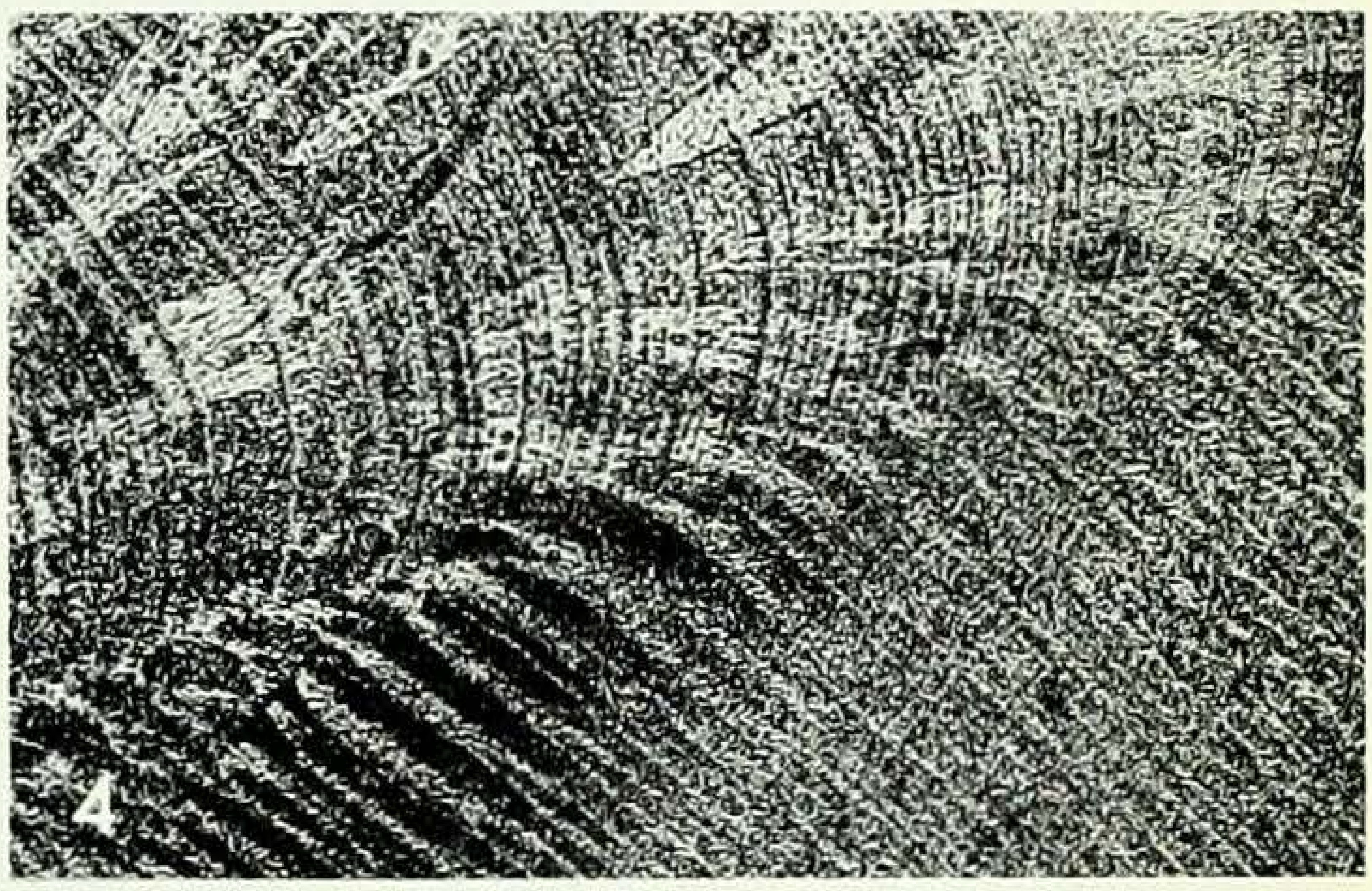
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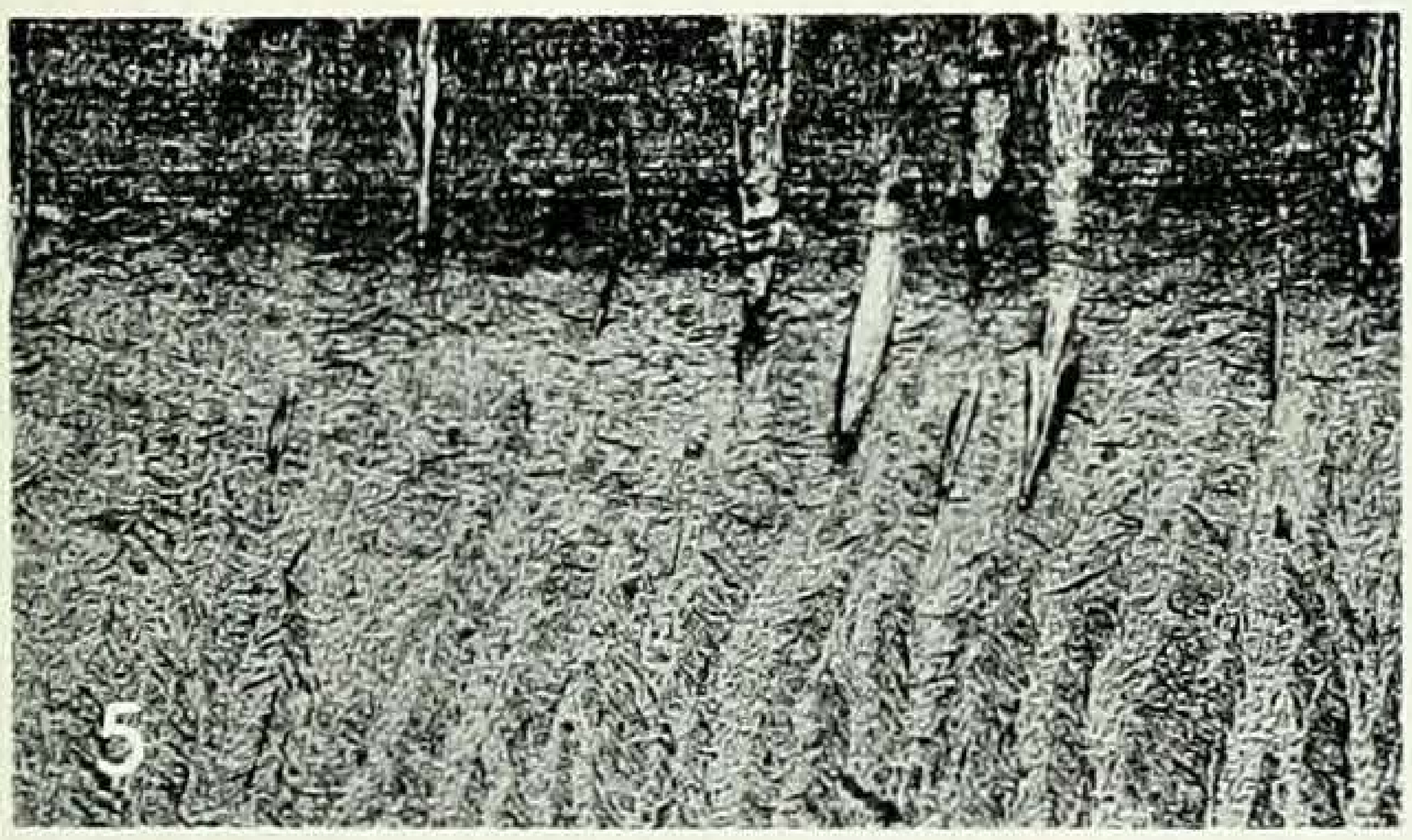
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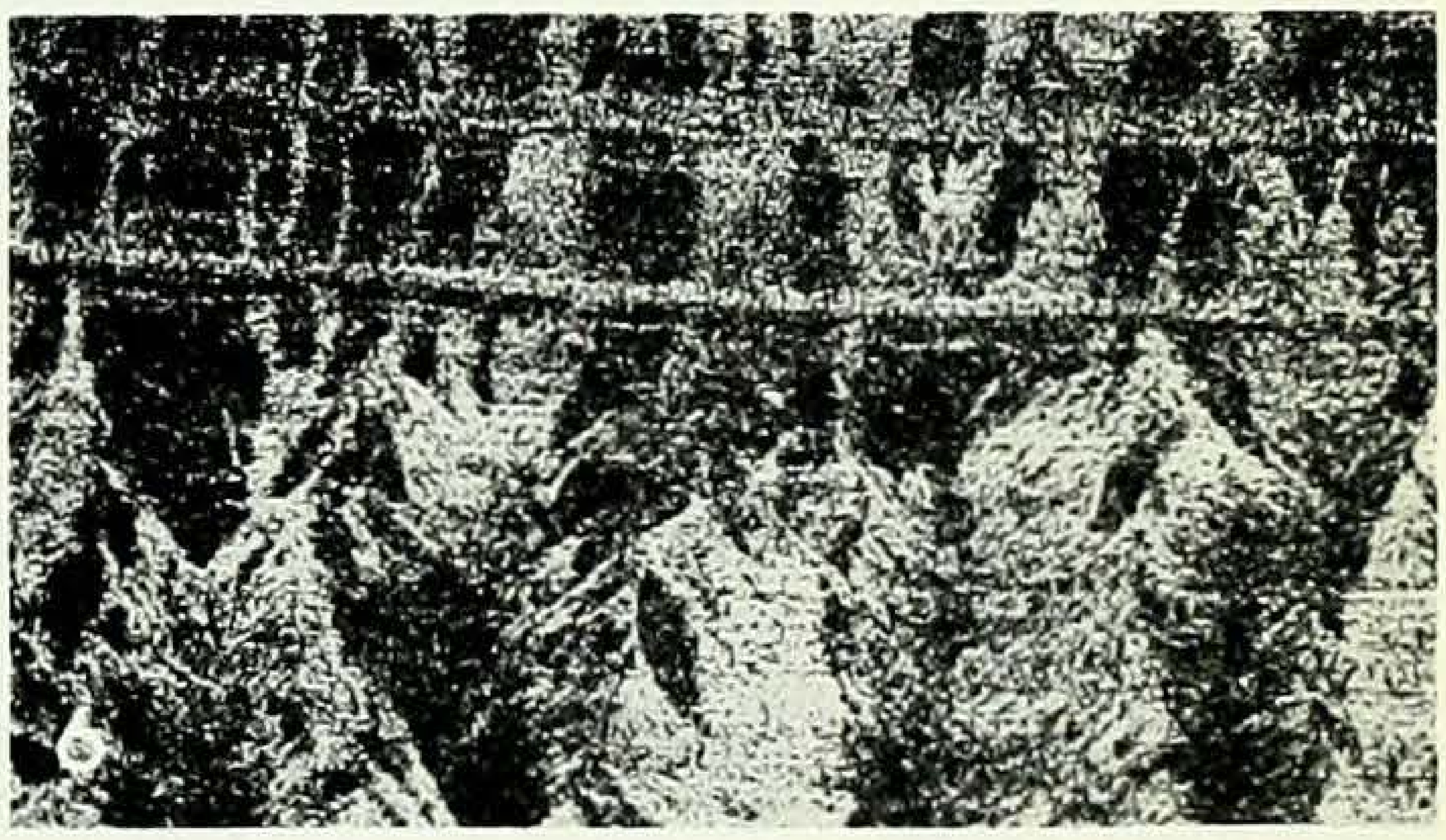
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PLATE 3

FIG. 1. Radial section of ***Trachycardium consors*** in the hinge showing the crossed-lamellar layer with two orientations of first order lamels (top and bottom) separated by a thin myostracum (probably pedal). Acetate peel, × 160.

FIG. 2. Radial section of the outer crossed-lamellar layer of ***Acanthocardia echinata*** showing the very fine, first order lamels intersected by prominent growth banding. Acetate peel, × 160.

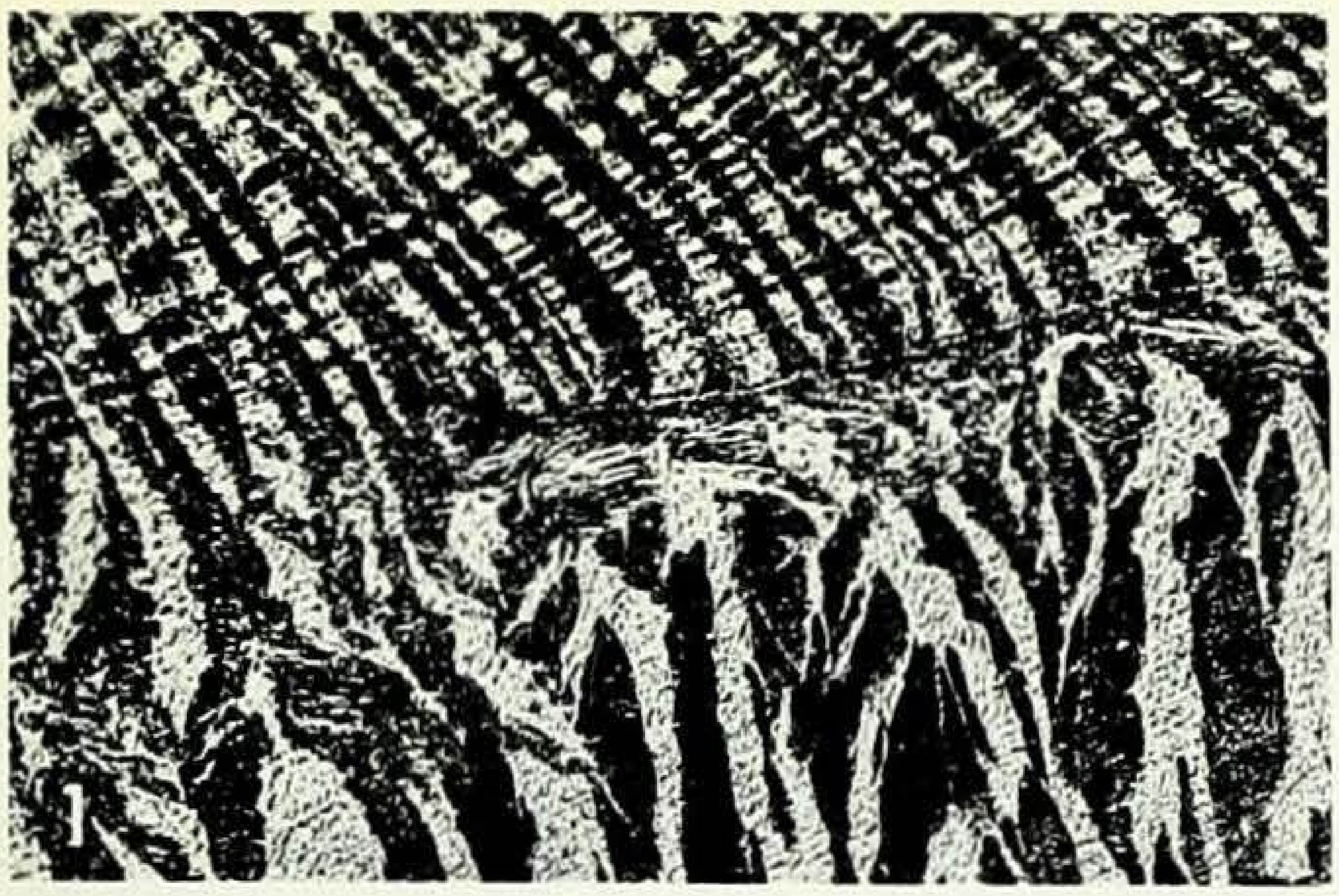
FIG. 3. Radial section of the outer crossed-lamellar layer of ***Laevicardium alternatum.*** Acetate peel, × 160.

FIG. 4. Inner complex crossed-lamellar layer of ***Cerastoderma edule***; radial section. Acetate peel, × 160.

FIG. 5. Radial section of the outer crossed-lamellar layer of ***Hippopus hippopus*** showing the change in orientation of first order lamels associated with strong ribbing. Acetate peel, × 40.

FIG. 6. Radial section of the outer crossed-lamellar layer of ***Tridacna squamosa*** showing several first order lamels with constituent lath-like, second order lamels inclined in opposing directions in adjacent first order lamels. Acetate peel, × 160.

FIGS 7 & 8. Radial sections of ***Hippopus hippopus***, inner layer. Fig. 7 is a scanning electron-micrograph (× 1,200) of the structure which in the optical micrograph (Fig. 8, × 160) appears homogeneous and banded. The banding consists of sheets of aragonite needles arranged with their long axes normal to the plane of the sheet.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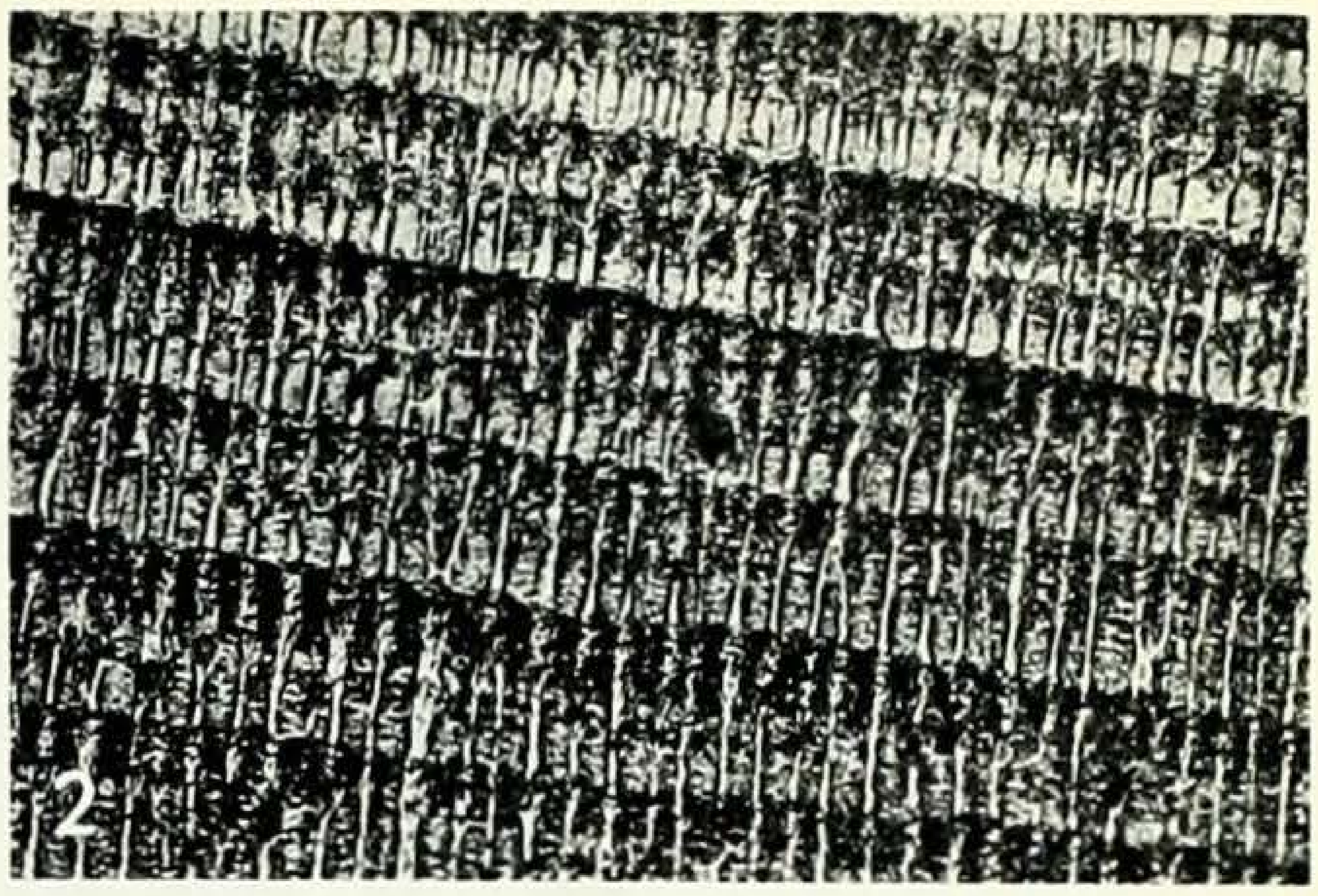
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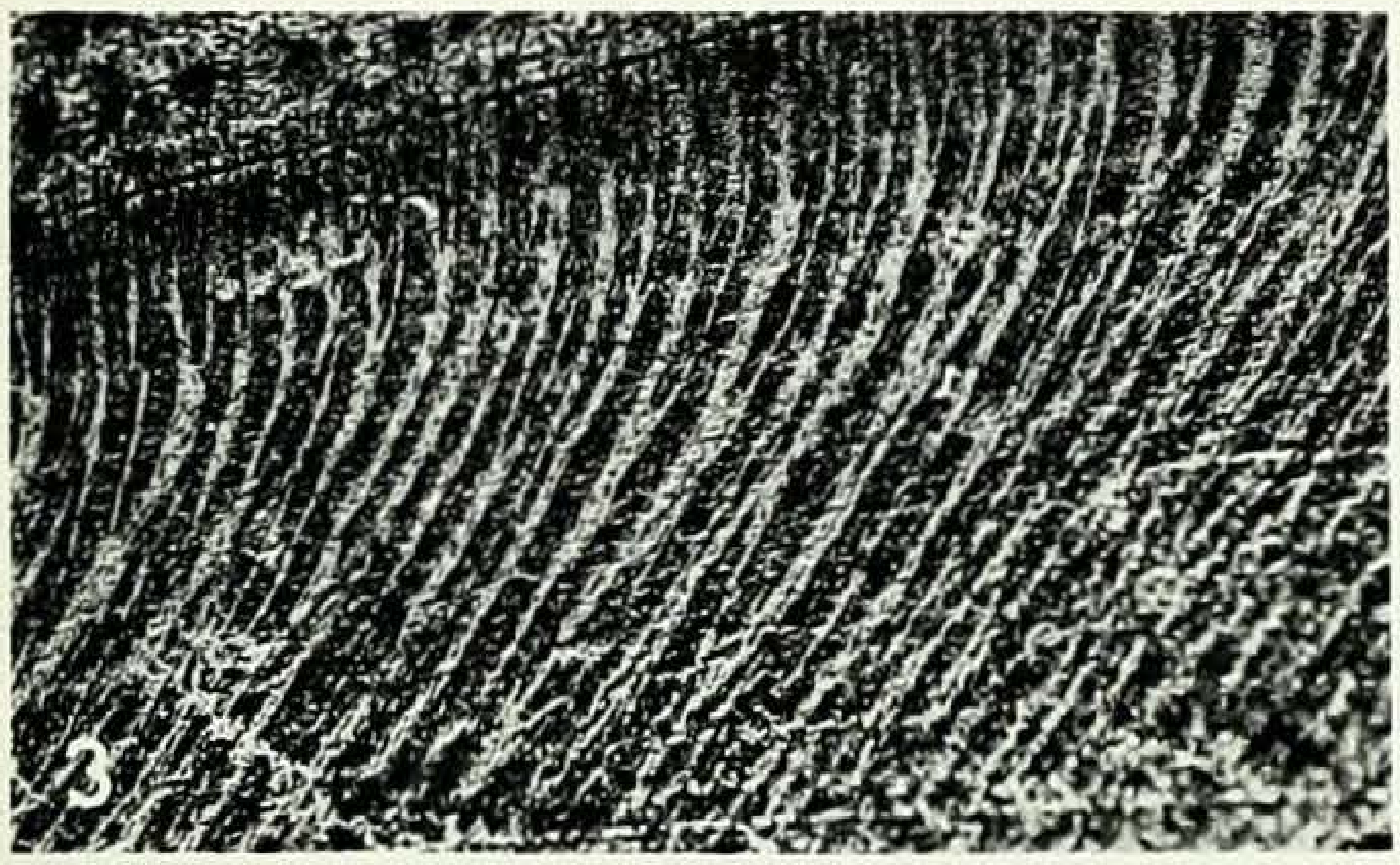
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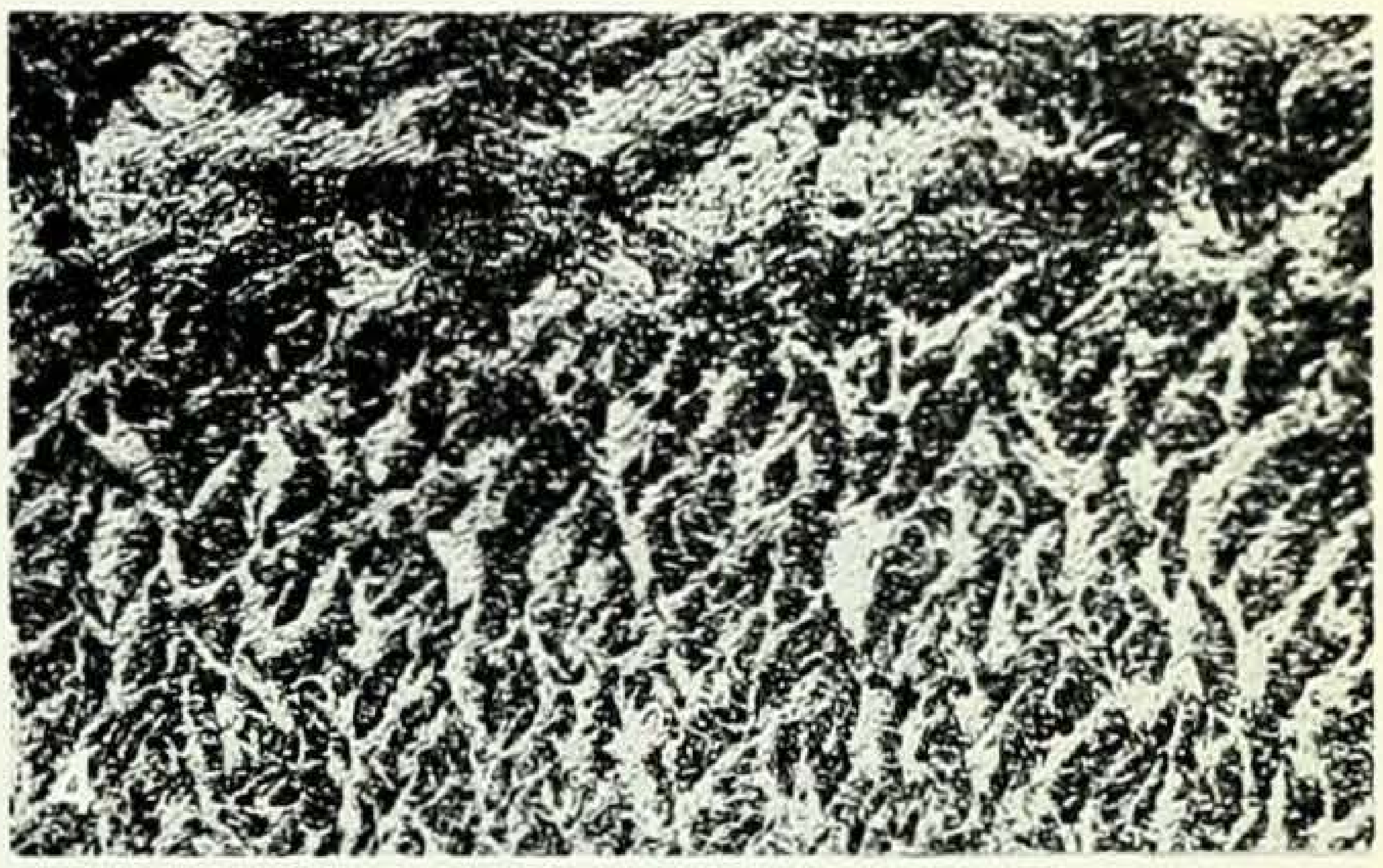
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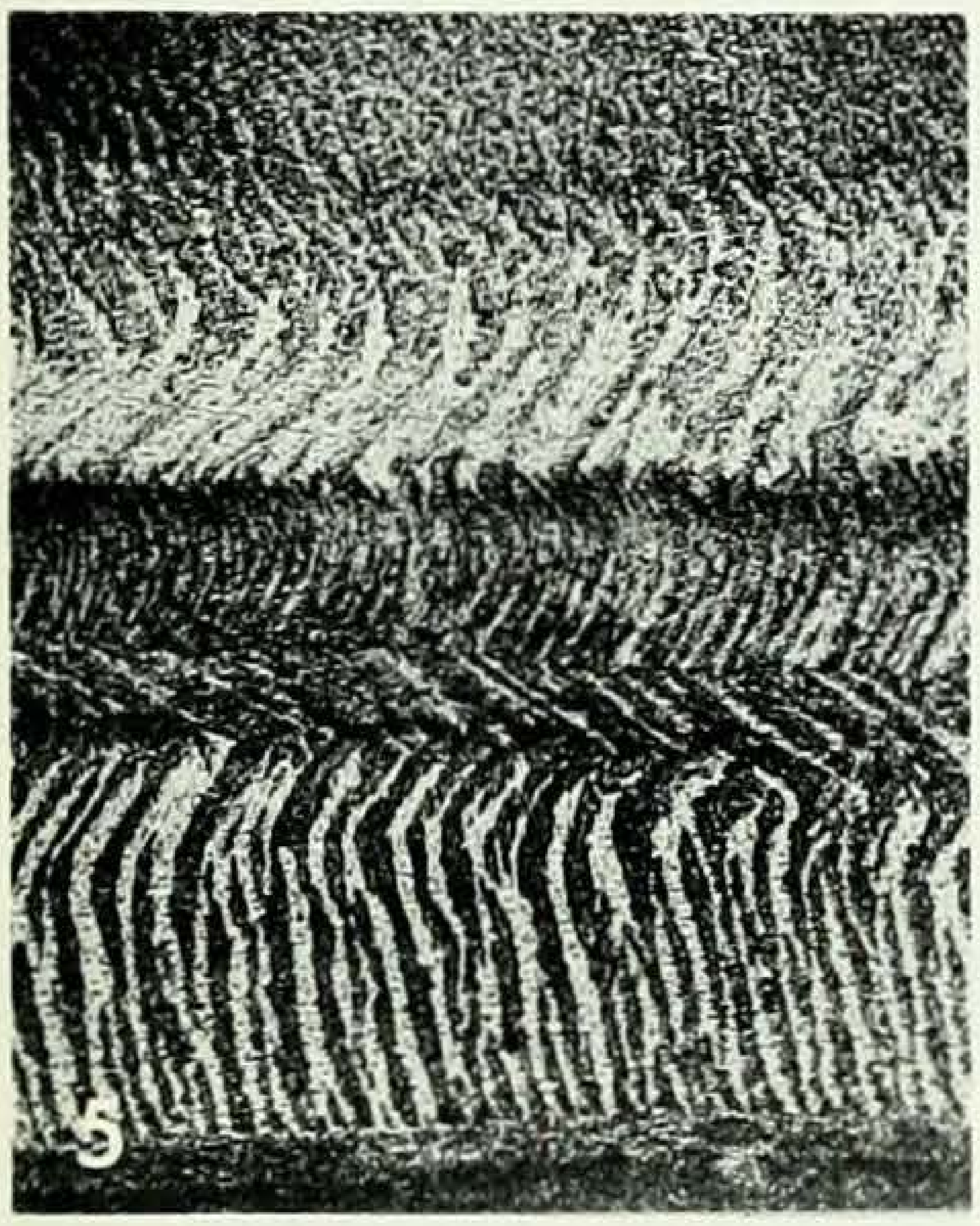
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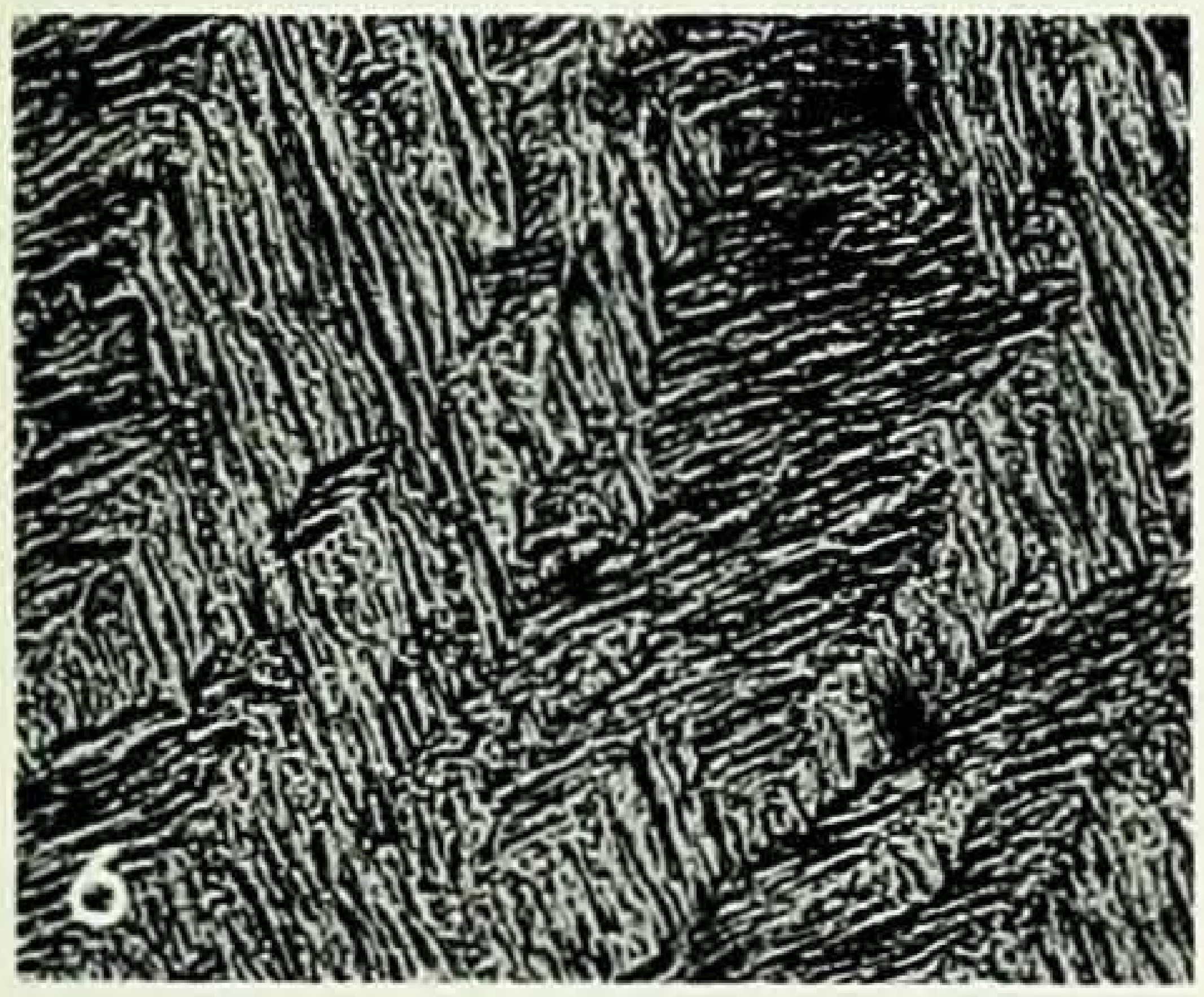
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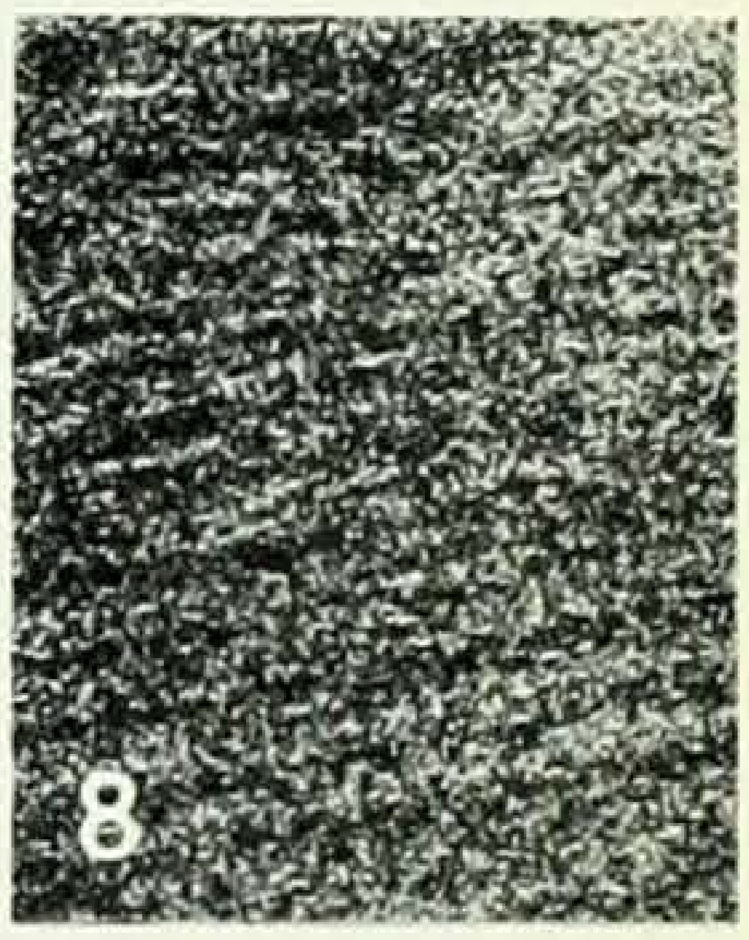
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PLATE 4

