Shell microstructures in Early Cambrian molluscs

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The affinities of a considerable part of the earliest skeletal fossils are problematical, but investigation of their microstructures may be useful for understanding biomineralization mechanisms in early metazoans and helpful for their taxonomy. The skeletons of Early Cambrian mollusc-like organisms increased by marginal secretion of new growth lamellae or sclerites, the recognized basal elements of which were fibers of apparently aragonite. The juvenile part of some composite shells consisted of needle-like sclerites; the adult part was built of hollow leaf-like sclerites. A layer of mineralized prism-like units (low aragonitic prisms or flattened spherulites) surrounded by an organic matrix possibly existed in most of the shells with continuous walls. The distribution of initial points of the prism-like units on a periostracum-like sheet and their growth rate were mostly regular. The units may be replicated on the surface of internal molds as shallow concave polygons, which may contain a more or less well-expressed tubercle in their center. Tubercles are often not enclosed in concave polygons and may co-occur with other types of textures. Convex polygons seem to have resulted from decalcification of prism-like units. They do not co-occur with tubercles. The latter are interpreted as casts of pore channels in the wall possibly playing a role in biomineralization or pits serving as attachment sites of groups of mantle cells. Casts of fibers and/or lamellar units may overlap a polygonal texture or occur without it. They may reflect an inner layer consisting of aragonitic fibers fused into more or less well-developed lamellar units. It seems that nacreous and crossed-lamellar aragonitic microstructures evolved in the Cambrian from such lamellar aragonitic microstructures independently in different groups of molluscs.

Key words: Biomineralization, molluscs, Early Cambrian.

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Introduction

Shells composed of hollow fused sclerites and isolated sclerites of various shapes are an integral part of the earliest skeletal assemblages. They have been interpreted as belonging to a monophyletic group, Coeloscleritophora, and are presumed to have been

secreted at a fixed size by a soft tissue from the inside (Bengtson & Missarzhevsky 1981). The shape and distribution over the body surface varied significantly among groups of coeloscleritophoran sclerites. Chancelloriids had saccate bodies covered with sclerites assembled in rosettes (Bengtson *et al.* 1990; Mehl 1996, 1998; Bengtson 1999). The dorsal armor of slug-like halkieriids consisted of at most three types of sclerites plus an anterior and a posterior plate (Conway Morris & Peel 1995). They have been suggested to be derived from slug-like(?) siphogonuchitids carrying less regularly arranged sclerites and shell-like structures built of fused sclerites (Bengtson 1992). The mineralized walls of coeloscleritophoran sclerites were probably originally aragonitic and mainly composed of fibers (Bengtson & Conway Morris 1984; Bengtson *et al.* 1990; Mehl 1996; Fig. 2 here) or platelets (a few tens of micrometers in size) (Bengtson 1999). These groups are considered close to the Mollusca (Bengtson 1992; Conway Morris & Peel 1995), whereas halkieriids have also been regarded to be related to the Annelida, and Brachiopoda (Conway Morris & Peel 1995).

The evolutionary development of conchiferan molluscs probably began with the earliest recognized cyrtoconic forms (*Latouchella*-like) in early Early Cambrian. Cap-shaped shells composed of fused sclerites, such as *Maikhanella, Purella, Postacanthella,* and *Rozanoviella* co-occur, or slightly predate, these in Siberia, Mongolia, and China (Rozanov *et al.* 1969; Missarzhevsky 1989; Qian & Bengtson 1989; Vassilieva & Rudavskaya 1989; Khomentovsky *et al.* 1990; Bengtson 1992; Rozanov & Zhuravlev 1992; Khomentovsky & Karlova 1993; Esakova & Zhegallo 1996). Recently the generic concept for *Latouchella* has been revised, and it is likely that the earliest recognized form of this group belongs to *Oelandiella* (Gubanov & Peel 1998, 1999). These forms are just slightly coiled (cyrtoconic) and relatively low. Taller and more coiled forms appeared later. Thus, a cyrtoconic shape appears to have evolved first.

Early Cambrian univalved forms having shells with continuous, solid walls show a great morphological diversity (Runnegar & Jell 1976; Pojeta 1980; Runnegar 1983; Runnegar & Pojeta 1985). Conical, cyrtoconic and coiled forms, relatively low or tall, with more or less isometric or laterally compressed apertures are recognized among them. A supposed mixture of exo- and endogastrically coiled forms within the 'Monoplacophora' has been critical in revision of the class. To distinguish between exo- and endogastrically coiled univalved shells, two new classes have been introduced respectively: Tergomya and Helcionelloida (Peel 1991). According to this classification, the forms with continuous bilaterally symmetrical shells regarded herein are to be assigned to the Helcionelloida. The direction of coiling, however, seems difficult to prove, owing to the absence of muscle scars. The controversy also exists because of opposing interpretations of exhalant and inhalant water currents through the shell, and a posterior placement of the ligament in *Pojetaia* and *Fordilla* derived from a longer convex dorsal zone of a laterally compressed helcionellid, *Anabarella* Vostokova, 1962 via *Watsonella* (Runnegar & Pojeta 1974; Peel 1991; Runnegar 1996). To satisfy the model a group Stenothecidae has been separated from the Helcionelloida (*sensu* Peel 1991) to incorporate laterally compressed exogastric univalves, such as *Anabarella* (Waller 1998). Laterally compressed *Watsonella* Grabau, 1900 is the most likely earliest representative of basically exogastric Paleozoic class Rostroconchia and the ancestor of first bivalvians, *Pojetaia* Jell, 1980, and *Fordilla* Barrande, 1881 (Waller 1998, but see Runnegar 1996). The presence of the Gastropoda in the Early Cambrian is questionable, because
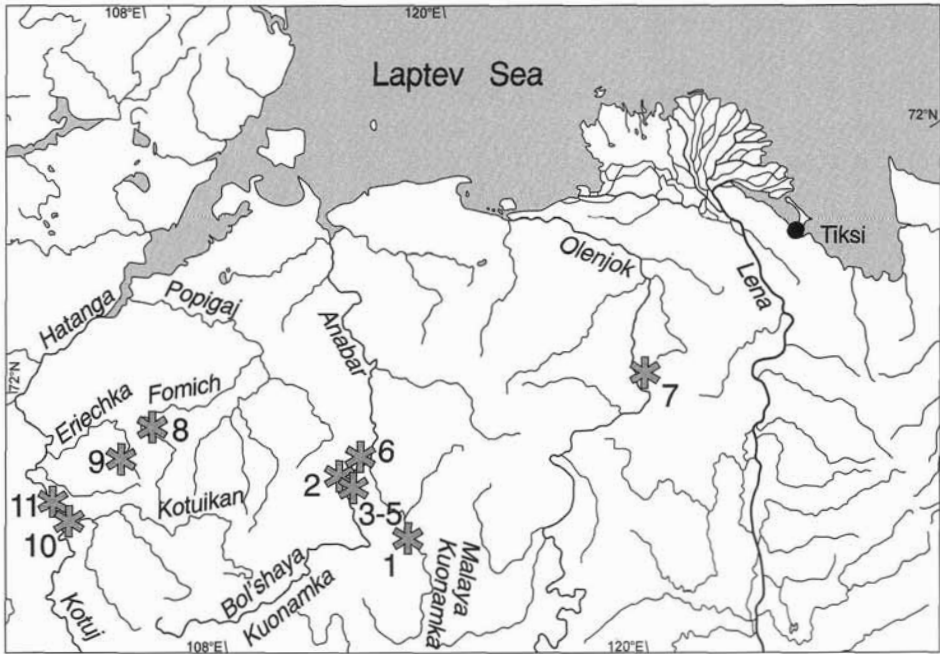
Fig. 1. Schematic map of localities on the northern Siberian Platform indicated in the text. 1. Locality 96-1: left bank of the Malaya Kuonamka River, at the Zhelinda village, eastern Anabar uplift (locality A-37 in Valkov 1975). 2. Locality 96-4: left bank of the Bol'shaya Kuonamka River, 1 km upstream of the mouth of the Ulakhan-Tjulen Brook, northeastern flanks of the Anabar uplift (locality A-51 in Valkov 1975). 3. Locality 96-5: mouth of a small left creek that feeds into the Ulakhan-Tjulen Brook about 1 km from the mouth of the latter, right bank of the Bol'shaya Kuonamka River, northeastern flanks of the Anabar uplift (locality A-50 in Valkov 1975). 4. Locality 96-5a: right side of the mouth of the Ulakhan-Tjulen Brook, at the right bank of the Bol'shaya Kuonamka River, northeastern flanks of the Anabar uplift. 5. Locality 96-6: right bank of the Bol'shaya Kuonamka River, 1,5 km downstream the mouth of the Ulakhan-Tjulen Brook, northeastern flanks of the Anabar uplift (locality A-53 in Valkov 1975). 6. Locality 96-7: left bank of the Bol'shaya Kuonamka River, 3 km downstream the mouth of the Ulakhan-Tjulen Brook, northeastern flanks of the Anabar uplift (locality A-54 in Valkov 1975). 7. Locality B-9 (Valkov 1975): right bank of the Oleniok River, 5.2 km upstream the Djogurdakh Brook. 8. Locality M314 (Rozanov et al. 1969): right bank of the Fomich River, about 6 km upstream the Afanasievsky lakes, northwestern flanks of the Anabar uplift. 9. Locality M321 (Rozanov et al. 1969): left bank of the Eriechka River, at the mouth of the Nemakit-Daldyn River, northwestern flanks of the Anabar uplift. 10. Locality M419 (Rozanov et al. 1969): right bank of the Kotujkan River, 2.5 km from the mouth, northwestern flanks of the Anabar uplift. 11. Locality M423 (Rozanov et al. 1969): mouth of the Kugda Brook, on the right bank of the Kotuj River, northwestern flanks of the Anabar uplift.

there is no reliable evidence of torsion typical of gastropods (Pojeta 1980; Runnegar 1981; Runnegar 1983). Asymmetrically coiled Early Cambrian forms interpreted as partially torted may be included in a new class Paragastropoda (Linsley & Kier 1984). Because of the ambiguity discussed above, in the descriptions that follow I refrain from using higher rank taxa.

After pioneering investigations by B. Runnegar on the microstructures of Cambrian molluscs (Runnegar 1983, 1985, 1989; Bengtson et al. 1990), the pace of study appears to have gone down. The well-preserved fossils from Arctic Siberia described herein provide new information on the shell structure of early mollusc-like animals.

Material and methods

The investigated fossils are deposited at the Swedish Museum of Natural History, Stockholm (abbreviated SMNH), under collection numbers Mo160403–Mo160429 and X3416 (see explanations of figures). The material derives from several outcrops on the northern Siberian Platform. The majority of the fossils was collected during an expedition to Siberia in 1996, in which S. Bengtson (Swedish Museum of Natural History), V.V. Missarzhevsky (Geological Institute of the Russian Academy of Sciences), S. Pelechaty (Massachusetts Institute of Technology), A.K. Valkov (Geological Institute of the Yakutian Academy of Sciences), and myself participated. The fossils were obtained from carbonate samples dissolved in 10% acetic acid at the Geological Institute of the Russian Academy of Sciences (Moscow). Additional material from the collections of V.V. Missarzhevsky, V.E. Savitzky and A.K. Valkov has been used. The age of fossils ranges from the Manykayan–Tommotian (samples: 96-4/27,5; 96-5/0; 96-5a/1,2; 96-5a/17,5; 96-5a/34,5; 96-5a/34,75; 1282; 1487; K1a/47; K2/24; K2/25; M314/6; M321/31) to Atdabanian (samples: 96-7/33; 96-7/36,7; 96B-6/66,2) and Botomian (samples: 96-1/5; 96-7/70; 96B-1/3) Stages (Rozanov *et al.* 1969; Valkov 1975, 1987; Bakhturov *et al.* 1988; Missarzhevsky 1989; Bowring *et al.* 1993; Khomentovsky & Karlova 1993, 1994; Knoll *et al.* 1995). The localities are indicated in the caption of Fig. 1.

Descriptions

Chancelloria eros Walcott, 1920

Chancelloria eros Walcott, 1920 is represented by an internal mold of an individual sclerite ray. The composite sclerite (rosette) seems to have originally consisted of 6–7 radial rays plus one central ray, corresponding to the normal sclerite type of *Chancelloria eros* (Bengtson *et al.* 1990). Fibers replicated at the surface are 2–3 µm wide and directed along the ray, but at the base they do not seem to have been oriented (Fig. 2A). Some of the fibers are fused into wider laths, and this fusion, possibly, took place during diagenesis. A basal opening of 10–15 µm in diameter forms the tip of a cone with smooth slopes (Fig. 2A, B; arrow).

