

Phosphate replicated and replaced microstructure of molluscan shells from the earliest Cambrian of China

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The earliest Cambrian Meishucunian phosphoritic succession in eastern Yunnan, China, contains well-preserved molluscan shells that offer insights into the early evolution of skeletonization. Phosphate internal moulds, phosphate replaced originally carbonate shells, and phosphate coatings show lamello-fibrillar structure, prismatic structure, and regularly foliated structure. The lamello-fibrillar structure appears earlier in the fossil record than laminar structures such as nacreous or foliated structures. It has been identified in fossil mollusks, which occur in China as early as the lower phosphate layer of the Zhongyicun Member of the Meishucunian. Therefore, the lamello-fibrillar structure appears to be primitive in mollusks. The lamello-fibrillar and prismatic aragonite is the most common shell material of molluscan skeletons in the Early Cambrian Meishucunian and equivalents around the world. Although the early molluscan microstructure is not so diverse as that of extant mollusks, it may be of use in high rank taxonomic classification as shown by the early conchiferan mollusks discussed here. These mollusks are characterized by the horizontal fibrillae that are layered and parallel, and thereby differ from hyoliths, in which the horizontal fibrillae appear to be in the form of the bundles of fibres that can branch or anastomose.

Key words: Mollusca, small shelly fossils, microstructure, biomineralisation, Cambrian, Meishucunian Stage, China.

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Introduction

The apparently sudden appearance of abundant and diverse small skeletal fossils in rock successions near the base of the Cambrian is an expression of the “Cambrian explosion”, a long-standing enigma in both geology and biology. The most spectacular difference between the latest Precambrian and the earliest Cambrian faunas is the advent of biomineral skeletonization. For this reason, research on the biomineralization characters of the early small skeletal fossils may provide significant information about the origin and early diversification of the major groups of the Metazoa.

Although in the last three decades Early Cambrian small skeletal fossils have been found in basal Cambrian rocks at numerous localities throughout the world, little is known about their biomineralization and diagenesis (Bengtson and Conway Morris 1992; Lowenstam 1989; Runnegar 1989). Previous studies commonly concentrated on morphological characters of “small shelly fossils”. More and more small skeletal fossils, such as *Microdictyon* (see Bengtson et al. 1986; Chen et al. 1989), *Wiwaxia* (see Bengtson and Conway Morris 1984; Butterfield 1990), and *Halkieria* (see Conway Morris and Peel 1990, 1995), have been proven to be dispersed hard parts (sclerites) covering bodies of relatively large animals. Their original taxonomic affiliation based on morphology of single sclerites appeared incorrect. Other Early Cambrian small skeletal fossils have been attributed to

many phyla, such as the Mollusca, Brachiopoda, and Hyolitha. Qian and Bengtson (1989) in a comprehensive review attributed the Meishucunian small skeletal fossils to a catalogue of morphological groups.

Those different major groups may have their own diagnostic characters of skeletonization, which can be used as evidence for identification and classification. Although most of the Early Cambrian small skeletal fossils are problematic due to incomplete preservation or unusual morphology, they may help in recognizing ancestors of later major taxa and reveal their phylogenetic relationships.

Mollusks, as a good example to start with, contributed a very important part to the earliest Cambrian small skeletal fossils. Pioneering work by Runnegar (1983, 1985a, b, 1989; Runnegar and Jell 1976) on the microstructures of Cambrian mollusks and works of other researchers (Müller 1975; Misarzhevsky 1989; Brasier 1990; Bengtson et al. 1990; Carter and Hall, 1990; Bengtson 1992; Li and Chen 1992; Kouchinsky 1999, 2000b; Feng 1998; Feng et al. 2000, 2001) have provided very useful information about early molluscan biomineralization. Our investigations are based on molluscan fossil materials from the Meishucunian in eastern Yunnan, southwestern China. The aim of this paper is to use diagenetic phosphate replication of the original mineral tissues to determine the original shell structure of early mollusks.

Material and methods

The Meishucunian is the basalmost Cambrian chronostratigraphic unit in the eastern Yunnan of China and corresponds, in ascending order, to Xiaowaitoushan, Zhongyicun, Dahai Members of the Dengying Formation and the Shiyantou Member of the Yuanshan Formation. Small skeletal fossils abruptly appear in abundance in the Zhongyicun Member.

The fossil material dealt with in this paper was collected in 1996 and 1999 from the Zhongyicun and Dahai Members of the Early Cambrian Meishucunian at Beideng of Anning County, Baizhai of Xundian County, and Dahai and Yulu of Huize County (Fig. 1). The rock samples were carbonates and phosphorites. Most of the fossil specimens were obtained by washing weathered rock with water. Acid maceration with 5–8% acetic acid was also applied. Observations were done under SEM (JSM-6300) in addition to Figs. 2B and 5B, C, taken with Philips X-30 at Uppsala University, Sweden. This paper adopts the standardized microstructure terminology set up by Carter et al. (1990).

Molluscan fossils used for the research on microstructure include the monoplacophorans *Ramenta cambrina* Jiang, 1982 (Luo et al. 1982), *Latouchella* cf. *korobkovi* Vostokova, 1962, *Papilloconus explanatus* Feng et al., 2000, *Ilsanella* cf. *orectes* (Jiang, 1982), *Ilsanella?* *rozanovi* Wang, 1994, *Watsonella yunnanensis* (He and Yang, 1982), and the paragastropod *Archaeospira ornata* Yu, 1979. *Watsonella* is considered to be a monoplacophoran based on the most complete phylogenetic analysis available (Carter et al. 2000). It is the link between the stenothecid monoplacophorans and the Bivalvia. It lacks a true pegma, which, as indicated by Pojeta and Runnegar (1974), is necessary for membership in the Rostroconchia, and its microstructure is in part much like that of *Pojetaia* and *Fordilla* (see Carter et al. 2000). All these specimens are housed in the Nanjing Institute of Geology and Palaeontology, Academia Sinica, abbreviated NIGP.