FIG. 1. Radial section of ***Mactronella exoleta*** showing boundary between outer crossed-lamellar and inner complex crossed-lamellar layers. Acetate peel, ×40.

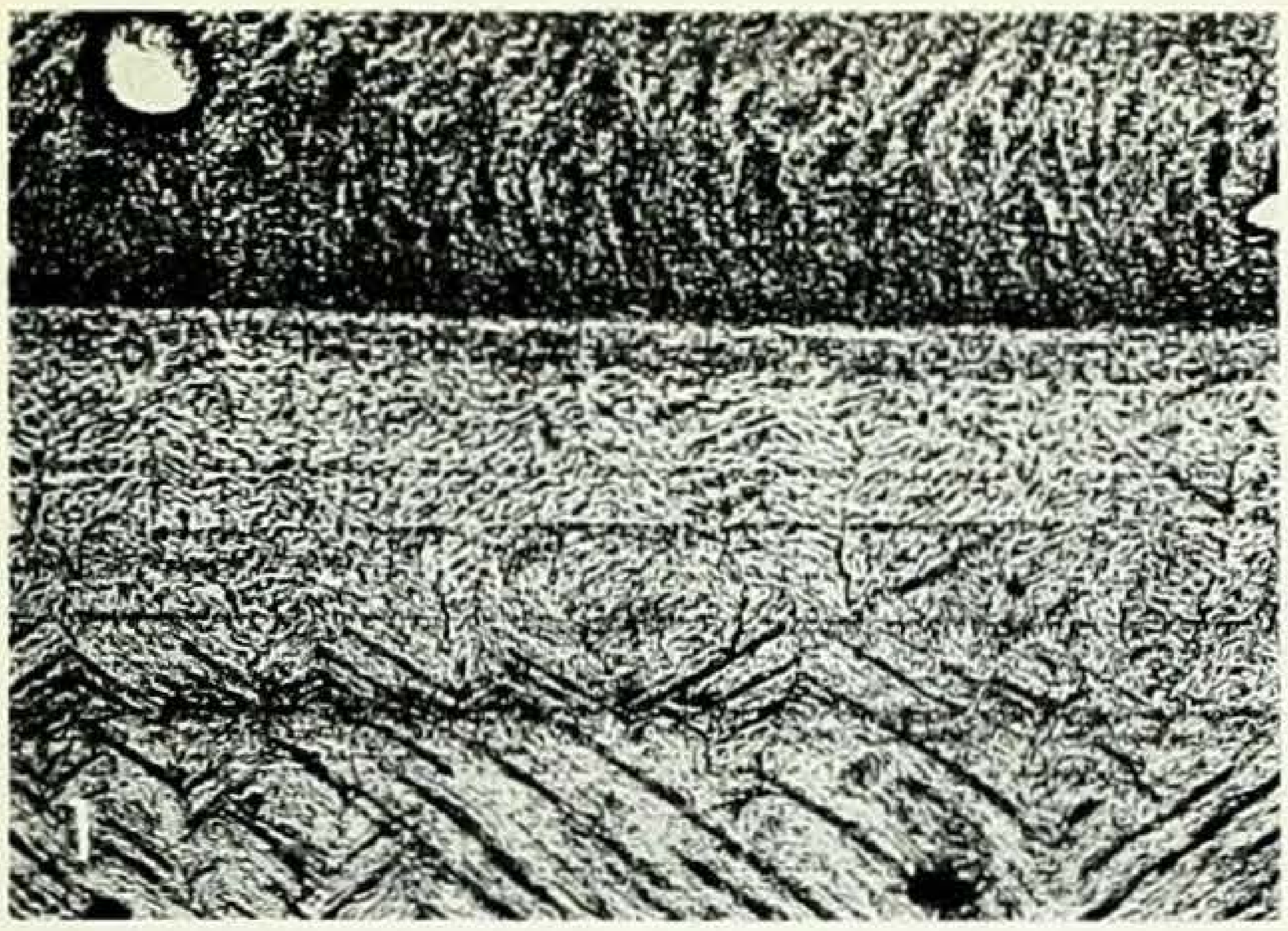
FIG. 2. Outer crossed-lamellar layer of ***Mactra producta*** showing the very thin lamels characteristic of this family. Acetate peel, ×80.

FIG. 3. Radial section of the inner layer of ***Ensis siliqua*** showing how this layer is built up of sheets of prisms, alternating with sheets of complex crossed-lamellar structure. Scanning electron-micrograph ×2,000.

FIG. 4. Polished, etched, radial section of the middle crossed-lamellar layer of ***Hecuba scortum.*** Scanning electron-micrograph, ×2,000.

FIG. 5. Radial section of the junction between the outer composite prismatic and the middle crossed-lamellar layers of ***Donax faba***. Scanning electron-micrograph, ×1,600.

FIG. 6. Radial section of the composite prismatic layer of ***Donax faba*** showing the long, lath-shaped units of this structure as found in this family. Scanning electron-micrograph, ×2,000.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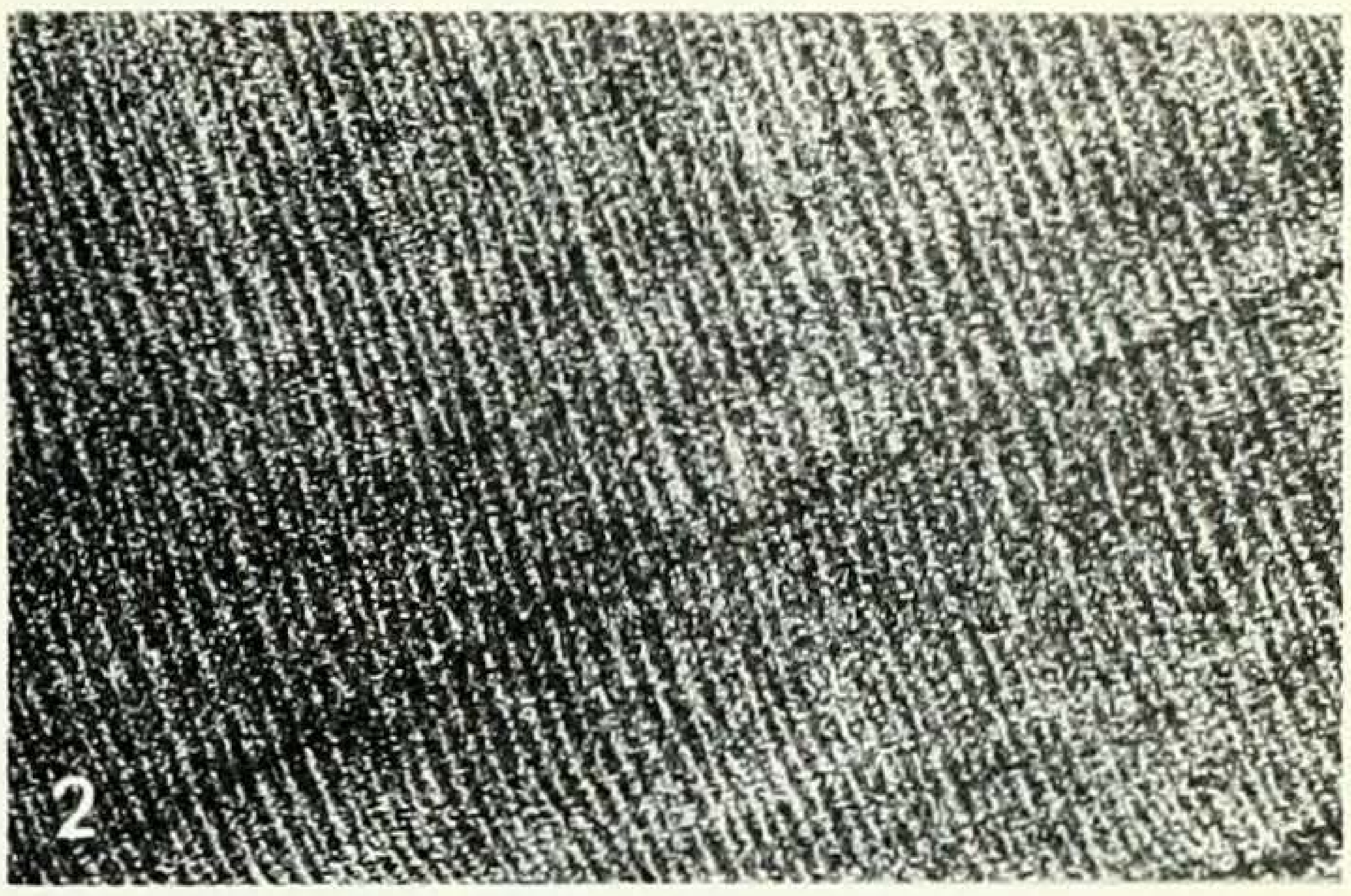
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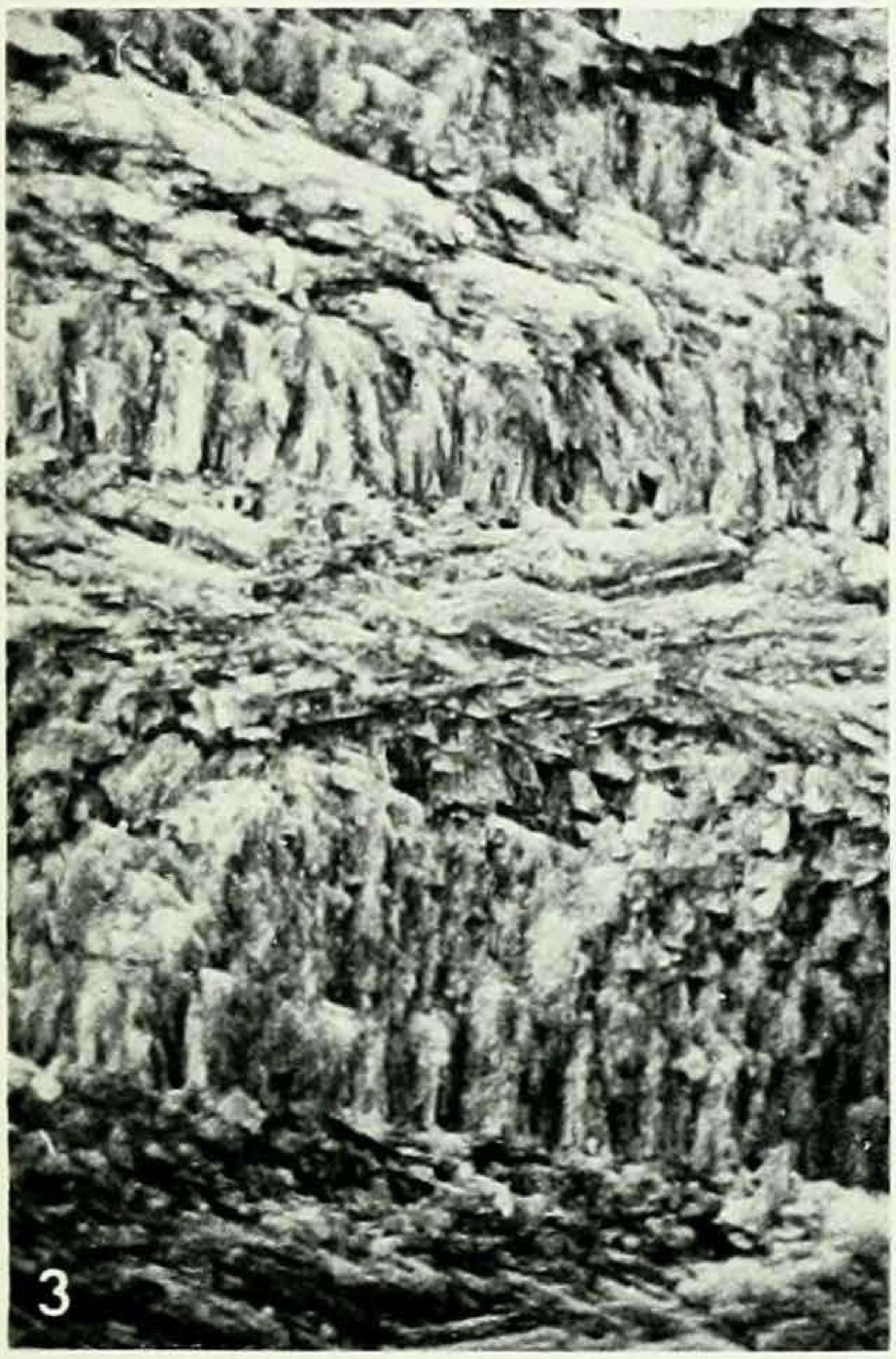
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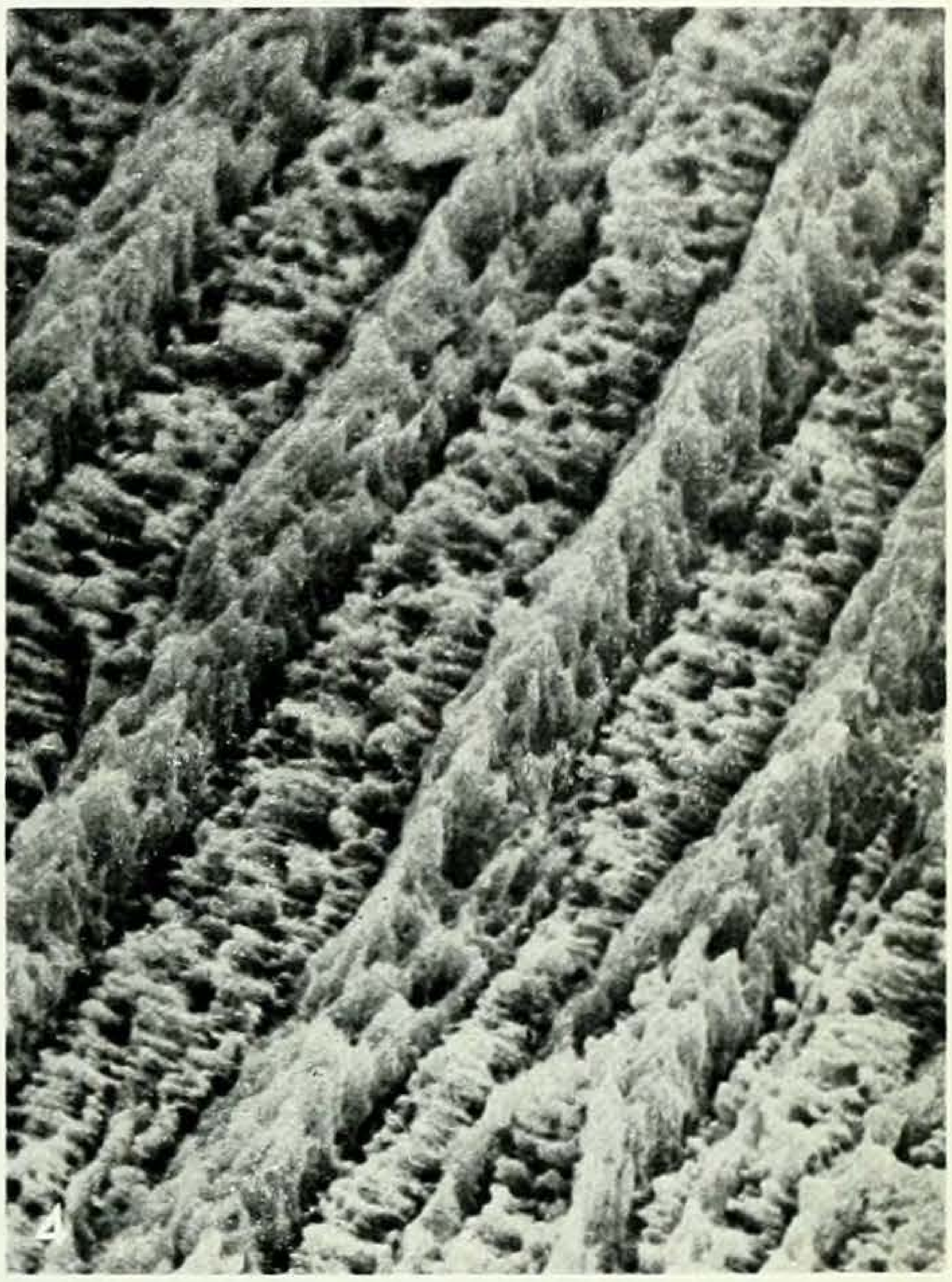
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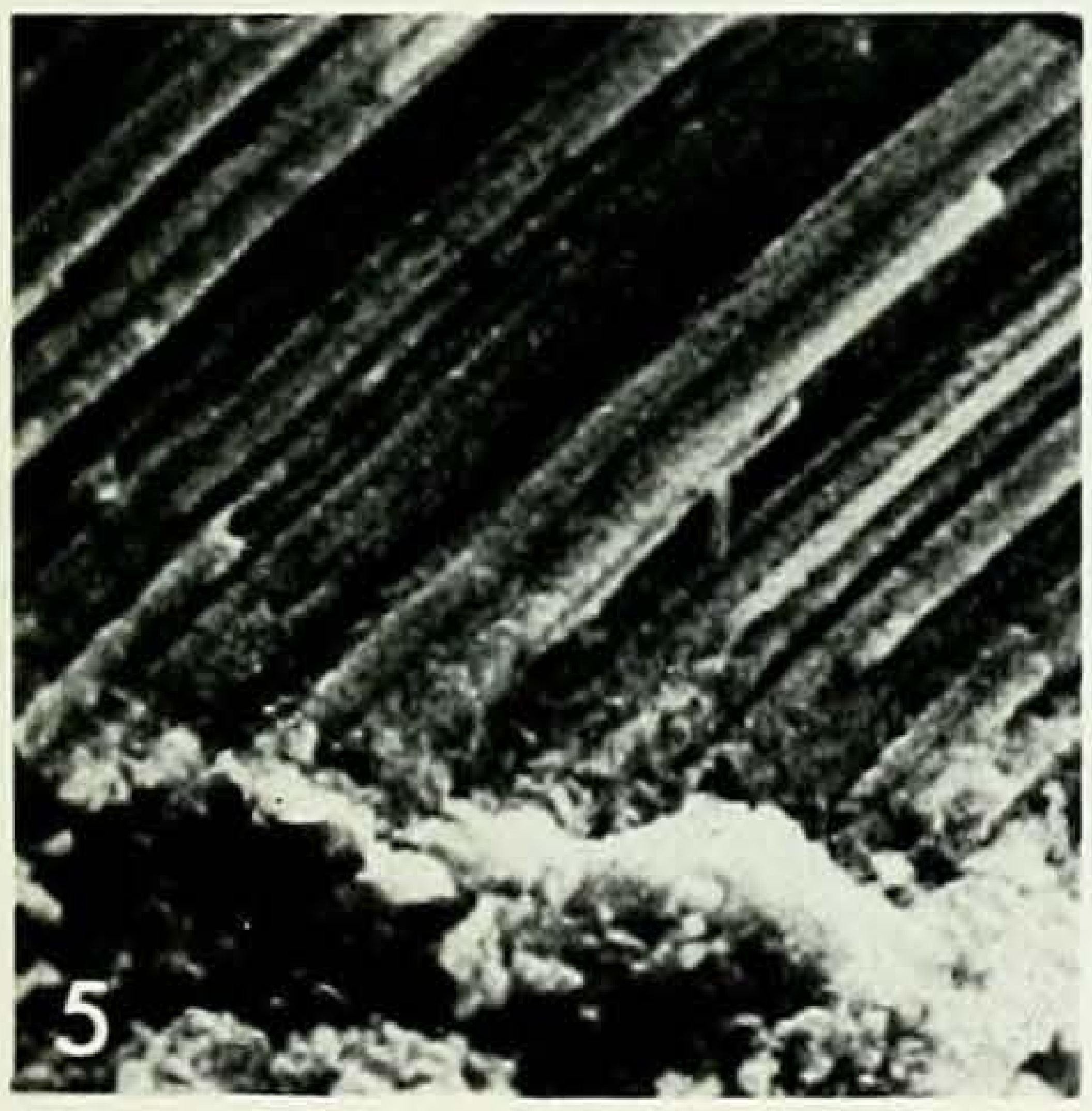
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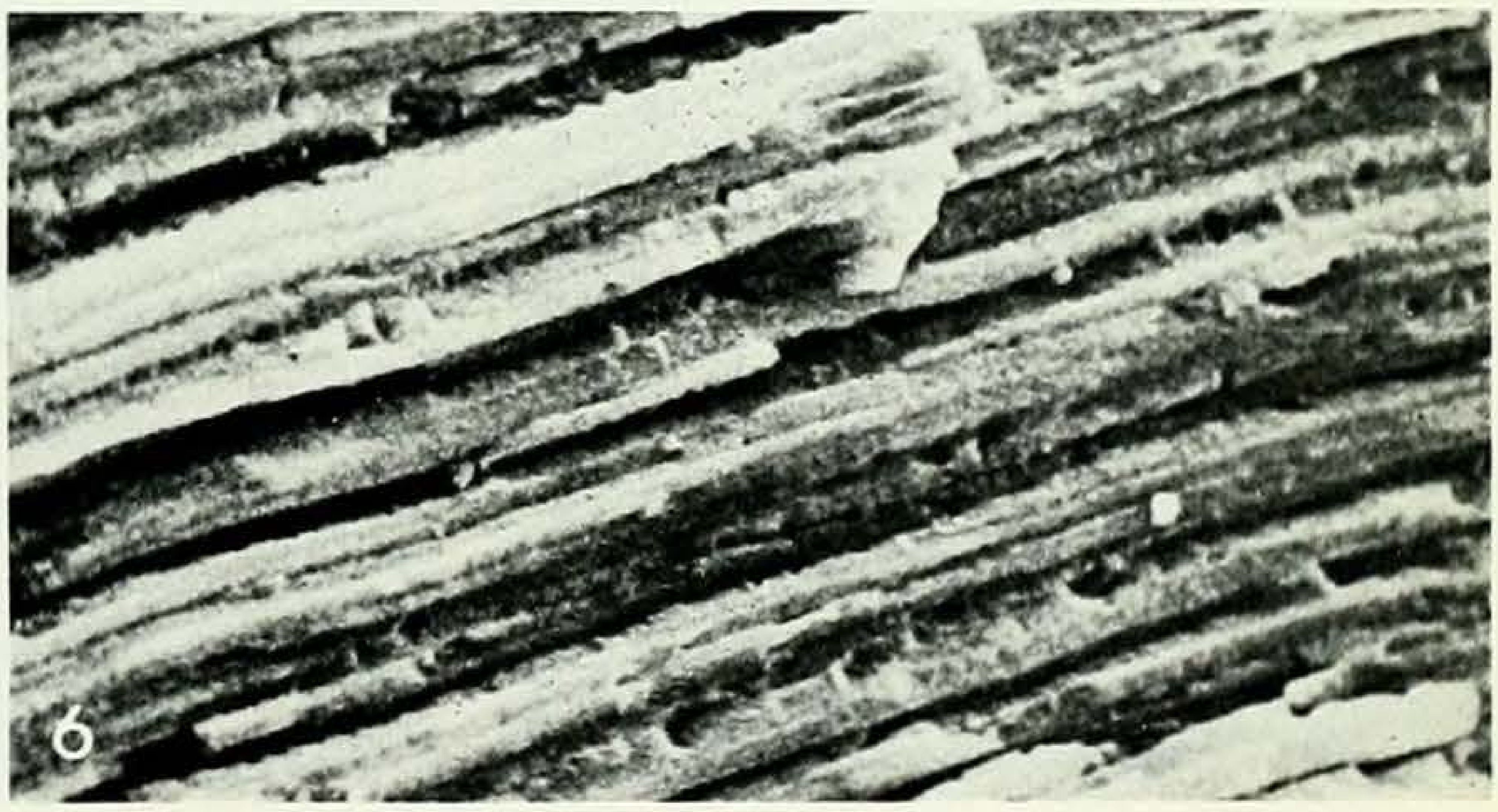
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PLATE 5

FIG. 1. Polished, etched, section of the inner prismatic layer (myostracal prisms) of ***Semele tortuosa.*** Scanning electron-micrograph, ×600.