Purella cf. *cristata* Missarzhevsky, 1974

Purella cf. *cristata* Missarzhevsky, 1974 is represented by cyrtoconic shells and internal molds (Figs. 3, 4). They fall within the limits of morphological variation of *Purella* Missarzhevsky, 1974 (Missarzhevsky 1974; Abaimova 1976; Kerber 1988; Qian & Bengtson 1989). The wall consists of two or three different zones (Fig. 3A, D). A juvenile shell is preserved as phosphatic matter below the umbo, penetrated by radial pores (Fig. 3H). This fabric may be interpreted as fused needle-like sclerites. Their diameter increases from 1–2 to 5–7 µm towards the periphery of the structure.

A smooth, bilaterally symmetrical sheet with fine radial striations covers a portion of the inner shell surface below the beak (Fig. 3D, F; arrow 1). This structure may be interpreted as a part of the juvenile shell.
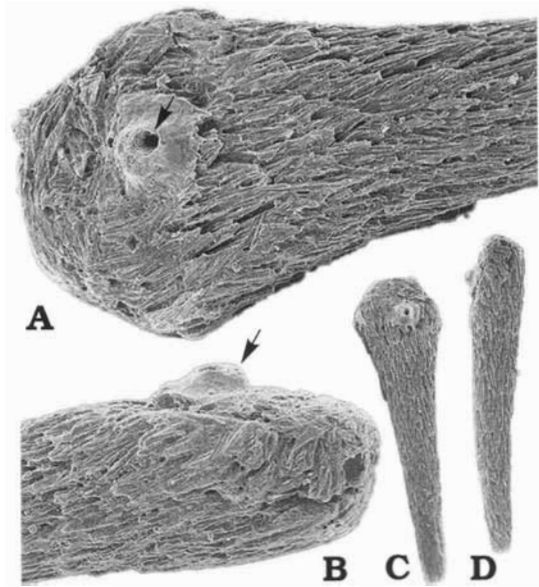
Fig. 2. *Chancelloria* cf. *eros* Walcott, 1920, internal mold of an individual sclerite with replicated fibers of the wall. Specimen SMNH X3416 from sample 96B-6/66,2, locality 96-6 (B. Kuonamka), Emjaksin Formation (upper part), Atdabanian. **A, C.** Basal surface with a foramen (arrowed). **B, D.** Lateral view (arrow points to a foramen). **A, B** × 130; **C, D** × 37.

At the boundary with the adult shell, the smooth zone (Fig. 3E) and needle-like sclerites pass into larger, flattened sclerites with their longer cross-sectional axes comarginal with the adult shell (Fig. 3D, arrow 2). At this transition boundary the openings are relatively short (up to 30 μm; Fig. 3E). At the shell exterior they correspond to relatively short and low sclerites at the beak (Fig. 4I, arrow). The openings are 5–10 μm wide and may be more than 100 μm long at lateral parts of the shell. In larger specimens they may reach more than 250 μm (Fig. 4G, H).

The sclerites are hollow and were possibly built of fibers oriented subparallel to their surface (Fig. 3G). The thickness of the sclerite walls is up to 5 μm (Fig. 3E, G). They have apparently fused bases and free distal ends directed towards the umbo. There is often phosphatized material attached to the outer surface of the shell, mostly in pockets between the sclerites (Fig. 4G, arrows). In one specimen (Fig. 4A–F) the exterior of the initial part shows flattened tubercles about 10 μm wide (Fig. 4F). There is a transition from the normal comarginally extended sclerites (Fig. 4D, lower left) to the tubercles (Fig. 4D, upper right). Replicas of needle-like sclerites may be observed at the initial part, where the wall has been broken (Fig. 4E).

Tuberculate shells

Three kinds of tuberculate shells are described here without formal names. The first form is represented by a cyrtoconic internal mold (Fig. 5A–F). The specimen is similar to *Punctella maidipingensis* Zhong Hua, 1978. It is also similar to *Aegides* Jiang, 1987, which has a surface sculpture consisting of concentrically arranged granules about 25 μm in diameter (Qian & Bengtson 1989; Bengtson 1992). The entire surface of the convex side and the lateral parts of the mold are covered with tubercles, about 20 μm wide and inclined towards the beak (Fig. 5D). There is approximately one tubercle per
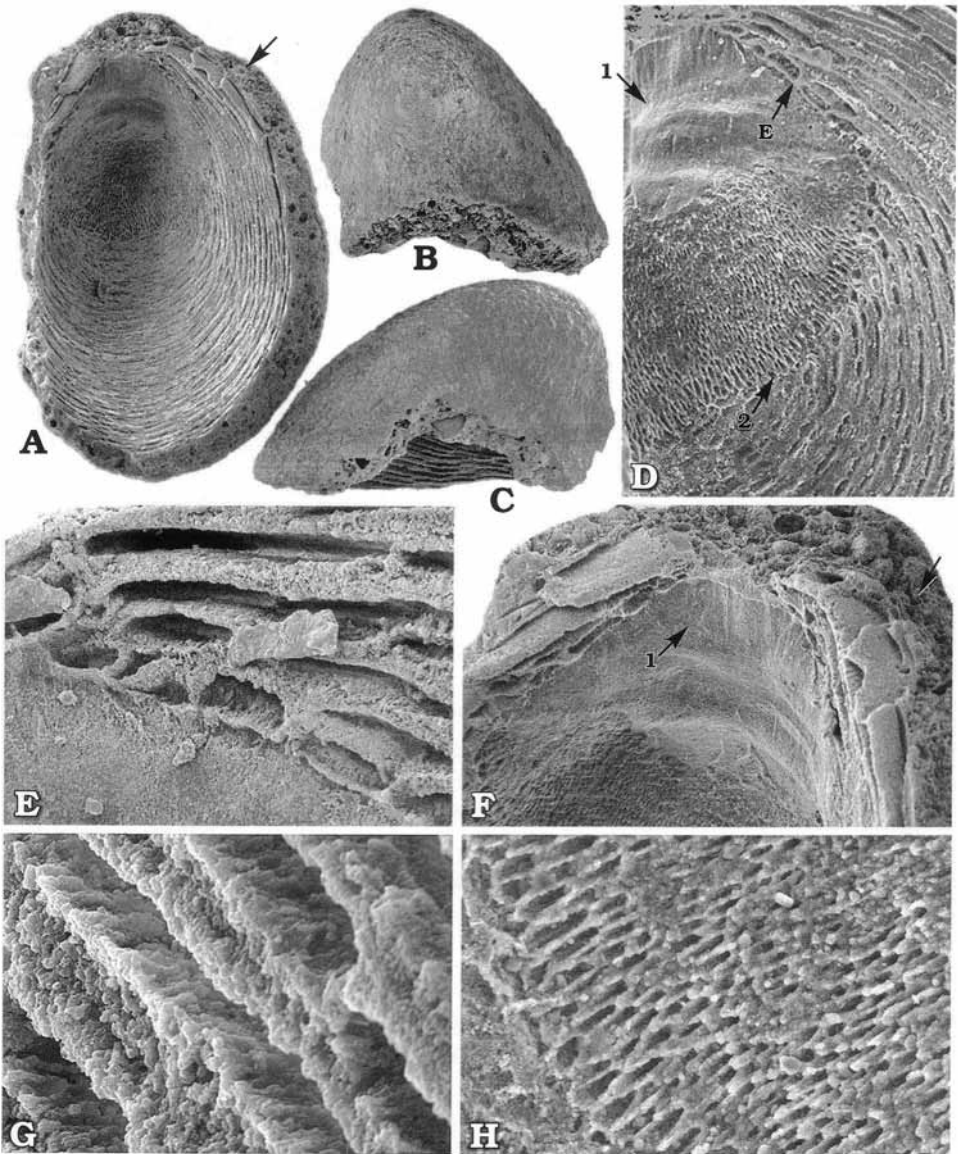
Fig. 3. *Purella* cf. *cristata* Missarzhevsky, 1974. Specimen SMNH Mo160403 from sample 96-4/27,5, locality 96-4 (B. Kuonamka), Emjaksin Formation (basal gravelstone), Manykayan. **A**. Inner surface of the specimen. **B**. Apical view. **C**. Lateral view. **D**. Enlargement of the area of inner surface showing transition from needle-like (lower left) to leaf-like sclerites (right). **E**. Contact between leaf-like sclerites and a smooth zone seen at the upper left part of D (arrow 1) and middle part of F (arrow 1) (close-up of the area arrowed in D). **F**. Imbricated leaf-like sclerites and a phosphatic crust covering them (arrowed). **G**. Enlargement of E showing basal openings of leaf-like sclerites. **H**. Needle-like sclerites. **A** × 63; **B** × 48; **C** × 52; **D** × 125; **E** × 350; **F** × 155; **G** × 1330; **H** × 425.

2000–3000 µm². The surface between the tubercles has a fibrous texture, with individual fibers around 1 µm wide and subradially oriented (Fig. 5E, F).
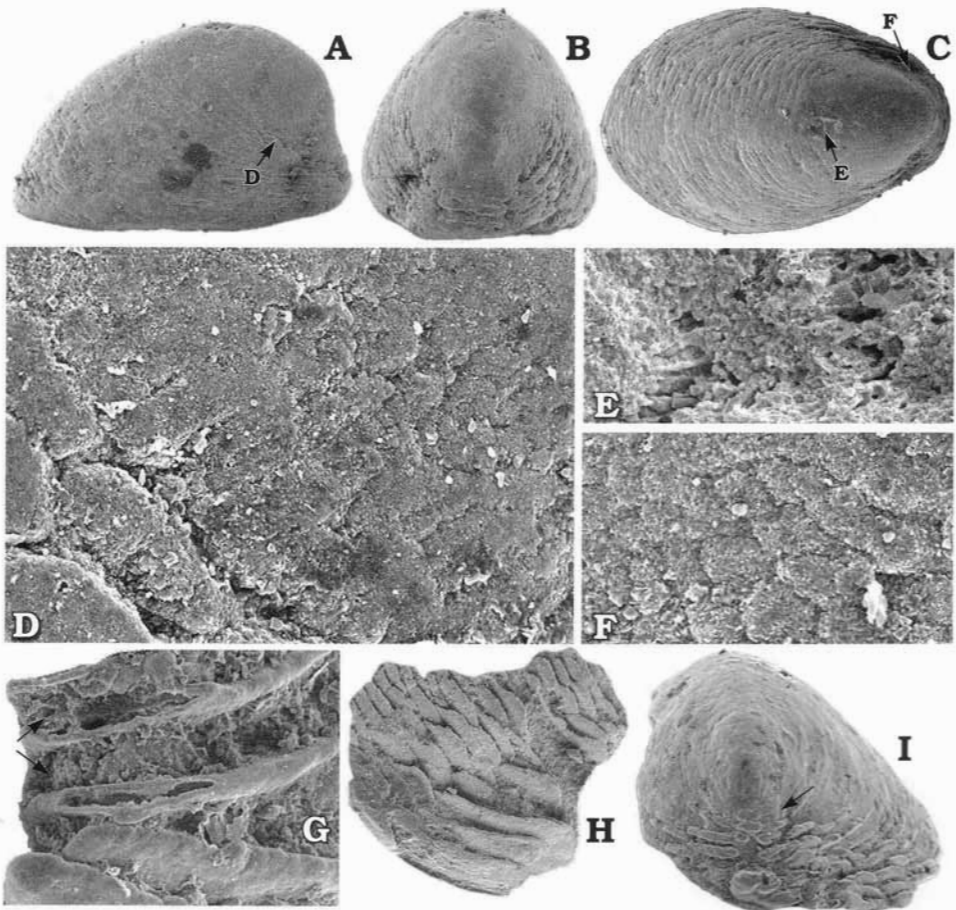
Fig. 4. *Purella* cf. *cristata* Missarzhevsky, 1974. A–F. Specimen SMNH Mo160404 from sample 96-5/0, lo-cality 96-5 (B. Kuonamka), Emjaksin Formation (basal gravelstone), Manykayan. A. Lateral view of the specimen. B. Apical view. C. View of the top. D. Enlargement of the apical area (arrowed in A). E. Casts of fibrous sclerites from the area arrowed in C. F. Tuberculate surface of the area arrowed in C. G. Specimen SMNH Mo160406 from sample K1a/47, locality M419 (Kotujkan), Nemakit-Daldyn Formation (upper part), Manykayan. Phosphatized hollow leaf-like sclerites. H. Specimen SMNH Mo160407 from the same sample. Fragment of the scleritic wall. I. Specimen SMNH Mo160405 from sample 96-5/0, locality 96-5 (B. Kuonamka). Sclerites reducing in size towards the beak. A, C × 52; B × 55; D × 710; E × 900; F × 930; G × 295; H, I × 45.

The second form occurs as an almost orthoconic internal mold (Fig. 5G–I). Tuber-cles, 10–15 μm in diameter, are scattered over the entire surface of the mold. There is ap-proximately one tubercle per 2000–2500 μm². The surface between the tubercles con-sists of concave polygons about 10 μm wide. A spiny texture in the polygons consists of replicas of fibers about 1 μm wide directed towards the apex of mold (Fig. 5J, K).