Mode of preservation

Phosphatization, so common in strata near the Precambrian–Cambrian boundary around the world, played a key role in preserving information on the original shell structure (Bengtson and Conway Morris 1992; Brasier 1990; Dzik 1994; Runnegar 1985a; Runnegar and Bengtson 1990). As a general rule, phosphatic replacement or filling occurs only in small specimens, whereas silicification affects specimens of all sizes (Yochelson 1999). Phosphate fillings of small shells can replicate very fine structures, up to 100 nm (Runnegar and Pojeta 1985). This allows determination of both the topography of the shell surface and its microstructure (Runnegar 1989). Crystal morphologies replicated on internal moulds were reported to be rather common in phosphate and carbonate successions of the earliest Cambrian (Runnegar

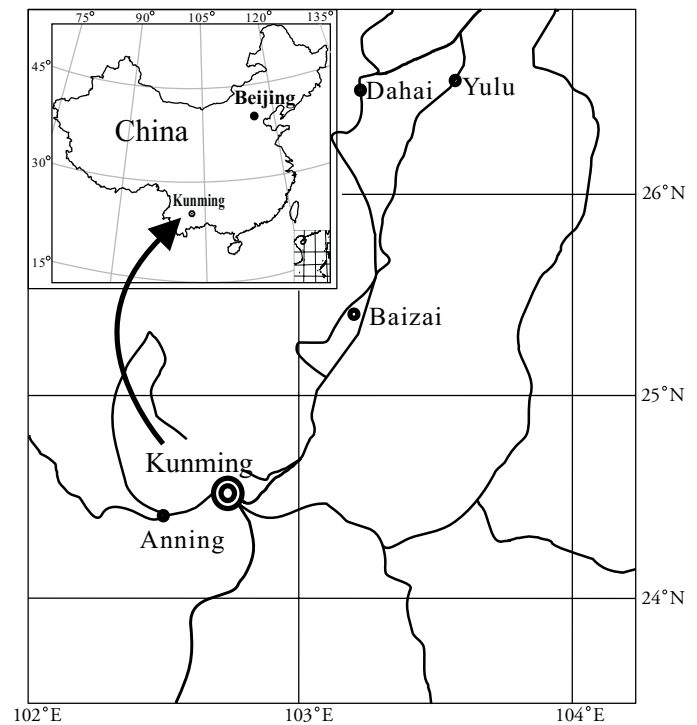


Fig. 1. Location of studied exposures of the Meishucunian in the Yunnan Province.

1989). Information about early molluscan microstructures is obtained mostly from the internal moulds of conchs (Table 1).

As typical for secondarily phosphatized small shelly fossils, the Meishucunian specimens usually show phosphoritic internal moulds, calcite-replaced original shell, and a phosphate coating of its exterior. In acid treated materials the calcitic shell is removed and represented by a narrow empty cavity between the mould and coating. The coating then easily exfoliates. Frequently the shell itself is also phosphatized. Each of these three kinds of phosphatic structures is potentially a source of information for original shell microstructure.

The external phosphatic coating, usually only roughly replicates the external shell morphology, but it can be sometimes recovered and observed from the inside (e.g., Olempska 1994; Hinz-Schallreuter 1995). It shows very fine details of the external shell surface in negative. In the case of mollusks these may be details of organic periostracum, if phosphatization was early enough. Frequently, internal moulds of cavities within the shell wall are attached to the coating. Mostly these are channels etched by endolithic cyanobacteria (e.g., Runnegar 1985b; Olempska 1986).

Phosphoritic internal moulds provide additional information, in this case replicating the internal shell structure (e.g., Runnegar 1985a).

In both of the above cases the information is rather reliable and relatively easy to interpret. Much more difficulty arises when the secondarily phosphatized shell wall is considered. The phosphatization, which may be late diagenetic in some cases, may replace the original organization of the shell or this

Table 1. Distribution of microstructures in the early molluscan fossils.

