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COMPOSITE PRISMATIC STRUCTURE IN BIVALVE SHELL

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Composite prismatic structure has been examined in Nuculidae, Lucinidae, Cardiidae, Tellinidae, Psammobiidae, Donacidae and Veneridae. This microstructure is divided into three basic structural varieties: typical composite prismatic, characteristic of Nuculidae (*Nucula*); fibrous composite prismatic, observed in Cardiidae, Tellinidae, Psammobiidae; and compound composite prismatic mainly characteristic of Donacidae and Veneridae. The observed differences within the structure, the orientation of prisms and the growth pattern are genetically determined. They may considerably supplement the criteria on which the taxonomy of the group is based. At the same time there exist phenotypic, environmentally controlled structural differences.

Key words: Bivalves, shell microstructure, prismatic layer.

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INTRODUCTION

Composite prismatic structure forms the outer carbonate shell layer of some bivalve molluscs. This type of microstructure is one of the most complicated. This term is not interpreted synonymously by different scientists. Böggild (1930) first suggested it to be a variety of prismatic structure and defined it as the structure which "consists of larger prisms (prisms of the first order) each of them being composed of fine prisms (of the second order)... The prisms of the first order are placed horizontally, in the radial direction, and only form one layer; the prisms of the second order diverge towards the margin. This structure is most typically developed in the upper layer of most members of *Nucula*" (op. cit. 249). When describing the structural type of separate systematic groups Böggild interpreted this structure more widely and recorded it in Donacidae, Lucinidae and Veneridae. These groups do not have such large prisms placed radially, and Böggild considered their structure to be transitional to simple prismatic structure. Later researchers (Kobayashi 1969, 1971; Taylor *et al.* 1969, 1973; Popov 1977; Carter 1980) regarded the composite prismatic structure as an independent type and, moreover, they recorded it in Tellinidae, Psammobiidae, Arcidae, Cardiidae and Gastrochaenacea. Carter (1980: 64) introduced the term "compound composite prismatic structure" for a structure with large horizontal prisms each composed of compound prisms radiating in three directions. In a paper on composite prismatic structure Suzuki (1982) suggested a restricted interpretation of this term. At the same time he stated that composite prismatic structure was absent in nuculids, the taxon of which Böggild considered to be typical of this structure!

The study of the three-dimensional, spatial structure carried out on the basis of numerous taxa demonstrated considerable variety in composite prismatic structure in different groups of molluscs.

The main terms used for the description of shell microstructure were introduced by Böggild and earlier authors. Electronic microscopy data led to structural verification of these types of microstructure and revealed some new ones (Taylor *et al.* 1969, 1973; Kobayashi 1969, 1971; Carter 1980).

MATERIAL AND METHODS

The shell structure of Recent and fossil members of 8 bivalve mollusc families in which composite prismatic structure was indicated, has been examined: Nuculidae (4 species of three genera), Arcidae (*Anadara brounghtonii* Schrenck), Lucinidae (22 species of 11 genera), Cardiidae (32 species of 12 genera), Tellinidae (21 species of 10 genera), Psammobiidae (5 species of three genera), Donacidae (2 species of *Donax*) and Veneridae (62 species of 35 genera). The examination was first carried out in acetate replicas. A shell was embedded in epoxy resin, and was cut in such a way as to get three main sections: radial (R); transverse (T) and horizontal (H). Then the shell was ground, polished on a cloth and etched with a 2—3% solution of hydrochloric acid till the surface became lustreless. Acetate peel was soaked either in dioxane or acetone and then a sample was put on it. Layer thickness, growth lines, major structural units, their change in ontogeny, the pattern of sculptural structure in the shell were photographed and drawn from peels under an optical microscope with oblique light.

Radial, transverse and oblique fractures, as well as polished and etched surfaces have been studied under the scanning electron microscope (MSM-9 and BS-300). The etching was carried out with a 5% solution of the phosphorus-tungsten acid. The etching of fracture surfaces lasted 30 seconds, the etching of polished surfaces 1.5—2 minutes.

RESULTS

Nuculidae

Two species of *Nucula* — *N. (Nucula) nucleus* (Linné)[1] from the Miocene of the Ukraine and *N. (Lamellinucula) sulcifera* Koenen, from the Oligocene of the Crimea were eaxmined; *Leionucula tenuis* (Montagu), Se of Okhotsk and *Acila (Truncacila) beringiana* Slodkewitsch, Kronotsky Bay, Kamchatka.

The structures of the main shell layers in all the nuculids examined is similar: the outer layer is composite prismatic; the middle one is built up of columnar nacre, and the inner one consists of sheet nacre (pl. 1: 3). At the same time there are evident differences in the structure of the outer layer. For instance in *N. nucleus* and *N sulcifera* it is built up of large prisms, the thickness of which is equal to the one of the whole outer layer (pl. 1: 1—5). On the outer shell surface of these species there are thin radial striations and fine marginal denticles. Each denticle corresponds to the end of the radiating prism (megaprism or first order prism according to Böggild). In *N. nucleus* each megaprism consists of fine acicular prisms diverging from the centre of the megaprism. In *N. sulcifera* these fine prisms are evidently organized in layer elements forming megaprisms in their turn.

Similar structure is characteristic of other *Nucula* (the Eocene species, *N. similis* — see Böggild 1930: pl. 2: 6, and according to this author, *N. nitida*, *N. mayeri*, *N. grippini*, *N. pectinata*).

Leionucula tenuis and *Acila beringiana* do not have radial striations, marginal denticles and megaprisms corresponding to the denticles. Their outer layers are built up of much finer irregular prisms with cross sections of 3—10 μm. These (first order) prisms diverge at a small angle from the middle of the layer in the radial section (pl. 2: 1), but they remain subparallel in transverse and horizontal sections. Sometimes the prisms are poorly defined, but they become visible due to etching revealing interprismatic organic matrix (pl. 1: 6, 7). First order prisms are built up of finer acicular subparallel to the edges of major prisms.

Arcidae

The composite prismatic structure in the family was only indicated in two species: *Anadara broughtonii* (Schrenck) (Kobayashi, Kamiya 1968; Kobayashi 1976; Suzuki 1982) and *A. ninohensis* (Otuka) (Kobayashi 1976). Of these species the structure of *A. (Scapharca) broughtonii* was examined. The shell structure of other species of arcids, where known, has only two types of structures: the outer layer is crossed-lamellar and the inner one

[1] Examined type species of genera are underlined.

is complex crossed-lamellar. In *A.* (*S.*) *broughtonii* the structure does not build up the entire outer layer. It is periodically replaced with the crossed-lamellar structure (pl. 2: 3). It apparently happens when the growth slows down in cold seasons. First order prisms are directed to the outer surface and are bent to the beak. They are rather large (with cross section up to 20 μm), irregular, and of varying thickness (pl. 2: 4, 5). In the photographs presented by the Japanese authors, the prisms are still larger (about 40 μm) and of a more regular form. Such differences might be accounted for by ecological reasons, in particular by warmer water in the Japanese basins.

Lucinidae

Twenty two species of 11 genera of lucinids have been examined: *Lucina pectinata Gmelin*, Recent, Cuba (2 samples); *L. orbicularis* Deshayes, Pliocene of Syria (2 specimens), *Megaxinus* (*Megaxinus*) *ellipticus* (Borson), Pliocene of Syria, (*Gibbolucina*) *transversus* (Bronn), Miocene of the Ukraine, *M.* (*Saxolucina*) *incrassatus* (Dubois), Miocene of Moldavia (2 specimens); *Loripes lacteus* (Poli), the Aegean Sea (2 specimens), *L. dujardini* (*Deshayes*), Miocene of the Ukraine (2 specimens) and Transcaspia; *Codakia orbicularis* (Linné), Recent, Cuba (2 specimens); *Ctena orbiculata* Montagu, Recent, Cuba; *C. decussata* (Poli), Pleistocene of Tunisia (subfamily Lucininae, according to Chavan 1969); *Lucinoma borealis* (Linné), Miocene of the Ukraine (3 specimens), *L. acutilineata* (Conrad), Miocene of Kamchatka; *Gonimyrtea michelotti* (Mayer), Miocene of the Ukraine (the subfamily Myrteinae), *Divaricella* (*Divalucina*) *huttoniana* Vanatta, Pleistocene of New Zealand; *Divaricella* (*Divalinga*) *quadrisulcata* (Orbigny), Recent, Cuba; *D.* (*D.*) *ornata* (Agassiz), Miocene of the Ukraine; *Divaricella* (*Boeuvia*) *pulchella* Agassiz; Eocene of Belgium (subfamily Divaricellinae); *Pegophysema schrammi* (Crosse); Pleistocene of Florida; *Anodontia edentula* (Linné), Red Sea; *Anodontia* sp., Indian Ocean; *A. fragilis* (Philippi), Miocene of the Ukraine (subfamily Milthinae).

The shell in all the species examined has three main layers. The middle layer of nearly all Lucinidae is crossed-lamellar. Only *Ctena decussata* has inner homogeneous sublayer, and *Anodontia edentula* has a complex crossed-lamellar sublayer. The inner layer is usually complex crossed--lamellar but with frequent interlayers of the irregular prismatic structure (or transprismatic, according to Kobayashi 1969). Quite often the latter builds up almost all the inner layer.

The outer layer in Lucinidae is usually rather thin, but its structure is the most diverse. In the majority of lucinids it is built up of fine fibrous prisms. Such structure is observed in *Lucina orbicularis*, *L. pectinata*, *Gonimyrtea michelotti*, *Megaxinus ellipticus*, *M. incrassatus*, *M. transversus*, *Loripes lacteus*, *L. dujardini*, *Pegophysema schrammi*, *Divaricella*

(Divalinga) quadrisulcata, *D.(D.) ornata* and *Ctena orbiculata*. At the same time three-dimensional structure in various genera varies. Thus prisms arranged in a fanlike manner beginning with the middle of the layer are only observed in *Divaricella (Divalinga) ornata* (pl. 3: 3, 4). In other species prisms are bent to the beak, at the same time preserving the direction towards the outer surface (pl. 3: 1, 2). In members of *Megaxinus* radiating divergence of prisms from a number of centers in horizontal sections is observed periodically (pl. 4: 1, 2). In other cases prisms are approximately parallel to each other. Some differences are also observed in the forms of prisms. In *Gonimyrtea michelotti* the distal ends of prisms close to the middle layer are lamellar in form. In *Megaxinus transversus* prisms have transverse substructure. In *Codakia orbicularis* the outer layer seems to be built up of larger prisms. However later prisms are poorly outlined and they are subdivided into parallel fibrous prisms.

Linga columbella has a very peculiar structure. The outer layer is built up of rather large, irregular simple prisms also bent to the beak (pl. 5: 6). Similar structure is observed in species of *Lucinoma* — *L. borealis* from the Tethys region and *L. acutilineata* from the Far East. But in these species prisms are shorter, irregular and grouped in blocks or packages (pl. 5: 1—3). Short, irregular prisms in the outer layer are also observed in *Divaricella (Divalucina) huttoniana* (pl. 3: 6). The three species of *Anodontia* examined have a structure that differ entirely it from other Lucinidae. They have the outer layer composed of fine acicular prisms, diverging fanwise from centres near the outer surface of the shell. Growth lines are also bent around these centres (pl. 2: 6).

Cardiidae

The microstructure of the shell in this family has been examined most thoroughly, covering members of nearly all genera and subgenera (150 species of 34 genera and subgenera). The structure of the majority of typical species has been studied. The results of this examination being published elsewhere (Popov 1977, 1980), the microstructure of members of only two subfamilies, Fraginae and Clinocardiinae, has briefly been described here.

A three-layer shell is characteristic of the subfamily Fraginae (including the genera of the Tethys origin; *Acanthocardia*, *Parvicardium*, *Plagiocardium*, *Orthocardium*, *Loxocardium* and (?) *Cerastoderma*). The inner layer of fragins, as well as all Cardiidae, is complex crossed-lamellar, the middle one is crossed-lamellar. The outer layer is built up of fine fibrous prisms diverging fanwise from the middle of the layer (Carter 1980: fig. 5). Transverse and horizontal sections of *Acanthocardia* (*A. aculeata*, *A. tuberculata*) show that fibrous prisms are assembled in horizontally oriented megaprisms (pl. 6: 2, 3, 5). In other genera megaprisms are not observed.

Moreover *Acanthocardia* and some *Cerastoderma* have an additional outermost sublayer, having a crossed-lamellar structure (pl. 6: 1). In *Fragum fragum*, *Plagiocardium granulosum* and some *Parvicardium* the outer layer of the fibrous-prismatic structure does not cover the entire outer surface of the shell. It is well developed only in the middle part of the ribs and interribs while on the slopes of the ribs the lamels of the cross-lamellar structure reach the outer surface.