The third form is represented by a laterally compressed cyrtoconic internal mold (Fig. 5M–O). The surface of the mold is covered with smooth comarginal rugae and tubercles about 10 μm in diameter (Fig. 5L). There is approximately one tubercle per 375 μm².
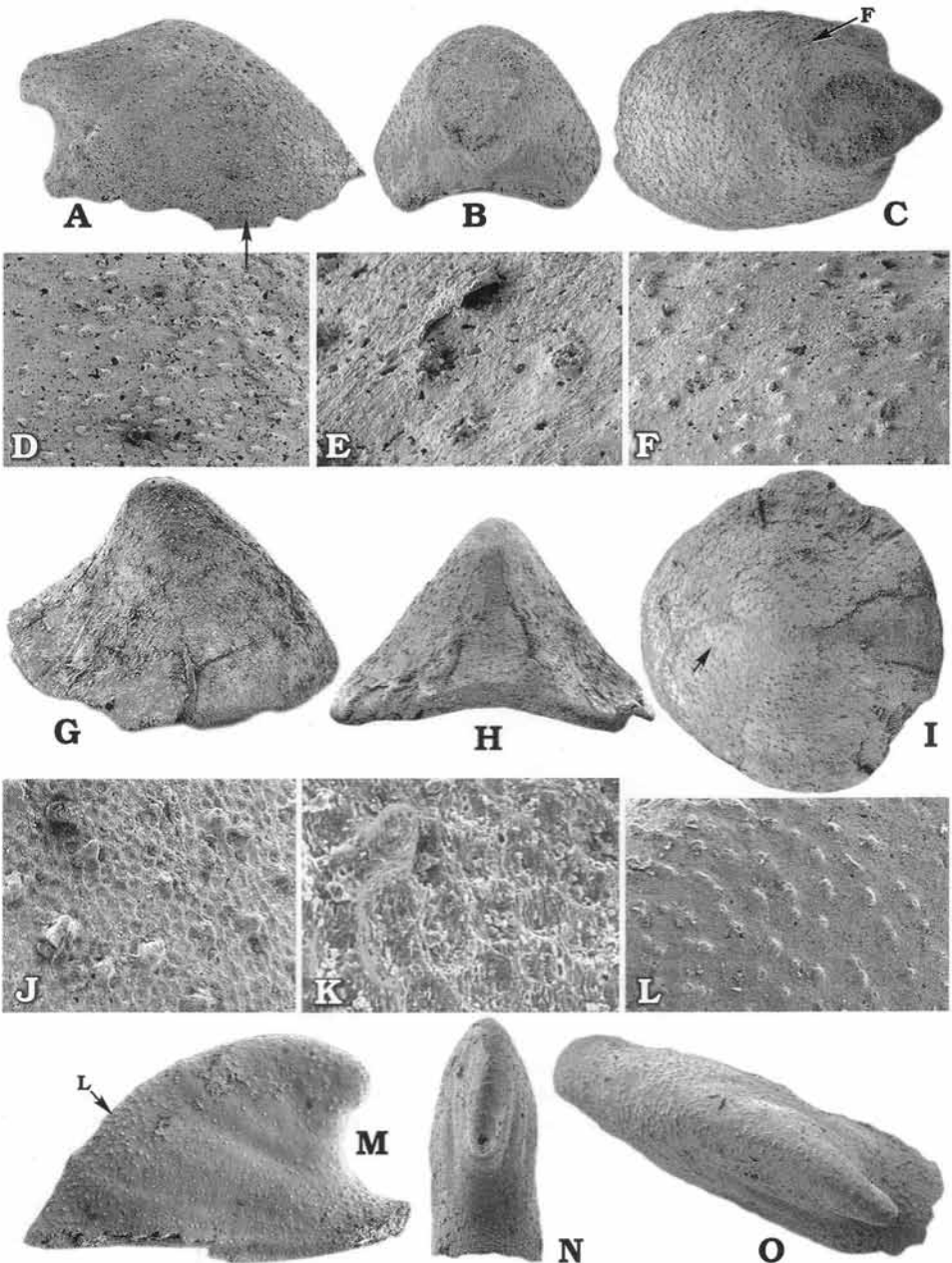
Fig. 5. A–F. Unnamed form 1. Specimen SMNH Mo160408 from sample M314/6, locality M314 (Fomich), Medvezhin Formation, Tommotian? **A**. Lateral view of the specimen. **B**. Apical view. **C**. View of the top. **D**. Enlargement of the area arrowed in A, with tubercles inclined towards the beak. **E**. Close-up of F showing tubercles and spiny texture between them. **F**. Enlargement of the area arrowed in C with isometrical tubercles. **G–K**. Unnamed form 2. Specimen SMNH Mo160409 from sample M321/31, locality M321 (Eriechka), Medvezhin Formation, Tommotian? **G**. Lateral view of the specimen. **H**. Apical view. **I**. View of the top. **J**. Close-up of the area arrowed in I. **K**. Enlargement of J. **L–O**. Unnamed form 3. ➤
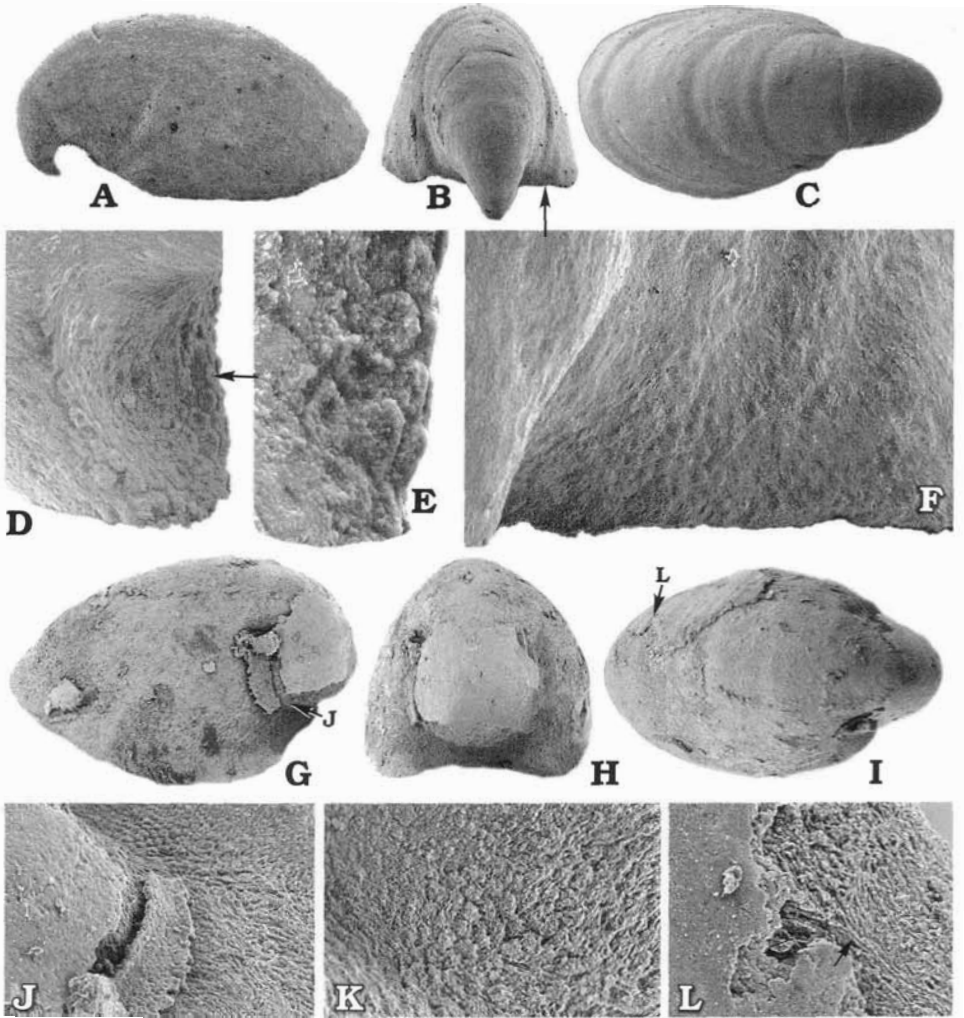
Fig. 6. A–F. *Securiconus* cf. *costulatus* Missarzhevsky, 1989. Specimen SMNH Mo160411 from sample 96-5a/1,2, locality 96-5a (B. Kuonamka), Emjaksin Formation (lower part), Manykayan? A. Lateral view of the specimen. B. Apical view. C. View of the top. D. Area with polygons under the beak. E. Enlargement of the area arrowed in D. F. Enlargement of the area arrowed in B. G–L. *Securiconus incertus* Bokova, 1985. Specimen SMNH Mo160412 (from the type series of *S. incertus*) from sample 1282, locality E-8 (Valkov 1975) same as M419 (Rozanov *et al.* 1969). G. Lateral view of the specimen. H. Apical view. I. View of the top. J. Close-up of the area arrowed in G. K. Enlargement of the upper part of J. L. Enlargement of the area arrowed in I with phosphatized fibrous fabric. A × 30; B, C × 33; D × 325; E × 785; F × 220; G–I × 60; J × 185; K × 415; L × 275.

Specimen SMNH Mo160410 from sample 96-7/70, locality 96-7 (B. Kuonamka), Emjaksin Formation (uppermost part), Botomian. L. Enlargement of the area arrowed in M. M. Lateral view of the specimen. N. Apical view. O. View of the top. A–C × 22; D × 63; E × 355; F × 110; G × 25; H, I × 23; J × 190; K × 665; L × 205; M, N × 48; O × 52.
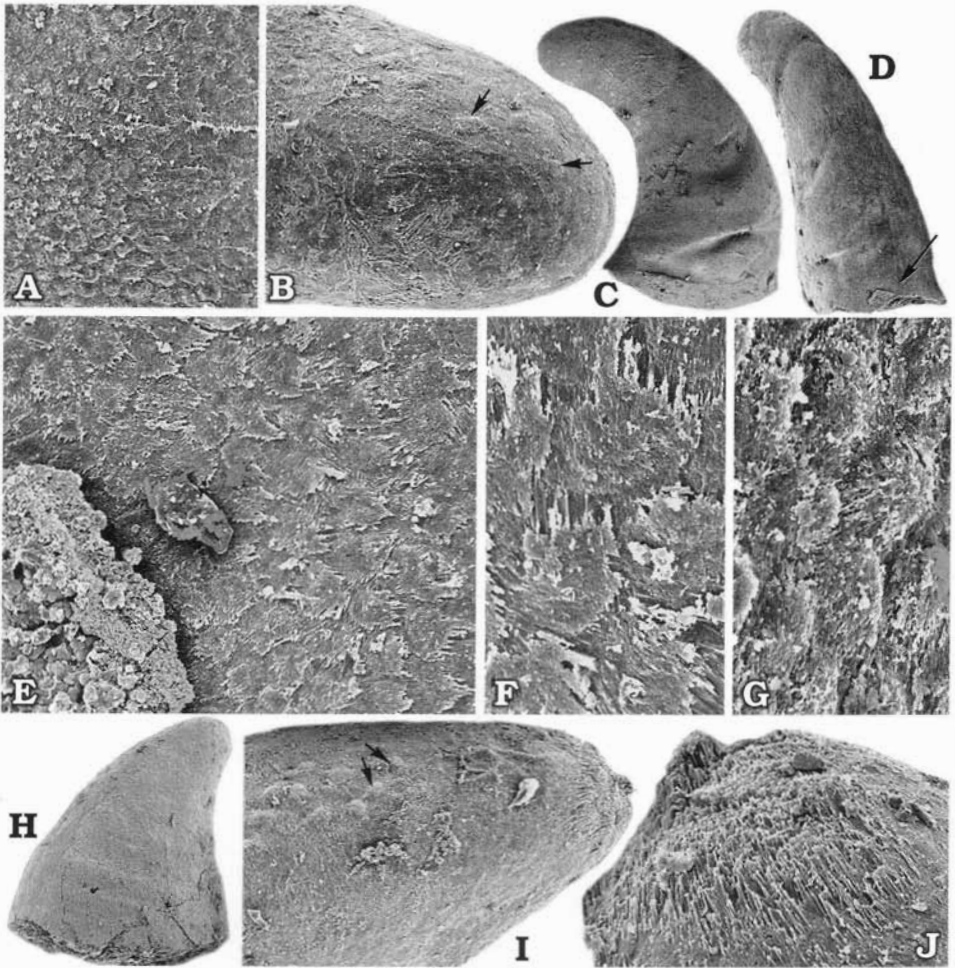
Fig. 7. A–G. *Ceratoconus* cf. *rusticus* (Valkov, 1987). Specimen SMNH Mo160413 from sample K2/25, locality M423 (Kugda), Medvezhin Formation, Tommotian? A. Enlarged area arrowed in D. B. Apex with arrowed flattened tubercles. C. Lateral view of the specimen. D. View of the convex side. E. Stepwise texture with casts of inclined fibers from the area arrowed in D. F. Close-up of E. G. Convex polygons with replicated fibers, close-up of the lower part of A. H–J. *Ceratoconus* sp., juvenile form. Specimen SMNH Mo160414 from the same sample. H. Lateral view of the specimen. I. Apex with tubercles (arrows) and spiny texture. J. Top of the apex showing aciculate elements. A × 340; B × 150; C, D × 30; E × 585; F × 1480; G × 1555; H × 48; I × 155; J × 480.