FIG. 2. As Fig. 1; showing middle crossed-lamellar layer and the inner prismatic layer separated by a thin sheet of myostracal prisms of the pallial myostracum. Scanning electron-micrograph, ×2,000.

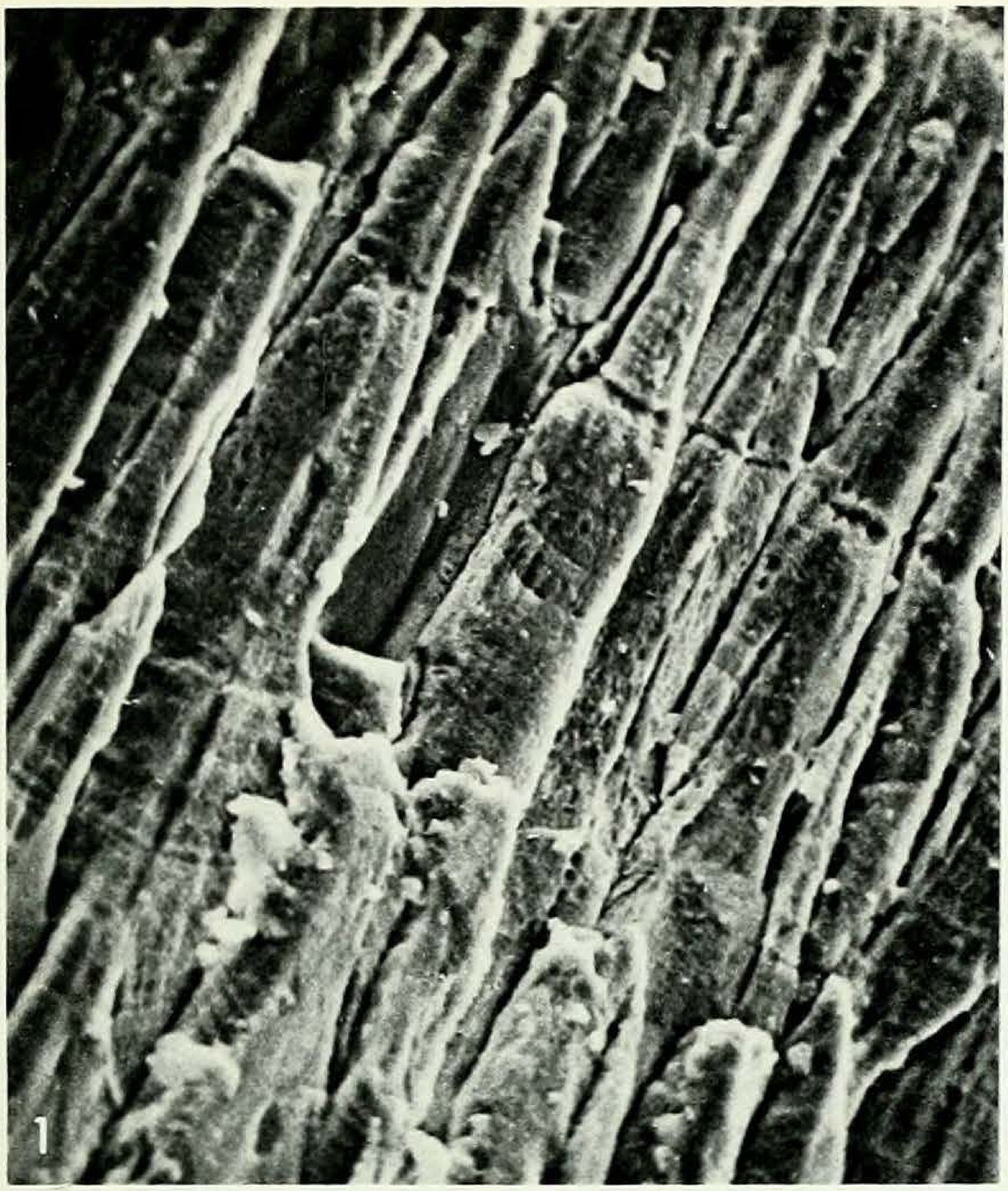
FIG. 3. Radial section of the middle crossed-lamellar layer of ***Solenotellina radiata*** showing very narrow first order lamels. Acetate peel, ×80.

FIG. 4. Radial section of ***Semele tortuosa*** with outer composite prismatic layer (top right), middle crossed-lamellar layer and an inner layer composed of myostracal prisms. Acetate peel, ×40.

FIG. 5. Complex crossed-lamellar inner layer of ***Asaphis deflorata.*** Acetate peel, ×40.

FIG. 6. Radial section of inner complex crossed-lamellar layer of ***Solenotellina radiata.*** Acetate peel, ×80.

FIG. 7. Radial section of the inner homogeneous layer of ***Tellina radiata*** showing lamellate character produced by organic sheets. Acetate peel, ×80.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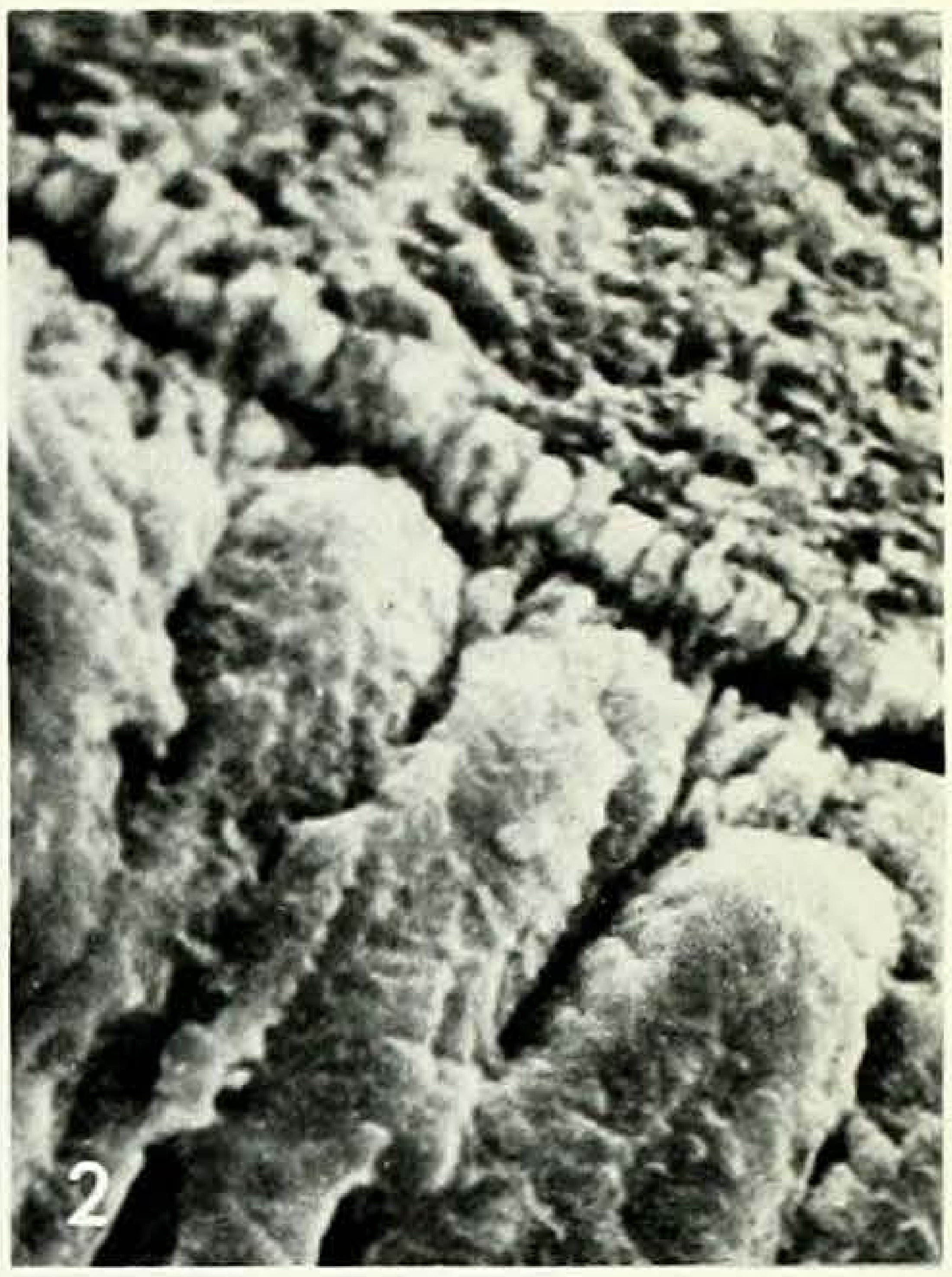
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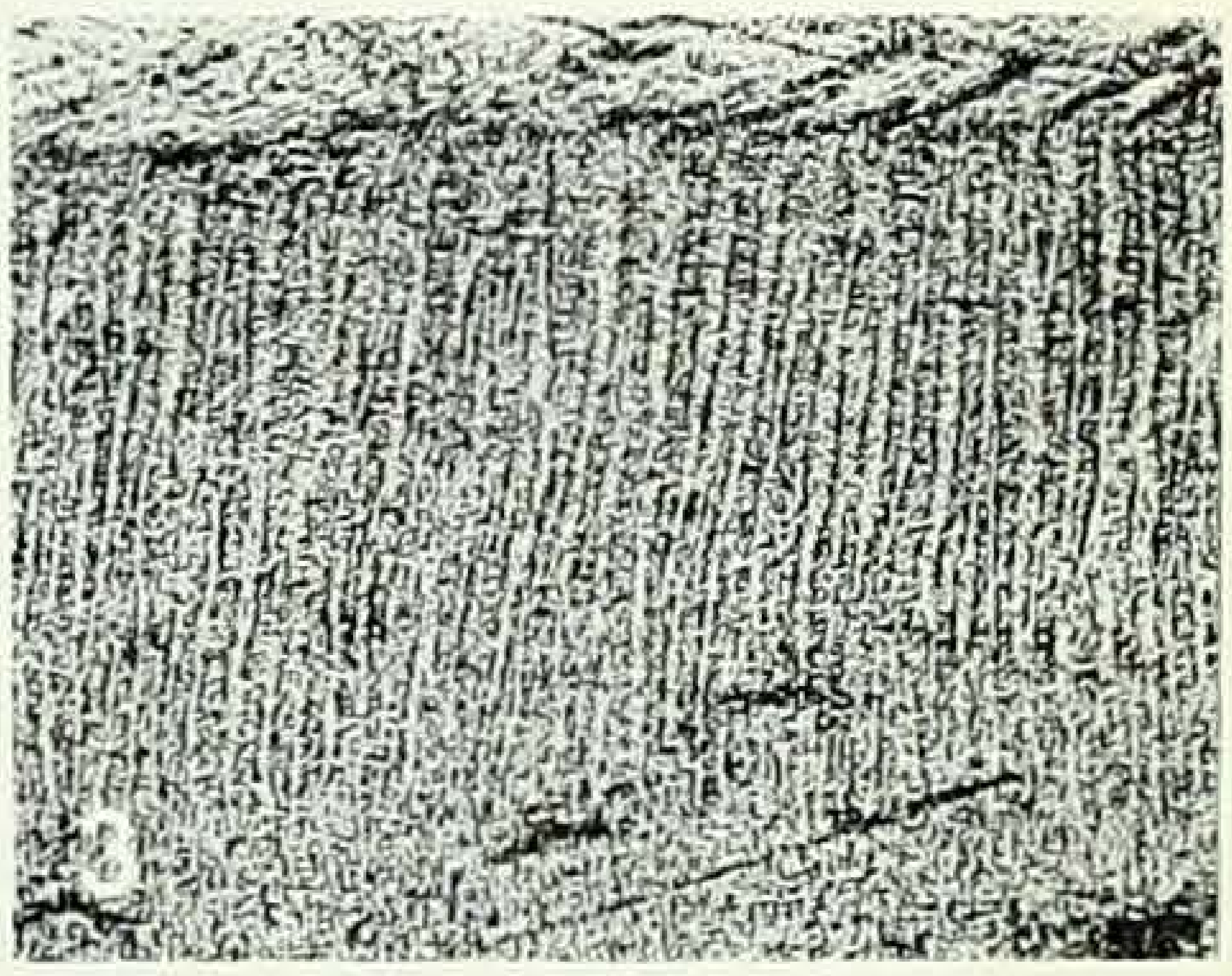
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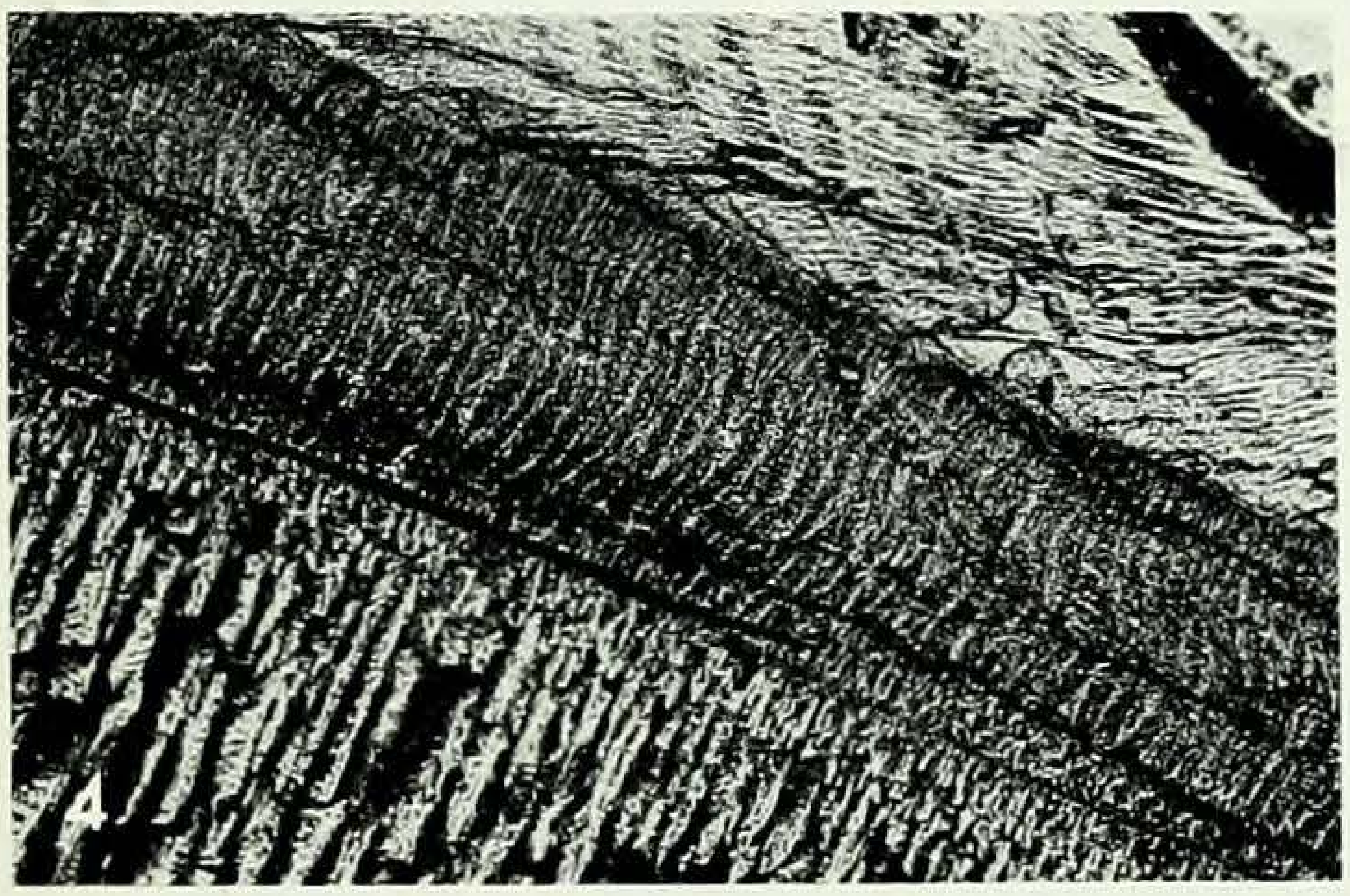
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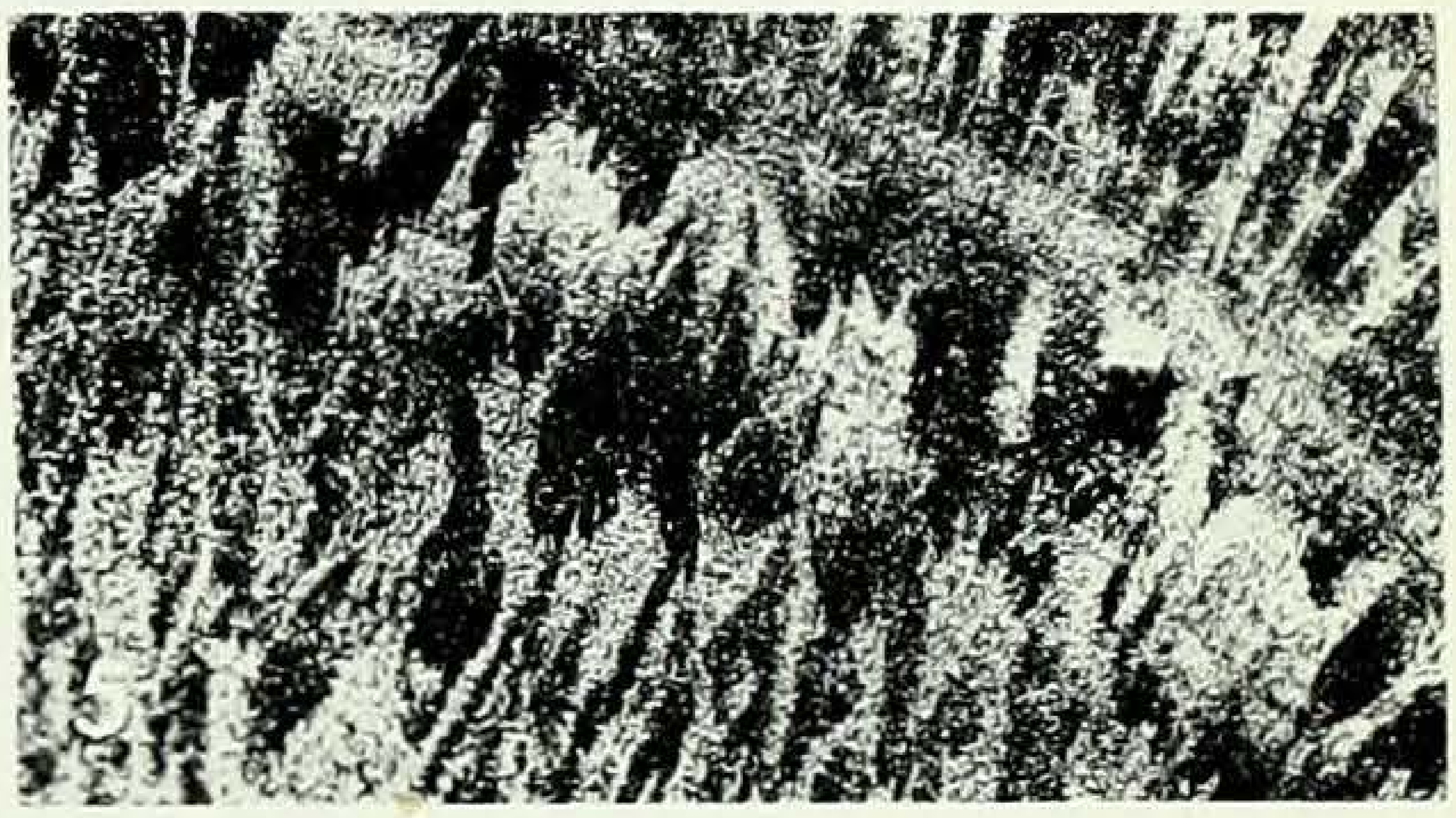
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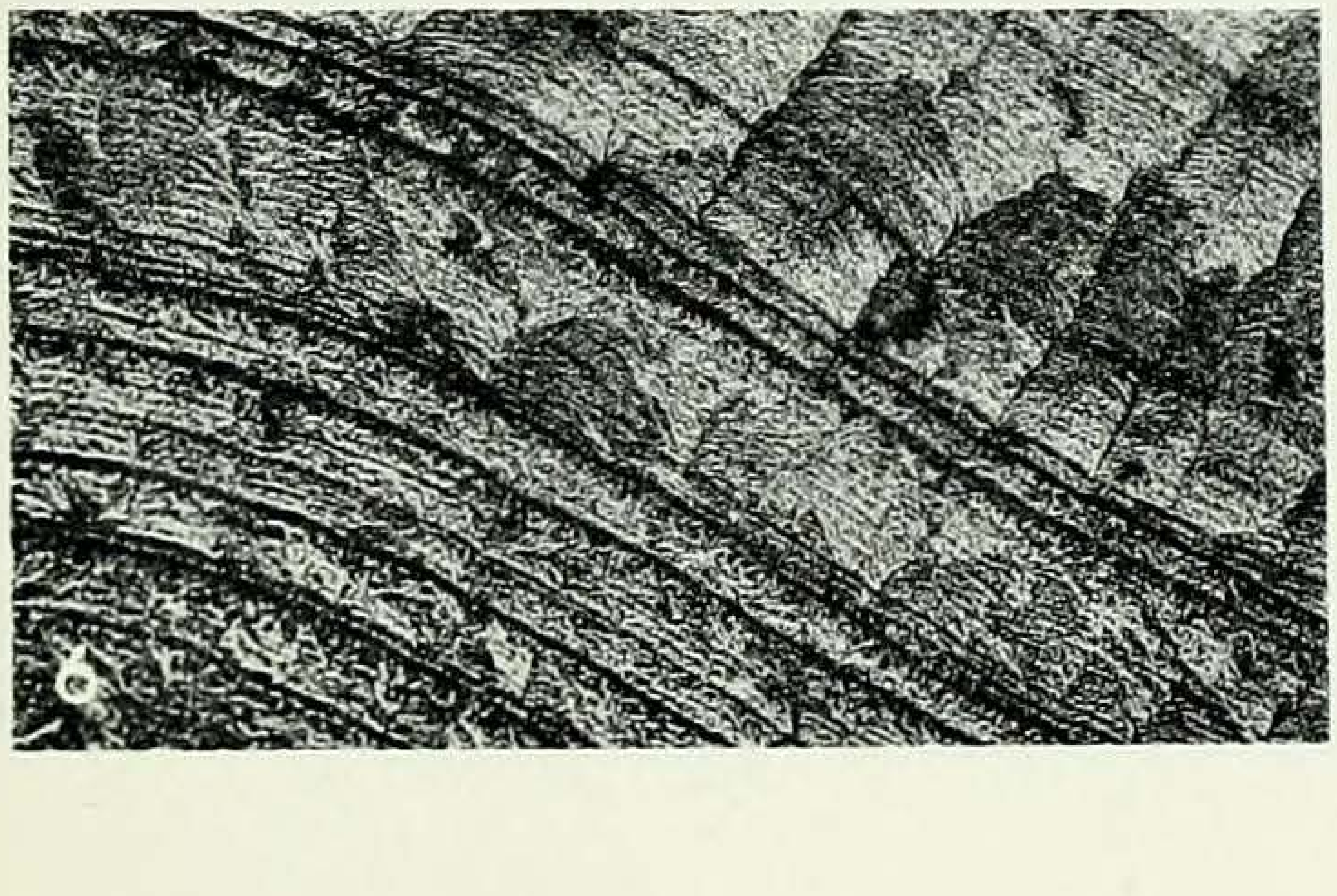
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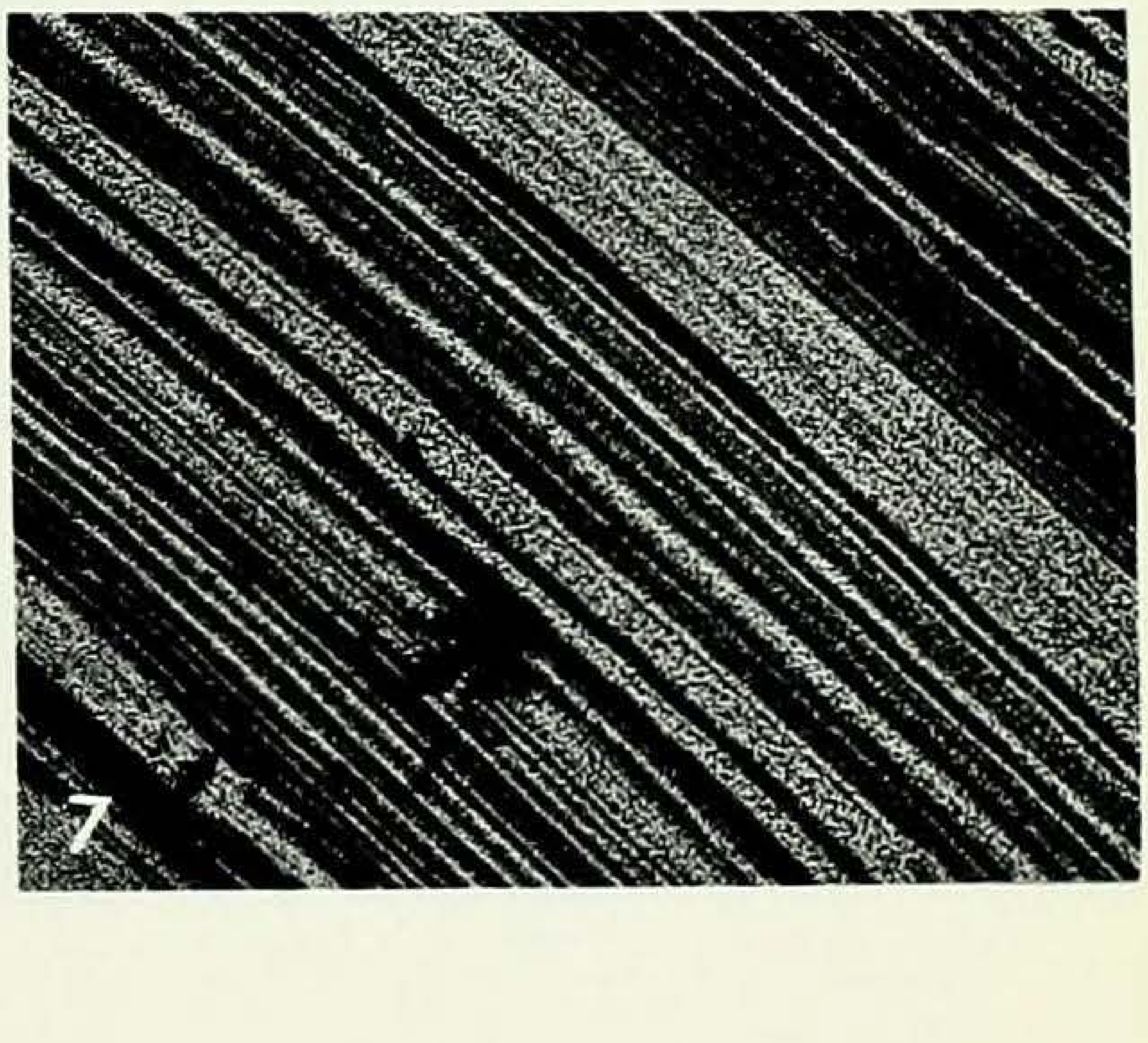
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PLATE 6

FIG. 1. Radial section of the outer crossed-lamellar layer of ***Glossus humanus***; pallial myostracum at bottom left. Acetate peel, × 80.

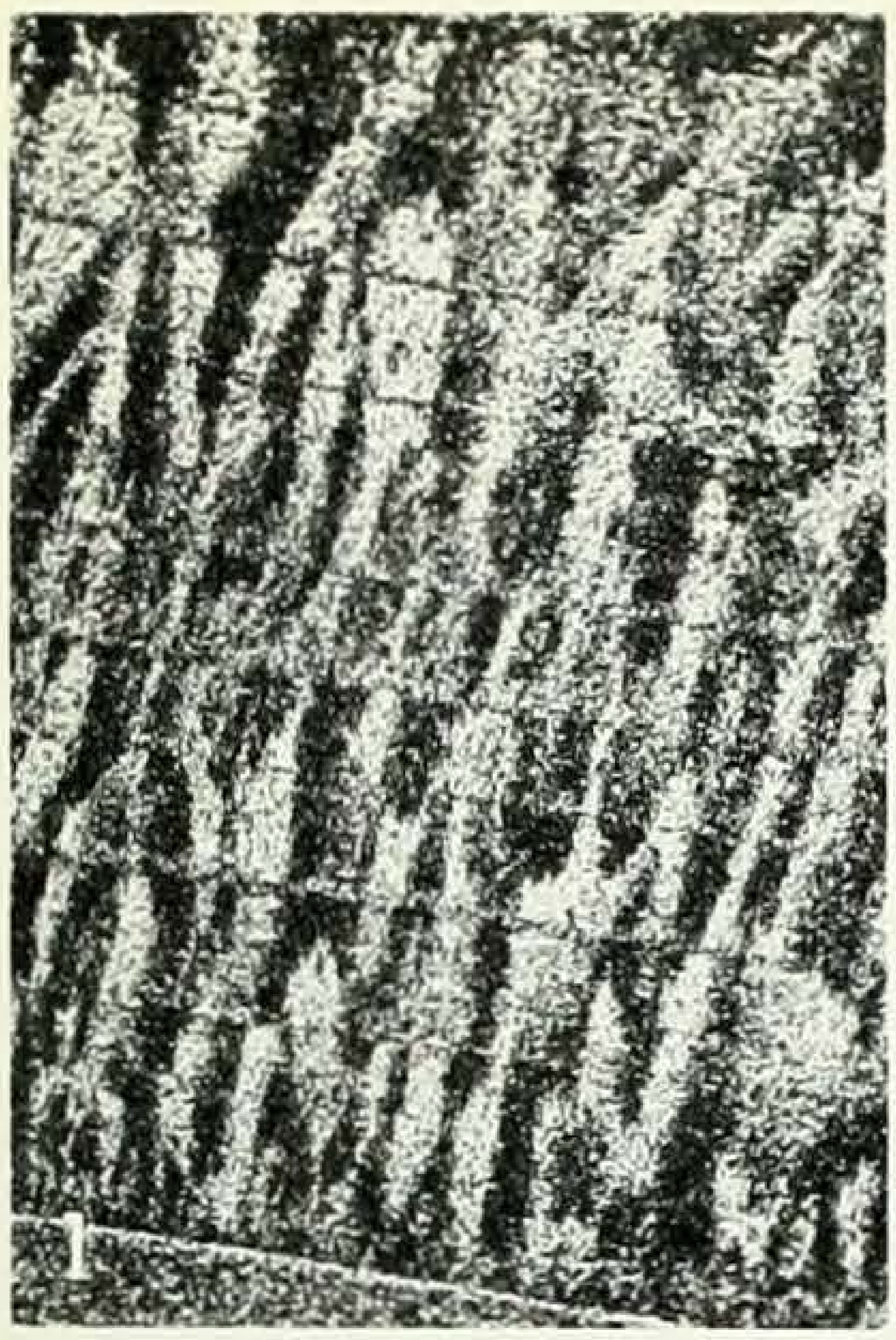
FIG. 2. Radial section of the inner complex crossed-lamellar of ***Polymesoda anomalata***. Acetate peel, × 80.