Species of *Clinocardium* and *Serripes* have a thick outer layer which is built up of fine prisms slightly bent to the beak and incurved in the radial ribs (pl. 7: 1). The prisms have a subsquare or more irregular cross section and are often compound, having substructure of short fine elements directed towards the middle of the prism (pl. 7: 2). Sometimes in the same shell the elements composing the prisms are not observed and the prisms seem to be fused (Popov 1977: pl. 5: 2a). The transition of prisms of one type into the other makes it possible to suppose that the changes in the construction of prisms might have been caused by seasonal changes of conditions under which the shell growth was taking place.

Tellinidae

In this family the shell structure of 21 species of 10 genera has been examined: *Tellina radiata* Linné Recent, Cuba (2 specimens), Florida; *Tellina incarnata* (Linné), the Adriatic Sea (2 specimens); *Angulus tenuis* (Da Costa), the Black Sea; *Angulus pretiosa* (Eichwald); Miocene of the Ukraine (2 specimens); *Angulus nysti* (Deshayes), Oligocene of Usturt; *Angulus fabula* (Gmelin), the Black Sea (2 specimens); *Angulus albicans* (Gmelin), the Adriatic Sea (2 specimens); *Oudardia compressa* Brocchi, Miocene of the Ukraine (2 specimens); *Peronaea planata* (Linné), the Mediterranean Sea (2 specimens); *Moerella donacina* (Linné), Miocene of the Ukraine (2 specimens); *Arcopagia crassa* (Pennant), Miocene of France; *A. corbis* (Bronn), Miocene of the Ukraine; "*Peronidia*" *lutea* (Wood), the Bering Sea; "*P*". *venulosa* (Schrenck), the Sea of Japan; *Quidnipagus palatam* Iredale, Recent, New Zealand (subfamily of Tellininae) and *Macoma calcarea* (Gmelin), the White Sea; *M. balthica* (Linné), the White and Baltic Seas; *M. orientalis* Scarlato, the Sea of Japan; *M. nasuta* (Conrad), Pleistocene of California; *M. incongrua* (Martens), the Sea of Japan; *Gastrana fragilis* (Linné), the Mediterranean Sea (2 specimens) (subfamily of Macominae).

The microstructure of tellinids is rather diverse and differs greatly between two subfamilies. The shell of tellinids is three-layered, often with additional sublayers. The inner layer is usually homogeneous, the middle one has two sublayers: crossed-lamellar and homogeneous. In *Tellina radiata* the crossed-lamellar structure in the middle layer is missing.

The outer layer in most tellinids is thin. Its structure varies in different species. The outer layer is usually built up of fine fibrous prisms diverging from the upper part of the layer. Cross section of the prisms is close to rounded or of irregular form with a diameter less than 1 μm. Electron microscopy reveals the substructure of transverse elements in prisms (pl. 8: 2). The outer layer in *Moerella donacina* and *Tellina radiata* is thicker. The prisms diverge from the middle of the layer. There are clearly outlined megaprisms only in *Angulus tenuis* and *A. nysti*. In *A. pretiosa* the fibrous prisms are bent to the beak at an angle of about 45°. Horizontal sections show that they are gathered in bundles (pl. 8: 1—3).

The most evident differences to structure are observed in Pacific species, usually referred to *Peronidia*: "*P.*" *lutea* and "*P.*" *venulosa*. The thick outer layer of these species is built up of irregular compound prisms of the first order, formed of fine prisms diverging from the middle of the first order prisms (pl. 9: 1, 2).

Unlike Tellininae the species of *Macoma* examined lack homogeneous structure and have a complex cross-lamellar inner layer. The structure of the outer layer is different. Some *Macoma* (*M. nasuta*, *M. incongrua*) have a two-layer structure. The outer layer is crossed-lamellar, the inner one is complex crossed-lamellar. If the shell is three-layered, the outer layer is of spherulitic structure (as in *M. calcarea*, *M. balthica*, *M. orientalis*) (pl. 9: 5, 6). The spherulites are fine at the outer surface, but the deeper they are, the larger they become.

Gastrana fragilis belonging to the subfamily Macominae are also characterised by a complex crossed-lamellar outer layer and crossed-lamellar middle layer. However the outer layer of this species is formed by fibrous prisms (pl. 9: 4).

Donacidae

Two species only have been examined, *Donax incarnatus* (Gmelin), Recent, Seychelles and *D. trunculus* Linné, the Black Sea. The structure of the outer layer in these species is different. In *D. incarnatus* it is built up of large fibrous prisms (the diameter is up to 1.5 μm) diverging fanwise from the upper part of the layer (pl. 10: 1, 2). In *D. trunculus*, the structure is evidently the same as in *D. variabilis* and *D. vittatus*, examined by Carter and Böggild; there are large complex prisms consisting of finer ones. These compound prisms radiate in three dimensions from the centre, thus forming megaprisms (Carter 1980: 10).

Psammobiidae

Five species have been examined: *Gari* (*Gobreus*) *depressa* (Pennant), the Adriatic Sea (2 specimens); "*Gari*" *labordei* (Basterot), Miocene of the Ukraine; *Asaphis deflorata* (Linné), Recent, Cuba (subfamily Psammobiinae) and *Sanguinalaria* (*Sanguinalaria*) *cruenta* (Lightfoot), Recent, Cuba;

S. (*Nuttallia*) *ezonis* Kuroda et Habe, the Sea of Japan (subfamily Sanguinalariinae). Members of these genera have different shell structures. In *Gari depressa* the thick outer layer is built up of prisms diverging fanwise from the middle of the layer, thus forming megaprisms (pl. 10: 5, 6). At the same time fine prisms meet in the lower part of the layer forming bent lamels. The middle layer of this species is crossed-lamellar, the inner one is complex crossed-lamellar. "*Gari*" *labordei* has quite a distinctive structure. The outer layer is very thin and is formed of fine acicular prisms. The middle layer has two sublayers: the outer one is crossed-lamellar with short irregular lamels and the inner one is homogeneous. The inner layer, separated by myostracum also has homogeneous structure. *Asaphis deflorata* has a thick outer layer, built up of fibrous prisms which do not form megaprisms. The middle layer is crossed-lamellar and the inner one is probably complex crossed-lamellar. The outer layer in species of *Sanguinolaria* consists of fine acicular prisms, directed toward the outer surface. In *S.* (*Nuttallia*) *ezonis* these prisms gather in bundles in the lower part of the layer. In both species examined this layer disappears periodically, and the lamels of the crossed-lamellar structure of the middle layer reach the outer surface. In the middle layer there is an inner sublayer of homogeneous structure. The inner layer in *S.* (*N.*) *ezonis* is complex crossed-lamellar, and in *S.* (*S.*) *cruenta* it is probably homogeneous.

Veneridae

The greatest diversity is observed in the shell structure of members of this large family. Altogether 62 species belonging to 35 genera and 10 subfamilies have been examined: *Venus (Venus) verrucosa* (Linné) (2 specimens), the Mediterranean Sea; *V. (Ventricoloidea) multilamella* (Lamarck), Pliocene of Italy; *Venus* sp., Miocene of the Ukraine; *Circomphalus subplicata* (Orbigny), Miocene of France; *C. basteroti* (Deshayes), Miocene of the Transcaspian, *Periglypta reticulata* (Linné), Recent, Australia; *Periglypta materna* (Iredale), Recent, Singapore (2 specimens); *Periglypta* sp. Recent, Australia; *Dosina zelandica* Gray, Recent, New Zealand, (subfamily Venerinae, according to Keen 1969). *Tapes (Tapes) literatus* (Linné), Recent, Japan; *T. (Ruditapes) decussatus* (Linné), the Adriatic Sea; *T.* (*R.*) *philippinarum* (Adams et Reeve), Sea of Japan (2 specimens), Singapore; *Venerupis* (*Venerupis*) *corrugata* (Gmelin), the Mediterranean Sea; *V.* (*Polititapes*) *rugata* (B. D. D.), the Black Sea; *V.* (*P.*) *vitaliana* (Orbigny), Miocene of the Ukraine (2 specimens); *V.* (*P.*) *merklini* Gontcharova, Miocene of Crimea, *Neovenerella usturtensis Gontcharova*, Miocene of Transcaspian; *Paphia* (*Paphia*) *vernicosa* (Gould), the Pacific Ocean, *Paphia* sp., Recent, Thailand; *Paphia* sp., Recent, Singapore (2 specimens); *P. (Callistotapes) vetula* (Basterot), Miocene of Moldavia; *P.* (*Paratapes*) *textile* (Linné), Recent, Manila, Indo-China; *Marcia* sp., the Pacific

Ocean: *Gomphomarcia taurica* (Bajarunas), Miocene of Crimea; *Eumarcia (Atamarcia) secunda* (Bogatchev) Miocene of Transcaspian; *Katelysia japonica* (Gmelin), Sea of Japan; *Irus (Irus) irus* (Linné), Miocene and Pleistocene of Crimea, Recent Black Sea; *I. (Notirus) mitis* (Deshayes), Recent, Japan; *Liocyma fluctuosa* (Gould), the Sea of Okhotsk (2 specimens) (subfamily Tapetinae); *Dosinia (Pectunculus) exoleta* (Linné), Miocene of the Ukraine; *D. (Asa) lupinus* (Linné), the Adriatic Sea; *Dosinia* sp., Recent, Singapore (subfamily Dosiniinae). *Cyclina sinensis* (Gmelin), Recent, China (subfamily Cyclininae). *Chione cancellata* (Linné), Recent, Cuba; *Ch. calophilla* Philippi, Recent, Singapore (2 specimens); "*Chione*" *amidei* Sacco, Pliocene of Italy; *Clausinella fasciata* (Da Costa), the Mediterranean Sea; *Anomalocardia (Cryptonemella) producta* Kuroda et Habe, Recent, Japan; *A. (Anomalodiscus) squamosa* (Linné), Recent, Singapore; *Chamelea gallina* (Linné), the Mediterranean Sea; *Protothaca staminea* (Conrad), Sea of Japan (2 specimens); *P. euglipca* (Sowerby), Sea of Japan; *Callithaca adamsi* Reeve, Sea of Japan; *Mercenaria stimpsoni* (Gould), Sea of Japan (2 specimens); *Tawera subsulcata* (Suter), Pleistocene of New Zealand; *Bassina (Callanaites) yatei* (Gray), Recent, New Zealand; *B. katherinae* Marwick, Pleistocene of New Zealand; *B. speighti* (Suter), Recent, New Zealand; *Timoclea (Timoclea) ovata* (Pennant), Pliocene of Italy; *T. (Parvivenus) marginata* (Hörnes), Miocene of Caucasus (subfamily Chioninae); *Callista (Callista) chione* (Linné), Miocene of the Ukraine; *C. (C.) latilamella* (Lukovich), the Eocene of the Transcaspian; *C. (Costacallista) erycina* (Linné), the Indian Ocean; *Macrocallista gigantea* (Gmelin), Recent, Florida; *Saxidomus purpuratus* (Sowerby), Sea of Japan; *Callista brevisiphonata* (Carpenter), Recent, Sakhalin, Sea of Japan (2 specimens) (subfamily Callistinae); *Gafrarium divaricatum* (Chemnitz), Recent, Singapore (5 specimens); *Gafrarium* sp., Recent, Singapore (3 specimens); *Circe minima* (Monterosato), the Black Sea (subfamily Circinae); *Meretrix petechialis* (Lamarck), Recent, Japan; *Meretrix* sp., Recent, Japan; *Tivelina* sp., Oligocene of Europe (subfamily Meretricinae); *Pitar rudis* (Poli), the Black Sea; *P. striata* Chemnitz, Recent, Singapore; *Pitar* sp., Recent, Singapore; *Cordiopsis westendorphi* (Nyst), Oligocene, the Transcaspian (subfamily Pitarinae); *Clementia* sp., Recent, Singapore (subfamily Clementinae).

A rather complex shell wall, formed by three, four and even five types of microstructure is characteristic of venerids. At the same time structural differences are observed at various taxonomic levels, even at the specific one.

The inner layer is usually homogeneous. It is either formed of irregular granules or has crossed-acicular structure. In some groups of venerids the inner layer is complex crossed-lamellar frequently with interlayers of irregular prismatic structure. The middle layer is often of homogeneous structure too. It may also consist of two sublayers — the inner one is homogeneous and the outer one is crossed-lamellar. Compound prisms are the most characteristic structure of the outer layer in most venerids. Prisms of the first order show a substructure of elongate subunits radiating in three dimensions from the central prism axis towards the depositional surface. The angle of divergence of these subunits is generally greater towards the edges of the prism than near the centre (pl. 11: 1, 2). Such prisms are usually parallel to the outer surface in the middle part of the outer layer. They diverge fanwise to the marginal parts of the layer and remain normal to growth lines (pl. 14: 2, 3, 6). The same structure is observed in members of various subfamiles of venerids: Venerinae, Chioninae, some Tapetinae, Callistinae. Sometimes such prisms radiate not from the middle but from the upper part of the layer (*Circomphalus subplicata*, *Dosina zelandica* — pl. 13: 3). In all species of the genus *Bassina* from New Zealand the compound prisms are nearly straight, and bent to the beak (pl. 12: 4, 5). In *Saxidomus purpuratus* the prisms are larger (up to 35 μm). They have irregular form and differ in thickness (pl. 14: 2).