Fossil name	Microstructures	Horizon	Reference
<i>Aldanella crassa</i>	Concave polygons and crossed fibres	Lower Cambrian	Kouchinsky 2000b
<i>Anabarella argus</i>	Prismatic outer shell layer	Lower Cambrian	Bengtson et al. 1990
<i>Anabarella plana</i>	Prismatic, crossed-lamellar	Lower Cambrian	Kouchinsky 1999
<i>Anabarella</i> sp.	Prismatic outer shell layer and “nacreous” inner shell layer	Lower Cambrian	Runnegar 1983 Runnegar 1985a
<i>Archaeospira ornata</i>	Horizontal and parallel fibrillae	Lower Cambrian	This paper
<i>Ardrossania paveyi</i>	Fibrous structure	Lower Cambrian	Bengtson et al. 1990
<i>Bellerophon</i> sp.	Shell aragonitic and predominantly aragonitic CL, cone CCL and irregular CCL with thin bands of irregular simple prisms	Upper Carboniferous	MacClintock 1967 Rollins 1967 Carter and Hall 1990
<i>Bemella? mirabilis</i>	Prismatic	Lower Cambrian	Runnegar 1985a
<i>Ceratoconus</i> cf. <i>rusticus</i>	Tubercles and transverse fibres	Lower Cambrian	Kouchinsky 2000b
<i>Chancelloria eros</i>	Radial rays plus one central ray	Lower Cambrian	Kouchinsky 2000b
<i>Enigmaconus</i> sp.	Convex polygons	Lower Cambrian	Kouchinsky 2000b
<i>Eotebenna pontifex</i>	Inner shell layer largely calcitic, regularly foliated	Lower Cambrian	Runnegar 1983
<i>Euphemites</i> sp.	Shell aragonitic and predominantly CL and CCL with sublayers of irregular simple prisms in the inner layer and possibly with an exterior optically homogeneous layer	Upper Carboniferous	MacClintock 1967 Rollins 1967 Carter and Hall 1990
<i>Fordilla troyensis</i>	Large tablet, imbricated nacre	Lower Cambrian	Runnegar and Pojeta 1992
<i>Watsonella varensalensis</i>	Polygonal texture	Lower Cambrian	Müller 1975
<i>Watsonella varensalense</i>	Prismatic and probably aragonitic shell	Lower Cambrian	Runnegar 1983 Runnegar 1985a
<i>Ilsanella</i> cf. <i>orectes</i>	Lamello-fibrillar structure	Lower Cambrian	This paper
<i>Ilsanella</i> sp.	Pits and polygonal texture	Lower Cambrian	Kouchinsky 2000b
<i>Ilsanella? rozanovi</i>	Prismatic structure	Lower Cambrian	This paper
<i>Lathamella symmetrica</i>	Prismatic, Crossed lamello-fibrillar structure	Lower Cambrian	Li Guoqiang 1992
<i>Latouchella</i> cf. <i>korobkovi</i>	Lamello-fibrillar structure	Lower Cambrian	This paper
<i>Latouchella</i> sp.	Prismatic outer shell layer	Lower Cambrian	Runnegar, 1985a
<i>Leptostega? corrugata</i>	Outer shell layer of prismatic structure	Lower Cambrian	Bengtson et al. 1990
<i>Mackinonia</i> sp.	Tubercles and concave polygonal texture	Lower Cambrian	Kouchinsky 2000b
<i>Mackinonia davidi</i>	Outer layer of narrow fibrous prisms, a middle layer of wider columnar prisms with thick interprismatic organic matrices and in the thicker parts of the shell an inner layer with no distinctive impression on steinkerns	Lower Cambrian	Bengtson et al. 1990 J.Carter personal communication
<i>Maikhanella multa</i>	Spicular fibres	Lower Cambrian	Bengtson 1992
<i>Mellopegma georginensis</i>	Outer columnar prismatic and inner rhombohedral (parallelogram) small tablet, sheet nacreous	Lower Cambrian	Runnegar 1983 Runnegar 1985a
<i>Obtusconus rostriptutea</i>	Prismatic structure	Lower Cambrian	Runnegar 1983 Runnegar 1985a
<i>Obtusconus</i> sp.	Pits and polygonal texture	Lower Cambrian	Kouchinsky 2000b
<i>Papilloconus explanatus</i>	Polygonal elevations	Lower Cambrian	This paper
<i>Pararaconus staiconum</i>	Polygonal elevations	Lower Cambrian	Bengtson et al. 1990
<i>Pelagiella</i> cf. <i>subangulata</i>	Fine radial continuous fibres and shallow concave polygons	Lower Cambrian	Kouchinsky 2000b
<i>Pelagiella deltoids</i>	Inner shell layer of flattened, elongated crystallites arranged in a spiral fashion	Lower Cambrian	Runnegar 1985a
<i>Pelagiella subangulata</i>	Outer radial and inner comarginal layer of fibrous crystals	Lower Cambrian	Runnegar 1985 Bengtson et al. 1990
<i>Pojetaia runnegari</i>	Outermost very thin, columnar prismatic layer and middle and inner layers large tablet, imbricated nacre, probably separated with myostracal irregular simple prisms	Lower Cambrian	Runnegar 1983 Runnegar and Bentley 1983 Runnegar 1985a Bengtson et al. 1990 Carter 1990
<i>Praematuratropis</i> sp.	Shell aragonitic and varies from fine CCL to irregular CCL in the outer layer, grading inward into cone CCL in the middle layer, and irregular CCL to cone CCL in the inner layer, with a thin, irregular simple prismatic innermost layer; inductura commarginal linear CL	Middle Devonian	Rollins 1967 Rollins et al. 1971 Carter and Hall 1990

Table 1 continued.

Fossil name	Microstructures	Horizon	Reference
<i>Pseudomyona queenslandica</i>	Largely regularly foliated calcite, columnar prisms	Middle Cambrian	Runnegar 1985a
<i>Ptomatis</i> sp.	Shell aragonitic with a thin, outer layer of nearly vertical, irregular simple prisms; a thick middle layer of cone CCL, and an inner layer of fine CCL and very faintly CL (?) structure, with a parietal shelf of irregular CCL	Middle Devonian	Carter and Hall 1990
<i>Punctella maidipingensis</i>	Concentrically arranged granules	Lower Cambrian	Kouchinsky 2000b
<i>Purella</i> cf. <i>crystata</i>	Fused needle-like sclerites	Lower Cambrian	Kouchinsky 2000b
<i>Ramenta cambrina</i>	Inner lamello-fibrillar structure	Lower Cambrian	This paper
<i>Retispira</i> sp.	Shell aragonitic and predominantly CL, cone CCL, irregular CCL, and fine CCL, with sublayers of irregular simple prisms	Middle Devonian	Rollins 1967 Carter and Hall 1990
<i>Securiconus</i> cf. <i>costulatus</i>	Positive polygonal relief and casts of fibres	Lower Cambrian	Kouchinsky 2000b
<i>Securiconus incertus</i>	Subradially oriented fibres and tightly packed spherulites situated under the beak	Lower Cambrian	Kouchinsky 2000b
<i>Tuarangia gravgaardensis</i>	Largely (regularly) foliated calcite	Middle Cambrian	Berg-Madsen 1987
<i>Tuarangia paparua</i>	Largely (regularly) foliated calcite	Middle Cambrian	MacKinnon 1982 Runnegar 1985a
<i>Watsonella</i> sp.	Prismatic, crossed-lamellar	Lower Cambrian	Kouchinsky 1999
<i>Watsonella yunnanensis</i>	lamello- fibrillar structure	Lower Cambrian	This paper
<i>Yochelcionella cyrano</i>	Prismatic structure	Lower Cambrian	Runnegar 1985a
<i>Yochelcionella</i> sp.	Tubercles and polygonal texture	Lower Cambrian	Kouchinsky 2000b
<i>Yuwenia bentleyi</i>	Outer shell layer of radially fibrous prismatic and inner shell layer of commarginal simple crossed lamellar	Lower Cambrian	Runnegar 1985a Bengtson et al. 1990