FIG. 3. Polished and etched radial section of the outer crossed-lamellar layer of ***Dreissena polymorpha*** showing five adjacent lamellae. Scanning electron-micrograph, × 2,400.

FIG. 4. Radial section (polished and etched) of the outer crossed-lamellar layer of ***Sphaerium lacustris.*** Scanning electron-micrograph, × 2,400.

FIG. 5. Inner surface of the inner homogeneous layer of ***Gaimardia trapezia*** showing a general alignment of granules towards the shell margin (top right). Scanning electron-micrograph, × 3,000.

FIG. 6. Fractured section of the inner homogeneous layer of ***Gaimardia trapezia.*** Scanning electron-micrograph, × 800.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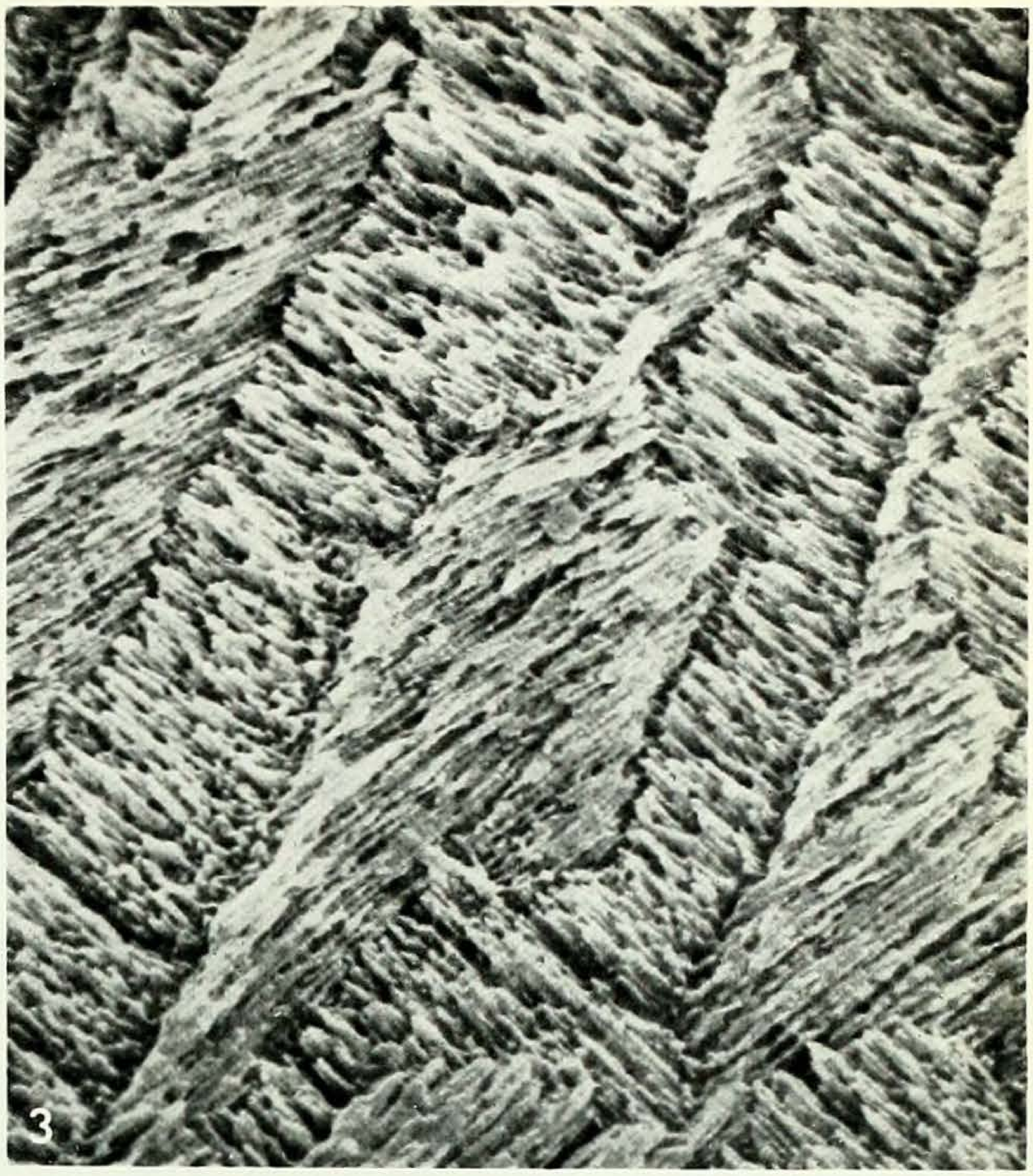
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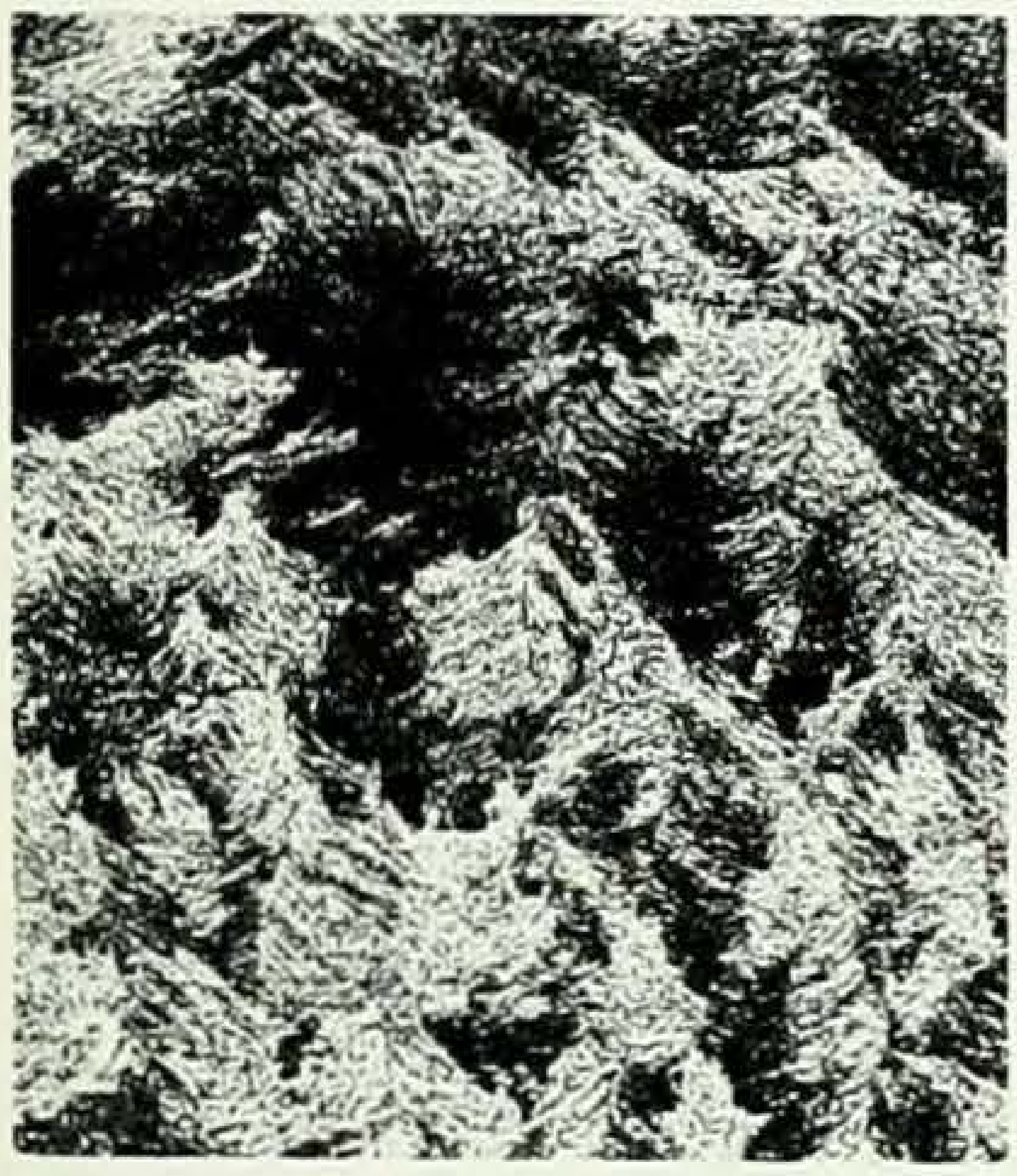

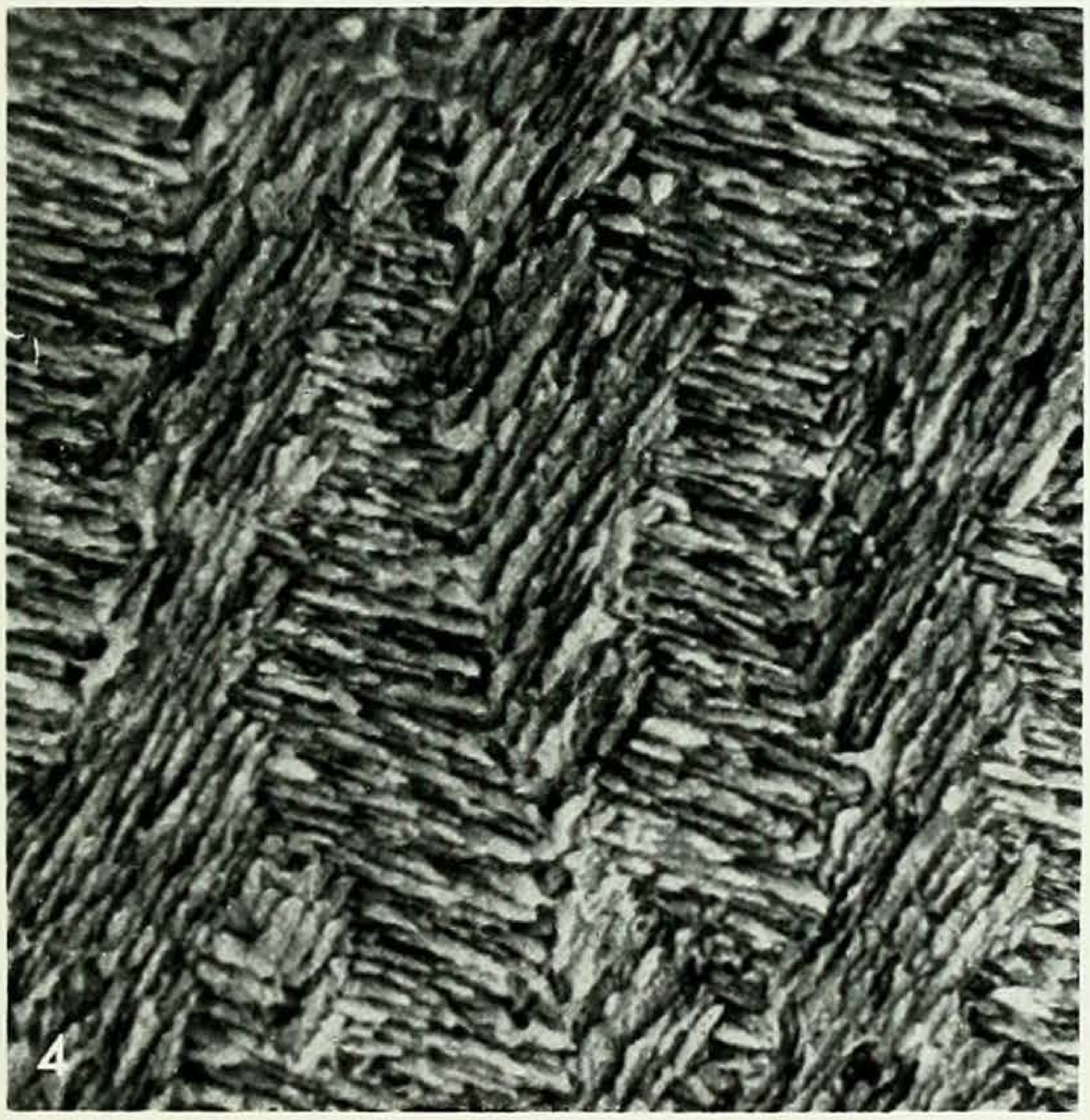
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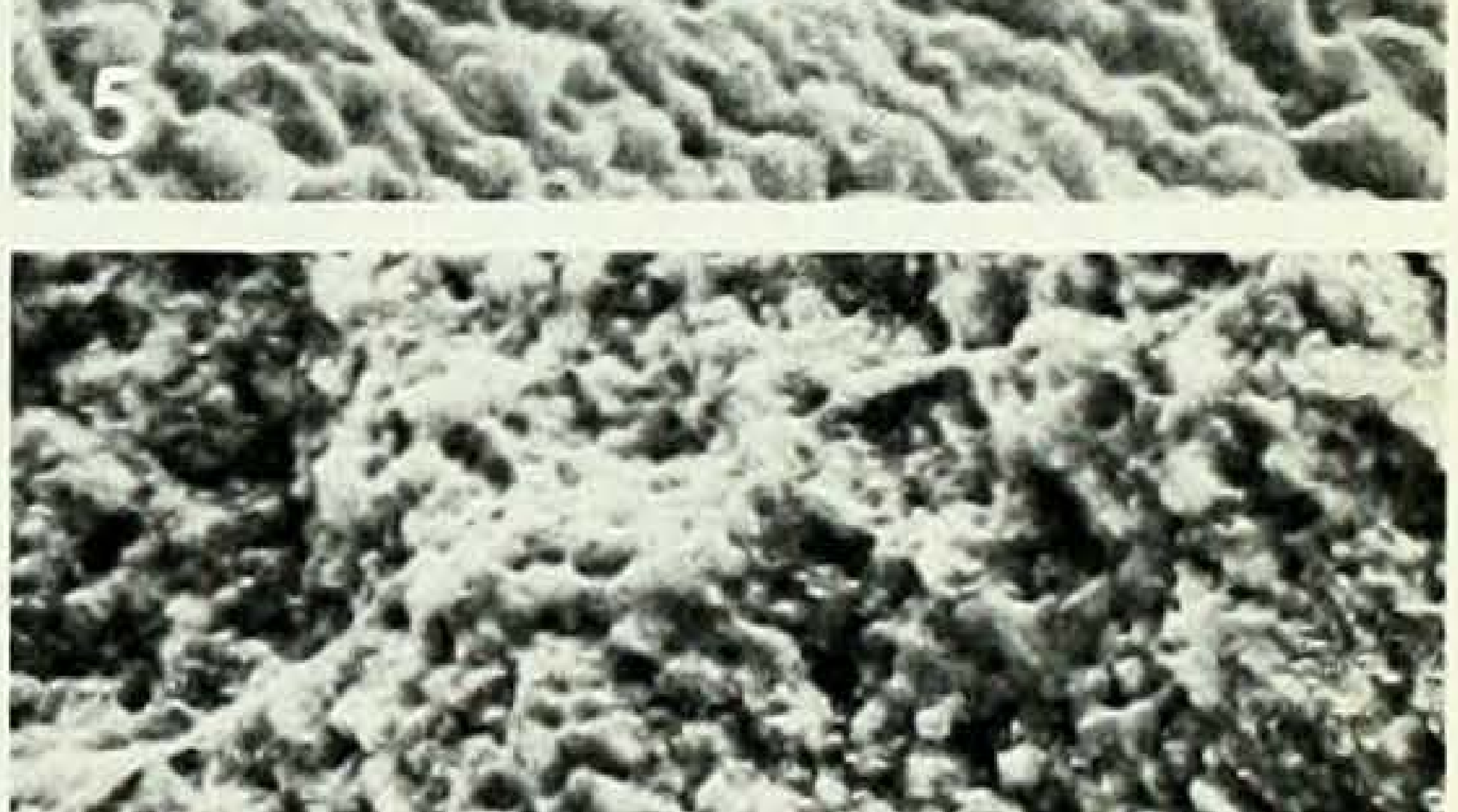
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PLATE 7

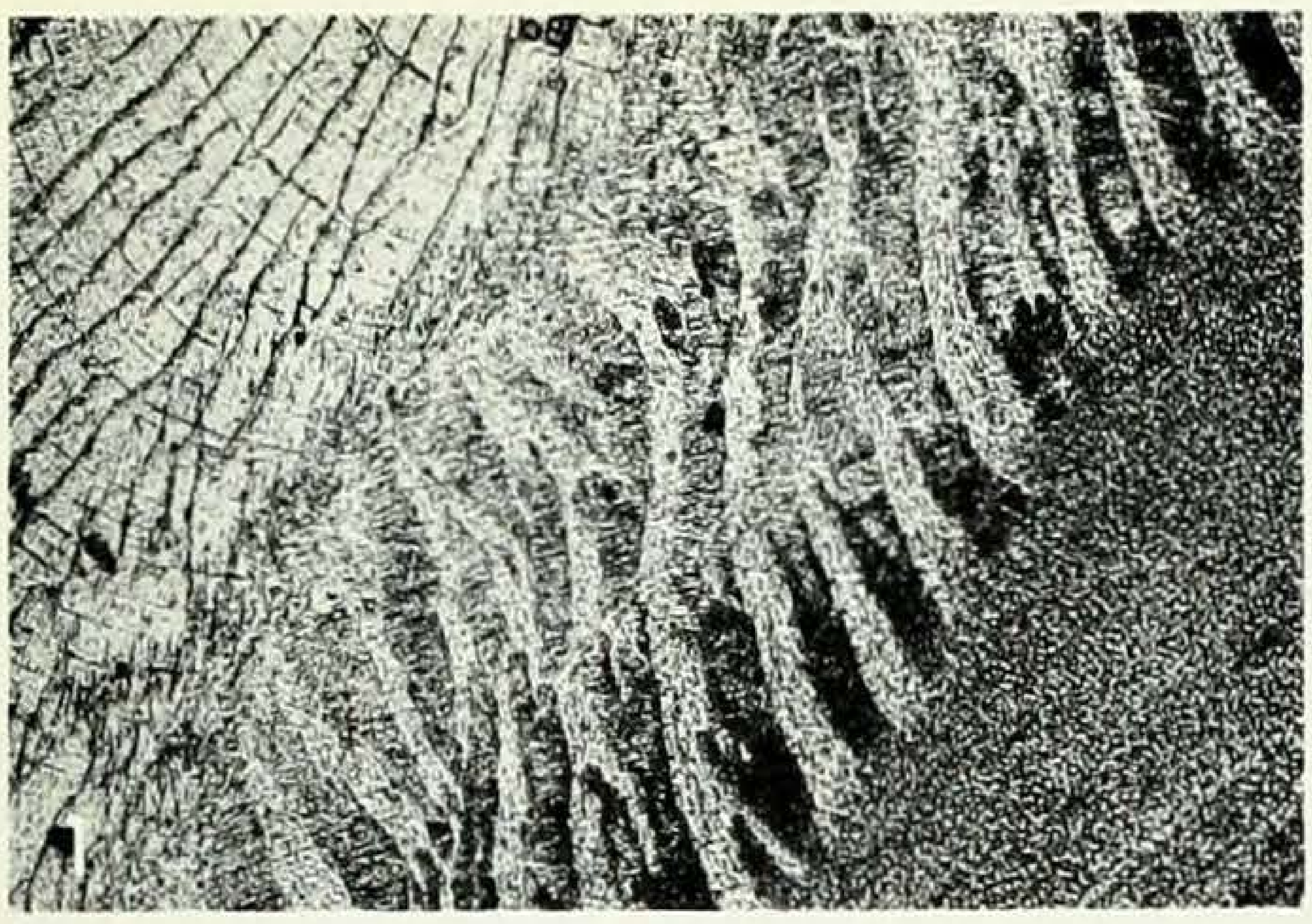
FIG. 1. Radial section of ***Venus striatula*** showing the outer composite prismatic layer (top left) and the middle crossed-lamellar layer which grades into homogeneous structure inwards (bottom right). Acetate peel, ×80.

FIG. 2. Radial section of ***Venus striatula*** showing the outer composite prismatic layer (top) and the middle homogeneous layer. Acetate peel, ×80.

FIG. 3. Concentric, polished, etched, section through the outer composite prismatic layer of ***Mercenaria mercenaria*** showing the large prism units made up of small crystallites. Scanning electron micrograph, ×2,400.

FIG. 4. Radial section (polished, etched) of the outer composite prismatic layer of ***Tivela hians*** showing first order units made up of smaller crystallites in a feathery arrangement. Scanning electron micrograph, ×1,400.

FIG. 5. As Fig. 4, showing the contact between the outer composite prismatic and the middle homogeneous layers. Scanning electron micrograph, ×3,000.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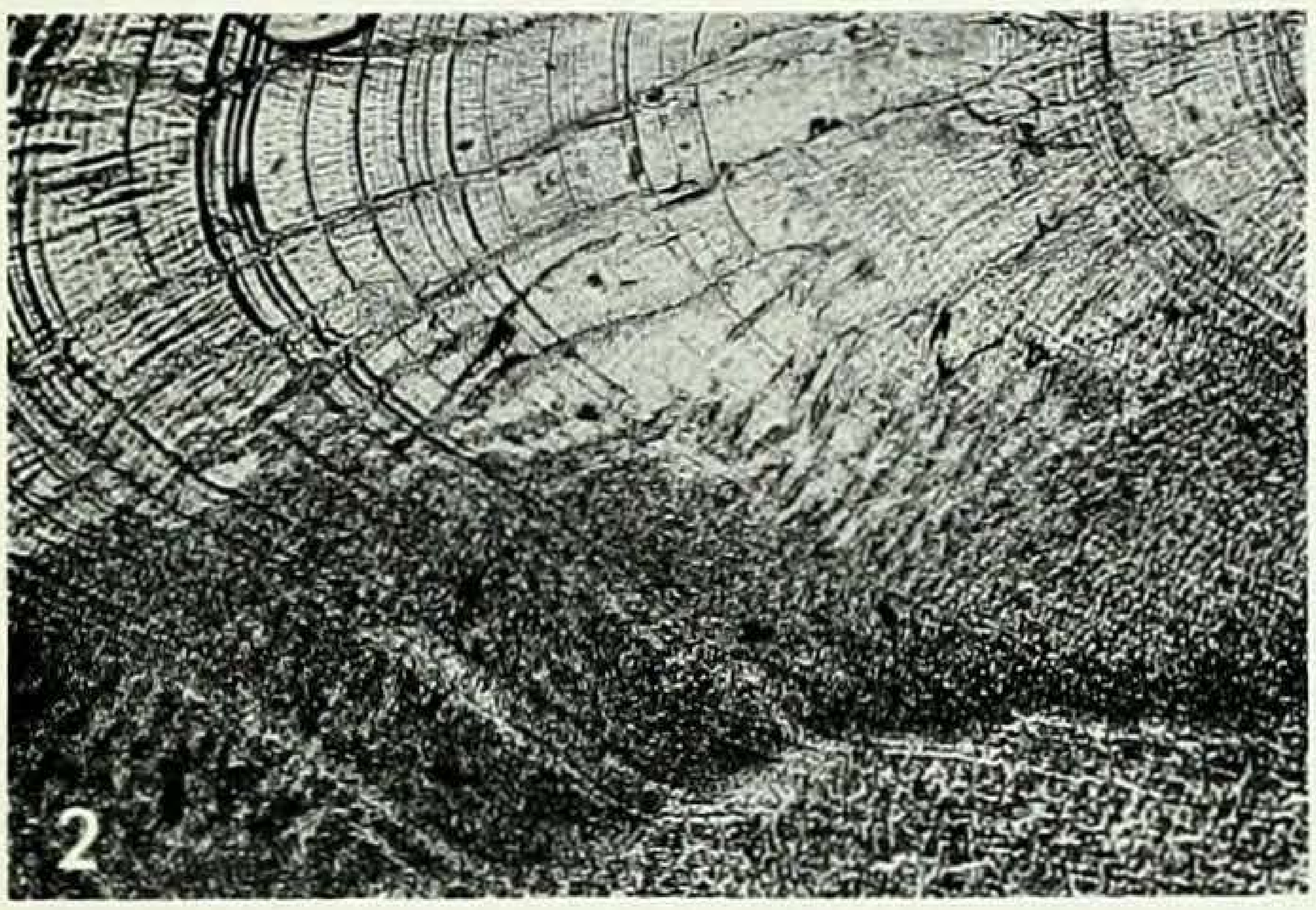
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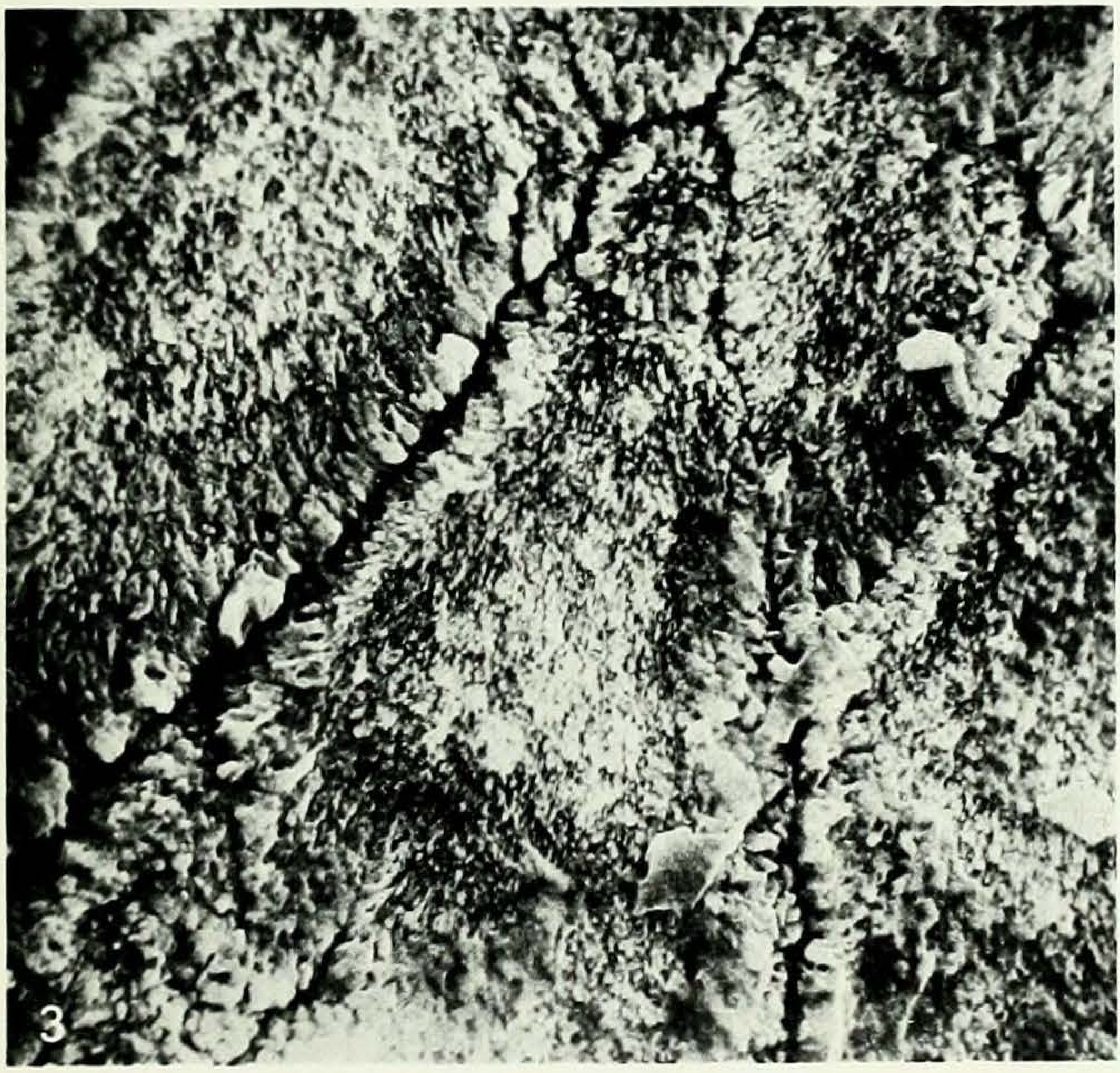
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PLATE 8

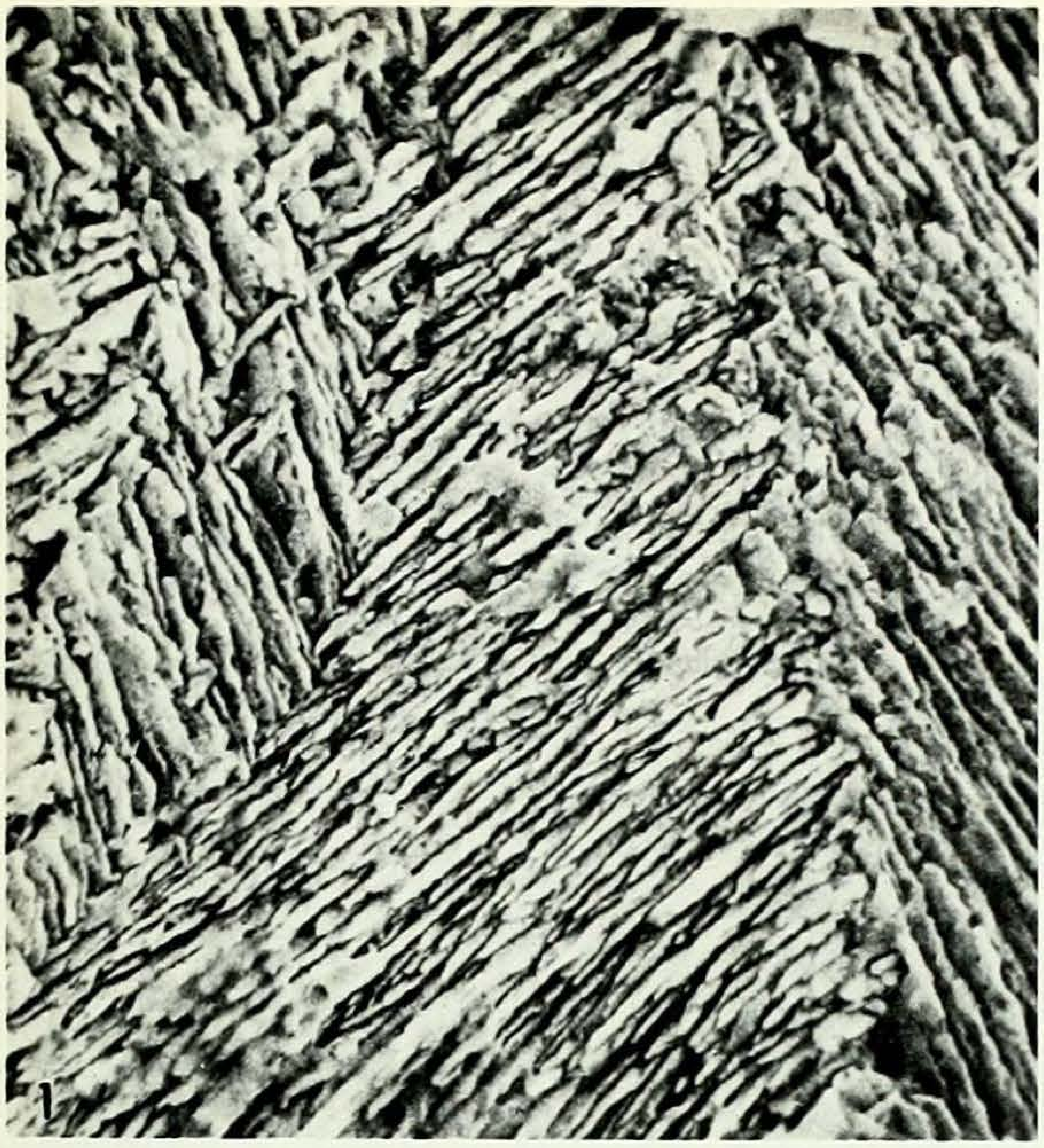
FIG. 1. Polished, etched, radial section of the crossed-lamellar middle layer of ***Mercenaria mercenaria*** showing the needle-like third order lamellae aligned in opposing directions in adjacent first order lamellae. Scanning electron-micrograph, × 2,400.