Members of the subfamilies Tapetinae and Dosiniinae have a peculiar structure in the outer layer. In *Venerupis* (*Polititapes*) *tricuspis*, *Paphia* (*Paratapes*) *textile*, *Marcia* sp., *Gomphomarcia taurica* and others, prisms of the type described above are developed only in the lower part of the layer. In the upper part they meet and form vertical radiating lamels elongated in the radial direction. Such lamels are formed of the same elongate subunits directed towards its central part (pl. 13: 1). Other species of tapetins and species of the *Dosinia* lack prisms, and the whole outer layer is built up of such thin lamels, radiating from the beak (pl. 13: 2, 5, 6). Japanese authors note the same structure in *Dosinia japonica* and *D. odosensis* (Kobayashi, Isogai, Omori 1968: 1, 2), whereas according to their data *D. kaneharai* differs in having an outer layer of the pseudo-crossed-lamellar structure. In some venerids, such as *Chione cancellata*, *Cyclina sinensis*, and *Periglypta reticulata* — there are no clearly outlined structural elements of the first order; the outer layer consists of fine elongate prisms which sometimes form bundles radiating from the middle part of the layer to its growth edge.

DISCUSSION

Examination of abundant and diverse material including all the main bivalve groups in which composite prismatic structure is known, leads to the conclusion that there are many evident differences within this structure. The common feature is that long axes of the constituent elements are directed from the beak to the growthing edge of the shell. In radial section they are disposed fanwise. According to the morphology of the elements building up this structure, it is possible to single out three main variations of composite prismatic structure (Table 1: A—G).

I. The structure is built up of fine acicular prisms forming megaprisms. Megaprisms have a horizontal disposition. They are elongated radially and their thickness corresponds to the entire outer layer. The outer layer in most nuculids has this structure, which Böggild considered to be the most characteristic of this structure type. It corresponds to the original description (Böggild 1930: 249), that is why it should be considered to be *typical composite prismatic structure*.

II. The structure is built up of fine fibrous prisms the cross section of which is many times less their length. Such fibrous prisms may form megaprisms similar to those in the preceeding structure. This is observed in some cardiids (*Acanthocardia*), tellinids (*Angulus*) and psammobiids (*Gari*). However megaprisms are more often missing, and the layer is built up of fibrous prisms diverging from the middle part as in most cardiids of the subfamily Fraginae, some tellinids (*Moerella*) and lucinids — *Divaricella* (*Divalinga*). In most tellinids such prisms diverge not from the middle part of the layer but from the upper one. All these variations of structure may be united under the term of the *fibrous composite prismatic structure*.

III. The outer layer is built up of rather large prisms with a section of 10—30 µm (prisms of the first order). At the same time these prisms have a compound structure. They are formed of acicular prisms diverging from the centre of the first order prisms to the edges. The latter may group in megaprisms, as in some *Donax*. Carter (1980: 64) propose the name *compound composite prismatic structure* for this fabric. In venerids such compound prisms do not form megaprisms. They diverge either from the centre of the layer or from its upper part to the edges. Compound prisms (first order) in venerids are usually regular with a subhexagonal cross section. Members of the subfamilies Tapetinae and Dosiniinae differ in the peculiar substructure of the outer layer. Instead of the compound prisms they have vertical radiating lamels.

In some tellinids (Pacific "*Peronidia*") and in *Saxidomus purpuratus* prisms are less regular, changing in thickness. Similar first order prisms are observed in some nuculids, which lack marginal denticles and megaprisms correspondingly to them (*Leionucula*, some *Acila*). However acicular prisms building up the first order prisms in nuculids, as in *Codakia orbicularis*, do not diverge to the edges, but are parallel to the sides of the prism.

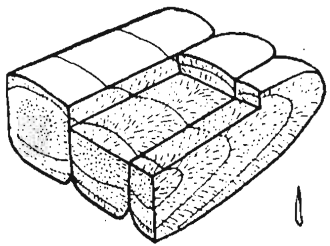
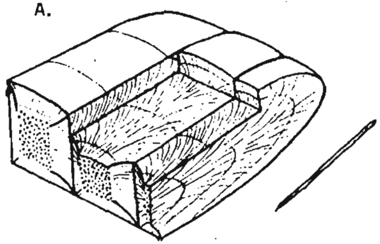
The structures described, in my opinion, should be regarded as varieties of the composite prismatic type. Besides that, there are structures with another disposition of prisms in the outer layer in the groups examined. Prisms built up of the same elements are oriented not to the beak, but to the outer surface of the shell; it is characteristic of simple prismatic microstructure.

Thus in some lucinids (*Anodontia*) and in psammobiids (*Sanguinalaria*)

Table 1

Summary of variations of composite prismatic and some similar structures

1:A

Main microstructural groups	Blockdiagrams of shell outer layer near growing edge	Elements of structure	Taxonomic distribution and references to figures
1	2	3	4
I. Acicular composite prismatic /typical/		Megaprisms have a substructure of elongate subunits-acicular prisms of 1-2x8-10 µm, diverging towards the depositional surface	*Nucula nucleus* / pl.1:1,2,5/ *N. similis* /Bøggild, 1930: pl. 2:6/ and some others nuculids
II. Fibrous composite prismatic	A. 	Megaprisms consist of: a/ fibrous prisms, with cross section 0,1-0,5µm b/ Larger fibrous prisms with cross section 0,5-1,5 µm	*Acanthocardia aculeata* /pl.4:5/ *A. tuberculata* /pl. 4:1-4/ *Angulus tenuis*, *Gari depressa* /pl.10:5,6/

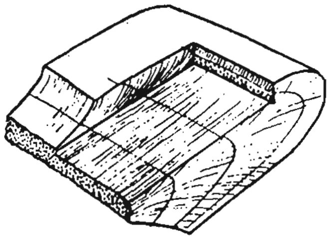
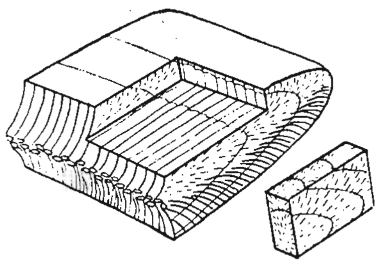
1	2	3	4
B.		Megaprisms are missing. a/ Fibrous prisms show orientation diverging from the middle of the layer	*Fragum subretusum* / Carter 1980:fig.5,6/ *Orthocardium porulosum* /Popov 1977: pl. 7:6 / *Plagiocardium latum* /ibid: pl. 8:3/ *Cerastoderma glaucum* / ibid: pl. 8:5a/ and other Fraginae /Cardiidae/ *Moerella donacina* / pl. 7:6/ *Divaricella ornata* / pl. 3:3,4/ *D. quadrisulcata* / pl. 3:5/
		b/ Fibrous prisms diverging from the upper part of the outer layer. Prisms are usually larger, as in a/	*Angulus fabula* / pl. 7:6/ *Peronaea planata* / pl. 9:3/ *Arcopagia corbis* / pl. 7:4/ *Gastrana fragilis* / pl. 9:4/ *Donax incarnatus* / pl. 10:1-4/ and some other Tellinacea

Table 1
(continued)

1:C

1	2	3	4
		c/ as in b/, but prisms are irregular of variable sizes d/ Smaller irregular prisms / cross section 3- 10 μm/ are subparallel to each other	*Saxidomus purpuratus*/ pl.14:2/ *"Peronidia" venulosa* / pl. 9:2/ *"P." lutea* /pl. 9:1/ *Leionucula tenuis* / pl. 1:6,7/ *Acila beringiana* / pl. 2:1,2/
C.		Prisms of the first order fused and form radiating lamels with the width from 10-20 μm to 50 μm	*Venerupis rugata* / pl. 13:1/ *Tapes philippinarum* / pl. 13:2,3,5/ *T. literata* /Carter, 1980: fig.11/ *Dosinia exoleta* / pl. 13:6/ and others Tapetinae and Dosiniinae /Veneridae/

1 : D

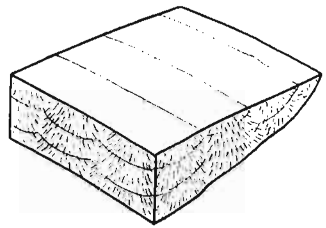
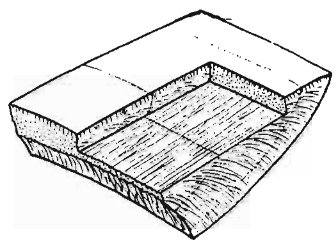
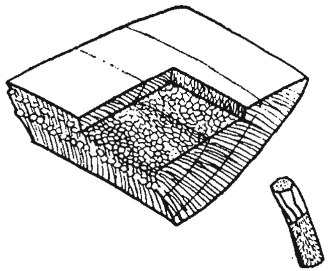
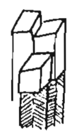
1	2	3	4
Prismatic structures distributed in the same families: Acicular prismatic		a/ Fine acicular prisms radiating in three dimensions from the centres on the periostracum surface /"spherulitic" prismatic according to Carter 1980: 646	*Anodontia edentula* *Anodontia* sp. /pl. 2:6/ *A. fragilis* *Spisula solidissima* /Carter 1980: fig.1/
		b/ The same elements have parallel orientation or show irregular bunches.	*Sanguinalaria ezonis* ? *S. cruenta* *"Gari" labordei*
Fibrious prismatic		a/ The thin fibrous prisms /cross section 0,5-1,5 μm/ bend towards the beak, frequently show bunch-pattern. Usually there is a thin prismatic outermost sublayer /mosaikostracum/	*Lucina orbicularis* /pl. 3:1/ *Megaxinus ellipticus* /pl. 4:1/ *M. incrassata* / pl. 4:2-5/ *Gonimyrtea michelotti* /pl. 3:2/ and other Lucinidae

Table 1
(continued)

1:E

1	2	3	4
		b/ Mosaikostracum is missing, prisms are of cross lamination	*Angulus pretiosa* /pl.8:1-3/ *"Tellina" incarnata*
Compound prismatic		a/ Regular compound first order prisms are bent to the beak and oriented towards external surface	*Bassina katherinae* *B. yatei* /pl. 12:4,5/
		b/ Prisms large are irregular /cross section from 10-20 μm to 50 μm/ consist of long acicular subunits	*Anadara broughtoni* /pl. 2:3-5/ *A. ninochensis*
		c/ Prisms are smaller /1-4 μm/, subsquare or irregular in cross section Sometimes one can see substruc - ture of fine acicular subunits	*Peronaea planata* / pl.9:3/ *Clinocardium nuttallii* / pl.7:1/ *Serripes groenlandicus* /pl.7:2/ and other Clinocardiinae /Cardiidae/

1:F

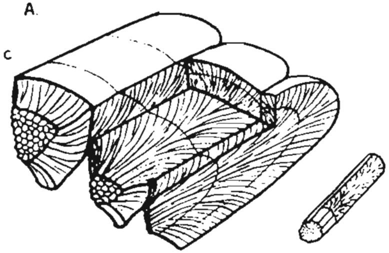
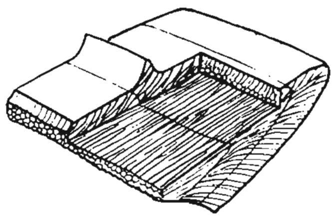
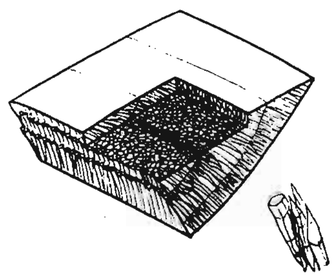
1	2	3	4
III. Compound composite prismatic	A. 	Megaprisms consist of compound prisms, with cross section 10-20 µm, having substructure of fine radiating acicular prisms of 0,1-0,4 x5-10µm	*Donax trunculus* *D. variabilis* /Carter 1980: 10/, *D. vittatus* /Bøggild 1930: pl. 6:6; pl. 7:1/
	B. 	Megaprisms are missing a/ Regular compound prisms with cross section 10-30 µm diverging from the upper part of the outer layer	*Circomphalus subplicata* /pl.11: 1,2/ *Dosina zelandica* / pl.11:5/ and some other venerids
		b/ Prisms diverging from the middle of the layer	*Circomphalus basteroti* *Timoclea ovata* / pl.11:6/ *Callistotapes vetulus* and some other venerids

Table 1
(continued)

1:G

1	2	3	4
IV. Irregular prismatic		Prisms are irregular, varying in thickness, without substructure	*Linga columbella* / pl.4:5, pl. 5:6/ *Lucinoma borealis* *Divaricella huttoniana* /pl.3:6/

fine acicular prisms are directed to the surface of periostractum. In most lucinids the outer layer is formed of fine fibrous or irregular prisms inclined to the beak. Their proximal ends reach the outer surface. Finally, some venerids (*Bassina*) and cardiids (*Clinocardium*, *Serripes*) have compound prisms, also directed to the outer surface. Larger irregular compound prisms in *Anadara brounghtonii*, *A. ninohensis* and simple irregular prisms in *Linga* and *Lucinoma* have the same orientation.