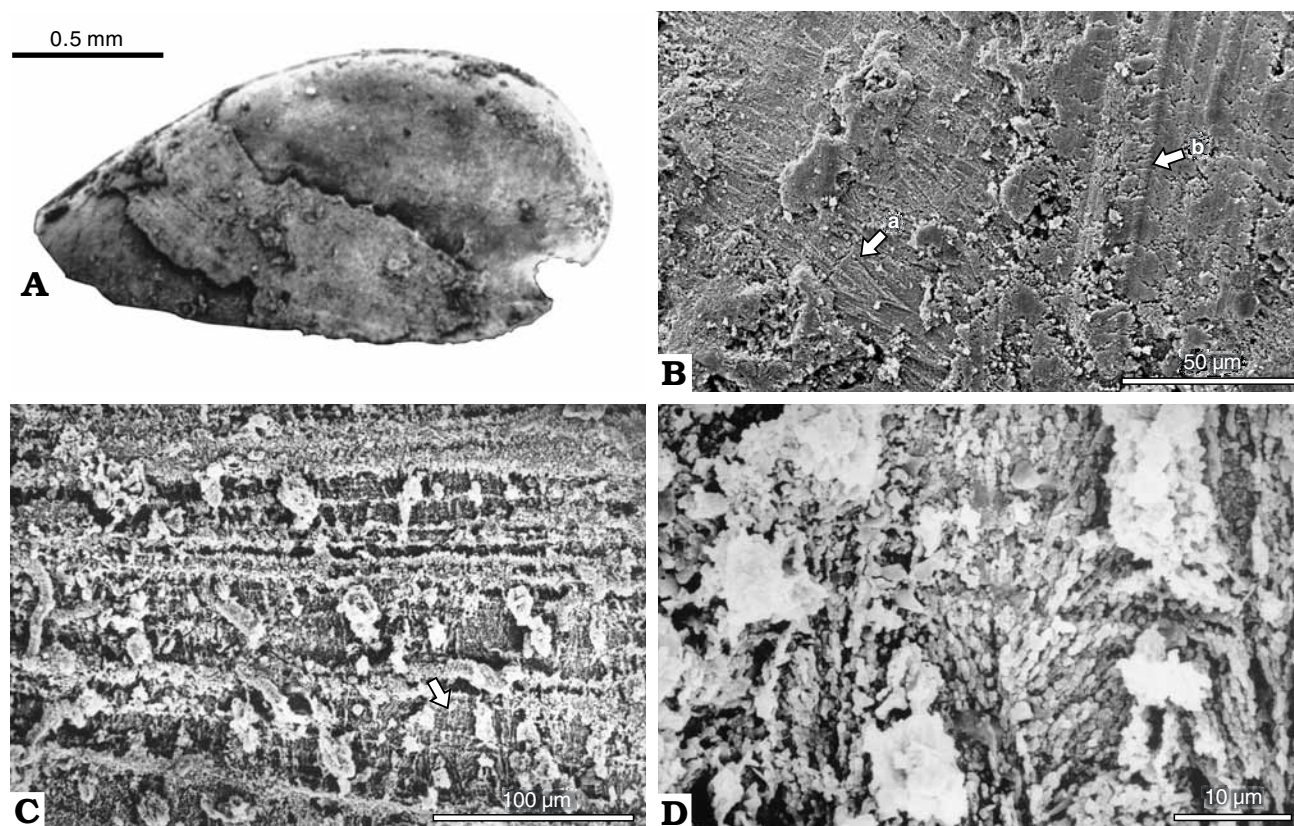


Fig. 2. *Ilsanella* cf. *orectes* (Jiang, 1982). Specimen NIGP Mo 131353 from sample yb96929-1, upper phosphatic bed of the Zhongyicun Member, Baizai Xundian in the eastern Yunnan, Meishucunian. **A.** Lateral view. **B.** Lamello-fibrillae (arrow a) approximately perpendicular to growth lines (arrow b). **C.** Microstructure of inner surface of external coating. **D.** Enlargement of place shown by arrow in C, note lamello-fibrillae.