FIG. 2. Radial section of the outer crossed-lamellar layer of ***Hysteroconcha dione*** showing the crossed-lamellar structure radiating from a central axis which is aligned parallel to the outer shell surface. Note the strongly reflected growth lines. Acetate peel, × 80.

FIG. 3. Radial section of ***Gafrarium pectinatam*** showing the transitional nature of the crossed-lamellar/homogeneous boundaries in the outer shell layer. Acetate peel, × 80.

FIG. 4. Radial section of the outer crossed-lamellar layer of ***Hysteroconcha dione*** showing the arrangement of lamellae in a spine. Acetate peel, × 80.

FIG. 5. Polished, etched section of the middle 'homogeneous' layer of ***Mercenaria mercenaria*** showing the orientated nature of the crystallites. Scanning electron-micrograph, × 3,200.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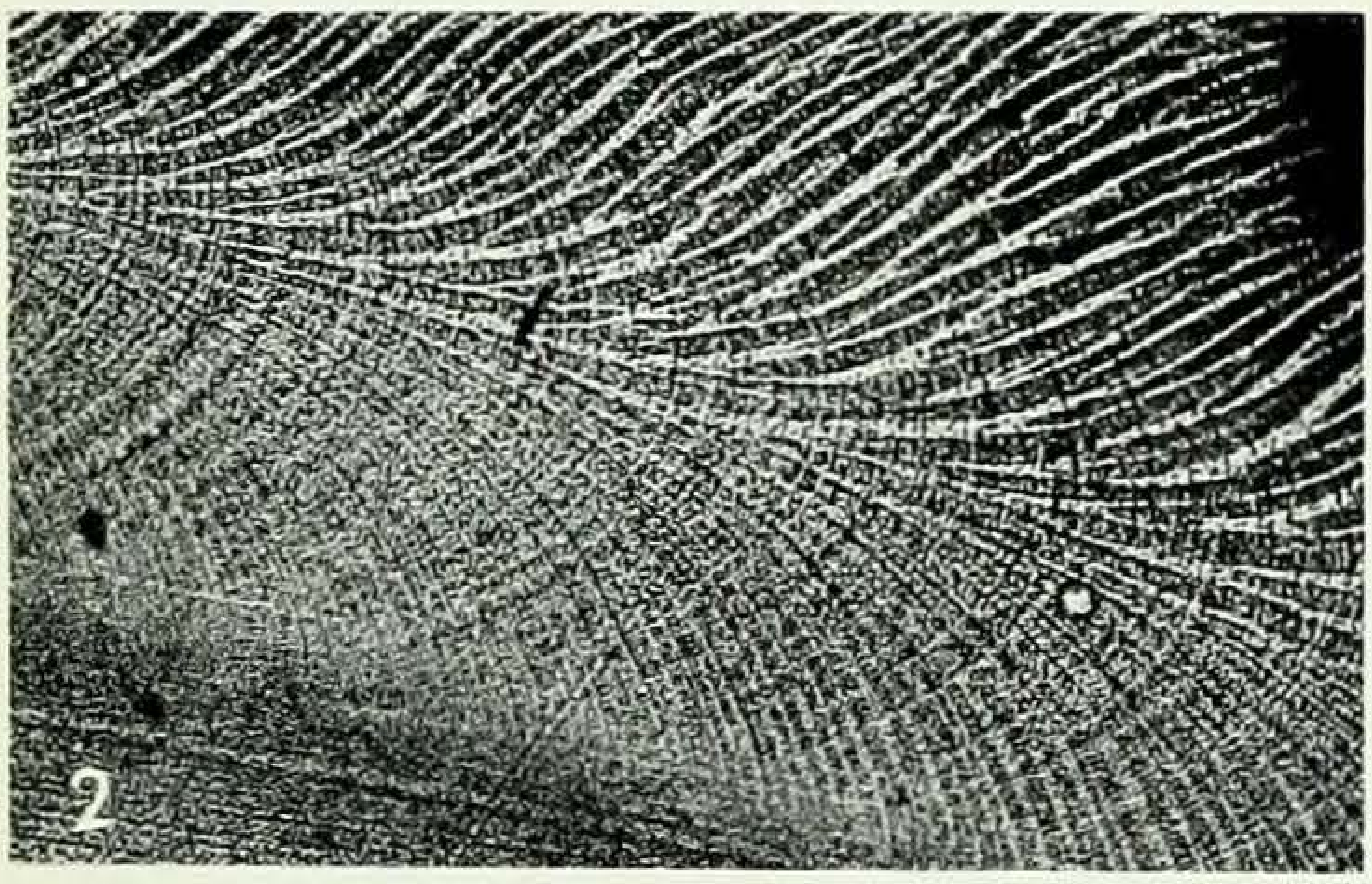
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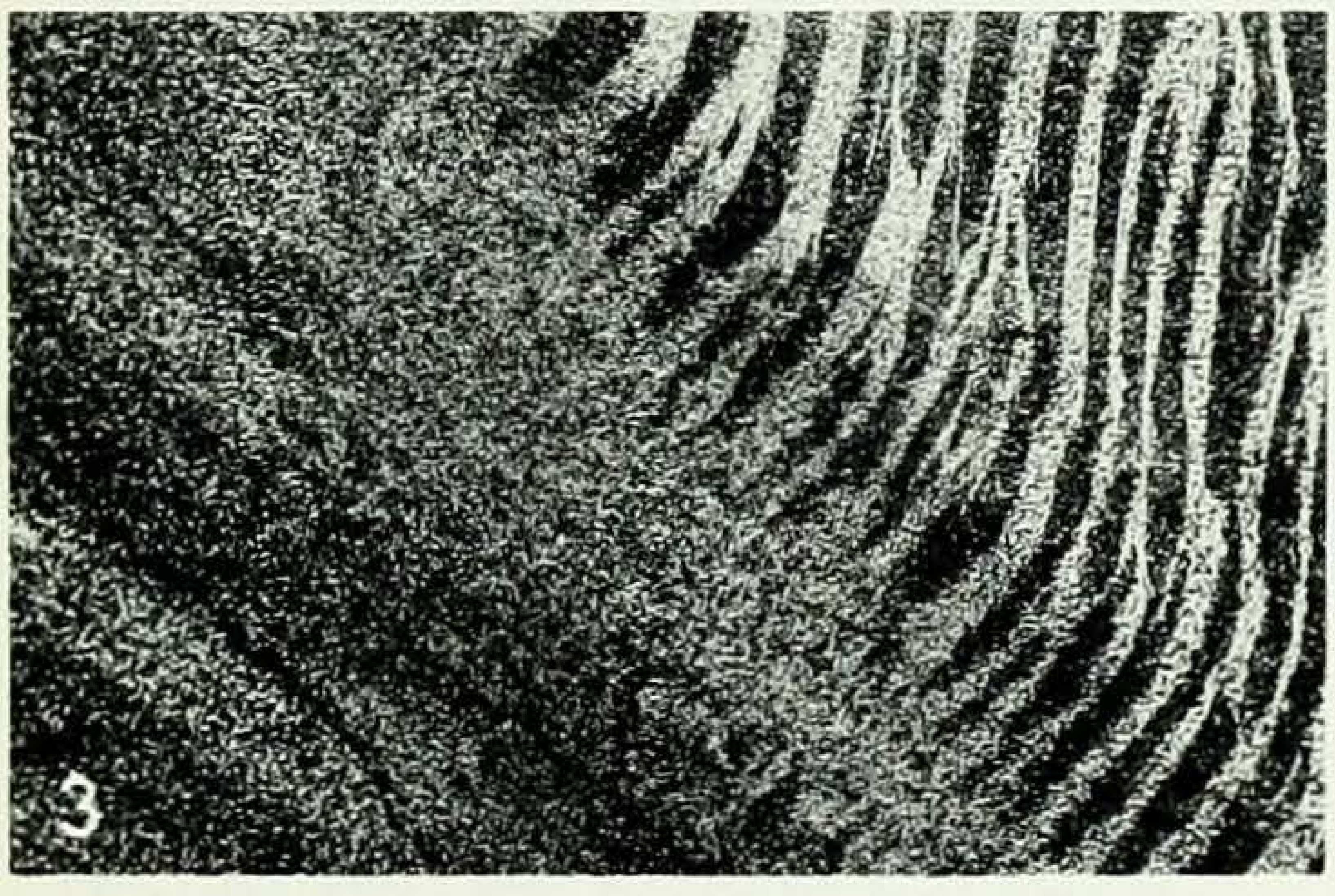
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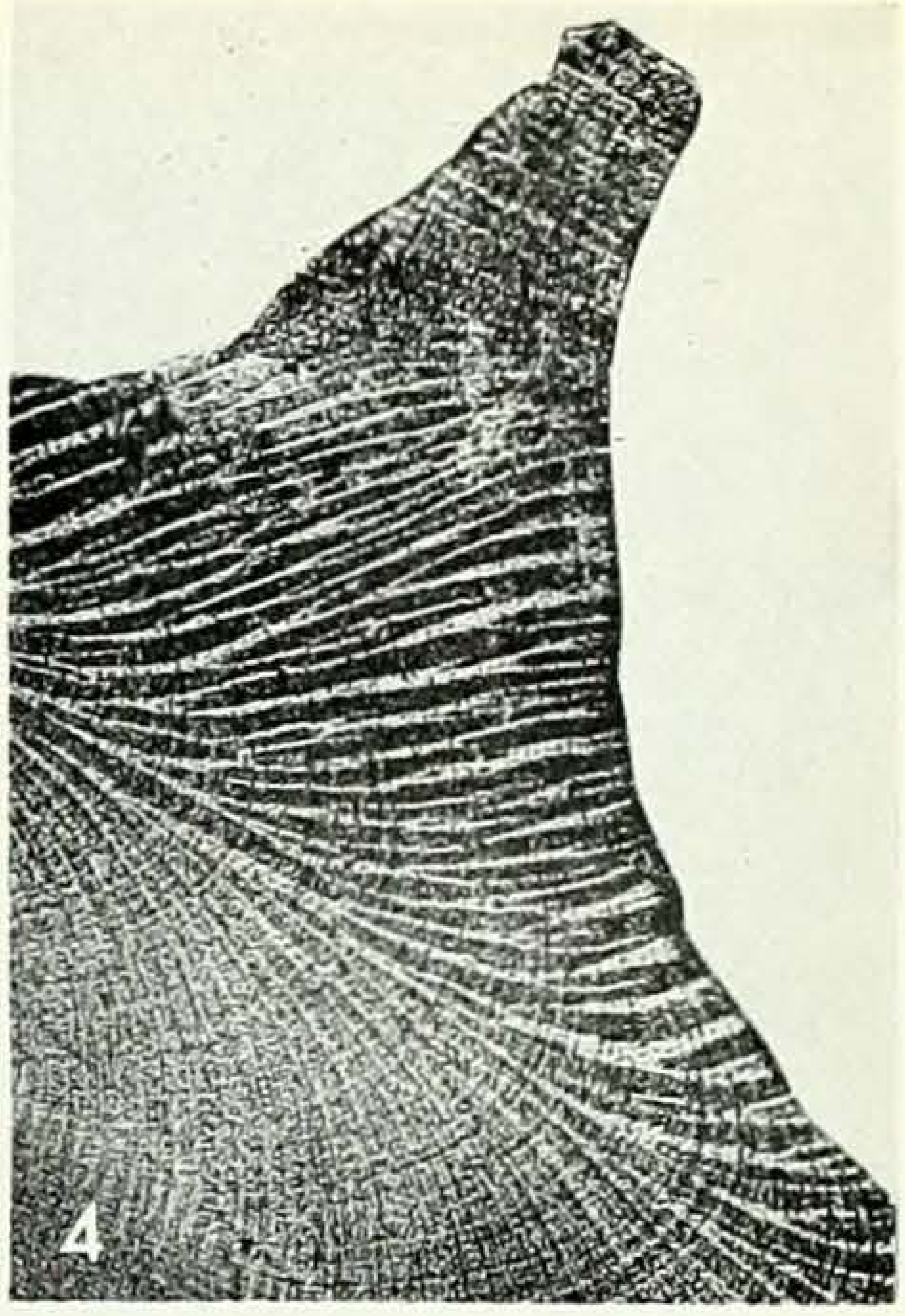
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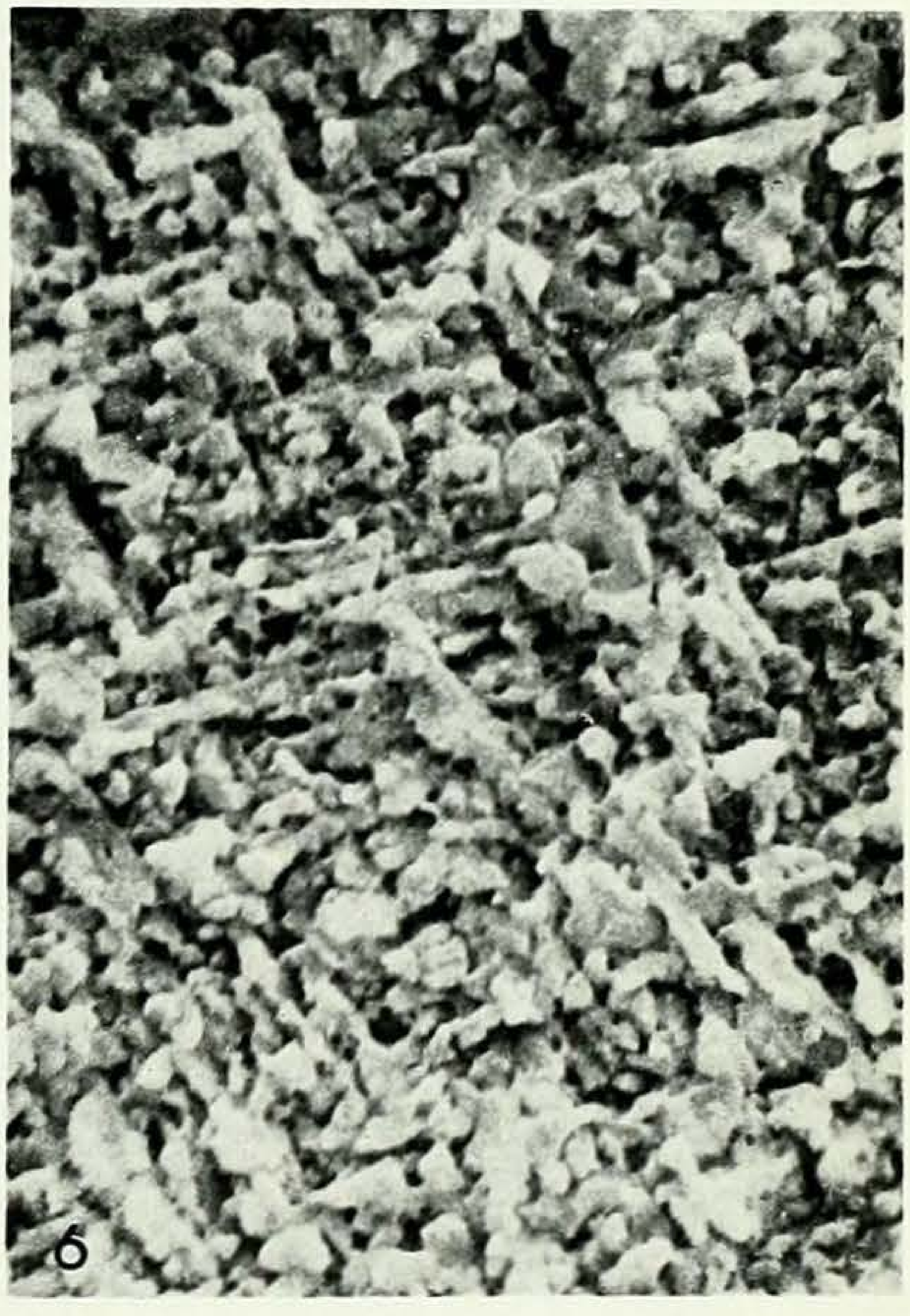
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PLATE 9

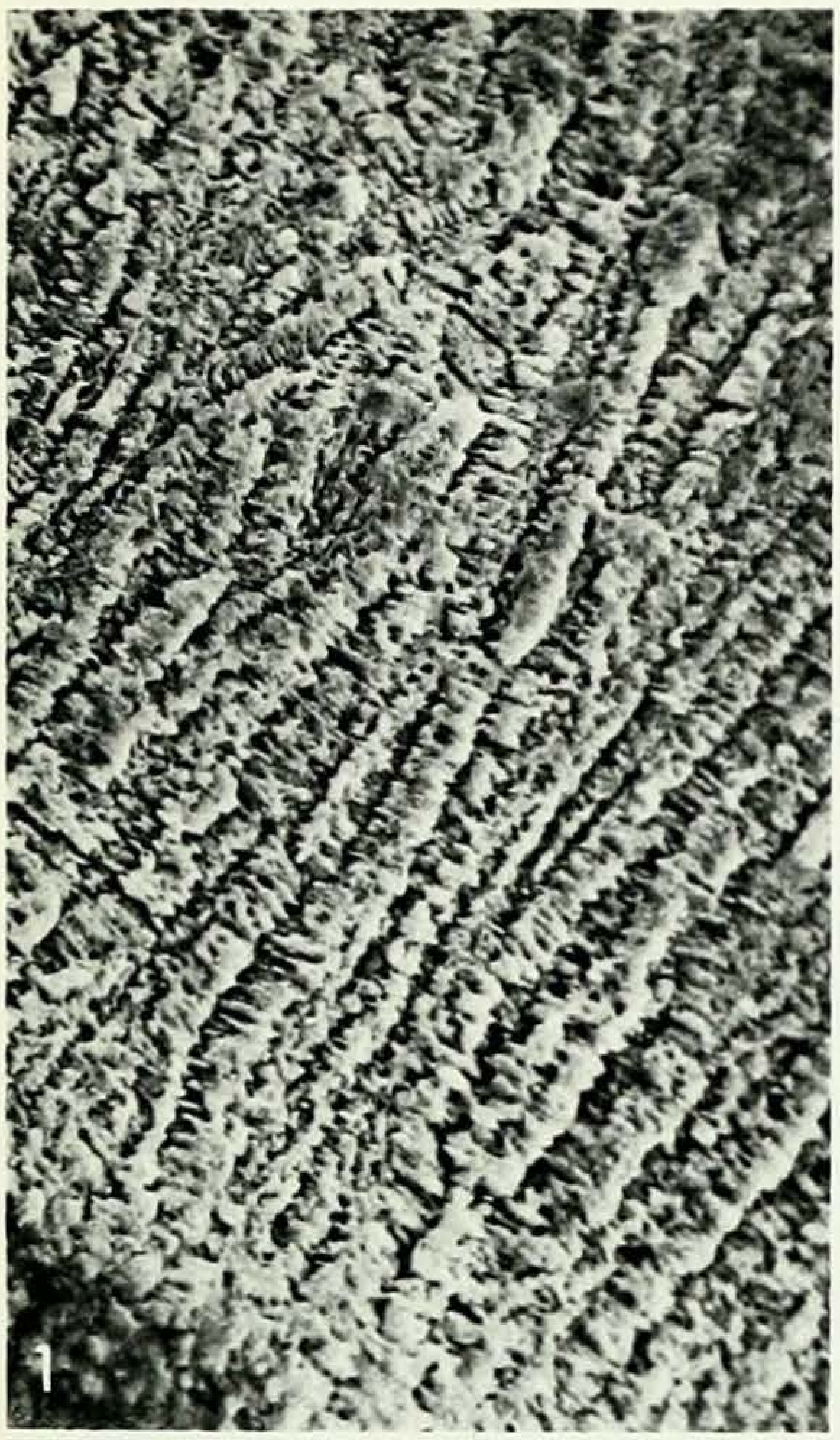
All figures are scanning electron-micrographs

FIG. 1. Polished, etched, radial section of the outer prismatic layer of ***Panopea zeylandica.*** Note the lack of a distinct interprismatic protein wall and the irregular orientation. ×650.

FIG. 2. As Fig. 1 but a detail of an individual prism showing its construction from nearly horizontal, platy crystals. ×1,200.

FIG. 3. Tangential section through a prism such as Fig 2 showing that the prism is constituted from platy crystallites which radiate from a central axis. ×1,300.

FIG. 4. Polished, etched, radial section of the inner "homogeneous" layer of ***Panopea zeylandica*** showing that at high magnifications it is made up of very fine complex crossed-lamellar structure. ×6,500.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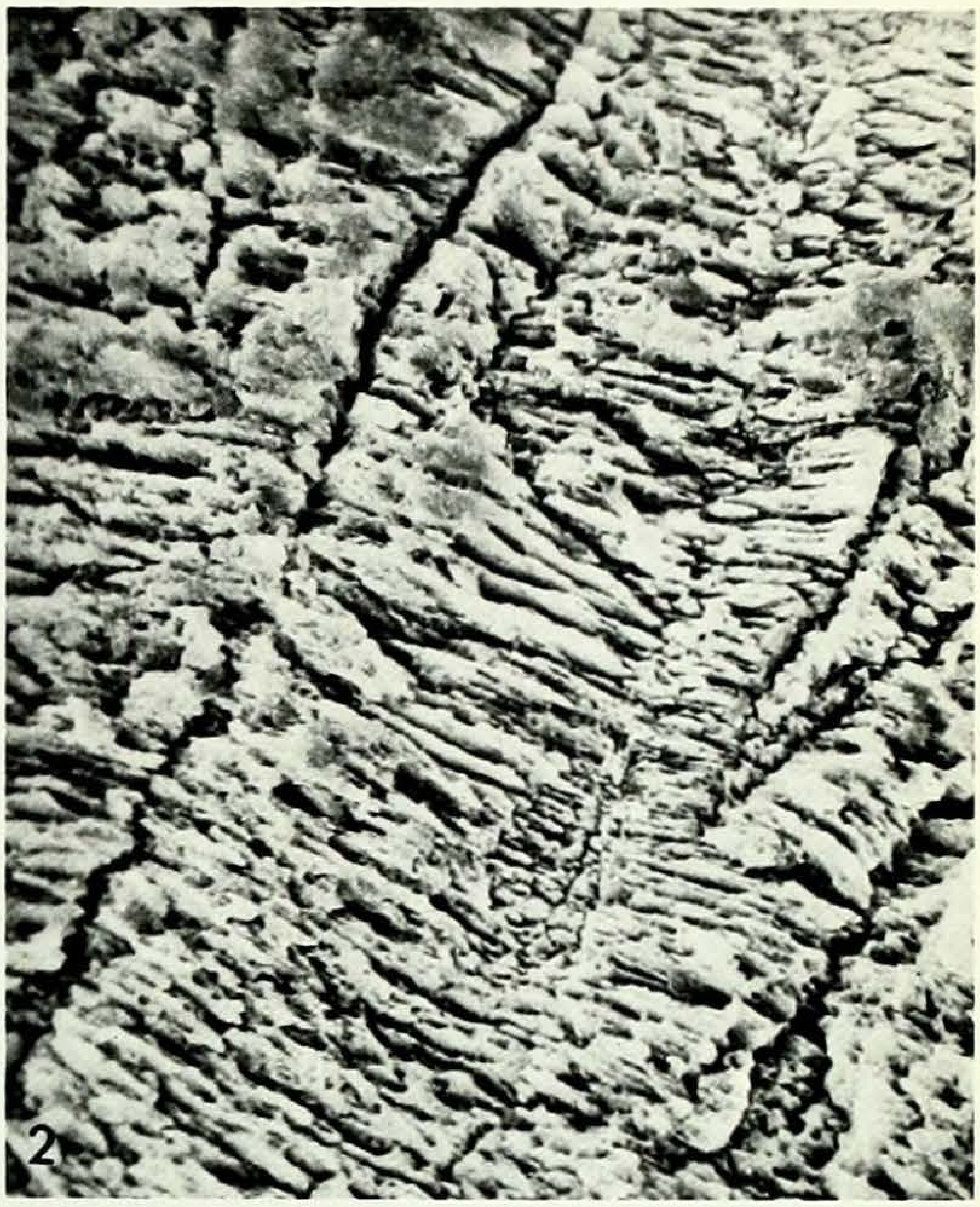
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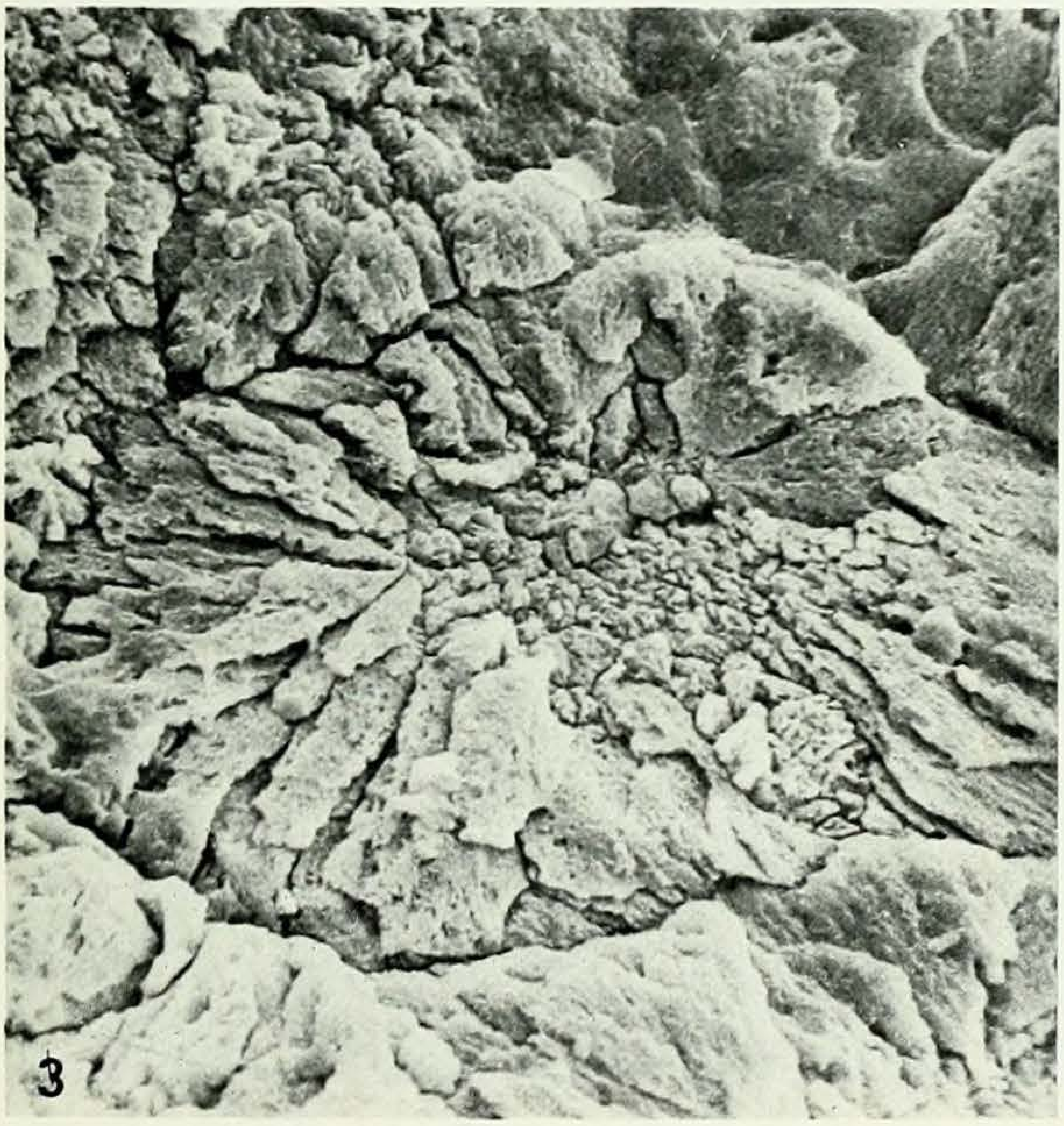
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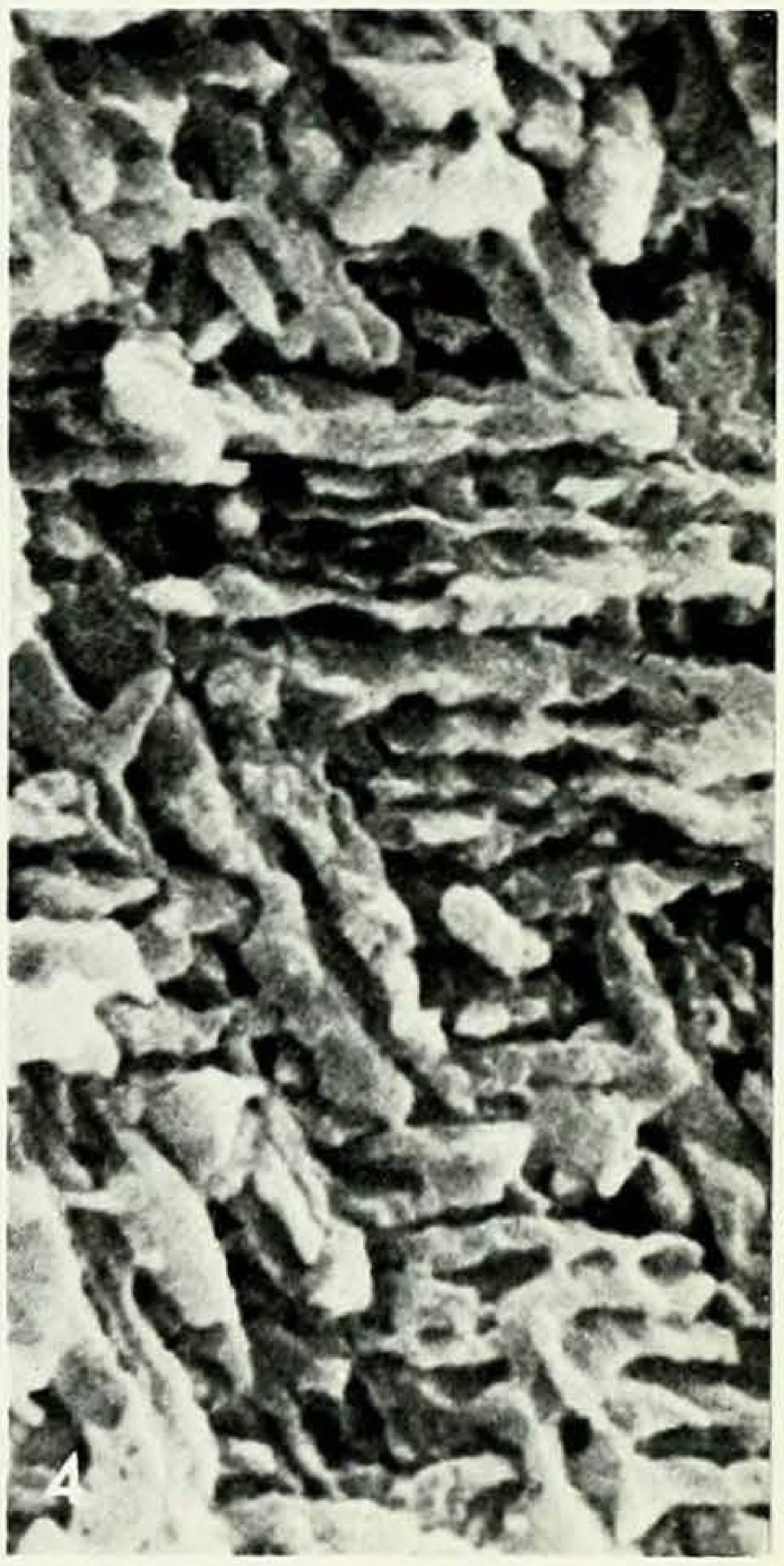
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PLATE 10

All figures are scanning electron-micrographs

FIG. 1. Polished, etched, radial section of ***Zirfaea crispata*** showing the outer layer (bottom left) consisting of elongate granules and the middle crossed-lamellar layer (top right). × 500.

