

On the Genus *Auricullina* Vassiljeva, 1998 and Shell Pores of the Cambrian Helcionelloid Mollusks

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Abstract—The genus *Auricullina* Vassiljeva, 1998 and its type species *A. papulosa* Vassiljeva, 1998 are redescribed based on new well-preserved material, which allows me to revise the generic diagnosis and greatly add to the morphological characterization of the type species. A new species, *A. granulosa* sp. nov., is described from the Botomian of Australia. The synonymy of the taxa is improved. The morphology and function of shell pores in Cambrian univalved mollusks are discussed.

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INTRODUCTION

The article continues the revision of Cambrian mollusks from Siberia undertaken by the author in his previous papers (Parkhaev, 2004, 2005). It includes the redescription of the genus *Auricullina* Vassiljeva, 1998 and its type species *A. papulosa* Vassiljeva, 1998 and the description of a new species, *A. granulosa* sp. nov. The first species is widely distributed in the middle part of the Tommotian Stage of the Siberian Platform and has a very peculiar morphology; thus, it is easily recognizable and may be useful for correlation. The second species is scarce, it is described on the base of two specimens from the Botomian of South Australia. The genus *Auricullina* should be redescribed because the original description (Vassiljeva, 1998) is based on five poorly preserved specimens of *A. papulosa*; hence, the diagnosis of the genus is not correct. New material of good preservation allows me to revise the generic diagnosis, to add new characters to the description of its type species, and, in addition, to improve the synonymy of these taxa. The morphology of shell pores in Cambrian univalved mollusks is discussed after the Systematic Paleontology section.

MATERIAL

The material studied is housed in the Paleontological Institute of the Russian Academy of Sciences (PIN), Moscow, under collection nos. 2019, 4664, and 5083.

SYSTEMATIC PALEONTOLOGY

CLASS GASTROPODA CUVIER, 1797

SUBCLASS ARCHAEOBRANCHIA
PARKHAEV, 2001

Order Helcionelliformes Golikov et Starobogatov, 1975

Superfamily Helcionelloidea Wenz, 1938

Family Helcionellidae Wenz, 1938

Genus *Auricullina* Vassiljeva, 1998

Auricullina Vassiljeva: Vassiljeva, 1998, p. 79 (non *Auricullina* Grateloup, 1838; non *Auricullina* Gray, 1847 [= *Ondina* de Folin, 1870]).

Punctella Zhong: Missarzhevsky, 1989, p. 176; Kouchinsky, 2000, p. 138; Feng and Sun, 2003, p. 24 (non Zhong, 1977, p. 122, 184).

Type species. *Auricullina papulosa* Vassiljeva, 1998 (by original designation); Lower Cambrian, Tommotian Stage, Siberian Platform.

Diagnosis. Shell cap-shaped, depressed, relatively wide. Apex pointed, shifted back beyond posterior apertural margin, and slightly bent downwards. Anterior field convex, lateral fields slightly convex or flattened, posterior field short and slightly concave. Aperture simple, without sinus, egg-shaped, with widely rounded anterior and extended posterior margins. Exterior shell ornamentation unknown. Internal mold covered by small papillae or cylindrical granules.

Composition. *A. papulosa* Vassiljeva, 1998 and *A. granulosa* sp. nov.

Comparison. The genus differs from all members of the family with a similar shell shape in the presence of small papillae or cylindrical granules on the surface of the internal mold.

Remarks. Zhong described the fossil *Punctella maidipingensis* from the Lower Cambrian of China and ascribed it to brachiopods (Zhong, 1977, p. 122, pl. 4, figs. 1, 2, 4). According to the original description, the species is represented by 1-mm-long bivalved biconvex shells with a smooth dorsal valve and more convex ventral valve, the surface of which is ornamented with fine, densely spaced pits. Along with that species, Zhong also described and illustrated shells ornamented with distinct, regularly placed granules or tubercles (Zhong, 1977, p. 122, pl. 4, figs. 3, 5). He referred to them as “brachiopod-like forms” without using any Latin

binomen. Subsequently, Missarzhevsky (1989) mistook these forms for *Punctella maidipingensis* Zhong. Kouchinsky (2000, pp. 123, 138) repeated this mistake (Kouchinsky, 2000, p. 123, 138), while Feng and Sun cited Kouchinsky (Feng and Sun, 2003, p. 24).