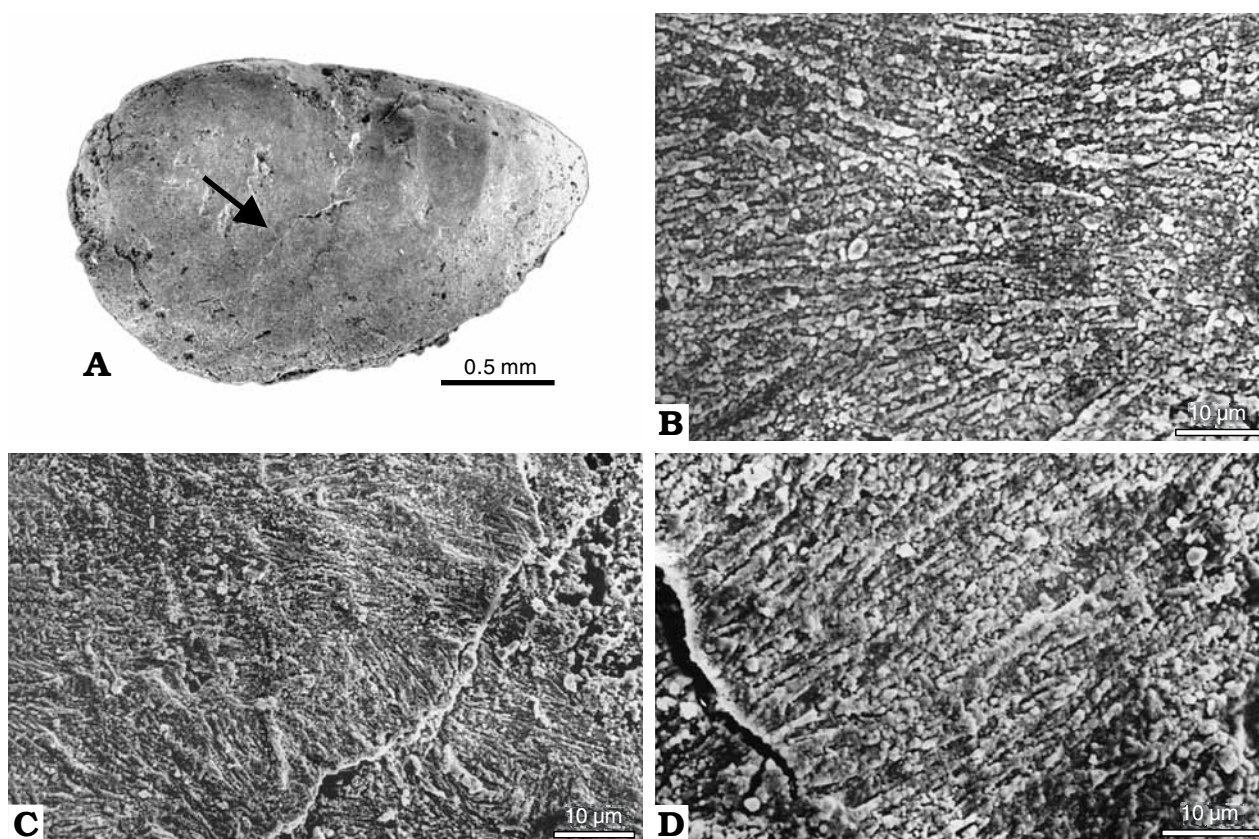


Fig. 3. *Watsonella yunnanensis* (He and Yang, 1982). Specimen NIGP Mo 131363 from sample yy9649-1, upper phosphatic bed of the Zhongyicun Member, Yulu of Huize in the eastern Yunnan, Meishucunian. A. Lateral view. B, C. Lamello-fibrillar structure. D. Enlargement of C.

may be completely obliterated by chaotically or perpendicularly growing apatite crystals. To be sure that the original structure is replicated, the matter must be sufficiently different from normal phosphate precipitation or replacement.

Description of structures

Structure of the external coating.—*Ilsanella* cf. *orectes* (Jiang) is represented by cyrtoconic internal moulds and an incomplete phosphatic coating (Fig. 2A). The inner surface of the coating shows fine details of microstructure (Fig. 2C, D). Several nearly parallel lines seem to represent growth lines (Fig. 2C). In close-up, the fibrillae obviously comprise a set of rice-shaped granules (Fig. 2D). These fibrillae are generally arranged in two directions. The rice-shaped granules are phosphatic in composition; they form the phosphatic coating.

Structure on the internal mould.—Microstructures replicated on the internal mould have been found in the monoplacophorans *Latouchella* cf. *korobkovi* Vostokova, *Ilsanella* cf. *orectes* (Jiang), *Ilsanella?* *rozanovi* Wang, *Papilloconus explanatus* Feng, *Ramenta cambrina* Jiang, *Watsonella yunnanensis* (He and Yang) and paragastropod *Archaeospira ornate* Yu. Two microstructural morphologies, lamello-fibrillar and simple prisms, are recognized.

Lamello-fibrillae are seen on the surface of internal moulds of *W. yunnanensis* (Fig. 3B–D), *R. cambrina* (Fig. 4C, D), *I. cf. orectes*, and *L. cf. korobkovi* (Fig. 5B, C). Commonly, the fibrillae are replicated as a crossed or branched pattern on the internal mould (Figs. 3B–D, 5B, C), but parallel fibrillae are visible as well (Figs. 3D, 5C). Crossed or branched fibrillae might be diagenetic artifacts from fine phosphate grains replicating fibrillae of different lamellae and then being compressed during diagenesis. Regardless of the seemingly branched fibrillae, they are distributed approximately along shell growth direction or perpendicular to growth lines (Fig. 2B). Horizontally parallel fibrillae can be also seen on the internal mould of *A. ornata* (Fig. 6A₂).

Another structural morphology replicated on the internal mould is a prism. This prismatic structure can appear in two replicated shapes. In *P. explanatus* Feng the prismatic preservation shows a positive relief. Ends of prisms resemble tubercles of diameter about 10 µm, very regularly exposed on the surface of the internal mould (Fig. 7B, C). This may reflect more intense weathering of the exposed prism facets than the destruction of organic material at their edges (Kouchinsky 1999). In *I.?* *rozanovi* Wang the prismatic structure is preserved in negative relief, as shown by a series of hexagons about 12–20 µm in diameter. The hexagon periphery, 1–2 µm in width, may represent an originally organic sheath sur-