FIG. 2. Detail of the outer layer of ***Zirfaea crispata***; heavily etched. × 1,400.

FIG. 3. Radial section (polished and etched) of the outer crossed-lamellar layer of ***Teredo navalis*** and the sharp ridges produced from this structure. × 260.

FIG. 4. Polished, heavily etched radial section of the middle crossed-lamellar layer of ***Teredo navalis.*** × 1,400.


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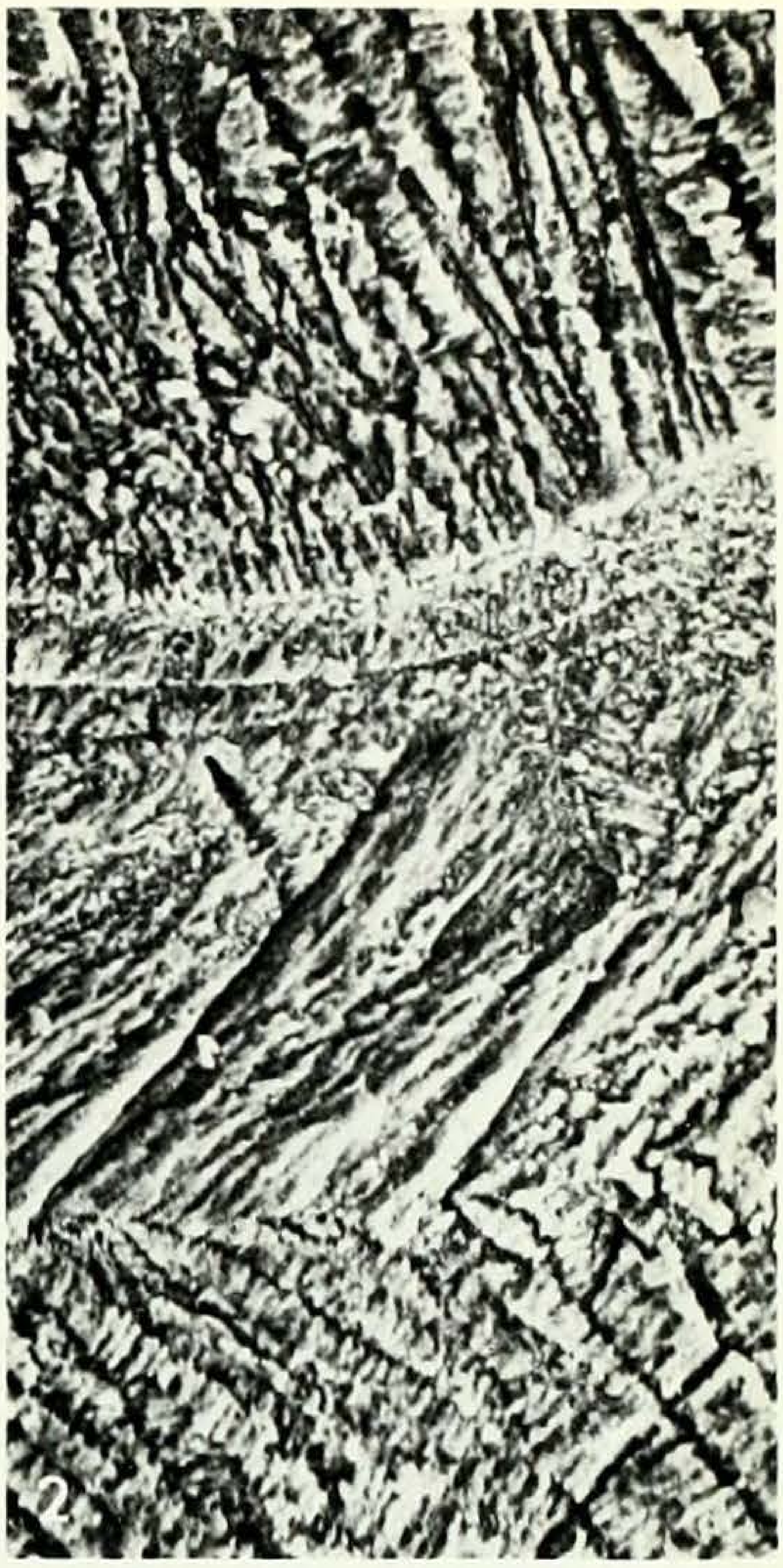
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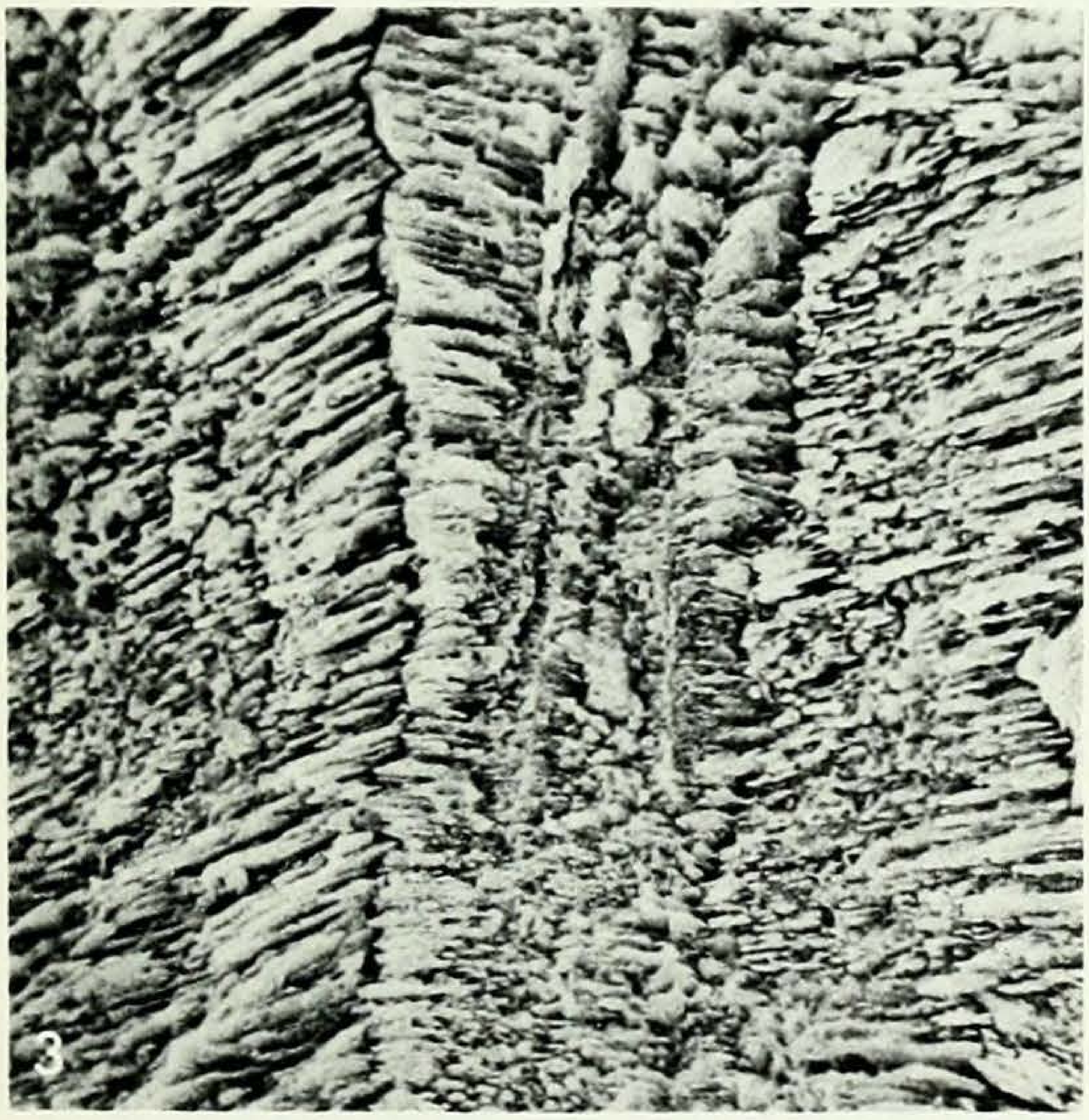
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4

PLATE 11

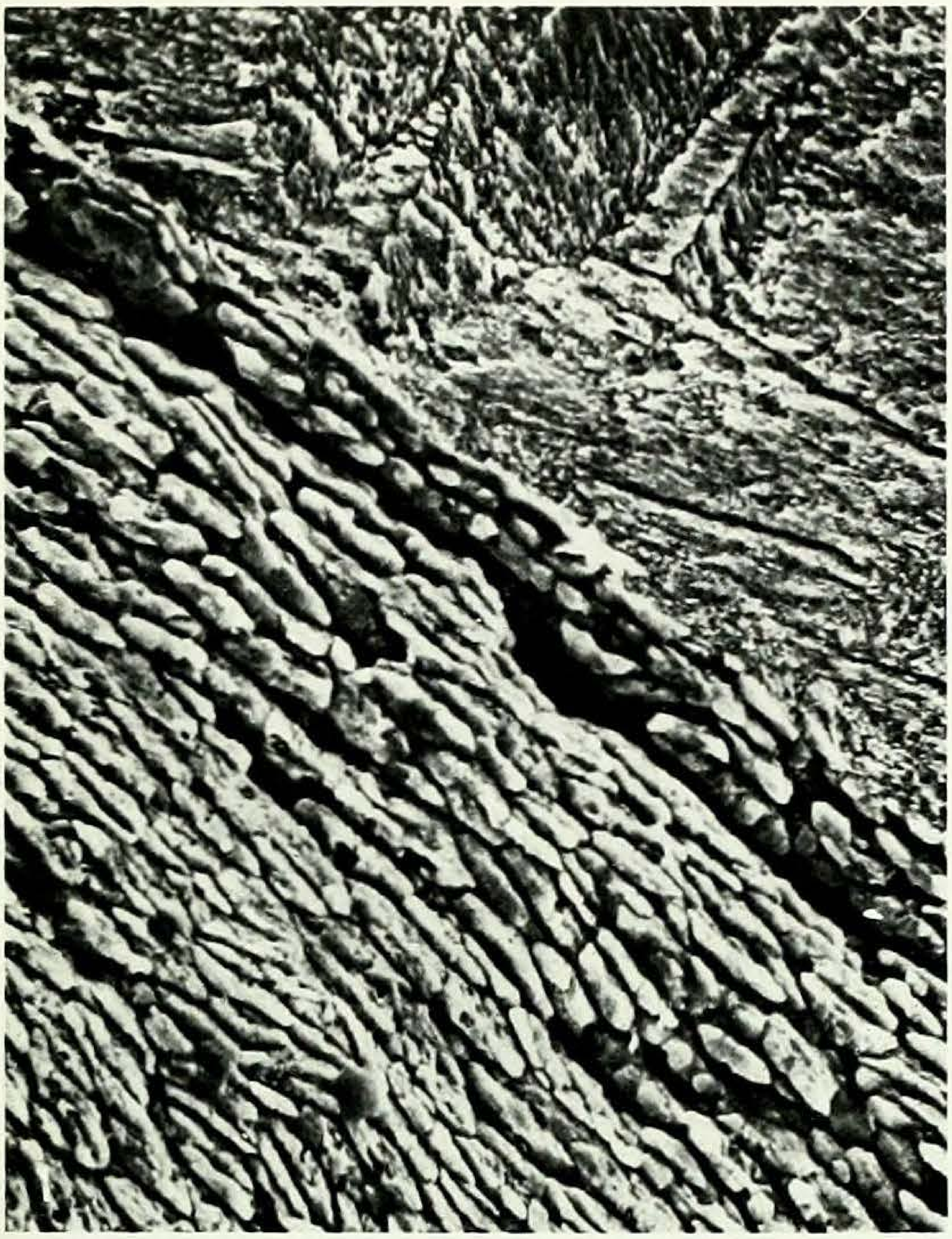
All figures are scanning electron-micrographs

FIG. 1. Radial section (polished and etched) of ***Barnea candida*** showing the outer prismatic layer (top half) and a "shoot" of the middle crossed-lamellar layer (see Text-fig. 28). The prisms are often, as shown arranged in radiating groups. ×850.

FIG. 2. As above, showing a "shoot" of the middle crossed-lamellar layer sandwiched between outer prismatic layer. ×850.

FIG. 3. Detail of the outer prismatic layer of ***Pholas dactylus*** (compare with Plate 9, fig. 2 of prisms in *Panopea*). ×1,100.

FIG. 4. Polished, etched, section of the outer grey homogeneous layer of ***Mya truncata*** illustrating the formation from irregular granular crystals. ×1,200.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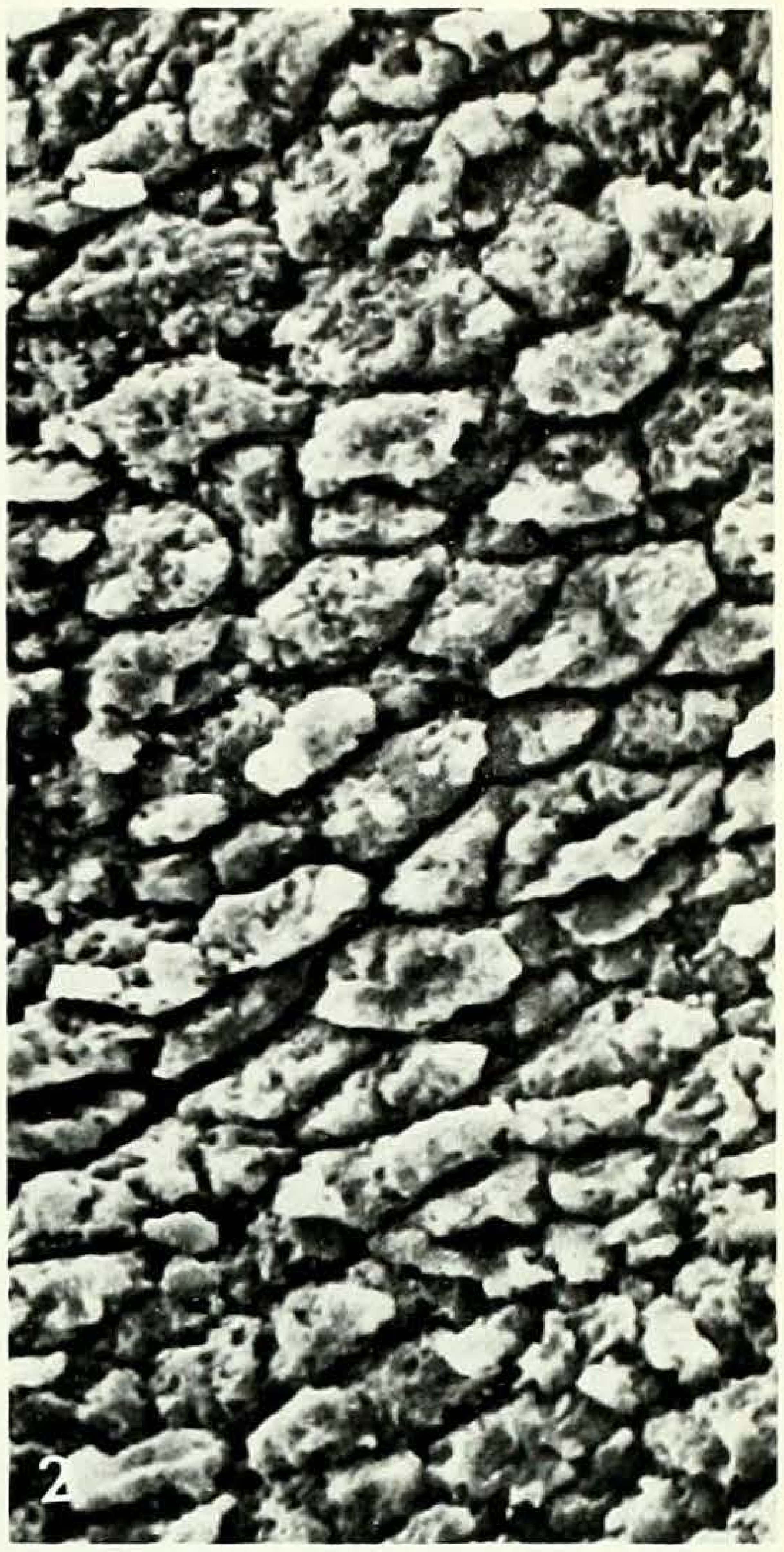
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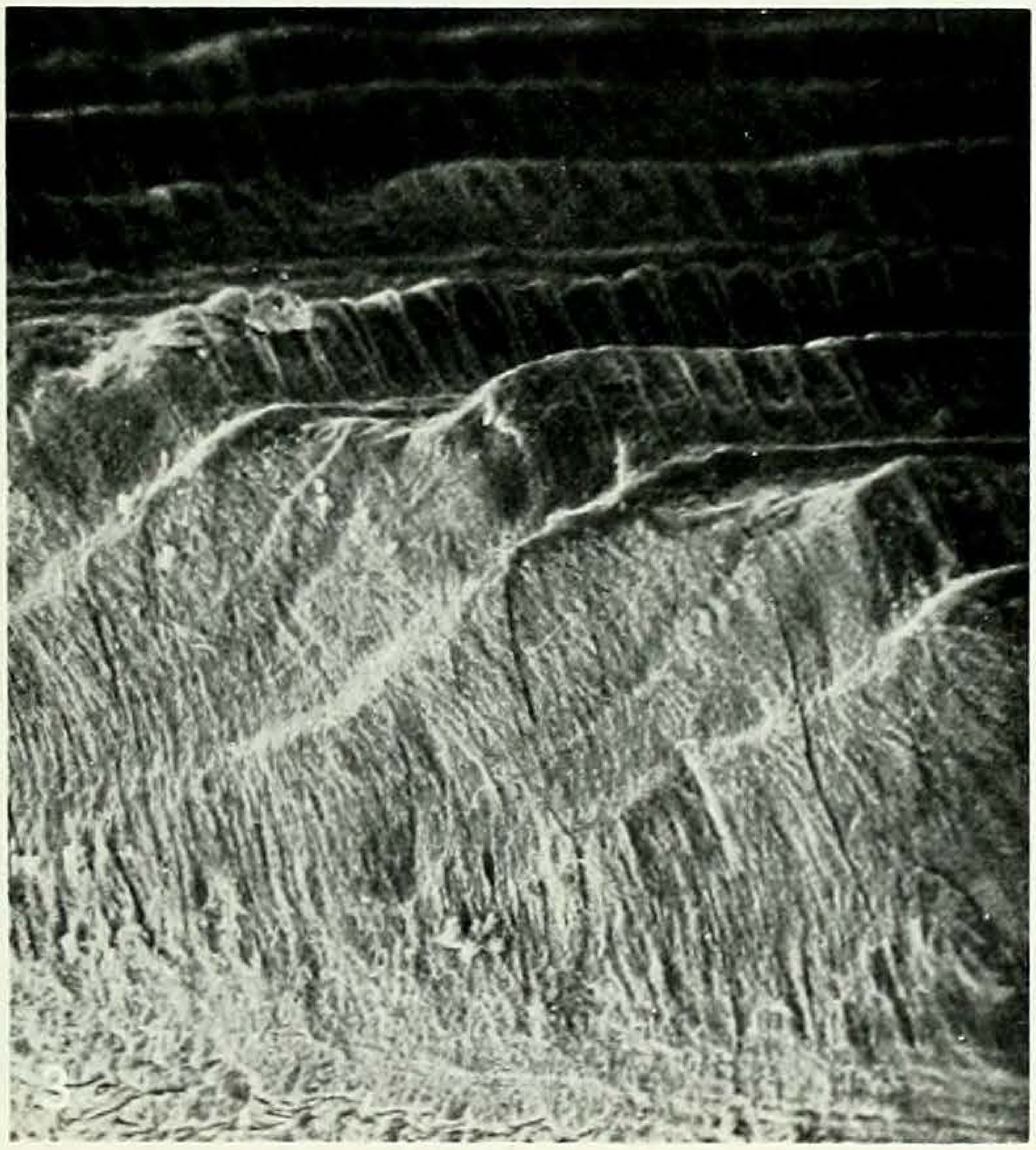
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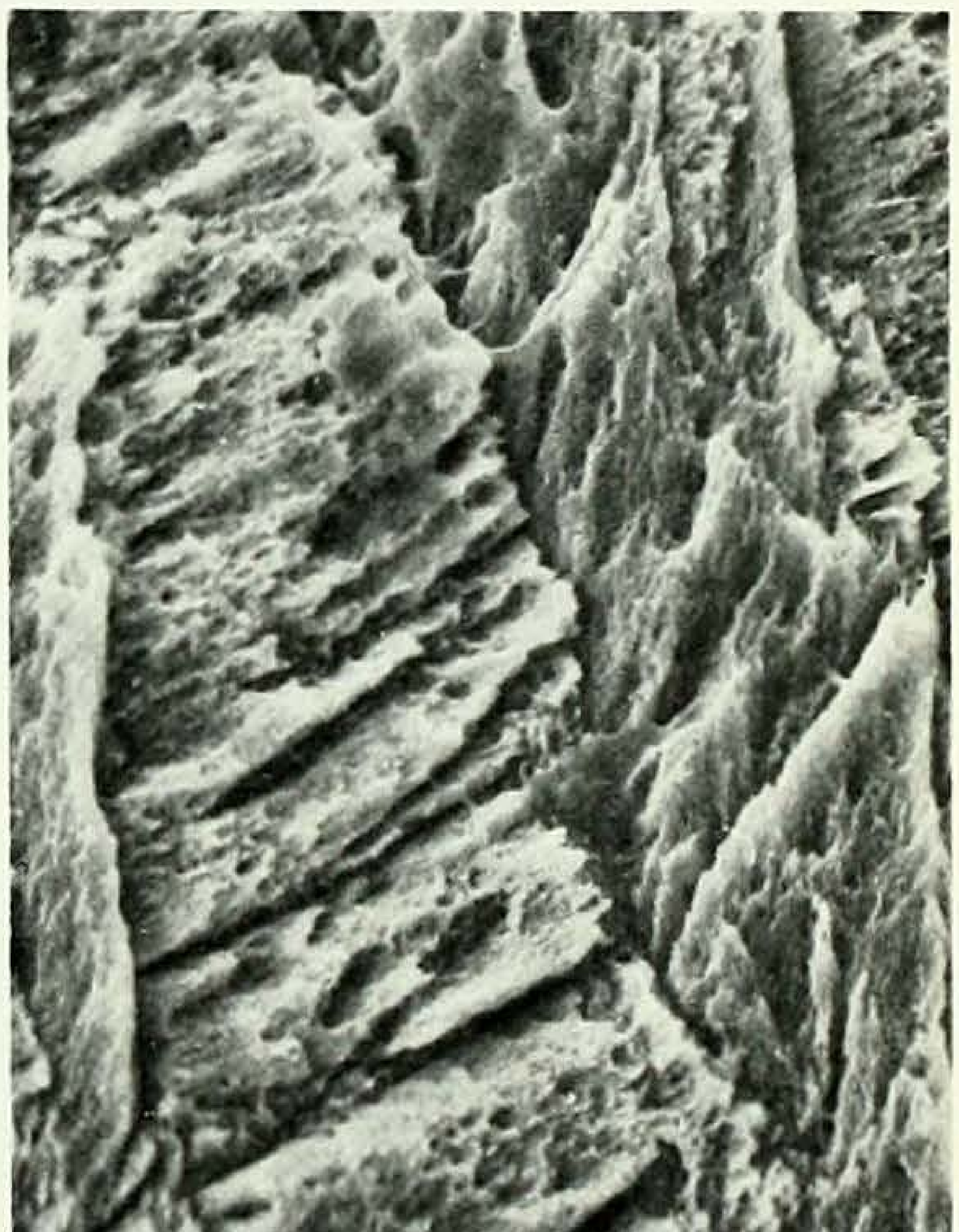
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PLATE 12

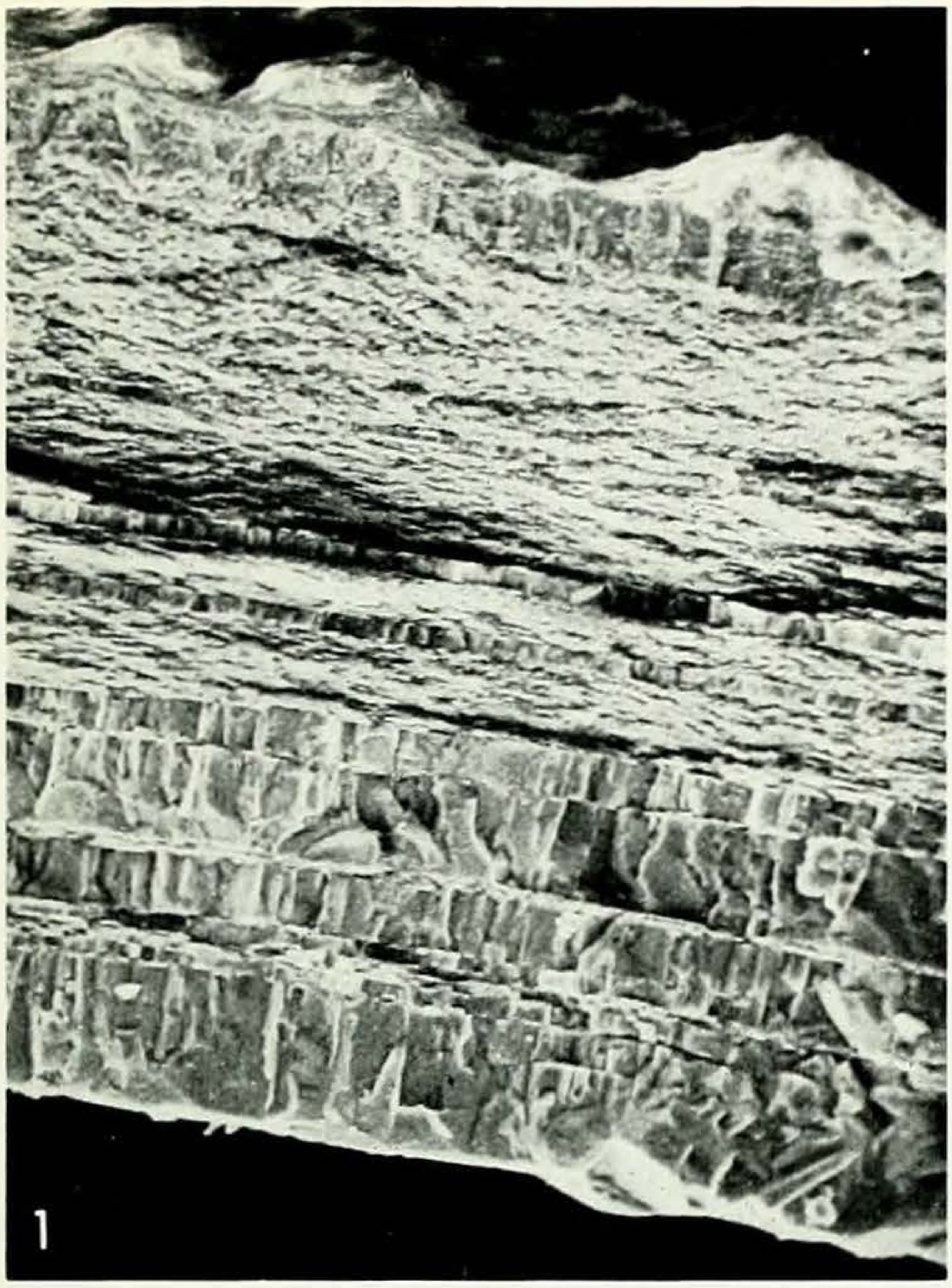
All figures are scanning electron-micrographs of ***Pholadomya candida.***

FIG. 1. Fractured radial section showing the outer simple prismatic layer (top), the middle nacreous layer, pallial myostracum, and an inner layer, consisting initially of nacre and then thick sheets of myostracal prisms. × 240.