Securiconus cf. *costulatus* Missarzhevsky, 1989

Securiconus cf. *costulatus* Missarzhevsky, 1989 is available as an internal mold (Fig. 6A–C). It is similar to *S. costulatus* (Missarzhevsky 1989: p. 175) in shape, but the width/length ratio of the aperture is greater than 1/2. The surface is smoothly comarginally folded. The concave side is bordered by two longitudinal folds, and carries a positive polygonal relief and casts of fibers. The polygons are about 10 μm in diameter.
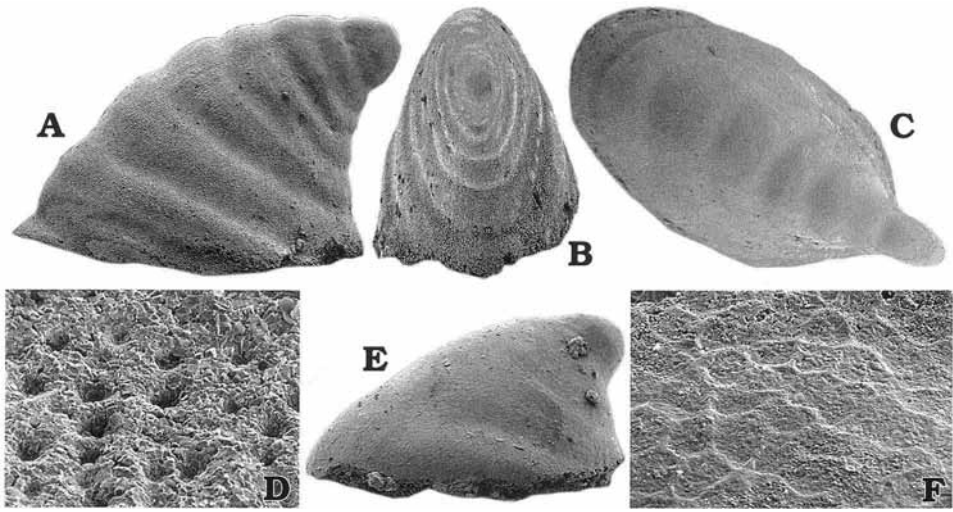
Fig. 8. *Ilsanella* sp. A–D. Specimen SMNH Mo160415 from sample 96-7/36,7, locality 96-7 (B. Kuo-namka), Emjaksin Formation (middle part), Atdabanian. A. Lateral view of the specimen. B. Apical view. C. View of the top. D. Enlarged area of the surface with pits. E, F. Specimen SMNH Mo160416 from the same sample. E. Lateral view. F. Enlarged area of the surface with polygons. A–C × 33; D × 1025; E × 40; F × 400.

They are better developed under the beak, where they additionally bear a depression in the center (Fig. 6D, E). Casts of fibers and convex polygons are expressed at the aperture, on the concave side of the mold in apical view (Fig. 6F).

Securiconus incertus Bokova, 1985

The most well-preserved specimen of *Securiconus incertus* Bokova, 1985 is an internal mold with phosphatized remains and replicas of shell wall (Fig. 6G–I). The surface of the mold is covered with subradially oriented fibers, 1–2 µm thick. In some places they appear to diverge from a single point (Fig. 6L, arrow). Tightly packed spherulites 5–10 µm in diameter are situated under the beak. They seem to transform into the fibrous fabric laterally (Fig. 6J, K). Other specimens of *S. incertus* from the sample, including the holotype, have the same but less well-preserved microstructures.

Ceratoconus cf. *rusticus* (Valkov, 1987)

Ceratoconus cf. *rusticus* (Valkov, 1987) is represented by an internal mold (Fig. 7A–G). The specimen differs from the type species *Ceratocomus rusticus* (Valkov, 1987) in having a less acute initial part (cf. Valkov 1987: pl. 15: 14–17). The outer surface of the mold is covered with smooth rugae, forming a sinus at the convex side (Fig. 7D). The lower half of the mold, at the convex and lateral sides, is covered with polygons, 5–10 µm wide (Fig. 7A, lower part). The polygons are convex at the convex part of the mold, where they have casts of radially arranged fibers, 0.25–0.50 µm wide (Fig. 7G). This texture gradually transforms laterally via flattened polygons with casts of transverse fibers into a stepwise pattern (Fig. 7A, E, F). There are 10 µm wide tubercles at the initial part of the mold (Fig. 7B, arrows).
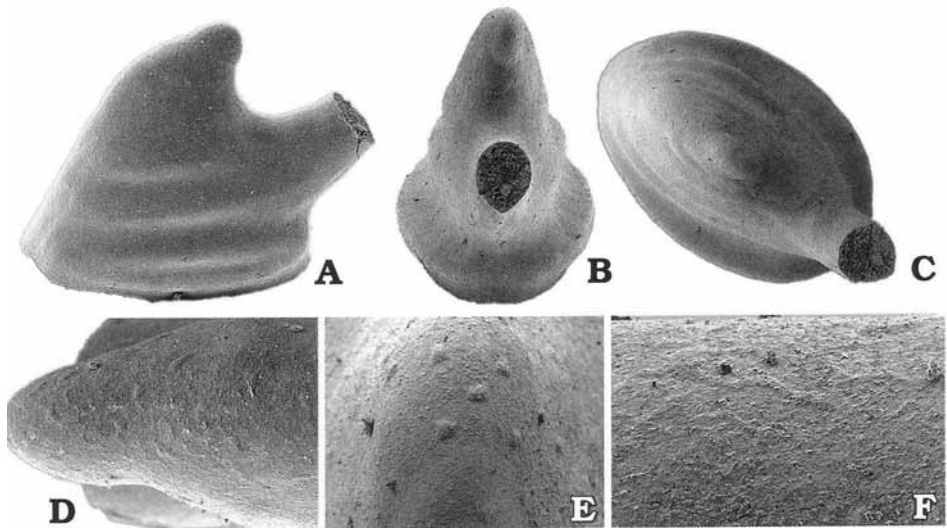
Fig. 9. *Yochelcionella* sp. A–F. Specimen SMNH Mo160417 from sample 96-7/36,7, locality 96-7 (B. Kuo-namka). A. Lateral view of the specimen. B. Apical view. C. View of the top. D. Apex with flattened tubercles and subdued polygonal texture. F. Surface of snorkel mold covered with polygons. E. Specimen SMNH Mo160418 from the same sample. Tubercles at the apex. A, B × 35; C × 40; D × 150; E × 175; F × 450.

The specimen in Fig. 7H probably represents a juvenile form of *Ceratoconus* sp. The entire surface is covered with tubercles of about 25 µm in diameter; these are better expressed and more densely spaced at the convex side of the mold (Fig. 7I, arrows). Casts of fibers, 0.5–1.0 µm wide, overlap the tubercles at some places and have a comarginal orientation with a slight inclination towards the beak (Fig. 7I). They are well preserved and radially oriented at the apex (Fig. 7J). The thickness of the fibrous layer at the apex was apparently 10–15 µm.

Ilsanella sp.

Ilsanella sp. is represented by internal molds with wide and smooth concentric ribs (*Ilsanella* Missarzhevsky, 1981, in Missarzhevsky 1989; Esakova & Zhegallo 1996). The entire surface of one large mold (Fig. 8A–C) is covered with pits approximately 5 µm in diameter and 10–20 µm apart (Fig. 8D). The surface between the pits is granulated. No pits have been found near the beak. A smaller mold from the same sample (Fig. 8E) displays a shallow polygonal texture, with centers of polygons 10–20 µm apart (Fig. 8F). The polygons are shallower than the pits on the bigger specimen.

Yochelcionella sp.

Yochelcionella sp. is available as two internal molds of equal size (Fig. 9A–C). There is a weakly preserved shallow polygonal pattern at the outer surface of the mold (Fig. 9D, F). The polygons are about 20 µm wide. Tubercles, 10–15 µm wide, are scattered over the beak (Fig. 9E). The form is close to *Y. cyrano* Runnegar & Pojeta, 1974, but differs from it in being a less curved and having a more inclined snorkel. *Y. daleki*
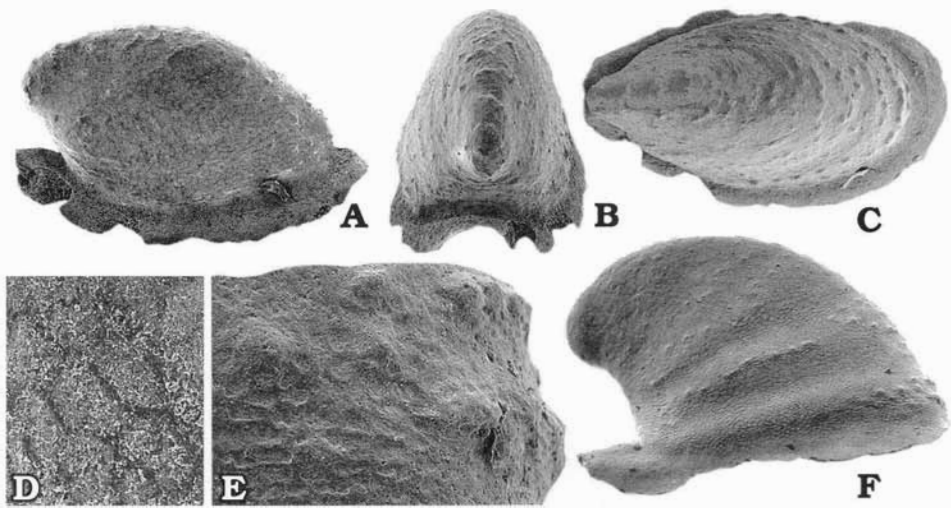
Fig. 10. *Mackinnonia* sp. A–D. Specimen SMNH Mo160419 from sample 96-7/70, locality 96-7 (B. Kuonamka). **A.** Lateral view of the specimen. **B.** Apical view. **C.** View of the top. **D.** Enlarged area of the surface with polygons. **E, F.** Specimen SMNH Mo160420 from the same sample. **F.** Lateral view of the specimen. **E.** Close-up of F showing tubercles and polygons. A×54; B, C×57; D×450; E×305; F×45.

Runnegar & Pojeta, 1976 is also similar but more compressed laterally (Runnegar & Pojeta 1976; Runnegar 1977).

Mackinnonia sp.

Mackinnonia sp. is represented by cyrtoconic internal molds. The surface of the smallest specimen (Fig. 10A–C) is covered by 10–20 μm wide tubercles that tend to be situated in comarginal rows, and a network of very shallow concave polygons of the same size range (Fig. 10D). The surface of the second mold is also covered with polygons and tubercles, with the latter mainly situated on comarginal folds of the mold (Fig. 10E, F). The specimens differ from *M. obliqua* Landing & Bartowski, 1996 and *M. davidi* Runnegar, 1990 in being tuberculate, and the latter is more curved and having a polygonal pattern on the entire surface of the molds (Bengtson *et al.* 1990: fig. 159; Landing & Bartowski 1996: fig. 5.10–5.18).

Obtusoconus sp.