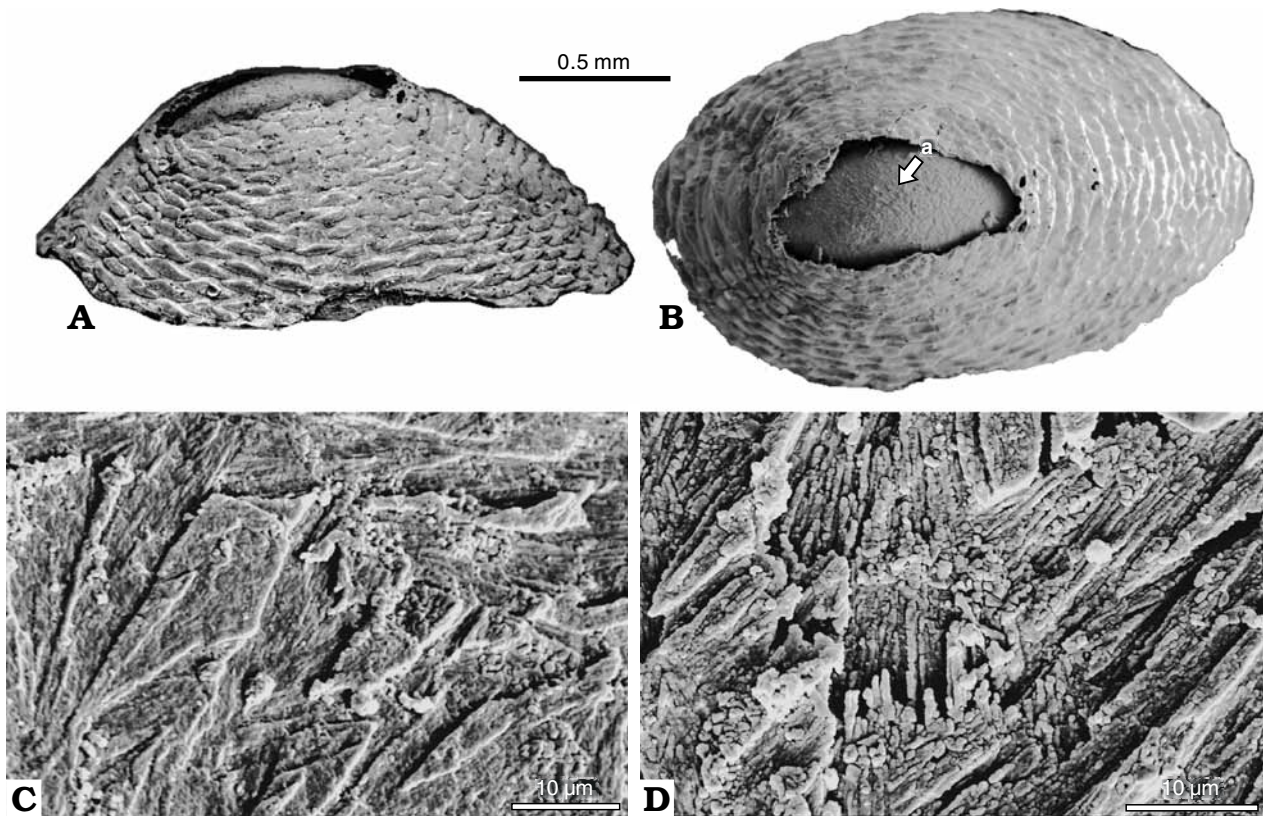


Fig. 4. *Ramenta cambrina* Jiang, 1982. Specimen NIGP Mo 131200 from sample yy9649-1, upper phosphatic bed of the Zhongyicun Member, Beideng of Anning in the eastern Yunnan, Meishucunian. A. Lateral view. B. Apical view. C. Enlargement of place shown by arrow a in B, note irregular polygonal convexity. D. Enlargement of C, note lamello-fibrillar structure.

rounding the prisms (Fig. 8C, D). The organic sheaths are very likely to have been decayed preferentially and were filled with a phosphatic matrix. A similar pattern of microstructural preservation has been reported in the early molluscan fossils from Siberia and Australia (Kouchinsky 2000b; Runnegar 1985a; Bengtson et al. 1990).

Phosphate replaced shell wall.—Phosphate replaced shell walls have been found in various Meishucunian fossils. In a specimen of *Ramenta cambrina* Jiang with an internal mould, a replaced shell and a phosphatic coating, the replaced shell wall is well exposed between the layer of the coating and the internal mould (Fig. 4C, D). The external coating replicated the surface sculpture while phosphatic re-

placement preserved lamello-fibrillae, where the fibrillae appear to be distributed in lamellae and arranged in two directions. Fibrillae in the same lamella are generally parallel to each other, but those in the adjacent lamella are arranged in another direction, thus forming a crossed pattern in dorsal view (Fig. 4D).

Phosphate replaced shell walls can be also seen in cross sections of several fractured specimens of *Archaeospira ornata* Yu. These shell sections comprise the outer and inner phosphate coatings and the phosphate replaced shell wall in between (Fig. 6B, C). Most of the shell wall has been filled with chaotically orientated phosphate granules, but the original fibrillae can still be recognized. They appear to be parallel to the shell surface (Fig. 6B, C).

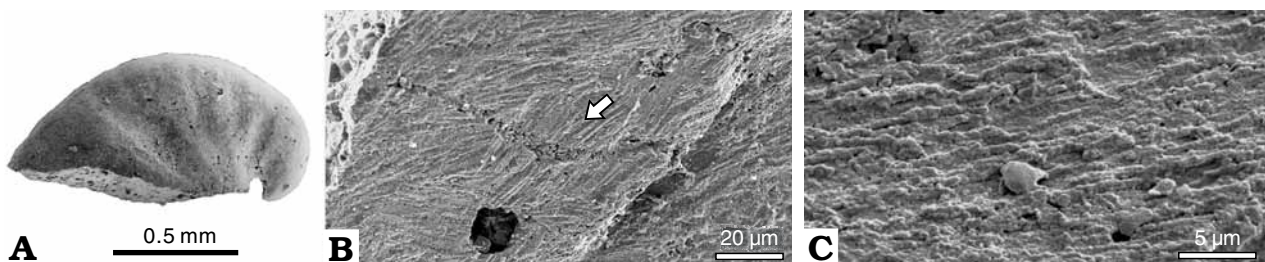


Fig. 5. *Latouchella* cf. *korobkovi* Vostokova, 1962. Specimen NIGP Mo 131371 from yd96924-8A upper part of the Dahai Member, Dahai of Huize in the eastern Yunnan, Meishucunian. A. Lateral view. B, C. Enlargement of place shown by arrow in B, note lamello-fibrillar structure.