CONCLUSIONS

Microstructural peculiarities are often more distinct and less prone to phenotypic variation than the external morphology of the shell. The shell structure gives independent qualitative features, which considerably broaden the basis used for the construction of the systematics and phylogeny of molluscs (especially at the level of families, subfamilies and genera). The great quantity of material examined permits us to conclude that the greatest structural diversity is observed in the outer layer of the bivalve molluscs. In addition to various types of microstructure, there is a great diversity within some structure types, especially composite prismatic structure. The similarity of structural details usually testifies to the taxonomic closeness of forms under examination. Thus, the similar and very peculiar structure of the outer layer in Tapetinae (Veneridae) proves this to be a natural grouping. The similarity of the shell structure of some tropical genera of cardiids (*Fragum*, *Corculum*, *Trigoniocardia*) and a group of mediterranean genera (*Parvicardium*, *Acanthocardia* and others), together with the closeness of their morphology, supports their assignment to the subfamily Fraginae (Popov 1977). On the other hand, the microstructural differences evident within other taxa (subfamilies of the family Lucinidae, genera and species in the subfamilies Chioninae and Laevicardiinae) may testify to the heterogeneity of these groups.

Some north pacific tellinids serve as another example of the use of microstructural data in the taxonomy. The two related species exist here, usually being referred to the genus *Peronidia* ("*P.*" *venulosa* and "*P.*" *lutea*). They are characterized by a peculiar structure of the outer layer (pl. 9: 1, 2). On this basis they differ greatly from the mediterranean species *Angulus* (*Peronidia*) *albicans*, the type species of the subgenus (or genus) *Peronidia*. Thus, for taxonomic revisions of bivalves, and, indeed, other mollusc groups, it will be useful to take into account microstructural data. It is worth remembering that together with structural differences that are genetically controlled, there may be features controlled by environmental factors. Seasonal conditions evidently account for variations in the sublayers of the outer layer in *Serripes groenlandicus*, dimensions of prisms in *Anadara brounghtonii*, etc. However, study of the influence of environment on the microstructure of mollusc shells is still in the early stages of investigation.

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SERGEI V. POPOV

ZŁOŻONA STRUKTURA PRYZMATYCZNA MUSZLI MAŁŻÓW

Streszczenie

Złożona struktura pryzmatyczna była badana u Nuculidae, Lucinidae, Cardiidae, Tellinidae, Psammobiidae, Donacidae i Veneridae. Wymieniona struktura występuje w trzech zasadniczych odmianach: typowa złożona struktura pryzmatyczna, charakterystyczna dla Nuculidae (*Nucula*); włóknista złożona struktura pryzmatyczna,

obserwowana u Cardiidae, Tellinidae, Psammobiidae oraz kombinowana odmiana złożonej struktury pryzmatycznej charakterystyczna głównie dla Donacidae i Veneridae. Takie różnice obserwowane w strukturze jak orientacja pryzm i sposób wzrostu wydają się być zdeterminowane genetycznie. Mogą one w znacznej mierze uzupełnić kryteria taksonomiczne badanej grupy. Równocześnie obserwuje się również fenotypowe różnice strukturalne podlegające wpływowi środowiska.

EXPLANATION OF PLATES 1—14

All photomicrographs, unless specially marked, are made with a scanning electron microscope. Orientation of sections and fractures is marked with letters on the photos: *R* radial, *T* transverse and *H* horizontal. Arrows show growth direction (from umbo to margin) for radial and horizontal sections. In block diagrams the magnification of the structure is much greater than that of the shell thickness.

Plate 1

1—5. ***Nucula nucleus*** (Linné): *1, 2, 5* — photomicrographs of typical composite prismatic structure; *1, 2* ×2000, *5* ×1000; *3* block diagram of shell structure; *4* scheme of orientation of the main sections.

6, 7. ***Leionucula tenuis*** (Montagu): compound composite prismatic structure; *6* ×3500; *7* ×4500.

Plate 2

1, 2. ***Acila beringiana*** Slodkewitsch: compound composite prismatic structure; *1* ×2000; *2* ×3000.

3—5. ***Anadara brounghtonii*** (Schrenck): *3* diagram of radial section shows periodic replacement of compound prismatic by crossed-lamellar structure in outer layer; *4, 5* prisms of first and second orders; *4* ×4000; *5* ×2000.

6. ***Anodontia*** sp.: acicular prismatic structure; ×1500.

Plate 3

1. ***Lucina orbicularis*** Deshayes: fibrous prismatic structure; ×800.
2. ***Gonimyrtea michelotti*** (Mayer): the same structure; ×1000.
3, 4. ***Divaricella (Divalinga) ornata*** (Agassiz): the same structure; *3* mosaicostracum (in the upper part of the photo), ×2500; *4* ×4500.
6. ***D. (Divalucina) huttoniana*** (Vanetta): irregular prismatic structure; ×1500.

Plate 4

1. ***Megaxinus ellipticus*** (Borson): bunches of prisms in fibrous prismatic structure; ×3500.

2—4. *M. incrassatus* (Dubois): *2* the same structure, acetate peel; ×400; *3* fibrous prismatic structure; ×1500; *4* myostracum, separating middle and inner shell layers; ×3000.
5. *Lucinoma acutilineata* (Conrad): the same structure, acetate peel; ×250.

Plate 5

1—5. *Lucinoma acutilineata* (Conrad): *1—3* irregular prismatic structure with packages of prisms; *1* ×700; *2* ×2000; *3* ×1000; *4* middle crossed-lamellar layer and myostracum (down); ×800; *5* inner irregular prismatic layer; ×800.
6. *Linga columbella* (Lamarck): contact of outer irregular prismatic and middle crossed-lamellar layers; ×1500.

Plate 6

1—4. *Acanthocardia tuberculata* (Linné): *1* outermost crossed-lamellar sublayer; ×2000; *2* contact of two megaprisms of fibrous composite prismatic structure close to the boundary of middle layer, ×2500; *3* the same structure, acetate peel, ×225; *4* middle crossed-lamellar and inner complex crossed-lamellar layers, acetate peel; ×150.
5. *A. aculeata* (Linné), contact of two megaprisms of the fibrous prismatic structure; ×4000.

Plate 7

1. *Clinocardium nuttalii* (Conrad): curved prisms of compound prismatic structure in radial ribs; ×350.
2. *Serripes groenlandicus* (Bruguiere): prisms of the same structure; ×4200.
3. Block diagram of fibrous composite prismatic structure.
4. *Arcopagia corbis* (Bronn): ×900.
5. *Moerella donacina* (Linné): ×1500.
6. *Angulus fabula* (Gmelin): ×700.

Plate 8

1—4. *Angulus pretiosa* (Eichwald): *1—3* fibrous prismatic structure; *1* ×2000; *2* ×10 000; *3* ×1500; *4* crossed-lamellar structure of the upper part of middle layer; ×2000.
5. *A. tenuis* (Da Costa); contact of the upper sublayer of crossed-lamellar structure and the lower homogeneous middle layer; ×5000.

Plate 9

1. "*Peronidia*" *lutea* (Wood): prisms of compound composite prismatic structure; ×2800.
2. "*P.*" *venulosa* (Schrenck): first order prisms and spherulites close to the contact with middle layer; ×1000.

3. *Peronaea planata* (Linné): fibrous prisms, having a fine substructure; ×7000.
4. *Gastrana fragilis* (Linné): fibrous composite prismatic structure; ×2000.
5. *Macoma calcarea* (Gmelin): spherulitic structure; ×4200.
6. *M. orientalis* Scarlato: larger spherulites close to the contact with the middle layer; ×1000.

Plate 10

1—4. *Donax incarnatus* (Gmelin): 1, 2 fibrous composite prismatic structure; *1* ×400; *2* ×10 000; *3, 4* contact with middle crossed-lamellar layer; *3* ×2000; *4* ×3000.

5, 6. *Gari depressa* (Pennant): fibrous composite prismatic structure; *5* ×400; *6* megaprisms; ×1000.

Plate 11

1—4. *Circomphalus subplicata* (Orbigny): *1, 2* prisms of first and second order of compound composite prismatic structure; *1* ×2000; *2* ×1000; *3* homogeneous structure; ×5000; *4* contact of crossed-lamellar and homogeneous structures; ×1500.

5. *Dosina zelandica* Gray: first order large prisms of compound composite prismatic structure; ×150.
6. *Timoclea ovata* (Pennant): tops of prisms of compound composite prismatic structure; ×3000.

Plate 12

1. *Protothaca staminea* (Conrad): tops of prisms of compound composite prismatic structure; ×700.

2, 3. *Anomalocardia producta* Kuroda et Habe: 2 second order prisms bunches in the outermost part of outer layer; ×5000; *3* first order prisms of compound composite prismatic structure; ×350.

4, 5. *Bassina yatei* (Gray): *4* first order prisms of composite prismatic structure; ×1500; *5* the same structure; ×700.

Plate 13

1. *Venerupis rugata* (B. D. D.): radial lamels of compound composite prismatic structure, acetate peel; ×200.

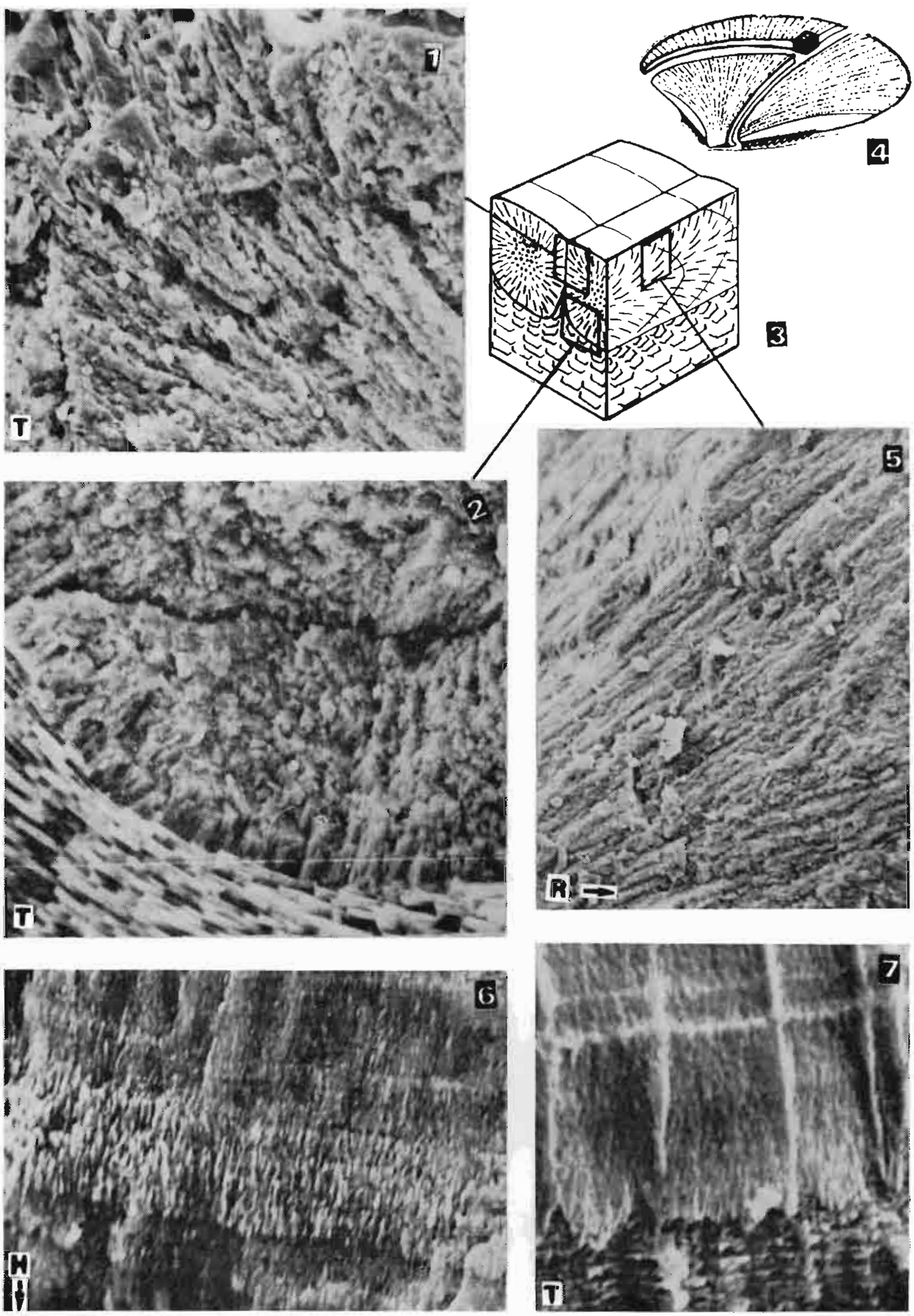
2—5. *Tapes philippinarum* (Adams et Reeve): *2, 3, 5* compound composite prismatic structure; *2* ×3000; *3* acetate peel; ×300; *5* ×3000; *4* homogeneous structure; ×5000.