Obtusoconus sp. is represented by an almost orthoconic internal mold with a shifted beak (Fig. 11A, B). The overall shape of the fossil, but its smooth exterior, fits the diagnosis of *Obtusoconus* Yu, 1979 (Missarzhevsky 1989; Esakova & Zhegallo 1996). The apertural part also resembles that of *Pararaconus staitorum* Runnegar, 1990 (Bengtson *et al.* 1990), a conical form with flared aperture and 5–10 μm wide tubercles situated at the surface of two ridges on each side of the internal mold. However, the molluscan affinity of *Pararaconus* is doubtful (Bengtson *et al.* 1990: fig. 161D–F). The surface of the mold is covered with polygons at the apex (Fig. 11E) and pits on the rest of the surface (Fig. 11C, D). The distance between centers of polygons and pits is 10–20 μm. The pits (depressions) and interior parts of the polygons and are rounded in
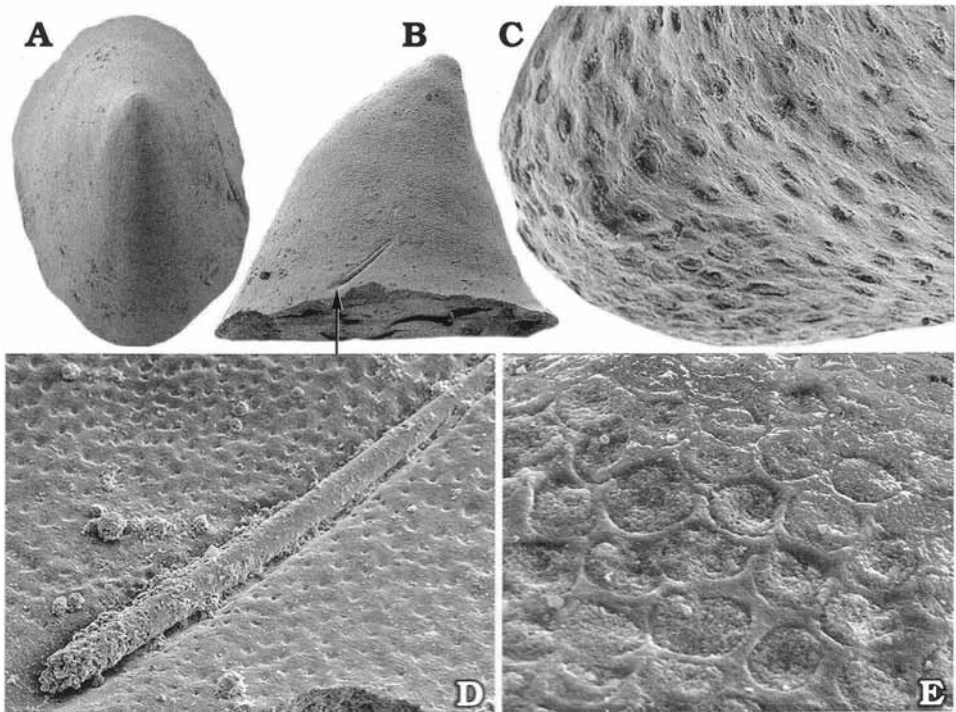
Fig. 11. *Obtusoconus* sp. Specimen SMNH Mo160421 from sample 96-7/70, locality 96-7 (B. Kuonamka). A. View of the top. B. Lateral view of the specimen. C. Area at the apex. D. Enlargement of the area arrowed in B with numerous pits and a spicular object. E. Area at the apex with polygons (close-up of the lowermost part of C). A, B × 30; C × 460; D × 350; E × 950.

shape and have a granulated surface formed by the phosphatized matrix of the shell mold (Fig. 11E). The surfaces between the polygons and pits are smoother and more elevated than the surface within the polygons and with fine replicas of comarginally oriented rugae (Fig. 11C). The distance between centers of the depressions apparently does not change, but the width of the areas between them increases from 1–2 μm on the beak to 5–10 μm at the aperture (Fig. 11D, E).

Enigmaconus sp.

Enigmaconus sp. is represented by an orthoconic internal mold (Fig. 12A–C). A narrow slit separates a flattened smooth structure with several thin transverse striae from the rest of the mold, and is probably left by a deep narrow transverse plate projecting ventrally from the shell wall (Fig. 12F, upper part). There is a fold of the mold at the opposite side of it (Fig. 12E, upper part). Almost the entire surface of the mold is covered with flattened convex polygons approximately 20 μm wide (Fig. 12D). The top of the mold is smooth, and the polygons gradually become smoother towards the upper part of the mold (Fig. 12F). The polygonal pattern has not been previously described from *Enigmaconus* MacKinnon, 1985, but the shape of the molds is consistent with its diagnosis (MacKinnon 1985).
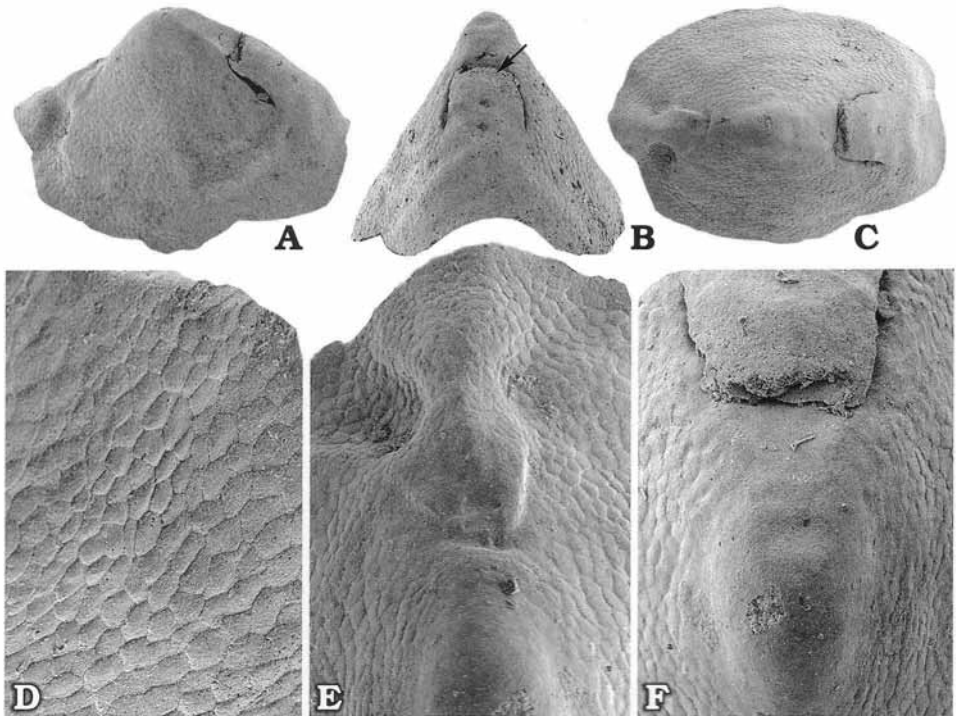
Fig. 12. *Enigmaconus* sp. Specimen SMNH Mo160422 from sample 96-7/70, locality 96-7 (B. Kuonamka). **A**. Lateral view of the specimen. **B**. View of a flattened emargination of the aperture (arrow). **C**. View of the top. **D**. Close-up of A showing polygons. **E**. Structure suggesting elastic deformation of the wall (upper part of the picture) enlarged from C. **F**. Polygons gradually smoothen towards the beak and apertural extension, enlarged from C. **A** × 40; **B** × 42; **C** × 39; **D** × 210; **E**, **F** × 110.

Aldanella crassa Missarzhevsky, 1969

Aldanella crassa Missarzhevsky, 1969, is available as two internal molds. On the specimen in Fig. 13B, shallow concave polygons around 40 μm wide, co-occur with replicated fibers on the surface of the first revolution (Fig. 13N, P). Replicas of adjacent fibers, 0.25–0.50 μm wide, may reflect lamellae; within a lamella the fibers are parallel to each other but crossed in adjacent lamellae (Fig. 13N–O, Q, R). The lamellae are up to 150 μm wide. The specimen in Fig. 13A is covered with crater-shaped polygons, up to 50 μm wide, visible for the first three-fourths of the whorl (Fig. 13L, M). Compared to *Aldanella* ex.gr. *attleborensis* from the same collection, *A. crassa* has fewer revolutions and a more rapidly expanding whorl (Rozanov *et al.* 1969; Missarzhevsky 1989).

Aldanella ex. gr. *attleborensis* (Shaler & Foerste, 1888)

Aldanella ex. gr. *attleborensis* (Shaler & Foerste, 1888) is available as several internal molds. On the specimen in Fig. 13C, convex polygons are exposed at external lateral and convex sides of the whorl. Polygons on the first revolution gradually decrease in expression from the initial part (Fig. 13F, I, J). The polygons are 30–50 μm wide, convex, with a smoothly folded surface.
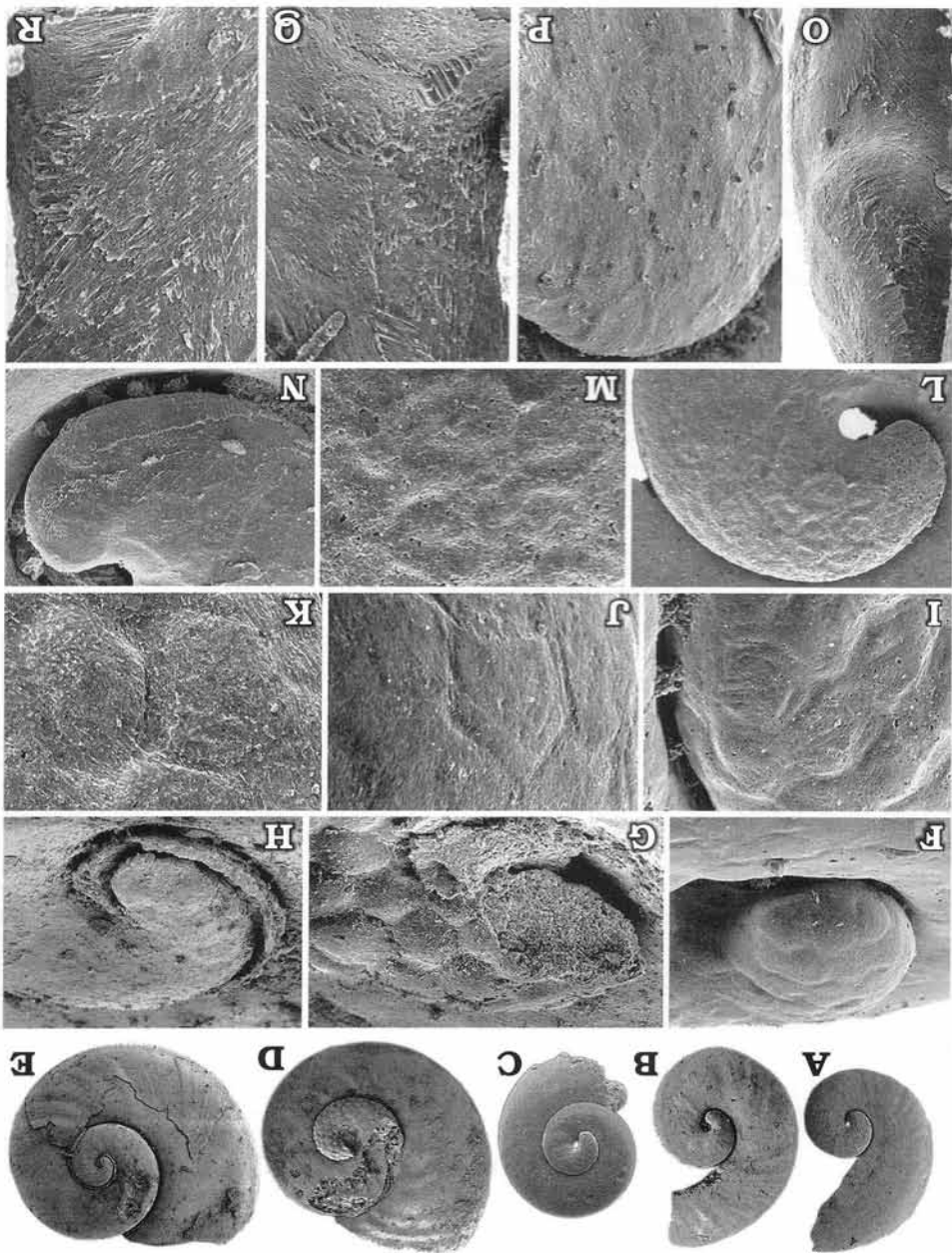
Fig. 13. A, B, I–R. *Aldanella crassa* Missarzhevsky, 1969. A, I, M. Specimen SMNH Mo160423 from sample 96-5a/1,2, locality 96-5a (B. Kuonamka). A. Overall view of the specimen. I. Close-up of the initial part showing polygons. M. Enlargement of I. B, N–R. Specimen SMNH Mo160424 from sample K2/24, locality M423 (Kugda), Medvezhin Formation, Tommotian? B. General view. N. Close-up of the initial part with traces of polygons and spiny texture. O. The initial part with a spiny texture. P. Polygonal texture overlapped by traces of fibers. Q, R. Spiny texture. C–K. *Aldanella* ex. gr. *attleborensis* (Shaler & Foerste, 1888). C, F, I, J. Specimen SMNH Mo160425 from sample 96-5a/17,5, locality 96-5a (B. Kuonamka), Emjaksin →

The specimen in Fig. 13K shows replicas of fibers, 1–2 μm wide, situated on the surface of convex polygons and between them, crossing their boundaries. The specimen in Fig. 13D carries convex polygons on the surface of first 1.5 revolutions. Transverse folds on the mold appear 1.5 revolutions from the apex. The polygons are 50–65 μm wide and have flattened or convex tops (Fig. 13G). The specimen in Fig. 13E represents a phosphatic internal mold covered with phosphatic diagenetic crust. There is a gap between crust and mold at the initial part corresponding to a leached wall (Fig. 13H).