FIG. 2. Detail of the inner layer showing the sheets of myostracal prisms separated by very thin sheets of nacre (interior of shell towards top of picture). × 600.

FIG. 3. Inner nacreous layer showing sheets of nacre crystals by a sheet of myostracal prisms. × 2,400.

FIG. 4. Middle nacreous layer, compare the short bent crystals with the step-like alignment with the more regular flat sheets of larger crystals of the nacre of the inner layer in Fig. 3. × 2,400.



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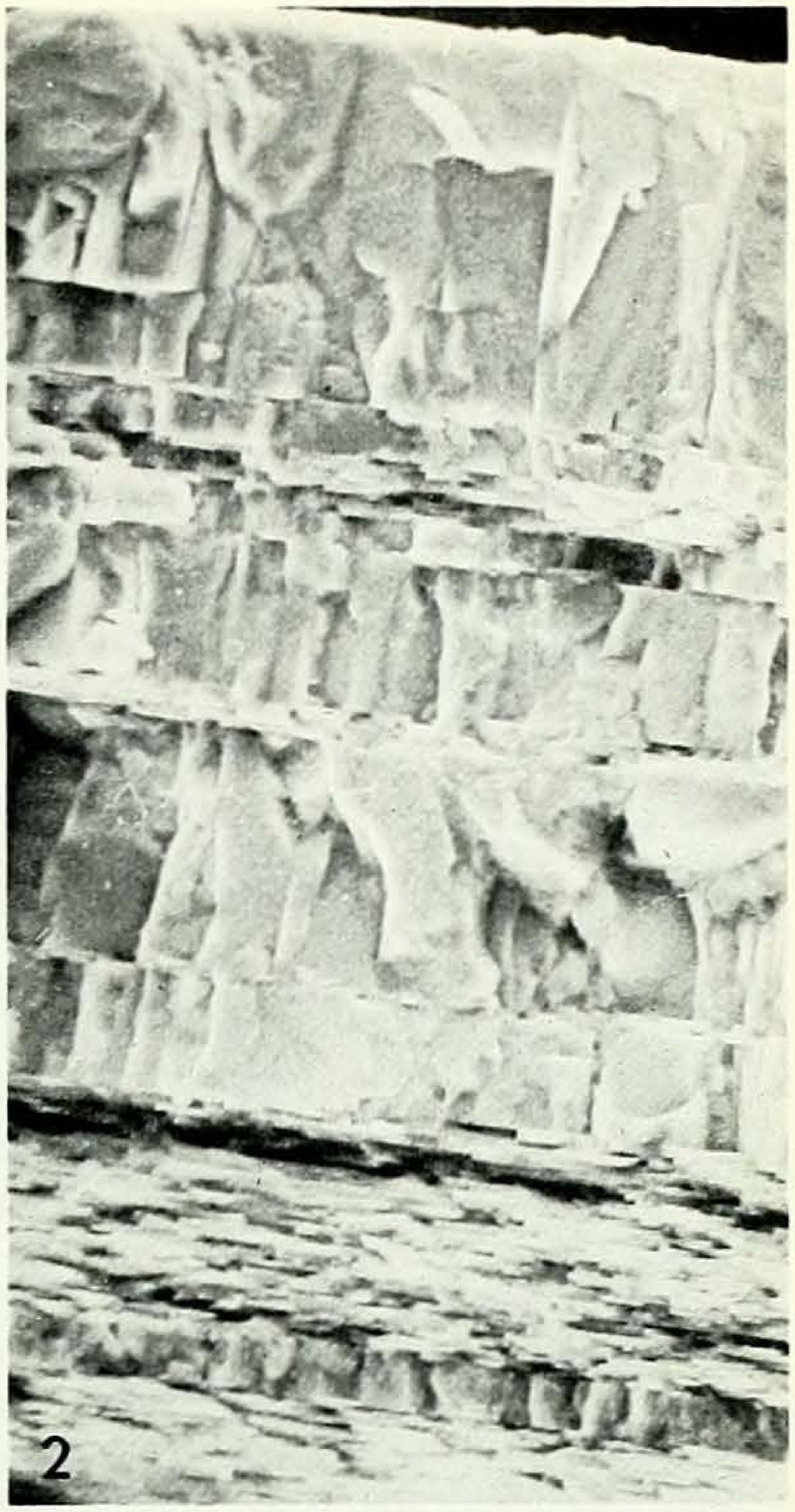

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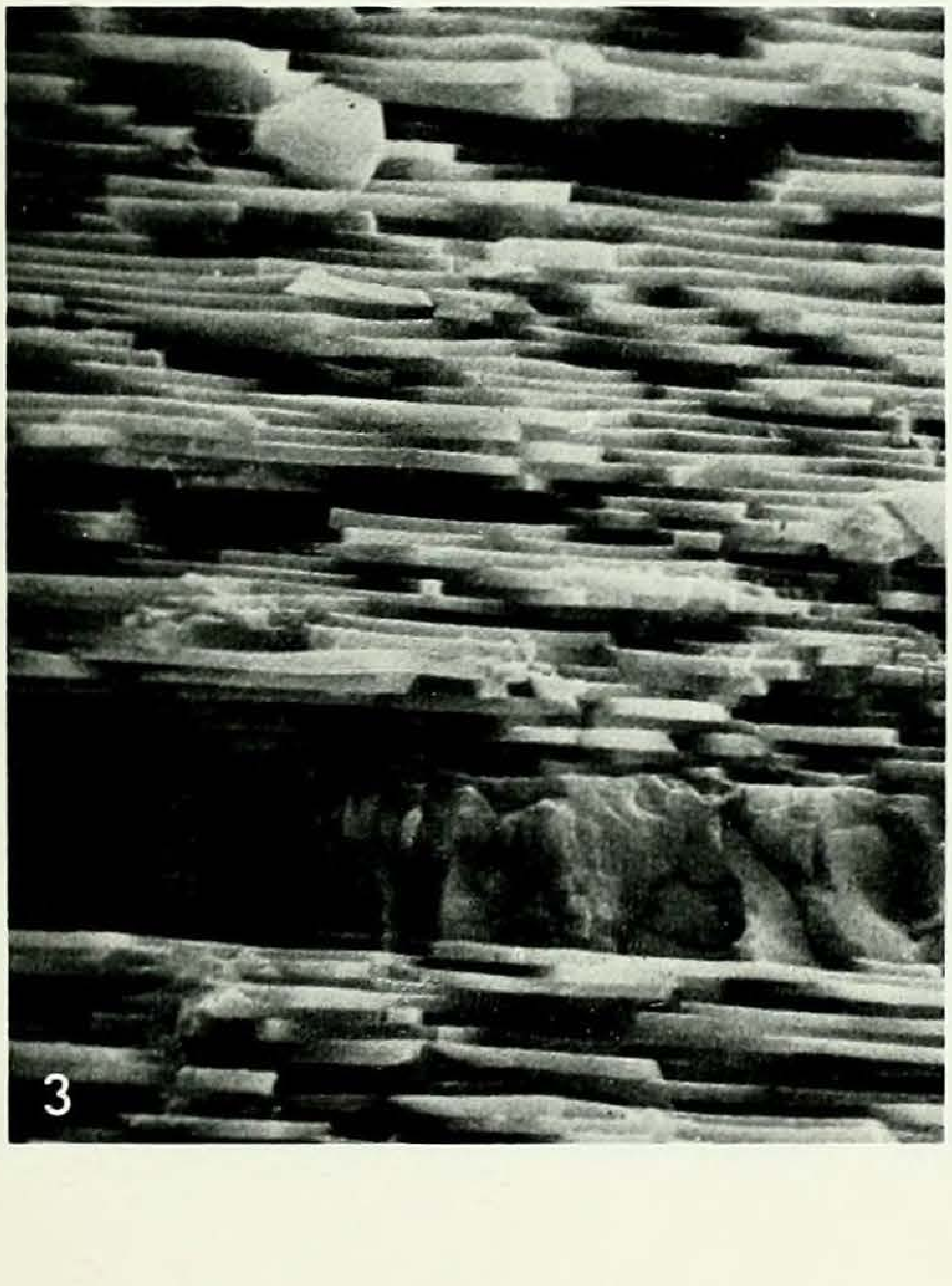

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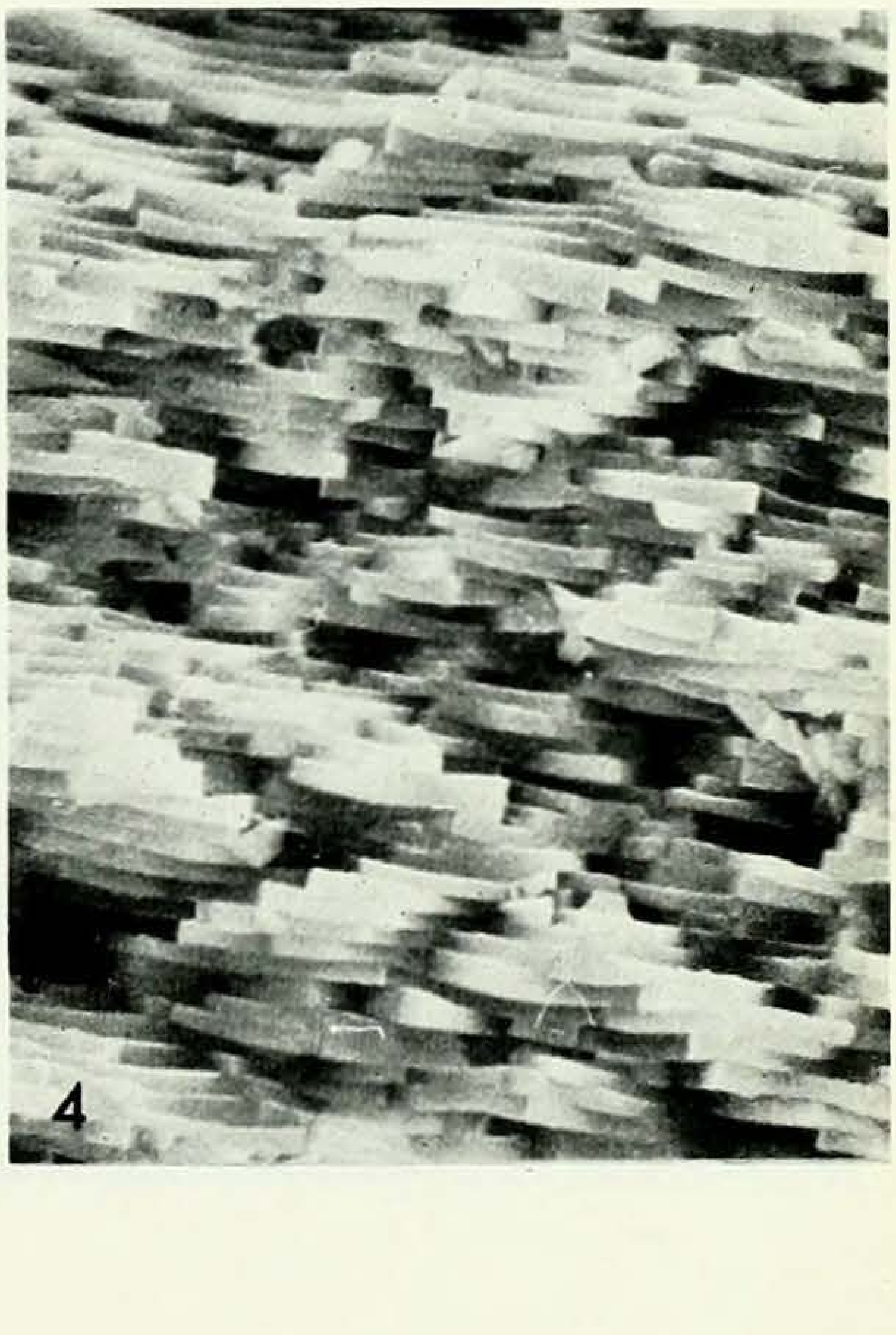

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PLATE 13

All figures on this plate are scanning electron-micrographs

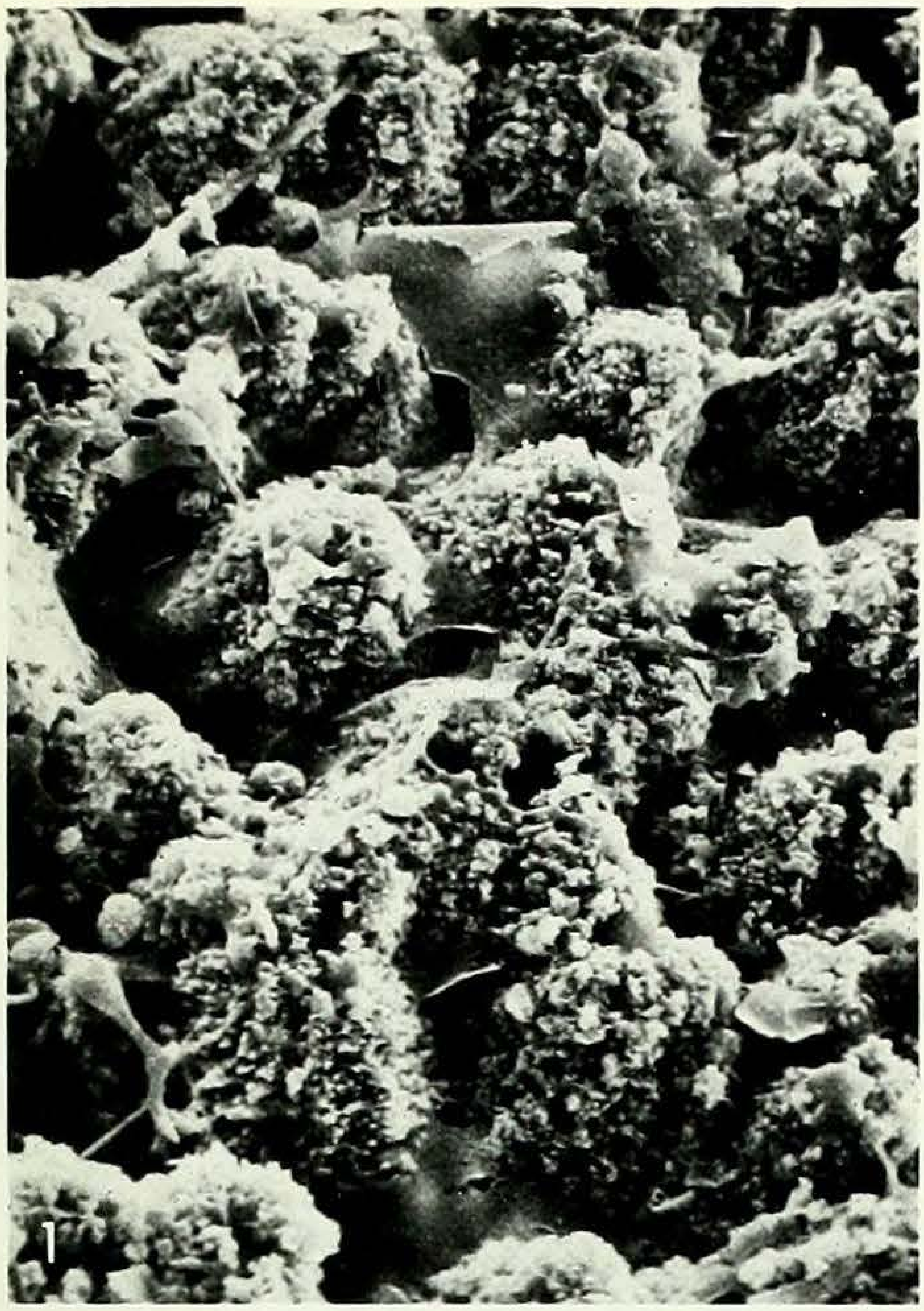
FIG. 1. ***Thracia phaseolina,*** inner surface of the outer shell layer showing individual spherulites separated by periostracum. ×1,100.

FIG. 2. Fractured section of the outer layer of ***Thracia phaseolina*** showing growing spherulites separated by sheets of periostracum. Inner shell surface to top right corner. ×800.

FIG. 3. As Fig. 2 but showing detail of growing spherulite on the inner shell surface. ×3,200.

FIG. 4. Outer shell surface of ***Thracia phaseolina*** showing spherulites projecting through the periostracum. ×260.

FIG. 5. Polished, etched, radial section of the outer prismatic layer of ***Euciroa eburnea*** showing how the prisms are made up of radiating needle-like crystallites. Note the lack of sharp boundaries between prisms. ×625.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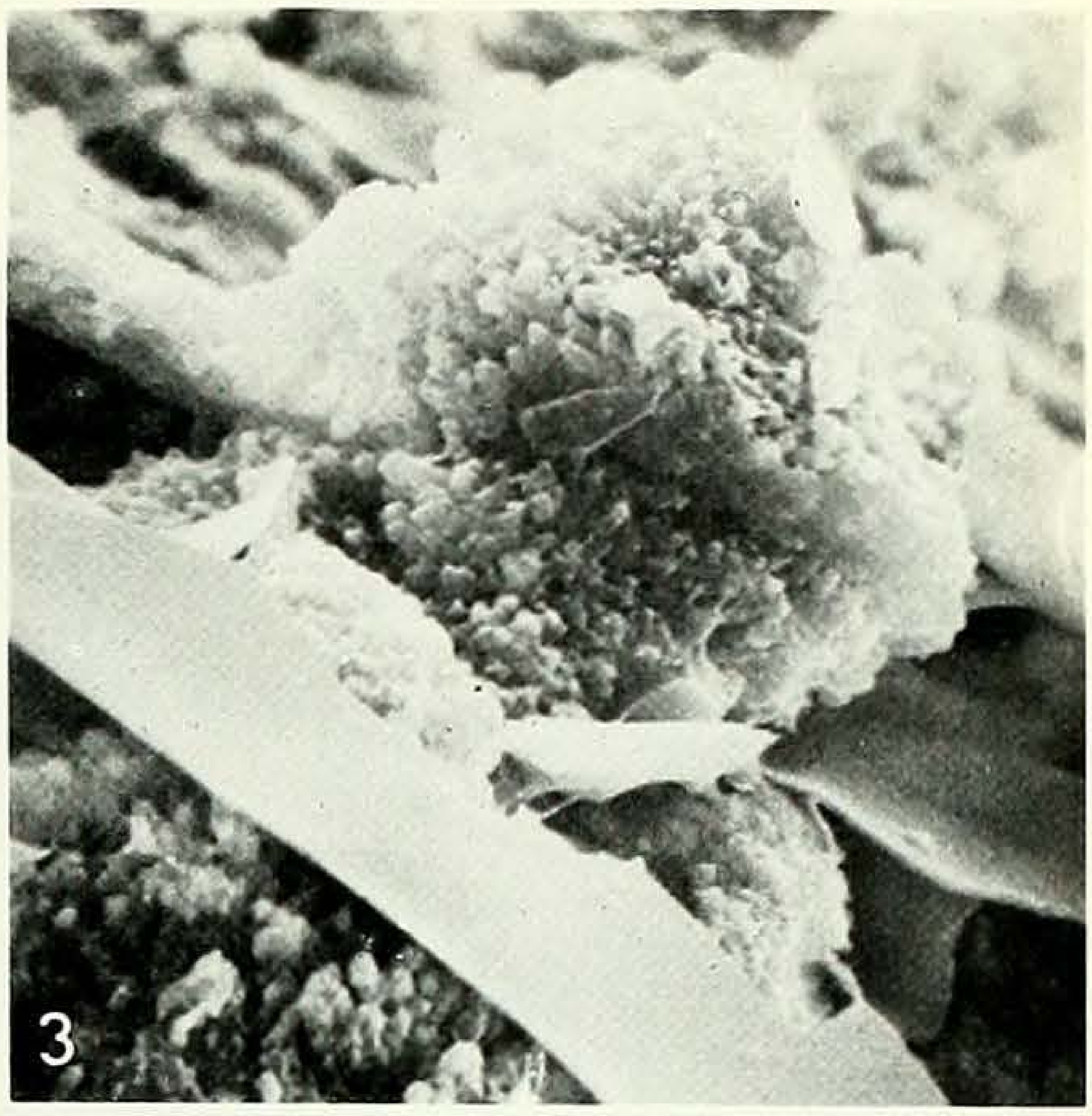
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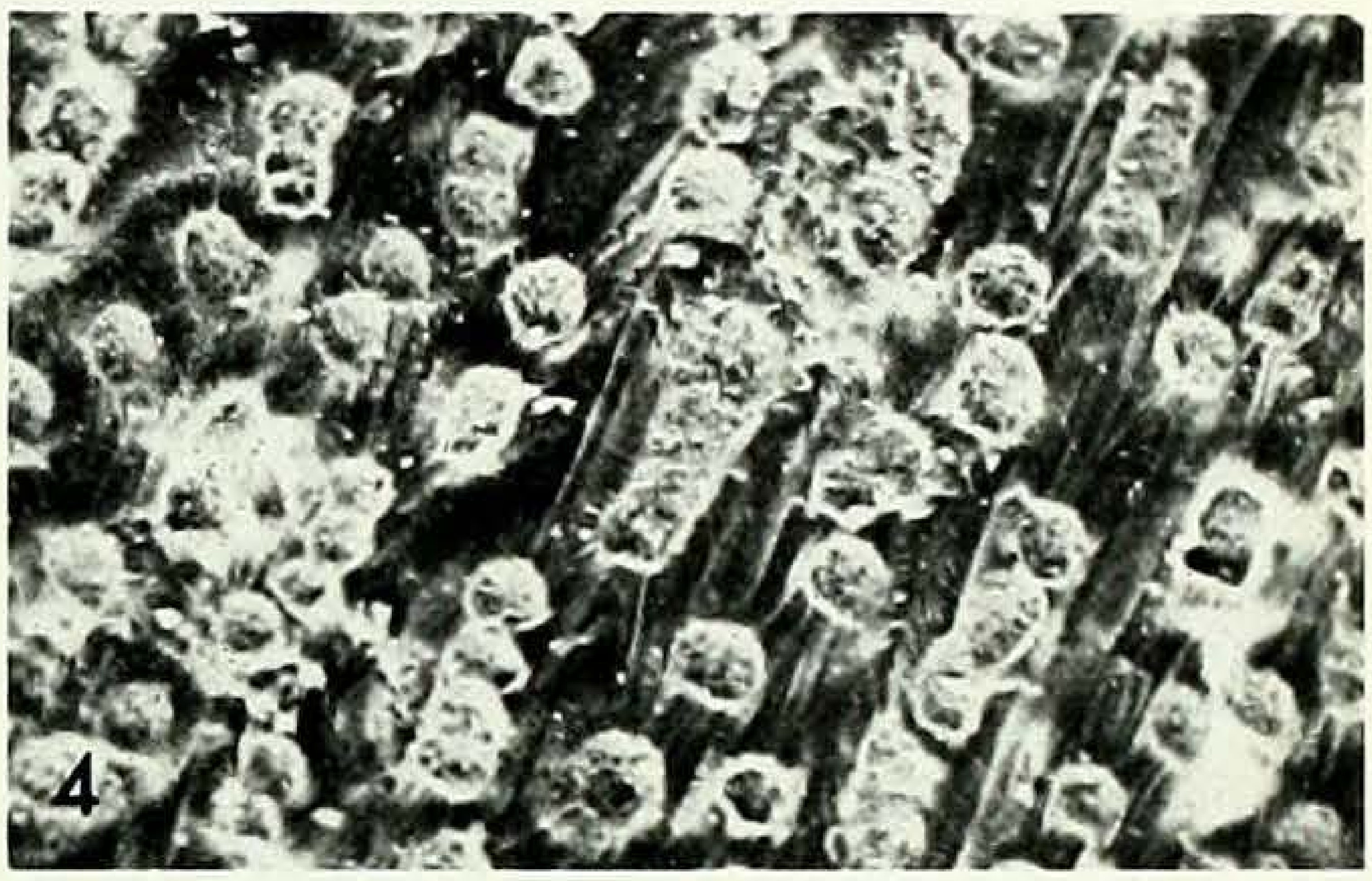
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PLATE 14

All figures are scanning electron-micrographs

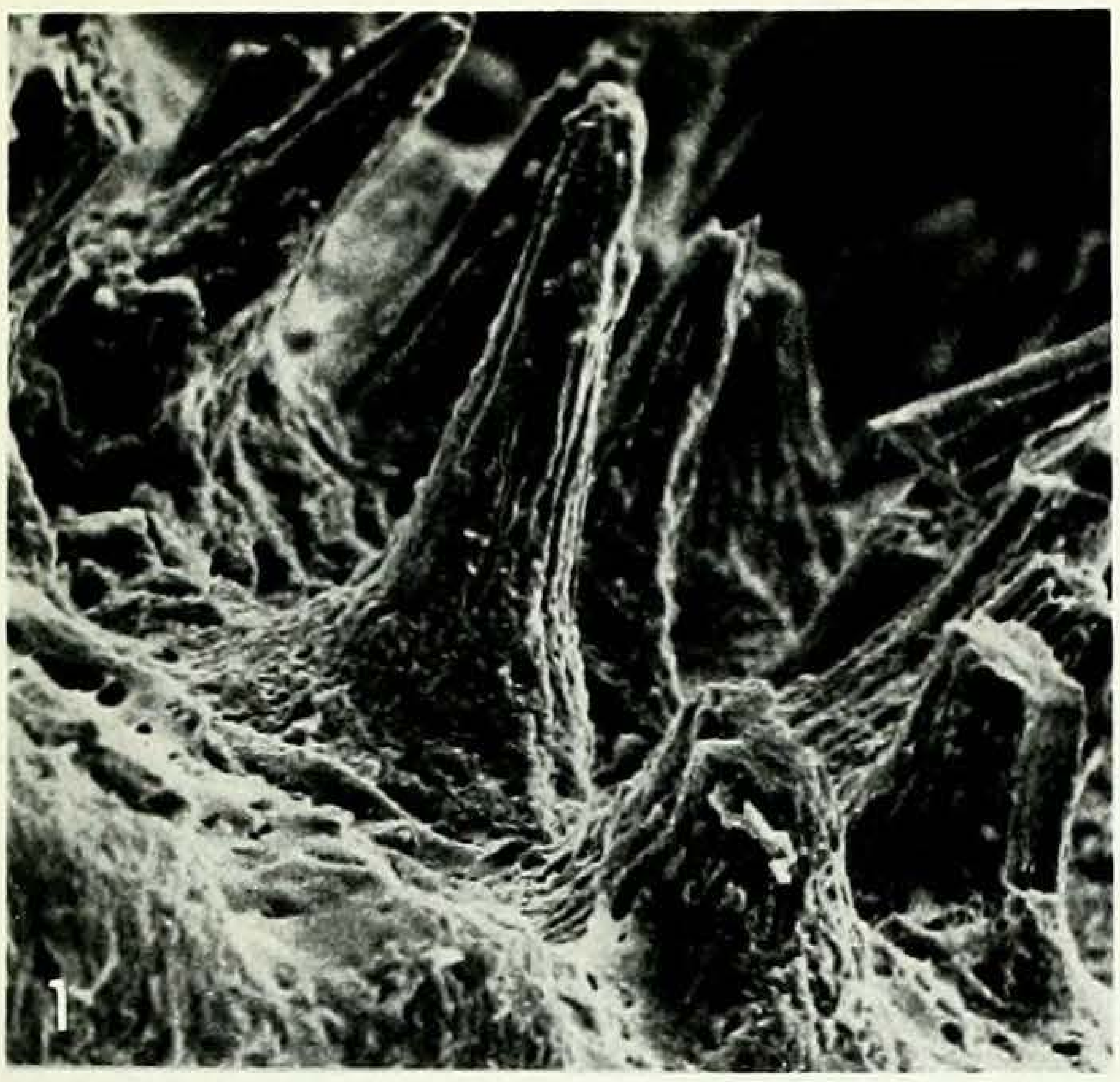
FIG. 1. Spines on the outer shell surface of ***Euciroa eburnea.*** ×220.

FIG. 2. Fractured section of the outer layer of ***Poromya granulata*** showing a section through a surface granule. ×1,100.

FIG. 3. Inner shell surface of the inner homogeneous layer of ***Cuspidaria cuspidata.*** ×6,600.

FIG. 4. Fractured section of the outer homogeneous layer and middle nacreous layer of ***Poromya granulata.*** ×1,100.

FIG. 5. Fractured section of ***Cuspidaria cuspidaria*** showing the outer homogeneous layer (bottom) and the inner layer resembling complex crossed-lamellar layer separated by a prismatic pallial myostracum. ×800.