6. *Dosinia exoleta* (Linné): radial lamels of compound composite prismatic structure; ×400.

Plate 14

1. *Paphia vernicosa* (Gould): polygonal sections of first order prisms of compound composite prismatic structure, acetate peel, ×150.

2. *Saxidomus purpuratus* (Sowerby): irregular first order prisms of compound composite prismatic structure; ×2500.
3, 4. *Paphia vetula* (Basterot): first order polygonal prisms of compound composite prismatic structure; *3* ×350; *4* ×1000.
5, 6. *Paphia* sp.: compound composite prismatic structure; *5* — the outermost part of outer layer without first order prisms, ×5000; *6* ×800.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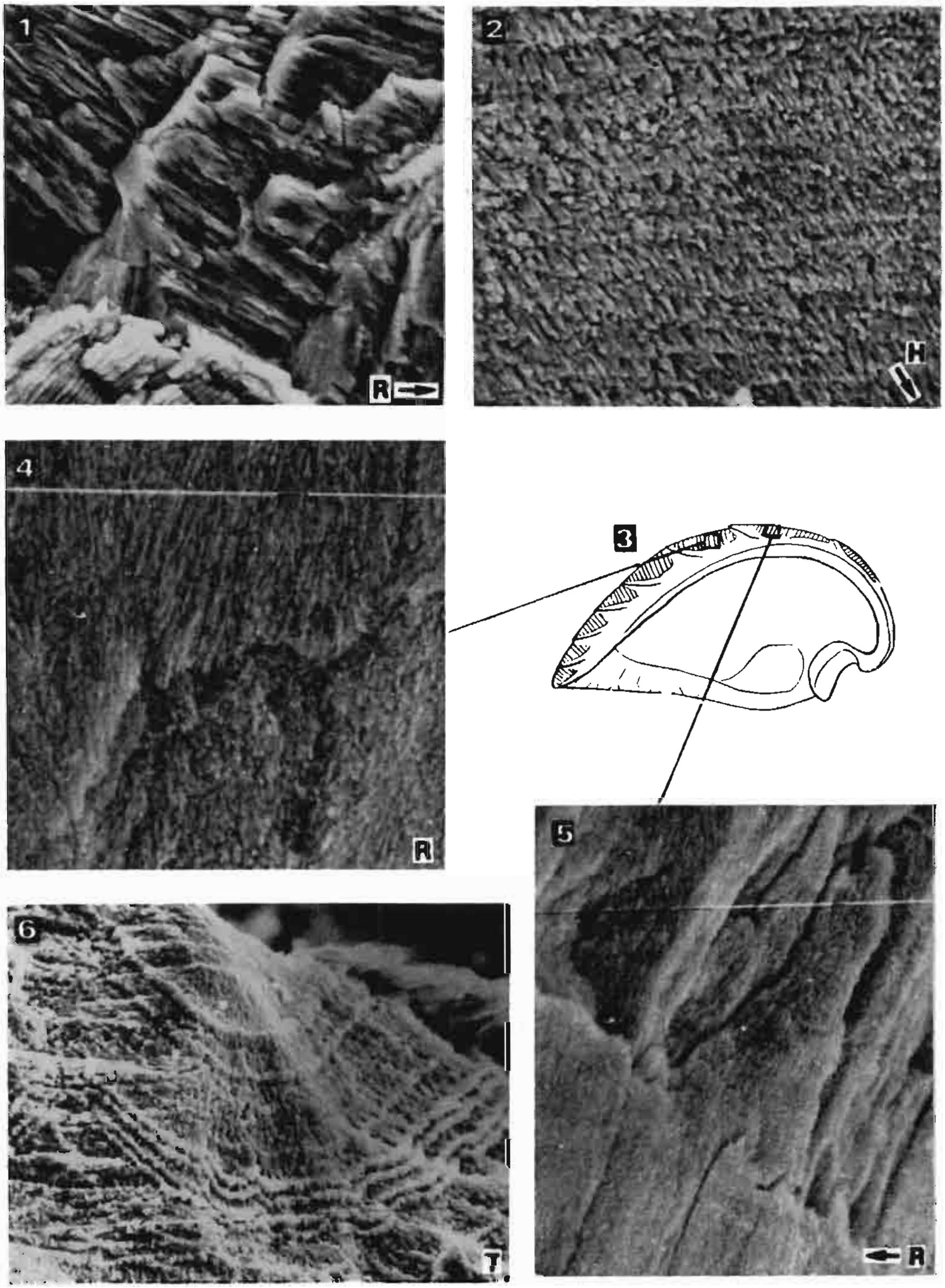
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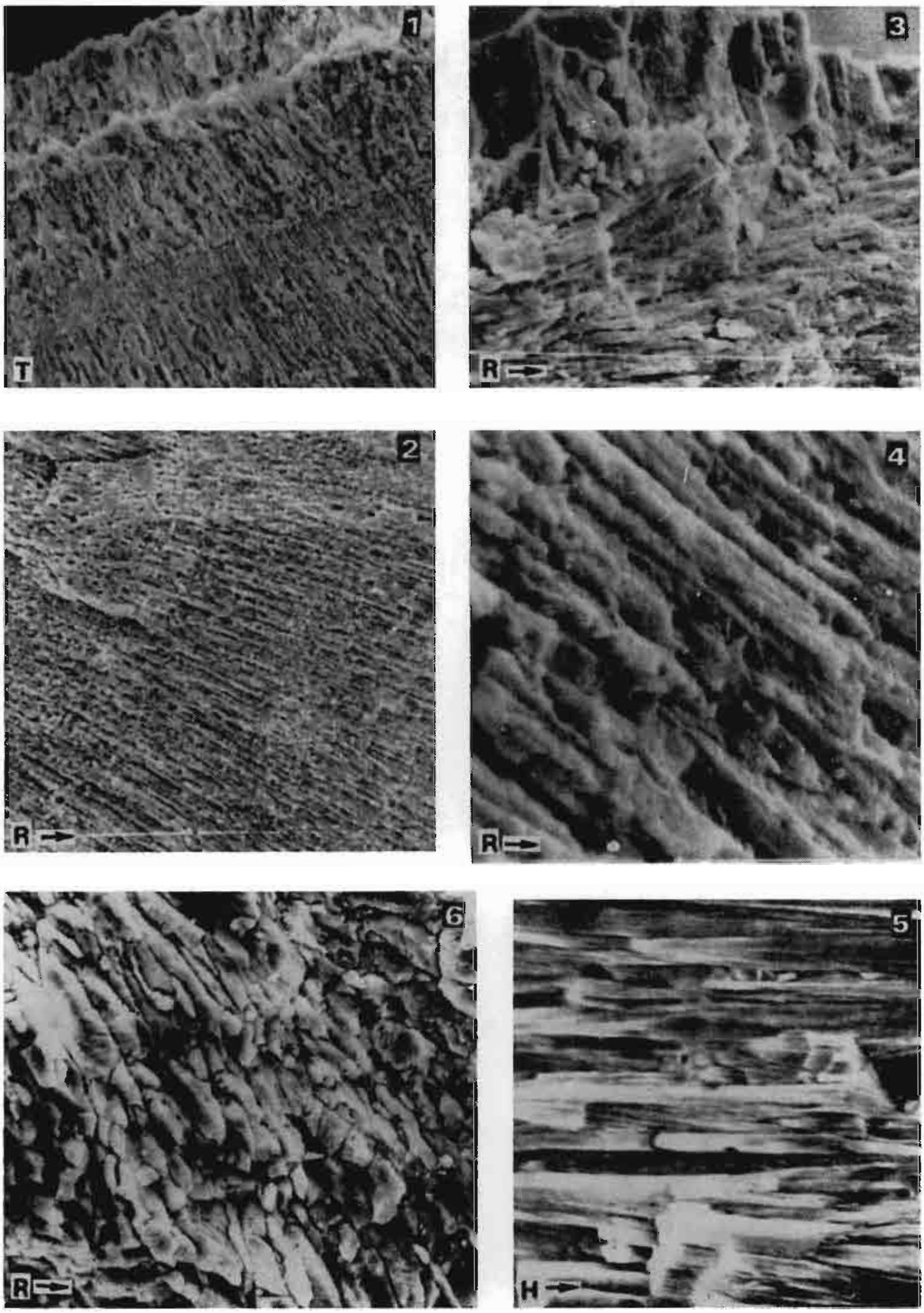
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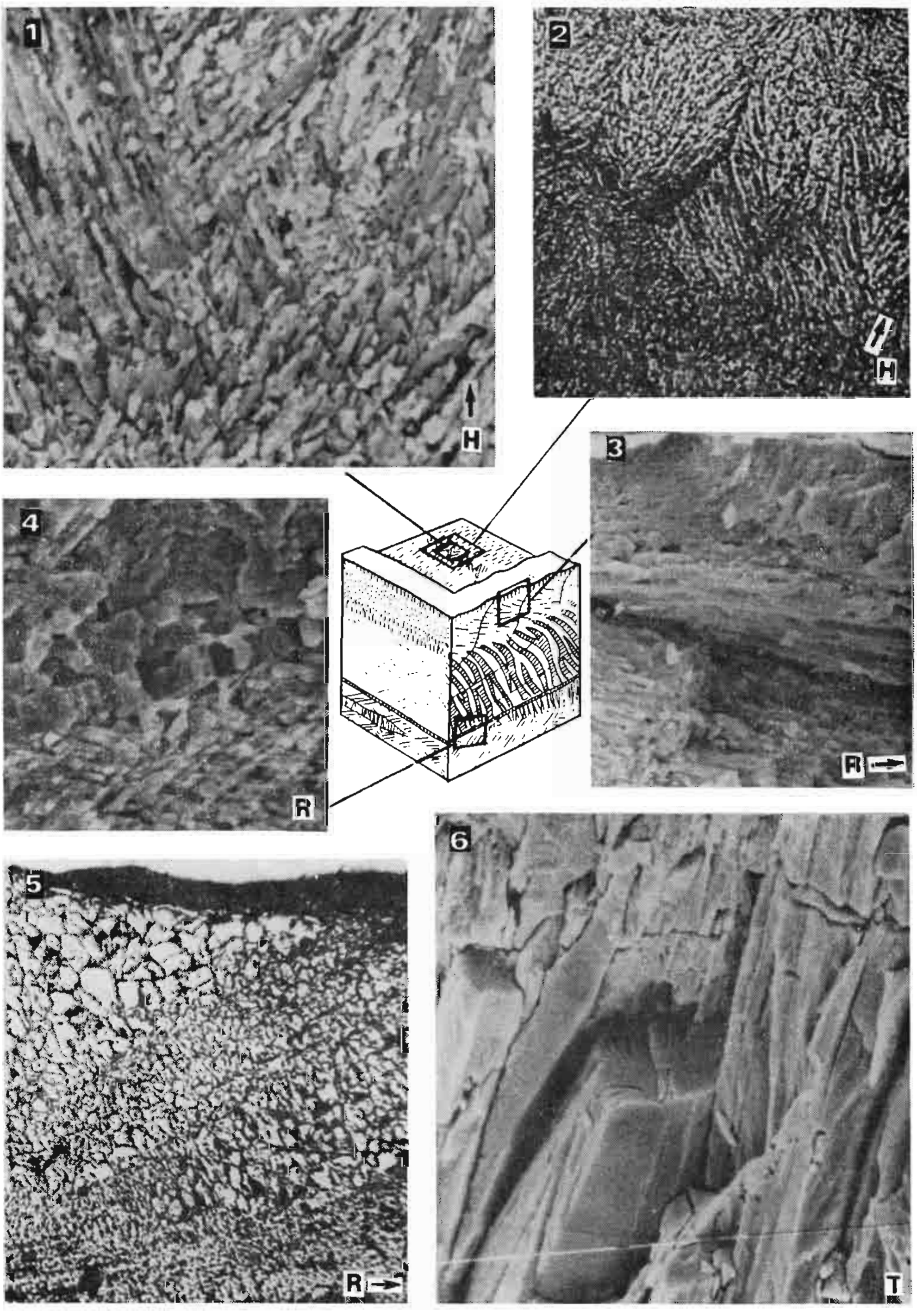