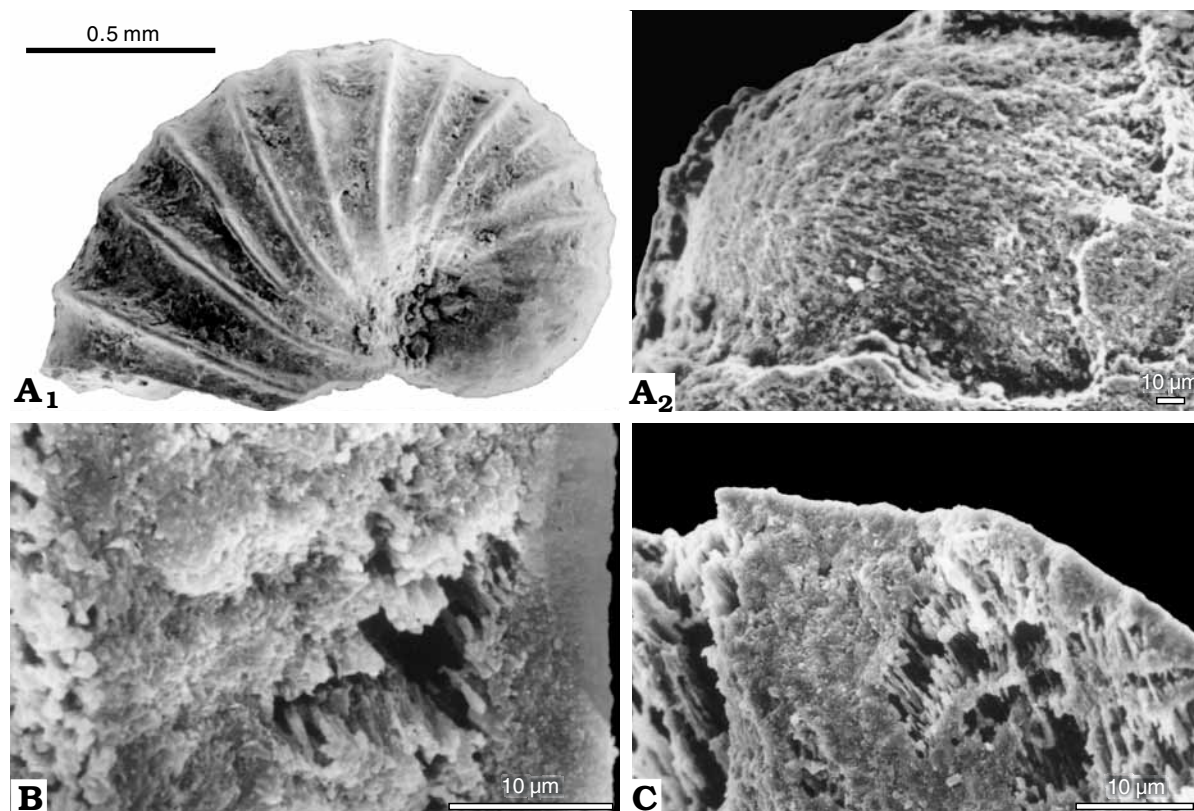


Fig. 6. *Archaeospira ornata* Yu, 1979. A. Specimen NIGP Mo 131370 from sample yd96923-10, upper part of the Dahai Member, Dahai of Huize in the eastern Yunnan, Meishucunian. Apical view (A₁); lamello-fibrillae at the apex (A₂). B. Specimen NIGP Mo 131370A from sample yd9649-2, upper phosphatic bed of the Zhongyicun Member, Yulu of Huize in the eastern Yunnan, Meishucunian. Lamello-fibrillae of the shell wall. C. Specimen NIGP Mo 131365 from yd96923-10, upper part of the Dahai Member, Dahai of Huize in the eastern Yunnan, Meishucunian (note fibrous structure).

Discussion

In this paper we show that phosphate coated and phosphate replaced shell walls from Meishucunian age mollusks can provide important information about original shell microstructure. The preservation of microstructure is rather complex due to diagenesis. It may reflect fine morphology of the inner layer's surface, or sometimes both inner and outer layers and different lamellae. This is because phosphatic granules may replicate fine structures of different layers as the inner layer is progressively destroyed. For example, prismatic and nacreous structures have been found in *Anabarella* sp. and *Mellopegma georginensis* Runnegar and Jell, 1976 (Runnegar 1983, 1985), prismatic and crossed fibrous structure in *Lathamella symmetrica* Li and Chen, 1992, *Anabarella plana* Vostokova, 1962, *Watsonella* sp. (Kouchinsky 1999), *Securiconus* cf. *costulatus* Missarzhevsky, 1989, *Securiconus incertus* Bokova, 1985, and *Pelagiella* cf. *subangulata* (Tate, 1982) (Kouchinsky 2000b), and outer vertical fibres and inner lamello-fibrillar structure in *Ramenta cambrina* (Jiang, 1982) (Feng et al. 2002). The replicated morphology of fine structure may be used to indicate the orientation of crystals and the distribution of organic matter between or within them prior to phosphatization (Fig. 8D). Positive and negative reliefs of

prismatic structure on many internal moulds from the Yangtze platform of China resemble those from the Siberian platform (Kouchinsky 1999: figs. 2B, 3F).

Different modes of phosphatization in the Meishucunian fossils offer information on various aspects of shell structure. For example, in *Ilsanella* the prismatic structure is known from internal moulds (Fig. 8C, D; see also Kouchinsky 2000b: fig. 8) and lamello-fibrillar structure is known from the inner surface of the coating (Fig. 2C, D). The inner and outer layers of the shell shown prismatic and lamello-fibrillar structures, respectively.

Lamello-fibrillar structure is commonly developed among Early Cambrian monoplacophorans and paragastropods (Table 1). However, it should be stressed that lamello-fibrillae are easily to be replicated as a crossed or branched pattern on internal moulds (Figs. 3B–D, 5B, C) due to the diagenesis. The present investigation of the phosphate replaced shell wall of *R. cambrina* clarifies the real aspect of the microstructure. Lamello-fibrillar structure is similar to the crossed lamellar structure of well known extant and fossil mollusks, but it is characterized by only two orders of arrangement and the latter by three orders. However, crossed lamellar structure without well-defined second-order lamellae is present in the Polyplacophora (Haas 1981; Poulicek and Kreusch 1986; Carter and Hall 1990). The polyplacophorans

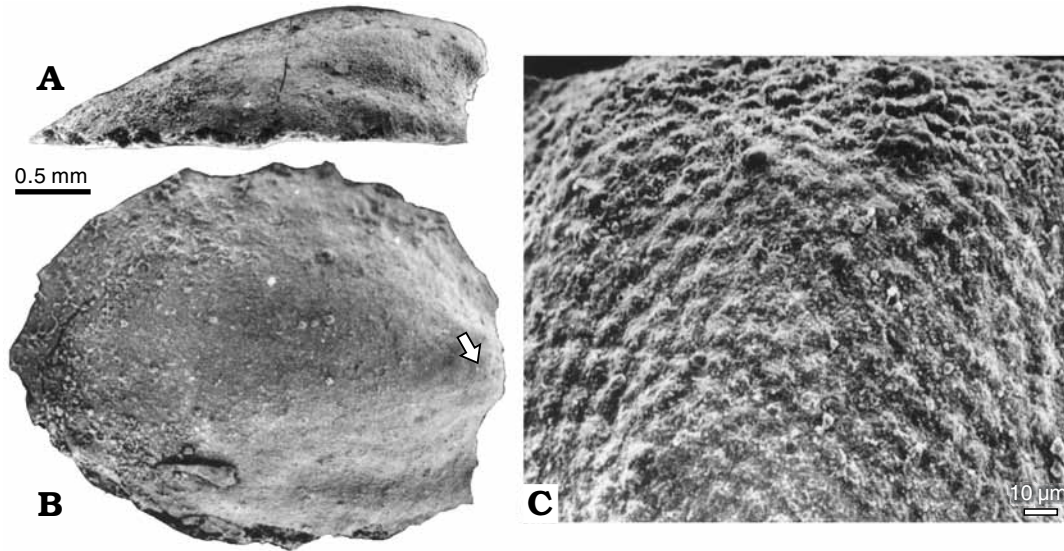


Fig. 7. *Papilloconus explanatus* Feng et al., 2000. Specimen NIGP Mo 131364 from sample yd96924, upper phosphatic bed of the Zhongyicun Member, Baizai of Xundian in the eastern Yunnan, Meishucunian. **A.** Lateral view. **B.** Apical view. **C.** Enlargement of place shown by arrow in B, note regular arrangement of nodules, corresponding to the end of prisms.