This group of fossils is referred to *Aldanella* ex. gr. *attleborensis* (*A. attleborensis* is the earliest described form in this group) and possibly includes different species. Species of the genus which are very close to *A. attleborensis* (Shaler & Foerste, 1888) are: *A. kunda* Öpik, 1926; *A. rozanovi* Missarzhevsky, 1966; and *A. costata* Missarzhevsky, 1989 (Rozanov & Missarzhevsky 1966; Rozanov *et al.* 1969; Golubev 1976; Posti 1978; Missarzhevsky 1989).

Pelagiella cf. *subangulata* (Tate, 1892)

Pelagiella cf. *subangulata* (Tate, 1892) is represented by an internal mold with a wide asymmetrical aperture (Fig. 14A–D). The surface of the mold is covered with traces of fine radial continuous fibers, 1–3 μm wide (Fig. 14G, H), and very shallow concave polygons, up to 50 μm in width, with tubercles, 5–10 μm in diameter, in their centers (Fig. 14E, F). The fibrous texture runs radially on lateral parts of the mold (Fig. 14G) and becomes comarginal on the convex side (Fig. 14H). A polygonal texture is developed unilaterally as a radially extended area on the mold between its convex and lateral sides (Fig. 14A, arrow E). Some polygons and tubercles situated more laterally have serrate edges oriented radially from the aperture (Fig. 14F). The shape of the shell was possibly similar to *P. subangulata* (Tate, 1892 in Bengtson *et al.* 1990). No polygonal pattern has ever been reported from internal molds of *Pelagiella* Matthew, 1895.

Coeloscleritophorans and the structure of shells composed of sclerites

Cap-shaped univalved shells composed of fused sclerites occur exclusively in the Precambrian–Cambrian transitional beds and Lower Cambrian, mainly the Manykayan and Tommotian Stages and their equivalents (Qian & Bengtson 1989; Bengtson 1992). They have been suggested to form an evolutionary link between the Early Cambrian coeloscleritophorans and 'monoplacophorans' (Missarzhevsky 1989). This comparison is based on a proposed process of gradual sclerite fusion in a siphogonuchitid shell. According to this scheme, individual or groups of hollow sclerites are homologous to

Formation (lower part), Manykayan? C. Overall view. F. Enlargement of the initial part with polygons. I, J. Polygons at different parts of the mold. D, G. Specimen SMNH Mo160426 from sample 1487, locality B-9 (Oleniok), Kessyusa Formation (upper part), Manykayan? D. Overall view. G. Close-up of the initial part with polygons. E, H. Specimen SMNH Mo160427 from the same sample. E. Overall view. H. Enlarged initial part with phosphatic crust (arrowed). K. Specimen SMNH Mo160428 from sample 96-5a/1,2. Polygons with transverse traces of fibers. A, B, E × 18; C, D × 15; F × 175; G × 195; H × 190; I ×265; J × 445; K × 550; L × 115; M × 320; N × 200; O × 425; P × 250; Q × 600; R × 870.
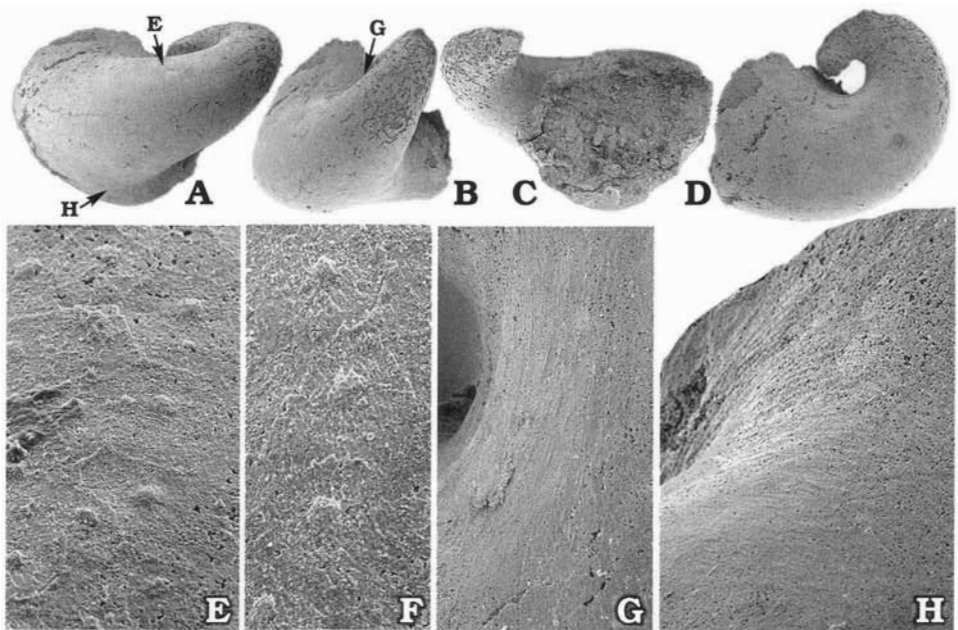
Fig. 14. *Pelagiella* cf. *subangulata* (Tate, 1892). Specimen SMNH Mo160429 from sample 96B-1/3, local-ity 96-1 (M. Kuonamka), Emjaksin Formation (uppermost part), Botomian. **A–D**. Different views of the entire specimen. **E**. Area with tuberculate polygons (arrowed in A). **F**. Tuberculate polygons with serrate edges. **G**. Radial fibrous texture from the area arrowed in B (aperture situated towards lower part of E–G). **H**. Comarginal fibrous texture at the aperture, from the area arrowed in A. **A–D** × 35; **E** × 400; **F** × 515; **G** × 170; **H** × 175.

shell prisms in 'monoplacophorans' (Missarzhevsky 1989). New details on the shell structure of *Purella* and some related forms provide more information on this account. At the juvenile stage the sclerites were needle-like (Fig. 3A, D). A central cavity suggests that the aragonite precipitated along an extended organic filament (Fig. 3H).

Some other scleritic forms have similar internal structures. On the inner surface of *Rozanoviella atypica* Missarzhevsky, 1981 there is a structure consisting of 4–5 μm wide fibers (Esakova & Zhegallo 1996: pl. 20: 5). In *Postacanthella pelmani* Zhegallo, 1996 thin elements radiate from the middle part of the shell interior (Esakova & Zhegallo 1996: p. 167, pl. 19: 9) and may also be interpreted as needle-like sclerites. There is a fibrous fabric on the inner surface of the scaly caps of *Canopoconus*? *radularis* Qian & Bengtson (Qian & Bengtson 1989: p. 94, fig. 59A4, 5).

Bengtson (1992) suggested that sclerites of *Maikhanella* Zhegallo, 1982 were em-bedded in a mineralized cuticular matrix. However, there is no distinction between the phosphatic matter of sclerite internal molds and the intermediate matrix consisting of 1–3 μm crystals and a finer grained material (Bengtson 1992, p. 406). The phosphatic matrix between the shell and phosphatic cover is apparently the same as in the internal mold of *Purella* (Figs. 3A–C, F, 4G). Therefore, a more likely interpretation of the inter-vening matrix in *Purella*-like shells is not as a mineralized cuticle, but as phosphatized sediment adhered to the sclerites before they were covered with a phosphatic film.

Shell microstructures of the Polyplacophora and Tergomya

Despite the fact that tergomyans, aplacophorans, and polyplacophorans are believed to be primitive within the Mollusca, microstructures of tergomyan shells and polyplacophoran plates are very different (Haas 1972, 1981; Poulicek & Kreusch 1986). The thin periostracum-like cuticle of polyplacophorans does not serve as a crystallization surface in biomineralization, as usually does the periostracum of conchiferans. Aragonitic aplacophoran and polyplacophoran spicules and polyplacophoran plates develop in crystallization chambers provided by individual cells or groups of cells below the cuticle. Nothing is known about shell microstructures of fossil Paleoloricata except for the vesicular microstructure of Late Cambrian *Matthevia variabilis* Walcott, 1885 (Runnegar *et al.* 1979; Carter & Hall 1990).

The shell-plates of modern polyplacophorans comprise at most three aragonitic layers. The outermost layer, tegmentum, is pierced by channels for aesthetes and has a spherulitic prismatic microstructure formed of rods of spherulitic sectors running parallel to the shell surface in the upper part and ventrolaterally in its lower part (Haas 1972, 1981). The innermost layer, termed hypostracum, may contain irregular spherulitic prismatic, irregular simple prismatic and crossed-lamellar microstructures (Haas 1972; Carter & Hall 1990). A middle shell layer, or articulamentum, appears as an intercalation in the hypostracum and has a spherulitic-type (Haas 1981; Poulicek & Kreusch 1986) or crossed-lamellar (Carter & Hall 1990) microstructure. A prismatic myostracum was observed in all polyplacophoran groups as a modification of the hypostracum for muscle attachment (Haas 1972, 1981). Homogenous and finely granular microstructures were attributed to the internal myostracum situated at the inner face of the shell-plates (Poulicek & Kreusch 1986). According to Carter & Hall (1990) the latter varies from irregular simple prismatic to homogenous. Crossed-lamellar microstructure is reported from myostracum disposed on both sides of the articulamentum (Poulicek & Kreusch 1986). Crossed-lamellar microstructure of polyplacophorans consists of rod-like third-order lamellae and lacks well-defined second-order lamellae (Haas 1981; Poulicek & Kreusch 1986; Carter & Hall 1990). However, the structure of polyplacophoran plates is rather specialized, complicated, and not likely to be primitive.

Recent representatives of the class Tergomya exhibit many characteristics that are not as primitive as was formerly thought and, thus, may not be considered 'living fossils' (Lindberg & Ponder 1996). Therefore, interpretations of skeletal microstructures of the Early Cambrian mollusc-like forms do not have to be restricted by those of modern relatives.

Below a relatively thick and well-developed periostracum, aragonitic shells of Recent tergomyans consist of an outer prismatic and inner lamellar nacreous layer (McLean 1979; Warén & Bouchet 1990; Warén & Hain 1992; Warén & Gofas 1996). The prisms, 15–45 µm wide, are polygonal in general and may be concentrically arranged following growth lines. Their height/width ratio ranges from 1/2 to 2. In rare cases the layer is homogenous. The nacreous layer may be thicker in the center of the shells and becomes thinner towards the periphery. It starts a short distance from the

margin of the shell. The thickness of the layer varies from 1–2 to 30 µm. In most cases a prismatic layer is a major part of the shell wall.

In a fossil tergomyan, *Pilina unguis* (Lindström, 1880) from the Silurian of Gotland, three layers were found. The outermost one is a 'thin apparently prismatic layer, followed by a thick nacreous layer which shows a pattern of polygons in horizontal section' (Erben *et al.* 1968: p. 4). A polygonal pattern in thin-section may also suggest, however, a prismatic nature of the layer. The polygons are 40–50 µm wide (Erben *et al.* 1968: pl. 10: 1). The innermost layer in this form and in *Tryblidium reticulatum* Lindström, 1880 consists of fine lamellae without visible subunits (Erben *et al.* 1968).

Pores in the wall

Punctella Zhong Hua, 1978 has been regarded as transitional between the scleritic stage and the solidly constructed exoskeletons of the Early Cambrian mollusc-like organisms (Missarzhevsky 1989). Missarzhevsky (1989) believed tubercles on the surface of internal molds of a fossil defined by him as *Punctella maidipigensis* to be outgrowths of the shell wall. However, investigation of the specimens from Missarzhevsky's collection showed that the tubercles represent casts of depressions or channels in the shell wall (Fig. 5A–F). Similar tubercles co-occur with different textures on internal shell molds of various morphologies (Fig. 5). Tubercles, 5–10 µm in diameter, were observed in shallow polygons of *Watsonella* sp. (Kouchinsky 1999: fig. 3E) and *Pelagiella* cf. *subangulata* (Fig. 14E, F). Larger polygons on an internal mold of *Aldanella* cf. *crassa* Missarzhevsky, 1989 are crater-shaped and contain a central elevation (Fig. 13L, M), which is broader and less distinct than tubercles in *Watsonella* sp. (Kouchinsky 1999: fig. 3E). In other forms the tubercles are not identifiable in polygons and not found in convex polygons (see Descriptions). It seems possible that at least some of the tubercles on internal shell molds reflect pore channels in the wall. Tubercles outside polygons may also represent attachment sites of groups of epithelial cells. Such a pitted interior shell surface corresponds, for example, with mantle attachment interior to the pallial line in some modern mytilids (J. Carter personal communication).