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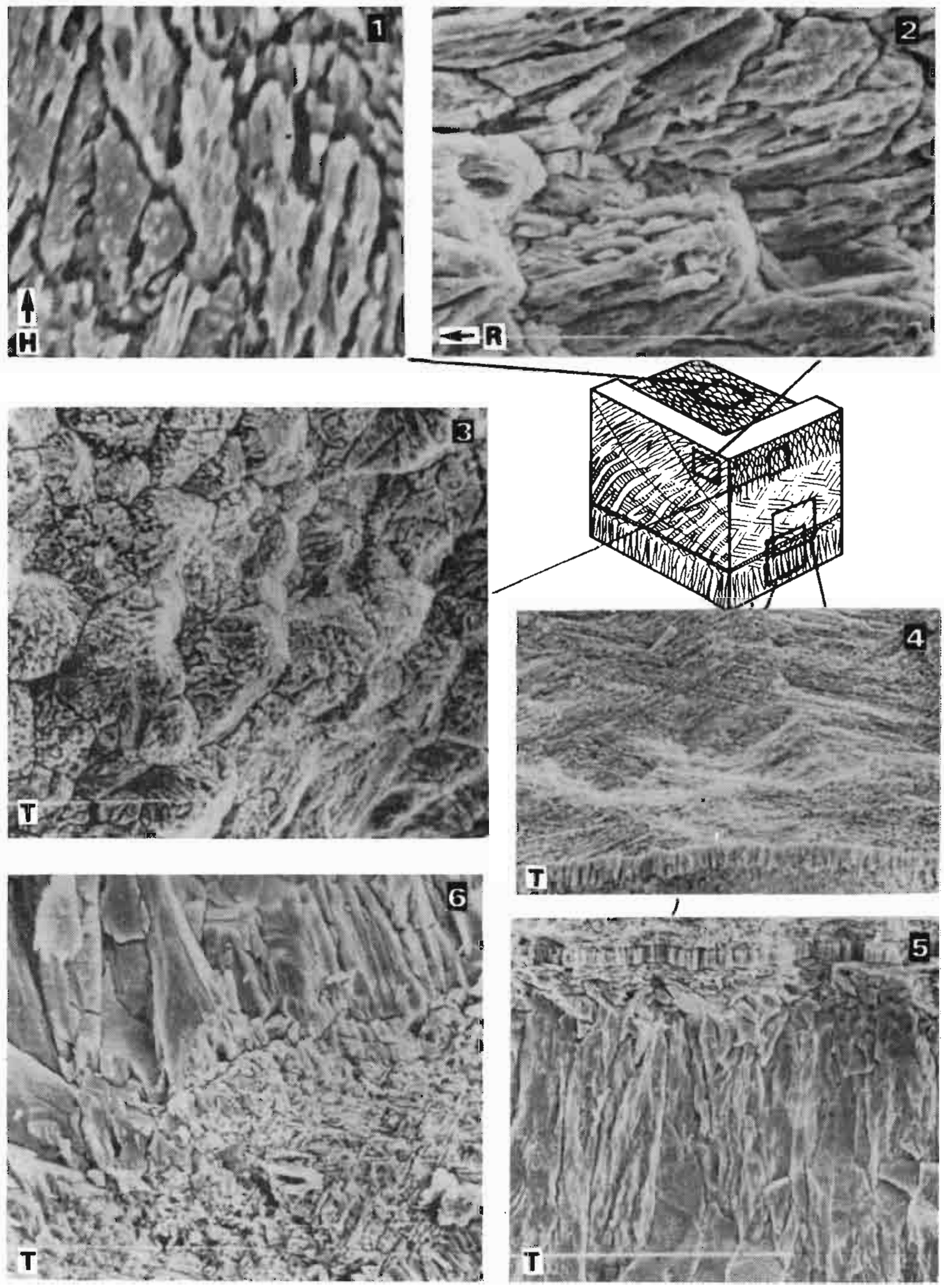
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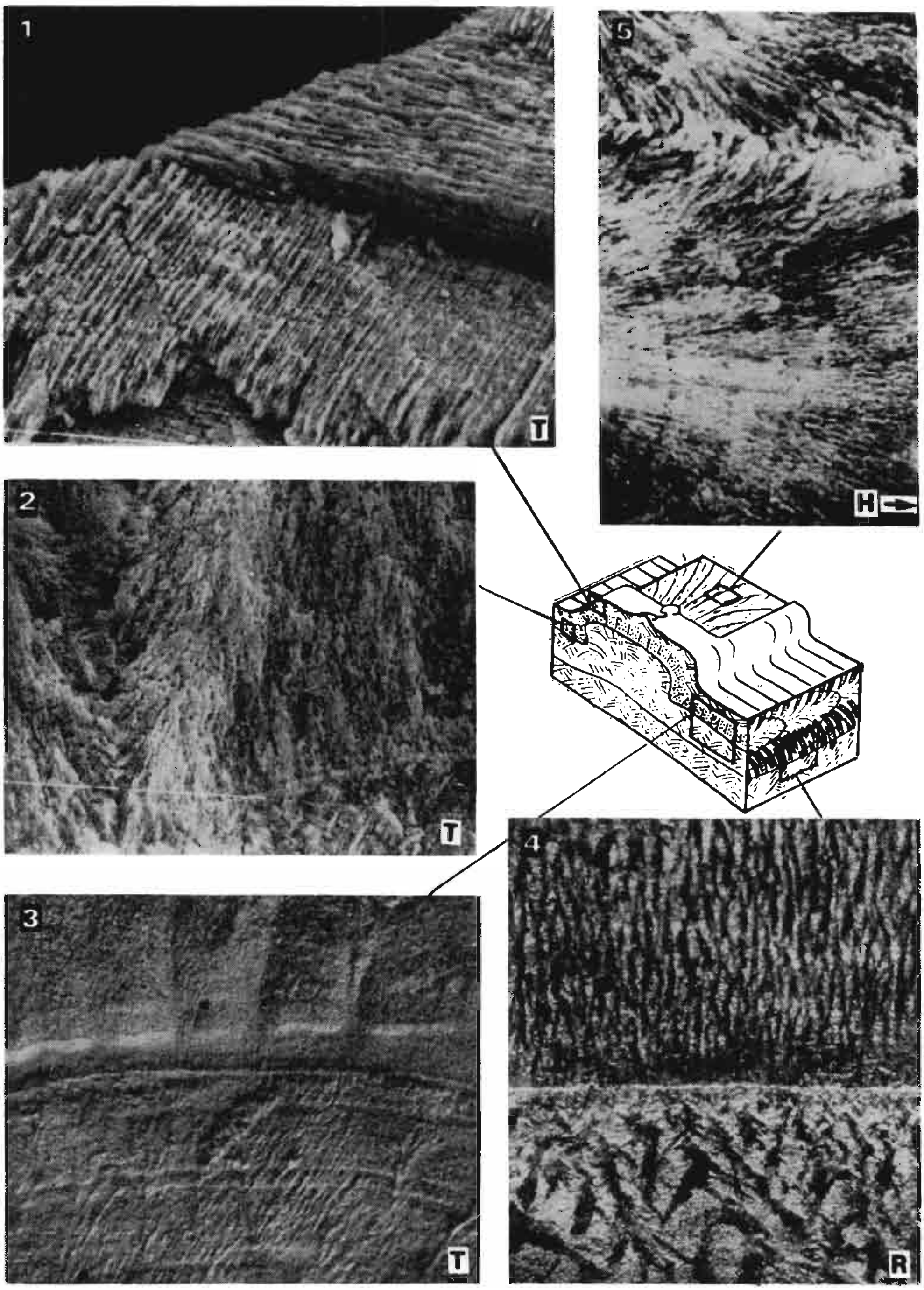
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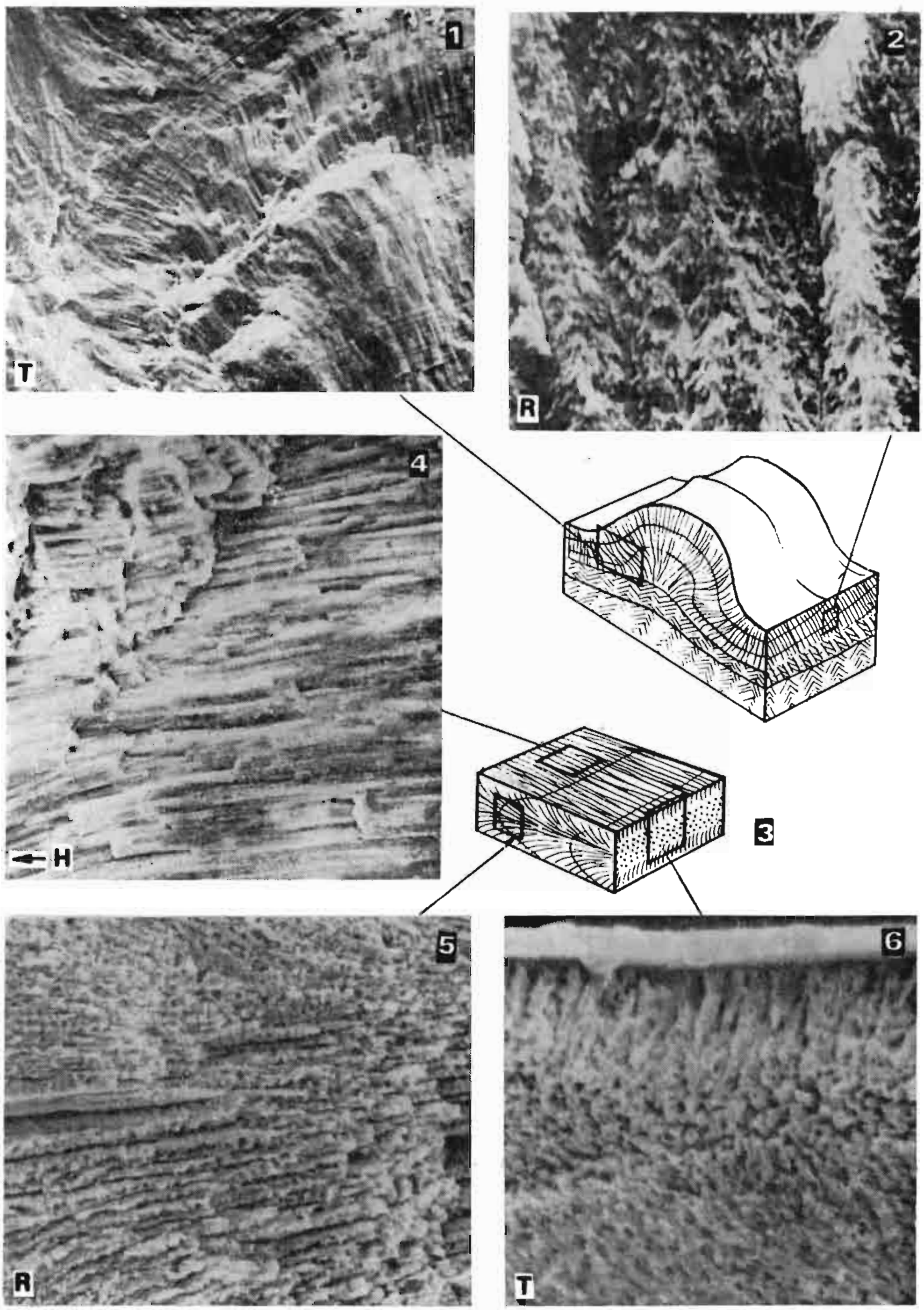
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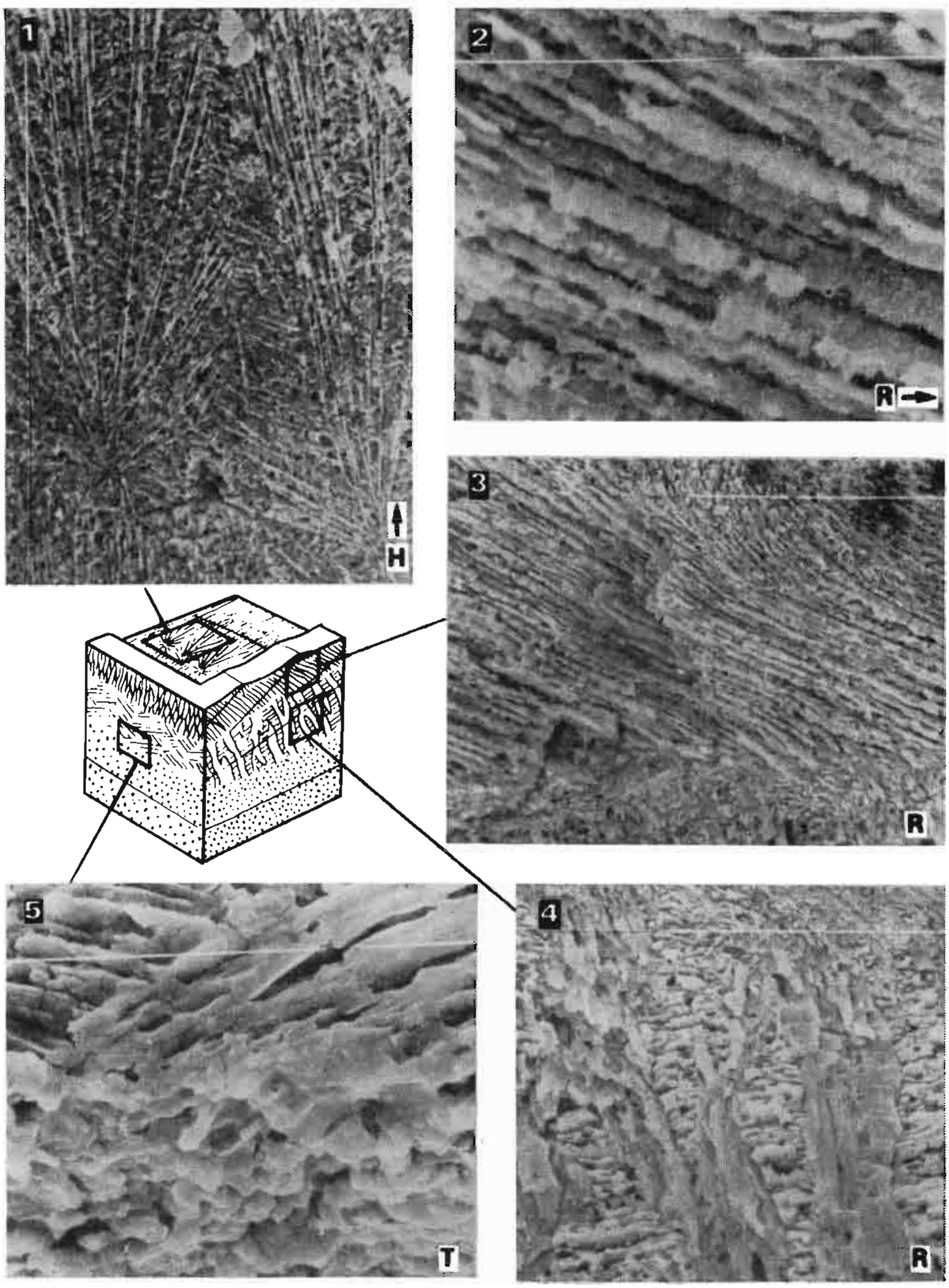
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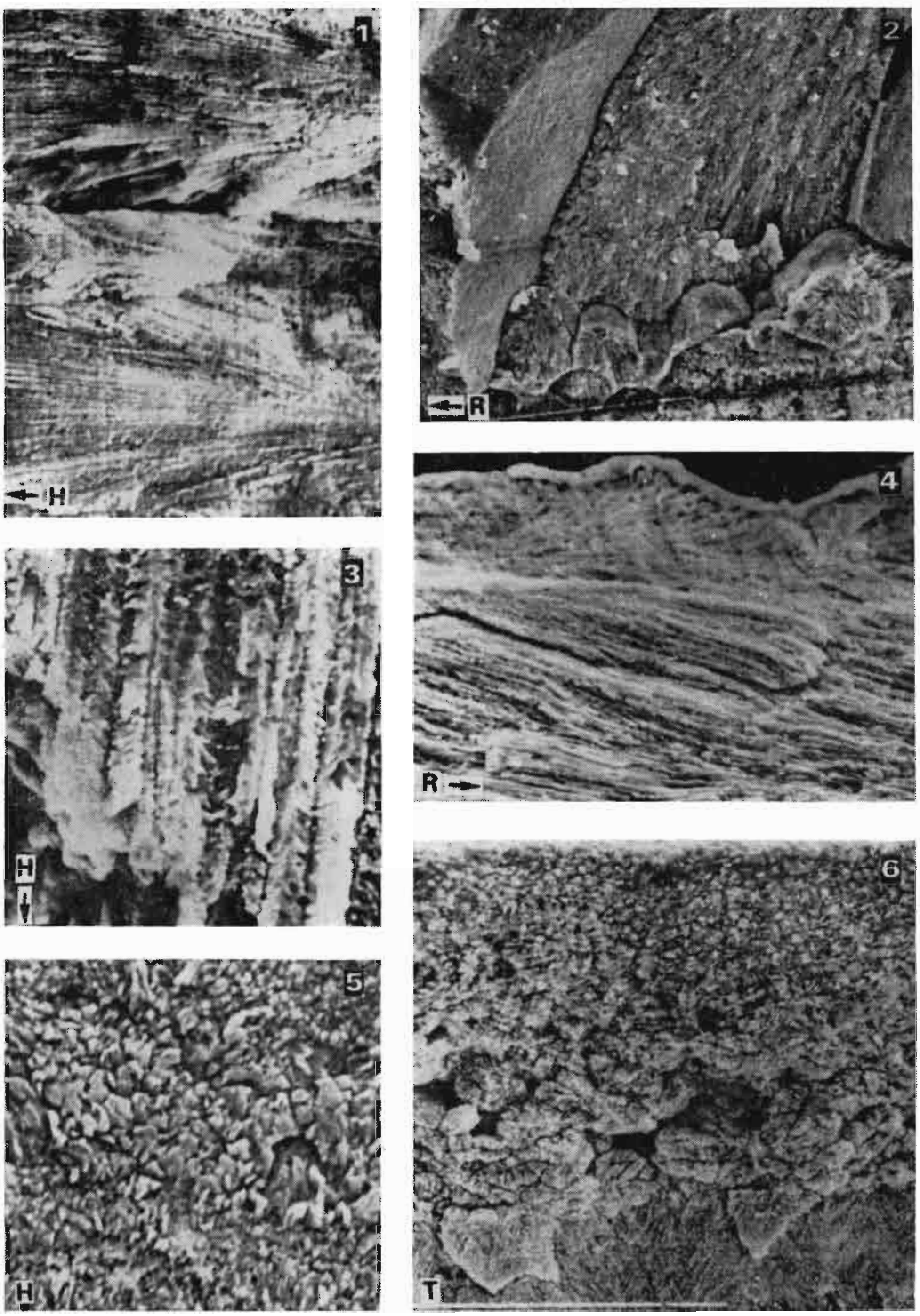
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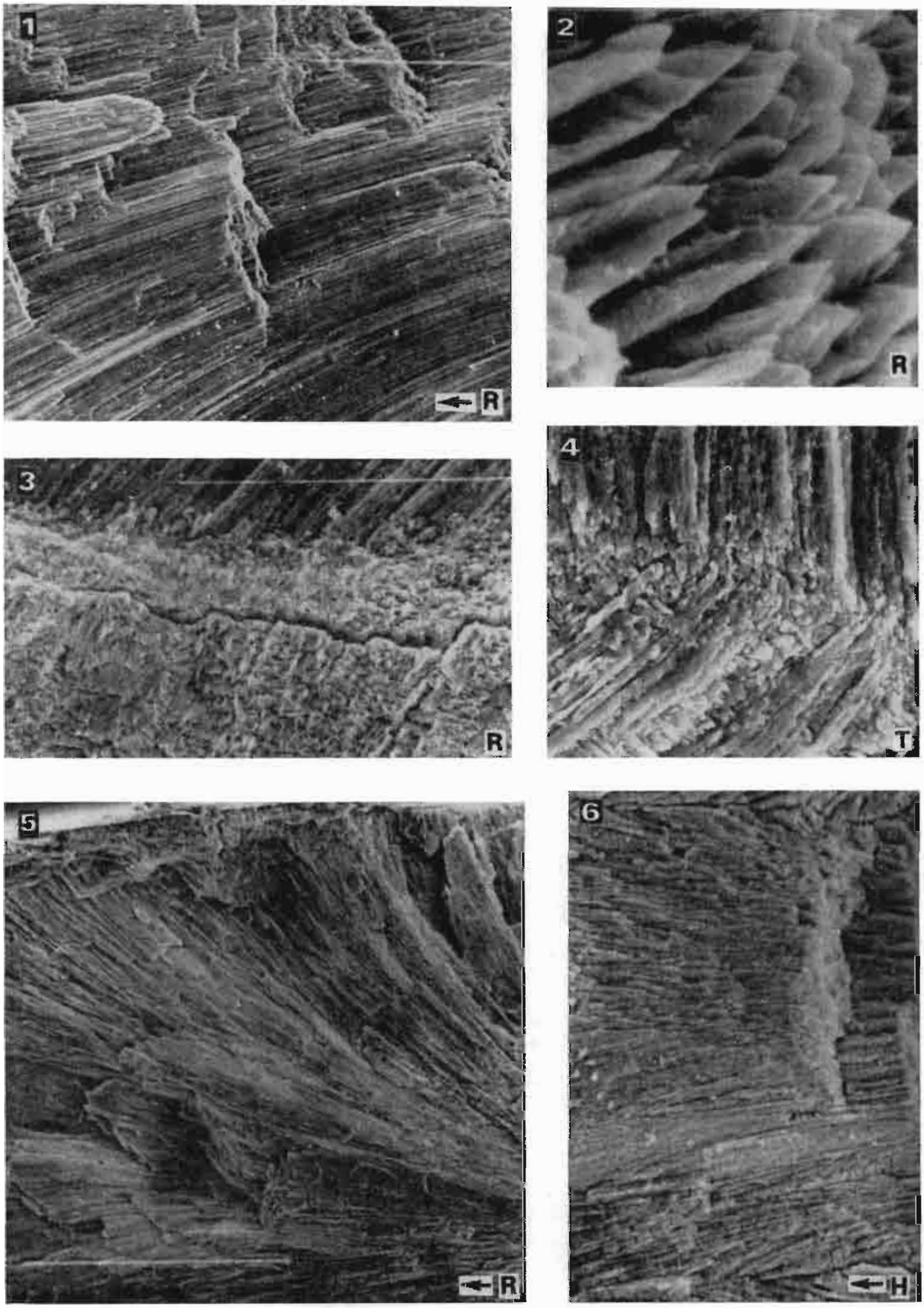