and aplacophorans are thought to be primitive within the Mollusca. The shell plates of the polyplacophoran seem to be more primitive than the conchiferan shell (Haas 1981). The thin periostracum-like cuticle of polyplacophorans does not serve as a crystallization surface in biomineralization, the

role usually performed by the conchiferan periostracum. Aragonitic aplacophoran and polyplacophoran spicules and polyplacophoran plates develop in crystallization chambers provided by individual cells or groups of cells below the cuticle. The lamello-fibrillar structure appeared earlier in the fos-

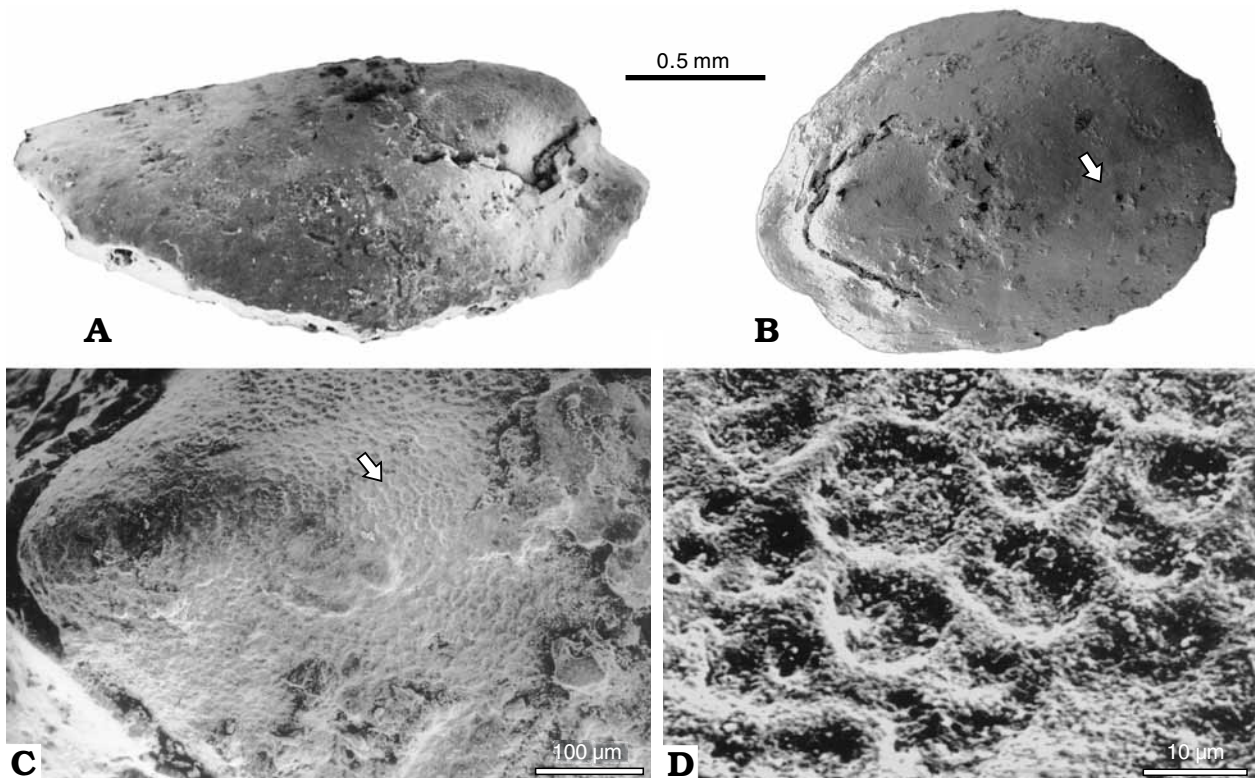


Fig. 8. *Ilsanella? rozanovi* Wang, 1994. Specimen NIGP Mo 131358 from sample yd96924-8, upper phosphatic bed of the Zhongyicun Member, Baizai of Xundian in the eastern Yunnan, Meishucunian. **A.** Lateral view. **B.** Apical view. **C.** Enlargement of place shown by arrow in B, note cross section of prism replicated by internal mould. **D.** Enlargement of place shown by arrow in C.

sil record than laminar structures such as nacreous or foliated structure. It has been identified in fossil mollusks in China as low as the lower phosphate bed of the Zhongyicun Member. Moreover, the nacreous structure of some extant mollusks consists of radial horizontal fibres (Mutvei 1983: fig. 4). Prisms seem to be secondary in evolutionary terms, as documented by the occurrence of fibres on convex polygons (Kouchinsky 2000b: fig. 7G). Therefore, the lamello-fibrillar structure appears to be very primitive in molluscan skeletonization.

Lamello-fibrillar and prismatic aragonite is the most common shell materials of molluscan skeletons in the Early Cambrian Meishucunian and its equivalents around the world. While developing such microstructures the earliest conchiferan mollusks made a leap forward in mechanical quality of their skeleton, especially compared with the uniform granular structure of *Cloudina* Germs, 1972 (Chen Zhe 1999), the only well known and widely distributed skeletal fossil of the latest Precambrian. Although the early molluscan microstructures are not so diverse as in extant mollusks, they may be useful in high rank taxonomic classification. In the early conchiferan mollusks discussed here, crossed lamello-fibres are generally layered and arranged parallel to one another. In hyolith shell the fibres appear to be in the form of bundles of fibres that branch or anastomose (Kouchinsky 2000a; Feng, Mu, and Kouchinsky 2001). The difference in fibre arrangement between early mollusks and hyoliths testifies that diversification within fibrous structures occurred before the beginning of the Cambrian.

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