Pore channels branching inwards are present in a thick outer layer of the tergomyan *Tryblidium reticulatum* Lindström, 1880, from the Silurian of Gotland (Knight & Yochelson 1960; Erben *et al.* 1968). Pores have also been described from Recent *Neopilina goesi* Warén, 1988 and *N. zografi* (Dautzenberg & Fisher, 1896), but these have not been studied in detail (Warén 1988). Pore channels are known from unmineralized and mineralized skeletons of other fossil and extant groups. A precise function of polyplacophoran aesthetes, gastropod and bivalvian tubules, and brachiopod caeca is not clear. They may be related to synthesis, storage and secretion of proteins and polysaccharides, as well as excretion, respiration, receptory functions, anaerobic metabolism, transport of dissolved organic matter to the body, and repair of the periostracum. They may be useful for supplying shell matrix, contact between shell and mantle, and defense against boring organisms (Reindl & Haszprunar 1996). They are associated with the formation of polyplacophoran spicules (Haas & Kriesten 1975).

Aesthetes of polyplacophorans were considered homologous with the tubules of conchiferans (Salvini-Plaven 1985). Later investigations revealed considerable cytological and developmental differences between shell pores among molluscs and suggested they had a polyphyletic origin (Reindl & Haszprunar 1996). In forms with continuous shells described herein, pores may have participated in biomineralization, for instance, in deposition and orientation of fiber crystals.

Microstructures of Early Cambrian molluscs with solid shells

Microstructures may be replicated on internal phosphatic shell molds (Runnegar 1983, 1985). The material considered here suggests that the diversity of textures on internal molds records the original spectrum of shell microstructures rather than results from diagenesis alone because of the following facts. Different textures may occur on internal molds of different morphologically distinct species from the same sample, implying very close preservation environments for all of these specimens (e.g., sample 96-7/70). The same textures may be observed on the same taxa from different localities, indicating originally similar or identical microstructures (e.g., *Aldanella*). Several types of textures may appear in one fossil, owing to prediagenetic differences in microstructures in different areas of a shell.

Replicated microstructures have been observed on molds of various Early-Middle Cambrian shelly molluscs. Aragonitic fibers seem to be very common basic microstructure units in the Early Cambrian forms described here, but some microstructures of molluscan shell from the Middle Cambrian are reported as calcitic. Foliated calcite was indicated for Middle Cambrian *Eotebenna pontifex* Runnegar & Jell, 1976; *Pseudomyona queenslandica* (Runnegar & Jell, 1976); *Tuarangia paparua* MacKinnon, 1982; and *T. gravgaerdensis* Berg-Madsen, 1987 (Runnegar 1985; Berg-Madsen 1987). The first form is univalved. The others developed a bivalved condition possibly independently from the Early Cambrian bivalves *Pojetaia* Jell, 1980 and *Fordilla* Barrande, 1881, having a different microstructure (Runnegar & Pojeta 1992; Cope 1996). Both aragonite and calcite prisms in the outer shell layer may be regarded as primitive (Runnegar 1985). The presence of forms with calcitic prisms in the Early Cambrian, especially Late Atdabanian–Early Toyonian seems possible, because geochemical conditions favored calcite deposition at this time (Zhuravlev 1993; Ushatinskaya & Zhuravlev 1994). However, Carter *et al.* (1998) indicated that temperature favors calcite evolution more than geochemical factors do. Unlike aragonite, calcitic prisms more likely represent single crystals, which tend to be prismatic, rather than fibrous. A fibrous habit and spherulitic growth is typical of aragonite (Runnegar 1989), but microstructures of the earliest molluscs do not seem to have consisted of spherulitic prisms nucleated randomly.

Securiconus incertus Bokova, 1985 (see Descriptions) seems to be the earliest known univalved mollusc with solid shell walls from the northern Siberian Platform (Fig. 6G–L). Two types of structures occur on its internal mold. The first consists of phosphatic fibers, diverging in some places (typical of spherulitic sectors) (Fig. 6L). The second represents spherulites attached to the mold below the beak and apparently

transforming into the first type outside the subapical area (Fig. 6J, K). Other forms display several types of textures and their combinations.

The polygonal texture consists of cells (polygons) ranging from less than 10 μm (in *Ceratoconus* cf. *rusticus*) to 65 μm (in *Aldanella* ex.gr. *attleborensis*) (see Descriptions). They likely represent casts of low prism-like units (low prisms or flattened spherulites), as the shell wall was relatively thin compared to the size of the polygons. In coiled forms, such as *Aldanella*, the polygons were 5–10 times wider than the thickness of the wall (Fig. 13E, H). They may be confined to particular parts of the mold or cover all or much of its surface. The polygons may be more or less concave or convex and co-occur with other textures. Adjacent polygons of most of the species considered herein are of similar size. This cannot be explained just by the rule of soap-bubble geometry. Inner ends of prism-like units would then have varied in size because of different stages of growth and competition for space.

Polygons with a positive relief betwee their boundaries (convex polygons) seem to have resulted from decalcification of prism-like units (Kouchinsky 1999: fig. 1G) and reflected a network of organic membranes around them. Convex polygons do not co-occur with tubercles of any kind, presumably because internal channels and pits in the mineralized units were destroyed (Figs. 6D–F, 7G, I, 12D–F, 13F, G). Replicas of fibers are sometimes observed on these polygons (Kouchinsky 1999: fig. 2B; Figs. 7G, 13K). The height of convex polygons and details of their relief may vary within the same internal mold (Fig. 13F, I, J). In *Securiconus* cf. *costulatus* Missarzhevsky (see Descriptions) convex polygons are developed in the vicinity of the beak, but under the beak each of them additionally has a rather well-expressed central depression (Fig. 6D, E). These depressions probably originated from remains of mineralized prisms completely decalcified in other areas of the shell. A flexibility of the wall reflected at some of the internal molds of *Aldanella crassa* (Fig. 13I) and *Enigmaconus* sp. (Fig. 12E) may have also resulted from a diagenetic decalcification.

Polygons having a negative relief between their borders (concave polygons) are possibly the result of preferential decay of organic sheets around prism-like units (Kouchinsky 1999: fig. 1F). In this case a replicating substance filled gaps between the prisms on the inner shell surface (Figs. 8F, 9F, 10E, 11E, 13P, 14E). Internal molds of *Anabarella plana* Vostokova and *Watsonella* sp. are covered with shallow polygons of 10 to 40 μm in width (Kouchinsky 1999). The largest polygons are situated at the apex (Kouchinsky 1999: fig. 1E). They probably reflect inner ends of tightly packed, regular, prism-like units perpendicular to the shell wall and constituting the outermost mineralized layer. Similar polygonal textures, with 10–20 μm wide polygons, have been observed at the edge of the aperture of *Planutella inclinata* Elicki, 1994 (Elicki 1996: pl. 5: 3, 9) and *Anabarella argus* Runnegar, 1990 (Bengtson *et al.* 1990: p. 251, fig. 164N). Casts of shell prisms about 10 μm wide have been described from internal molds of *Mackinnonia obliqua* Landing & Bartowski, 1996 (Landing & Bartowski 1996: fig. 5.10–5.18), and on elevated portions of the internal molds of *Mackinnonia davidi* Runnegar, 1990, *Leptostega? corrugata* Runnegar, 1990 (Bengtson *et al.* 1990: fig. 160D), and *Stenotheca taconica* Landing & Bartowski, 1996 (Landing & Bartowski 1996: fig. 10.2–10.3). In thin-sections, *Mackinnonia davidi* Runnegar, 1990 shows an outer even exterior and a comarginally folded interior of the shell wall. This sug-

gested that the polygons were left by prism-like units of the outer shell layer (Bengtson *et al.* 1990: p. 234, fig. 159).

Small depressions (pits) are found on internal molds of *Ilsanella* sp. (Fig. 8D) and *Obtusoconus* sp. (Fig. 11D). Similar pits were indicated for *Obtusoconus foliaceus* MacKinnon, 1985, *Helcionella* sp., *Latouchella* cf. *accordionata* Runnegar & Jell, 1976, *L.* cf. *orientalis* (Walcott, 1905) (MacKinnon 1985), and *Latouchella* sp. (Peel 1991: fig. 24) from the Middle Cambrian. Internal molds of *Yuwenia bentleyi* Runnegar, 1981 have paired pits scattered over the surface (Bengtson *et al.* 1990: fig. 171D–F). Their origin, however, was explained as borings of microbial endoliths, phosphatized channel fillings of which are attached to the surface of the molds (Bengtson *et al.* 1990). Pits on the surface may be interpreted as initial growth stages of prism-like units regularly distributed over the surface. A gradual transformation of pits into polygons possibly demonstrates how the prism-like units, seeded on a periostracum-like organic sheet, expanded during growth (Fig. 11C–E).

Stepwise texture consists of elements arranged in a stepwise fashion, each containing parallel transverse marks of fibers and having serrate edges. The texture is known from internal molds of *Anabarella plana*, *Watsonella* sp. (Kouchinsky 1999), *Fordilla troyensis*, *Pojetaia runnegari* (Runnegar & Bentley 1983), and *Ceratoconus* cf. *rusticus* (see Descriptions). The oriented stepwise pattern at the apical part and aperture of *Anabarella plana* and *Watsonella* sp. may be interpreted as replicated portions of the second- and third-order lamellae. Each lamella included several parallel second-order units of variable thickness consisting of third-order lamellae or laths. The angle of inclination of fibers (basal elements) to the depositional surface and their orientation within a first-order lamella remain stable, as well as the inclination and orientation of the second- and third-order units. Angles of dip and orientation are different in adjacent first-order lamellae (Kouchinsky 1999: figs. 2E, 4G, H).

The lamellar microstructure likely originated from a spherulitic or prismatic one. In *Ceratoconus* cf. *rusticus* relatively small convex polygons with radial casts of fibers at the convex side of the mold imply a spherulitic growth of the fibers (Fig. 7G). These polygons transform into those with oriented marks of fibers, possibly formed by inclined spherulitic prisms (Fig. 7E, F). Further laterally they transform into a pattern similar to the stepwise texture of *Anabarella plana* and *Watsonella* sp. (Fig. 7E). In the latter case the texture was probably not produced by polygons but flattened imbricated lamellae. It seems likely that these variations are caused by differences in growth rate of the shell margin. The situation may be the same as described for fibrous prisms (Ubukata 1994): the higher the growth-rate, the more inclined the prisms.

On the surface of internal molds of *Pojetaia runnegari* there are irregular polygons arranged in a stepwise fashion, having anteriorly oriented serrate edges and containing transverse marks (Runnegar & Bentley 1983). In *Fordilla troyensis* the cells are more elongated radially (Runnegar & Pojeta 1992). The polygons are comparable in diameter (ca. 30 μm) to the shell prisms of many extant bivalves. However, inner prism terminations do not display stepwise relief even if the surface is extremely curved (Carter *et al.* 1990). Despite statements by Runnegar & Pojeta (1992), inclined irregular to regular simple prisms in juvenile shells of a Middle Devonian paleotaxodont, *Palaeoneilo filosa* (Conrad, 1842) are not like the shell microstructure in the inner shell layer of *Pojetaia*, mainly because they are not imbricated on the depositional surface, and

interfinger with an underlying fibrous prismatic sublayer (Carter 1990a; J. Carter personal communication).

Large nacre tablets may be considered as an alternative explanation of the stepwise pattern (Carter *et al.* 1990, but see Runnegar & Pojeta 1992). The shell microstructure of primitive bivalves from the subclass Paleotaxodonta Newell, 1965 is mainly a prismato-nacreous aragonite (Cope 1996, 1997). A possible nacreous microstructure is reported from recrystallized shells of an Ordovician paleotaxodont, *Deceptrix levata* (Hall) (Carter *et al.* 1990: p. 303). *Palaeoconcha* sp. from the Late Ordovician retained phosphatized nacre tablets, which, in contrast to Recent bivalve nacre, are of variable size and arrangement, with crystalline laths commonly radiating and rarely parallel or subparallel to each other (Mutvei 1983b; Carter *et al.* 1990).

Replicated fibers or laths showing several alternating dip directions occur in lateral parts of the molds of *Anabarella plana* and *Watsonella* sp., from the dorsal area to the aperture (Kouchinsky 1999: fig. 2A). Spiny and polygonal textures do not transform into one another. Fibrous fabric clearly overlaps polygons (figs. 1C, 3C, F therein). Fibrous aggregates, replicated as a spiny texture, were situated at the inner surfaces of prism-like units and probably constituted an inner layer. The absence of a spiny texture in the dorsal groove suggests that at the dorsal margin the inner layer was reduced or did not exist. This may also be evident from a recrystallized shell wall of *Watsonella* sp. (fig. 4 therein). There is a gradual transition between spiny and stepwise textures on internal molds of *Anabarella plana* and *Watsonella* sp. (fig. 2D therein). Spiny texture, however, was not found on internal molds of *Pojetaia* and *Fordilla*.