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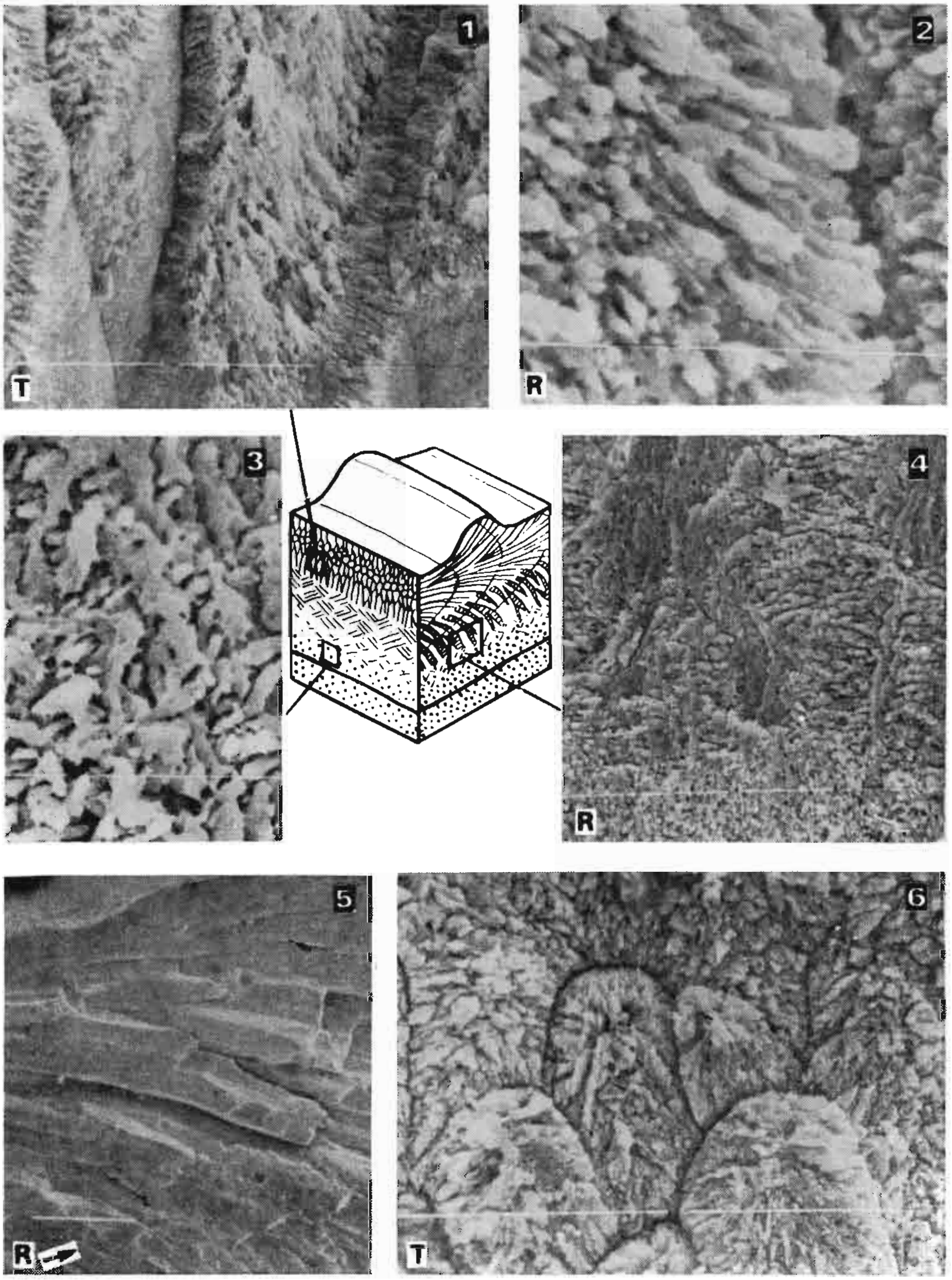
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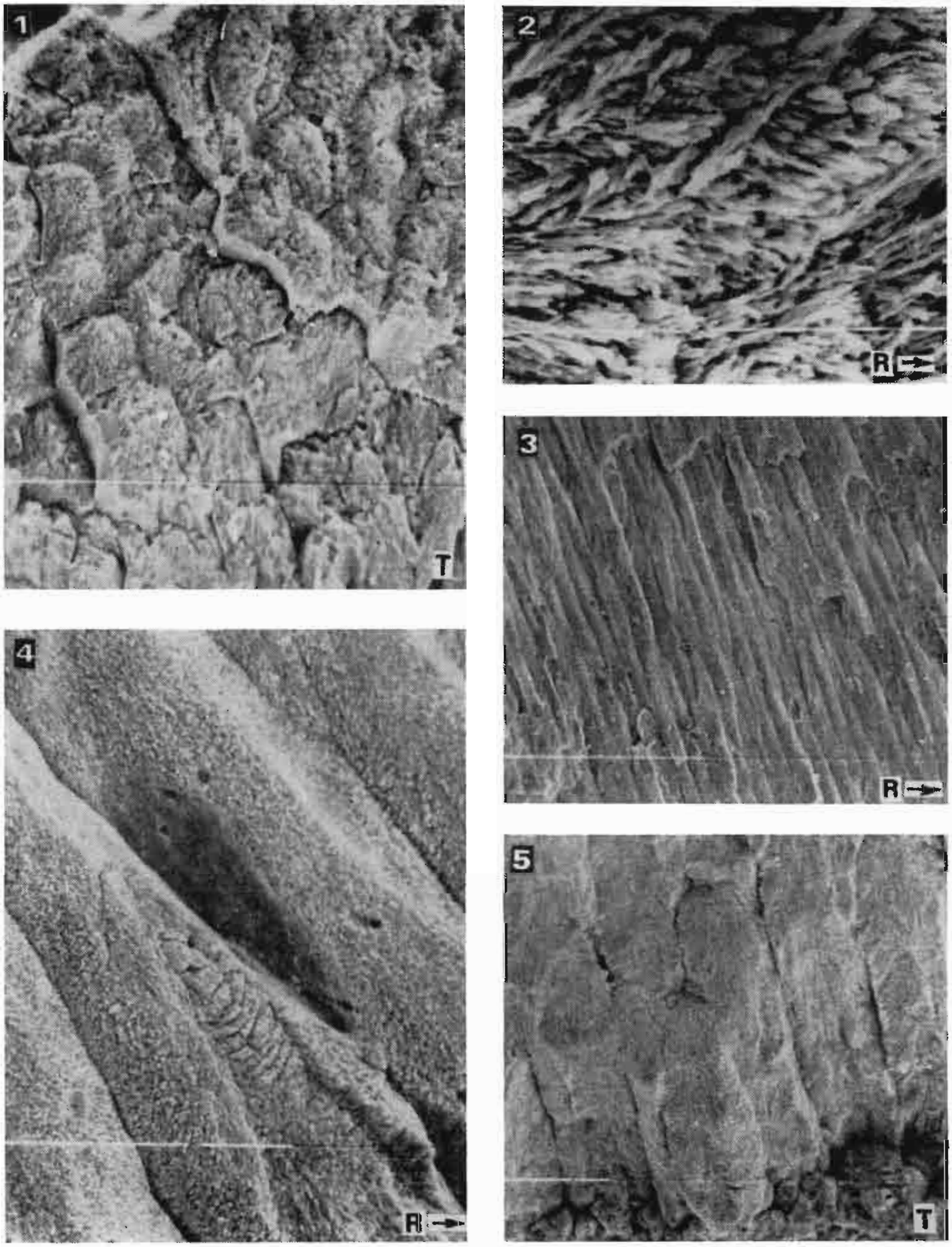
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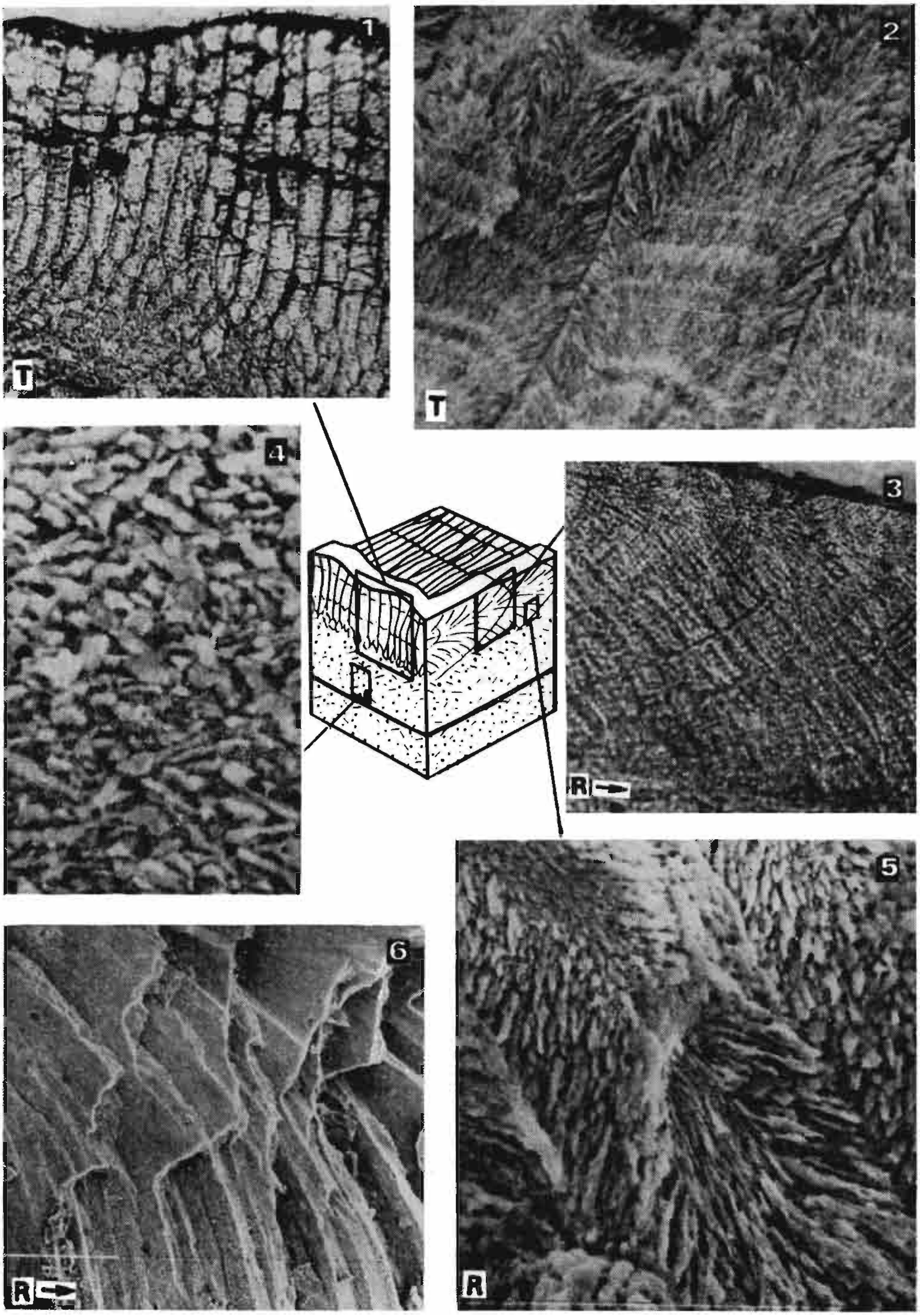
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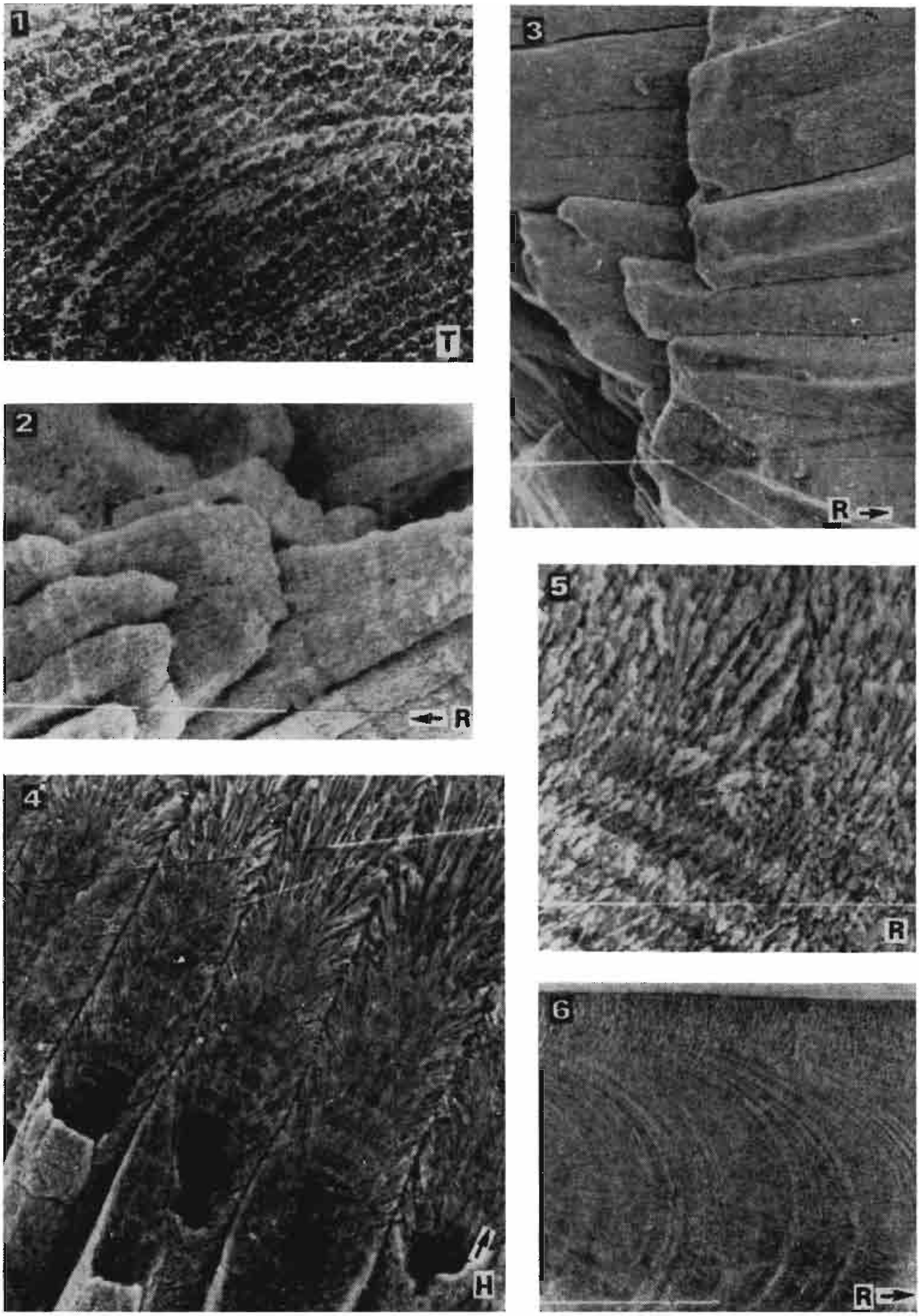
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