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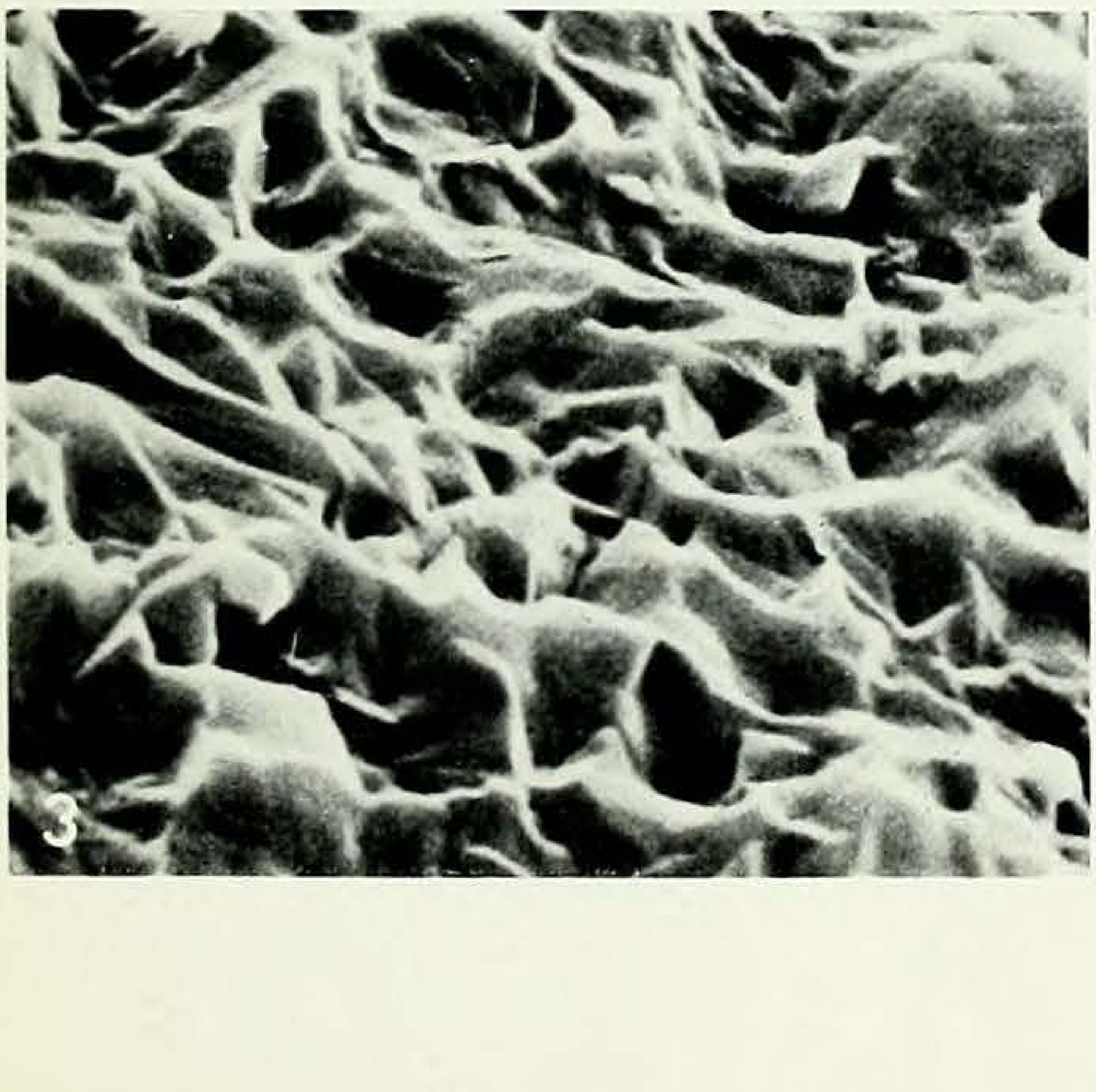

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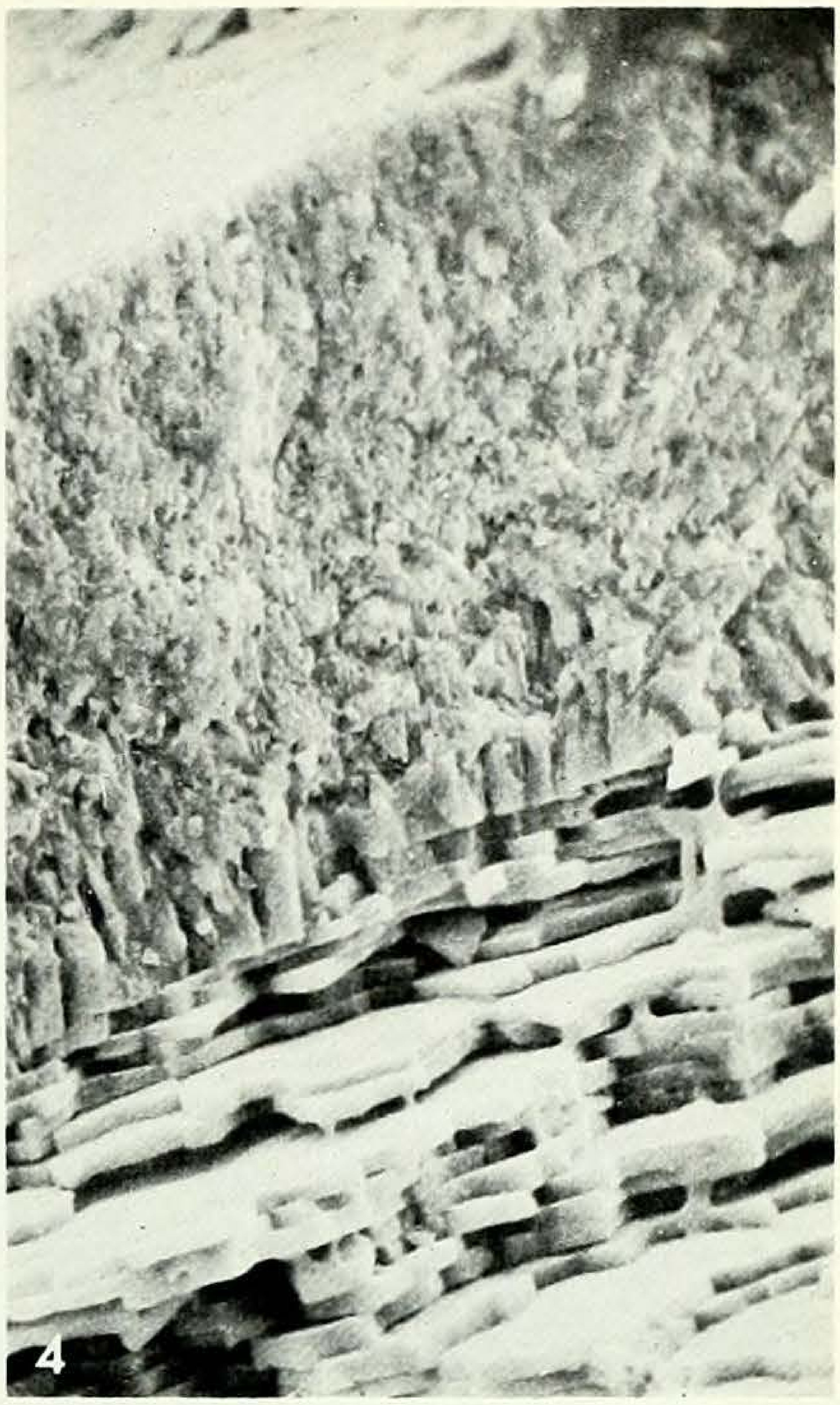

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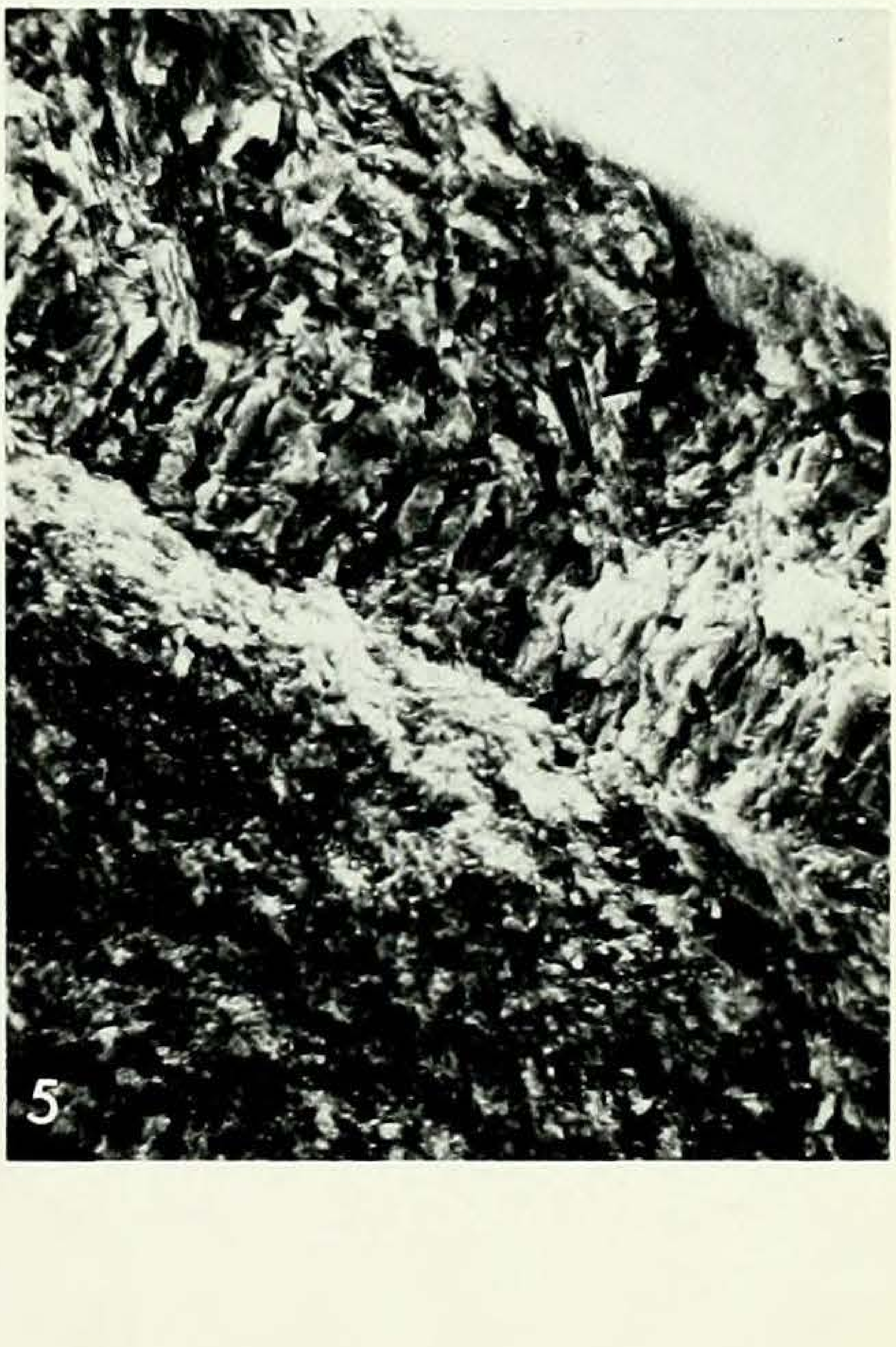

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PLATE 15

All figures are scanning electron-micrographs of ***Penicillus*** sp.

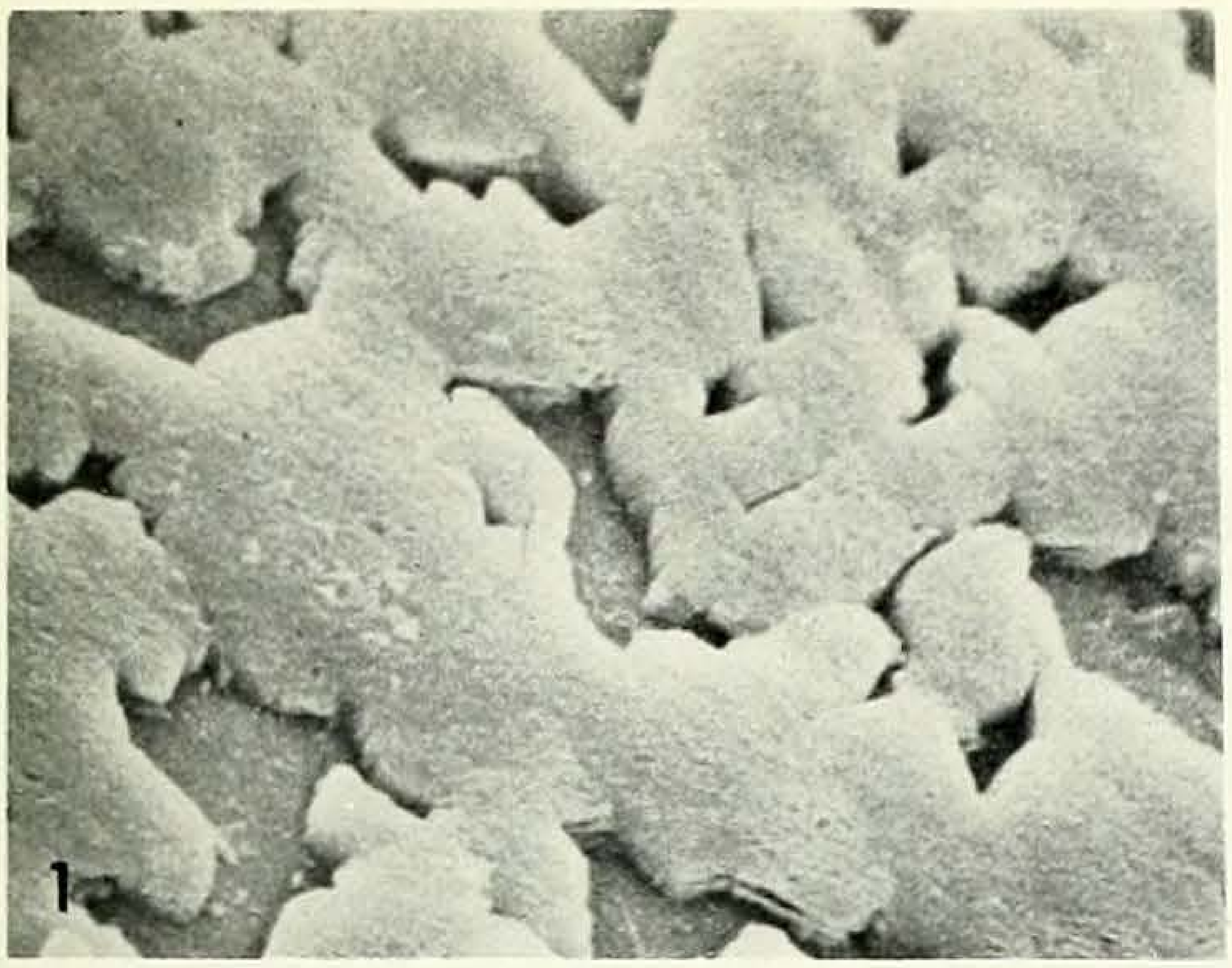
FIG. 1. Inner surface of nacreous layer. × 2,300.

FIG. 2. Fractured section of nacreous layer of valves showing sheet nacre. × 2,400.

FIG. 3. Fractured section of the tube showing the flat platy crystallites. × 2,400.

FIG. 4. As Fig. 3 but showing the stacks of platy crystallites. × 1,200.

FIG. 5. Surface granules, covered by periostracum on the outside of the true valves. The granules are arranged in rows which radiate from the umbo. × 1,300.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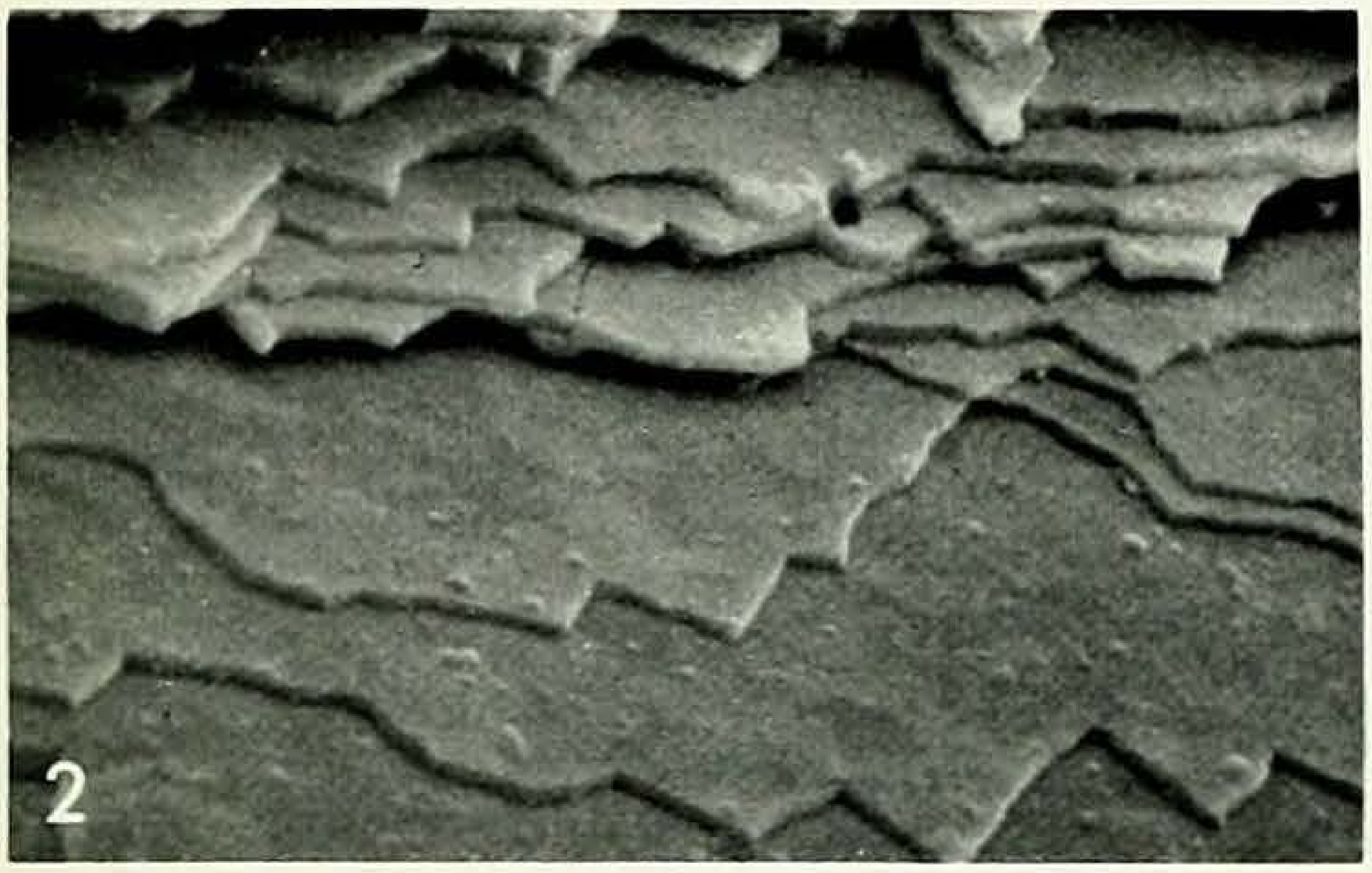
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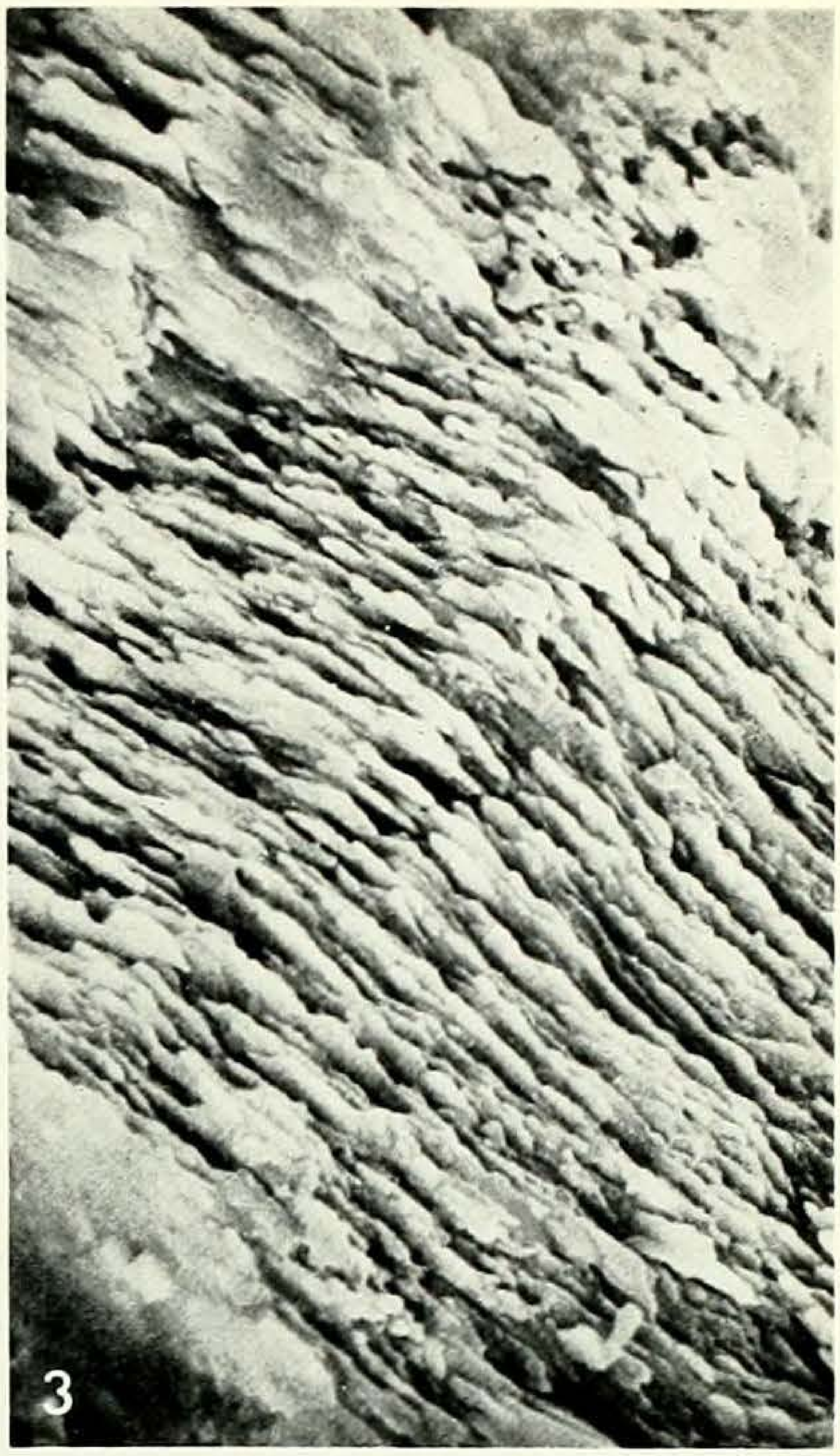
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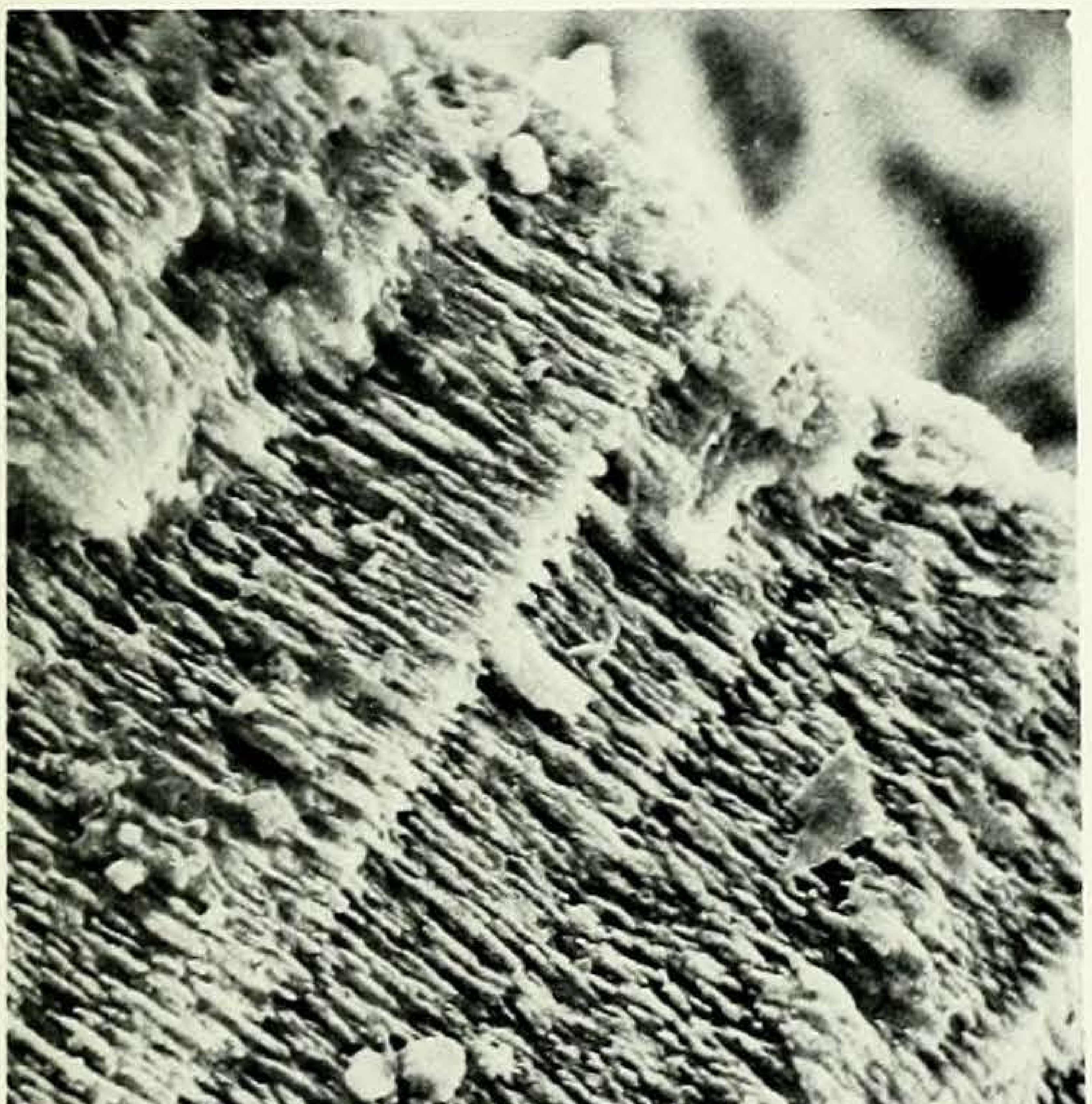
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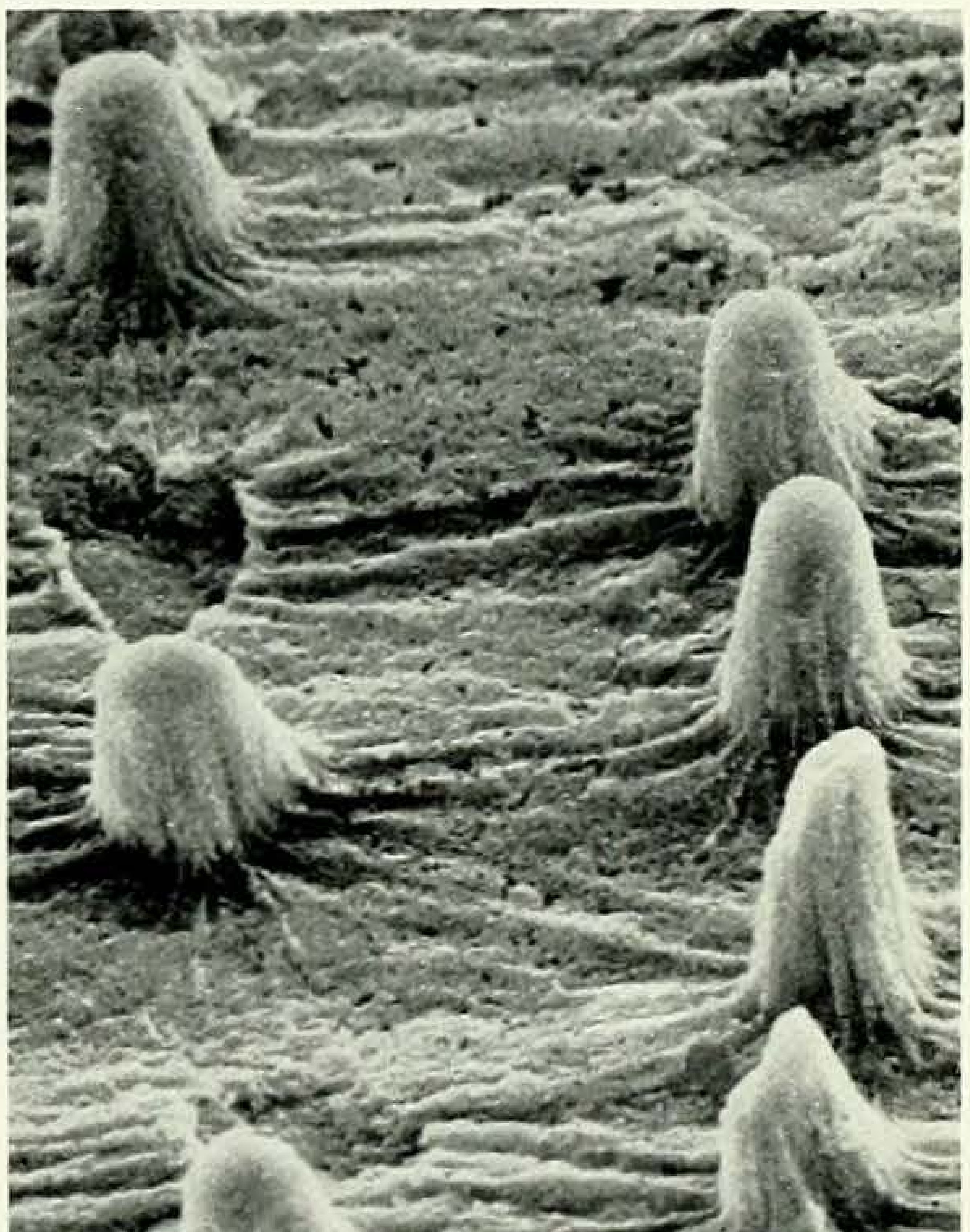
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