Two or more dip directions of lamellar subunits relative to the depositional surface are typical of crossed-lamellar, lamello-fibrillar, and matted laminar microstructures (Carter 1990b: pp. 611–612). The crossed-lamellar inner layer likely consisted of two zones different in prevalent orientation and angles of dip of sublamellae and fibers, integration of fibers into second-order lamellae, and degree of interpenetration of adjacent first-order lamellae. These zones produced either stepwise or spiny textures. A chevron-like spiny pattern on the surface of *Anabarella plana* and *Watsonella* sp. was likely formed by fibers and laths of complex crossed lamellae.

The inner layer of *Aldanella* may also have been built of individual fibers and fibrous lamellae. Fibers cross boundaries of polygons (Fig. 13K) and may also be arranged into crossed first-order lamellae (second-order lamellae are not defined) having different angles of dip and orientation of acicular elements reflected on the internal molds of *Aldanella crassa* and *A.* ex. gr. *attleborensis* (Fig. 13O, Q, R). In *Aldanella rozanovi* the inner layer consisted of similarly oriented recrystallized units (monocrystals) 0.5–1 µm wide. The thickness of the layer is 10–15 µm. The outer layer is 3–3.5 µm thick, and its microstructure is not distinct (Zhegallo 1980). Similar polygons were described from the surface of the first revolution of an internal mold of *Aldanella attleborensis*, where they co-occur with another cancellate texture consisting of smaller units 1–2 µm in diameter (Golubev 1976: pl. 3: 9). They are likely replicas of inner ends of aragonitic fibers. The texture observed at the first half of the first revolution in *A. crassa* is absent from molds of *A. utchurica* Missarzhevsky, 1969, a form with a taller whorl, from the same section (Golubev 1976: p. 35). From the initial part of the latter form, a microstructure similar to the prismatic one was reported (fig. 15, therein). Fibers, 1–1.5 µm wide, were also ob-

served at the initial part of a sinistrally coiled *Nomgoliella rotunda* Zhegallo, 1982 (Esakova & Zhegallo 1996: pl. 22: 7).

Tangentially arranged continuous fibers described from *Pelagiella* Matthew, 1895 and *Yuwenia* Runnegar, 1981 seem to be quite a different type of microstructure. In *Yuwenia bentleyi* Runnegar, 1981, internal and external molds show traces of continuous fibrous crystals (Runnegar 1985; Bengtson *et al.* 1990: fig. 172A, B). The crystals were likely aragonitic and oriented perpendicularly to growth lines in the outer layer, and parallel to the growth lines in the inner layer of the wall (radially and comarginally oriented aragonitic fibers). In *Pelagiella* two crossed layers of continuous fibers have been described (Runnegar 1985; Bengtson *et al.* 1990). Shells of *Pelagiella subangulata* (Tate, 1892) are reported to have consisted of an outer layer of aragonitic fibrous crystals arranged perpendicularly to the growth lines and at an angle to the spiral ornament (Bengtson *et al.* 1990: figs. 167F, G, 170). The inner layer may have included comarginally oriented fibrous units (fig. 167C therein). The innermost foliate microstructure has also been indicated for *P. subangulata* (fig. 169B therein).

This fibrous microstructure has been interpreted as tangentially arranged aragonitic fibers resembling dendritic growth in a two-dimensional space and believed to be a precursor of the crossed-lamellar microstructure, because it was generally similar to a crossed-lamellar aragonite, but differs from it in having no first-order lamellae and very acute angles of dip (Runnegar 1985).

The primitiveness of nacre and crossed-lamellar microstructure

It has been suggested that nacreous microstructure of the inner layer of conchiferan shells was primitive (Taylor 1973; Haas 1981; Runnegar 1985). This assumption is generally based on the fact that modern tergomyan shells are composed of an outer prismatic and inner nacreous aragonitic layers (McLean 1979; Bouchet *et al.* 1983; see also foregoing discussion), and that many of the oldest bivalves, gastropods, and cephalopods are nacreous (Mutvei 1983b; Runnegar 1985).

Columnar nacre replaced by phosphate in early diagenesis is known from the Late Ordovician cephalopod *Isorthoceras sociale* (Hall) and gastropod *Murchisonia* sp., and the Middle Ordovician cephalopod *Catoraphiceras* sp. (Mutvei 1983b). The main feature of columnar nacre in these Ordovician forms is its porosity, because of a weakly mineralized or unmineralized organic matrix that occupied spaces between adjacent stacks of tablets. Therefore, the nacre and shell were more flexible (Mutvei 1983a). A combination of spherulitic aragonite and nacre was found in other primitive representatives of gastropods and cephalopods (Runnegar 1985). Replicated nacreous tablets were reported also from the surface of internal mold of a Middle Cambrian stenothecid, *Mellopegma georginensis* Runnegar & Jell, 1976 (Runnegar 1985, 1989) placed with *Anabarella* in a group Stenothecidae of tergomyan molluscs by Waller (1998).

Nacre is known from modern gastropods, cephalopods, and bivalves. Nacre tablets in Recent gastropods and *Nautilus pompilius* Linnaeus consist of 2–50 radiating crystalline sectors, formed of parallel laths polysynthetically twinned within a sector. Organic membranes surround the sectors and envelop tablets. The center of each tablet is

perforated by a cavity about 1 mm in diameter, filled with a granular mineralized sub-stance representing an accumulation of mineralized organic matrix. The growth of the nacreous layer takes place on a marginal zone of the shell aperture. The nucleation of a new tablet at a concave surface of a preceding tablet in its middle part is determined by a central organic accumulation. Nacre tablets form vertical columns (Mutvei 1978, 1980, 1983a, b). Spherulitic aragonitic prisms and nacre columns may be very similar in shape. Initial portions of aragonitic prisms often form thin hexagonal tablets, 2–4 mm in diameter, resembling nacreous tablets, and, as in nacre, some of these initial tablets are subdivided into a varying number of sectors consisting of granules arranged in parallel rows (Mutvei 1991). Moreover, prismatic and nacreous microstructures may grade into one another (Bandel 1990).

Bivalve nacre grows on most of the inner shell surface. There are no organic mem-branes between the crystalline sectors. In Recent forms the tablets are of regular size and consist of parallel crystalline laths (Mutvei 1983b). New tablets are deposited on the peripheral portion of the preceding tablet (Mutvei 1978). Therefore the tablets in bivalves usually have a brick-wall arrangement in vertical sections and a terrace-like succession of nacreous sheets in a plane view. Potentially, these terraces may be repli-cated as a stepwise relief, similar to that on internal molds of *Fordilla* and *Pojetaia*. In the latter two, as well as in *Anabarella* and *Watsonella*, the stepwise texture may well correspond to a microstructure that was very close to certain laminar microstructures, especially of lamello-fibrillar (Carter 1990b: p. 611, fig. 12), *Sepia* sp. laminar (p. 611, fig. 14 therein), and matted types (p. 612, fig. 17 therein). Possibly containing aragonitic fibrous twins parallel to each other within one second- or third-order lamella this microstructure may be a precursor to laminar (nacreous) ones and precede the na-cre of bivalves.

On the other hand, *Anabarella-Watsonella* lamellar microstructure is apparently close to complex crossed-lamellar ones. Apart from polyplacophorans, crossed-lamellar microstructures are known from gastropods, scaphopods and bivalves. The initial miner-alized shell deposited under a periostracum usually consists of basic microstructural units like those in crossed-lamellar microstructures. Its transition into a crossed-lamellar microstructure may be gradual or abrupt (Iwata 1980; Togo 1984; Bandel 1990). At later stages these fibers fuse and form lamellae. Adjacent nacreous and complex crossed-lamellar microstructures have been found in a Devonian cyrtodontid bivalve, *Ptycho-desma* (Carter & Tevesz 1978). Carter & Hall (1990: pls. 104, 130) described nacre and complex crossed-lamellar microstructure in the crassatellid *Eodon* and in the gastropod *Bembexia*. Newell & Boyd (1990) described nacreous microstructure sandwiching a crossed-lamellar layer as a main feature of the Limipectininae, and nacre adjacent to crossed-lamellar leyers in some trigonioids. There has been noted a direct transition from nacreous to crossed-lamelar microstructure in a Carboniferous scallop (Carter 1990a: p. 246, fig. 44C). However, microstructural intergradation does not necessarily signifies phylogenetic origin despite Bandel's (1990) assumption, because there is al-ways microstructural intergradation where two aragonitic shell layers are in direct con-tact (J. Carter personal communication). Nacreous microstructures may have appeared as alternative to a crossed-lamellar microstructure in the Cambrian (Batten 1990), and both microstructures may have evolved independantly in different groups of molluscs from an *Anabarella-Watsonella*-type lamellar precursor.

Conclusions

Biomineralization in Early Cambrian molluscs did not apparently produce as much variation in microstructure as in modern forms. Therefore, it appears reasonable that these earliest microstructures should have greater phylogenetic significance than younger ones. However, the morphology of an early shell does not necessarily correspond to a particular microstructure.

It is unlikely that a univalved solid shell originated through fusion of sclerites into a prismatic wall. Juvenile shells of *Purella* and related forms composed of needle-like sclerites are possibly homologous with solid plates at the anterior and posterior ends of halkieriids. The morphology of fibrous sclerites is quite distinct from the fibrous fabric that occurs in integrated solid shells.

The earliest solid mineralized shell discussed herein was cyrtoconic and apparently consisted of 5–10 μm wide aragonitic spherulites observed on the concave side of the internal mold. Away from the subapical area, the spherulites transformed into inclined spherulitic sectors consisting of diverging fibers running almost parallel to the shell surface in a subradial direction. The difference may have been caused by different growth rates at the shell margins. It is possible to derive other microstructures of Early Cambrian shells from such a basic type.

Most of the forms with continuous shells had a layer of mineralized prism-like units (low aragonitic prisms or flattened spherulites) surrounded by organic matrix. The prisms grew and expanded from a periostracum-like sheet. The units may be replicated on the surface of internal molds as shallow concave polygons with or without a more or less expressed tubercle in their centers. Larger tubercles are not enclosed in polygons and may occur on smooth molds or co-occur with spiny or polygonal textures. Convex polygons seem to be a result of decalcification of prism-like units. They do not co-occur with tubercles. The latter are interpreted as casts of pits or pore channels in the wall. The growth rate of prism-like units and the distribution of their seed points were mostly regular. This is supported by the similar size of adjacent polygons and implies a certain amount of biological control over biomineralization in the earliest molluscs.

Casts of fibers and/or lamellar units may overlap a polygonal texture or occur without it. They may reflect an inner layer consisting of aragonitic fibers fused into more or less well-developed lamellar units. It seems likely that nacreous and crossed-lamellar aragonitic microstructures evolved in the Cambrian from lamellar and fibrous aragonitic microstructure independently in different groups of molluscs.

Acknowledgments

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Микроструктуры раковин раннекембрийских моллюсков

АРТЁМ КУЧИ НСКИЙ

Содержание

Исследование микроструктур древнейших скелетных беспозвоночных представляется весьма важным как для понимания процессов биоминерализации у ранних многоклеточных, так и для систематики этих, в большинстве своём, проблематичных организмов. Стенка раковин раннекембрийских моллюскоподобных форм состояла из добавлявшихся по периферии в ходе увеличения размеров мягкого тела арагонитовых ростовых ламелл либо склеритов. Некоторые раковины со стенкой из склеритов строились на своих ранних стадиях развития из удлинённых, игловидных элементов, тогда как на более поздних стадиях роста раковины образовывались листовидные склериты. Внешний слой из минерализованных низких арагонитовых призм или уплощённых сферулитов, окружённых неминерализованным матриксом, вероятно, существовал в большинстве раковин с монолитными стенками. Распределение начальных стадий роста этих призмоподобных элементов на периостракуме и темп их развития были в основном закономерными, а не хаотичными, что отражает существенный биологический контроль. Элементы микроструктуры могли в деталях отпечатываться на фосфатной плёнке, возникавшей в процессе раннего диагенеза между внутренним осадочным заполнением ядра раковины и её внутренней поверхностью. В одних случаях, призматические образования отпечатывались на поверхности внутренних ядер в виде полигональной сетки с неглубокими ячейками. В таких ячейках бывают выражены бугорки (туберкулы), по одному в центре каждой. Туберкулы могут встречаться и вне полигонов, сочетаясь с репликами иных микроструктур. В других случаях, возможно, при растворении минеральной составляющей внешнего слоя, образовывалась полигональная сетка с положительным рельефом ячеек. При этом отсутствуют туберкулы. Последние могут быть интерпретированы как отпечатки поровых каналов в стенке раковины, которые могли играть роль в биоминерализации или отражать места прикрепления мантии к раковине. Отпечатки фибр или ламелл могут перекрывать ячеистый рельеф или встречаться отдельно и свидетельствуют о наличии внутреннего слоя, состоявшего из фиброзного арагонита, объединённого в более или менее обособленные ламеллы. Рассматривается возможность возникновения в раннем кембрии в разных группах моллюсков перламутровой и перекрещенно-пластинчатой арагонитовых микроструктур от рассматриваемой ламеллярной арагонитовой.