Auricullina papulosa Vassiljeva, 1998

Plate 3, figs. 1–4

Auricullina papulosa Vassiljeva: Vassiljeva, 1998, p. 79, pl. 10, figs. 1–6.

Punctella maidipingensis Zhong: Missarzhevsky, 1989, p. 176, pl. 10, fig. 4; Kouchinsky, 2000, p. 138; Feng and Sun, 2003, p. 24 (non Zhong, 1977, p. 122, 184, pl. 4, figs. 1, 2, 4).

Unnamed form 1: Kouchinsky, 2000, p. 126, text-figs. 5A–5F.

Undetermined steinkern: Steiner *et al.*, 2004, p. 261, fig. 4.12 (non fig. 6.14).

H o l o t y p e. VNIGRI, no. 732/140, internal mold; Russia, Yakutia, Anabar Region, Olenek River, Boroulakh Section; Lower Cambrian, upper part of Tommotian Stage, Erket Formation, lower part.

D e s c r i p t i o n (Fig. 1). The shell is cap-shaped, rapidly and evenly expanding from the apex towards the aperture, wide (about 1.5 times as wide as long) and rather low (about 2.0 times as long as high). The apex is pointed, shifted backwards to extend beyond the posterior shell edge for a distance of one-fifth to one-sixth of the shell length, and slightly bent downwards. The anterior field of the shell is evenly convex; the lateral fields are slightly convex; the posterior field is short, slightly concave, and flattens below the apex. The aperture is simple, without sinus, egg-shaped, with widely rounded anterior and extended posterior margins. The outer shell surface is unknown. The protoconch is unknown. The surface of the internal mold has mammillated microornamentation, represented by small, closely spaced papillae, which are 7–15 μm wide, 20 μm long, and pointed apically. The base of each papilla is located in a wide (30 μm in diameter) pit. The mammillated microornamentation is replaced by a polygonal relief in the apical area (Fig. 1e) and in the posterolateral corners (Figs. 1c, 1d) of the internal mold. In the apical area the polygonal relief looks like a smooth net composed of narrow (3- μm -wide) balks, which divide shallow polygonal depressions, 15 μm in diameter. The posterolateral areas of the mold bear distinct polygons, 5–6 μm in diameter, divided by narrow (1- μm -wide) furrows. Possibly, the smoothed polygonal microrelief of the apical area of the internal mold is an impression of the epithelial cells of mantle, while the more distinct polygonal microrelief of the posterolateral areas is an imprint of the pallial myostracum, which has a prismatic structure (Ushatinskaya and Parkhaev, 2005). Sometimes, the surface of the internal mold has faint radial folds.

M e a s u r e m e n t s in μm :

| Specimen no. | Shell length | Shell height | Shell width |
|--------------|--------------|--------------|-------------|
| 5083/0038 | 810 | 370 | 630 |
| 5083/0039 | 735 | – | 480 |
| 5083/0040 | 690 | 340 | (425) |
| 5083/0335 | 1923 | 1125 | 1225 |

C o m p a r i s o n. The species differs from *A. granulosa*, with a similar shell shape, in the posterior field flattened in the subapical area and in the mammillated (instead of granulated) microornamentation of the internal mold surface.

O c c u r r e n c e. Lower Cambrian, Tommotian Stage of the Siberian Platform and China (Shaanxi Province, Ningqiang County, Yuanjiaping).

M a t e r i a l. Over dozen internal moulds and fragments from different localities in the Anabar Region (Fomich River, coll. N.P. Meshkova; Olenek River, coll. G.A. Karlova); from the middle reaches of the Lena River (Tiktirikteekh Creek, coll. V.V. Missarzhevsky); and from the Uchur–Maya Region (Dzhanda and Khobolokh rivers, Mt. Konus, coll. G.A. Karlova; Aldan River, N.P. Meshkova).

Auricullina granulosa Parkhaev, sp. nov.

Plate 4, figs. 1 and 2

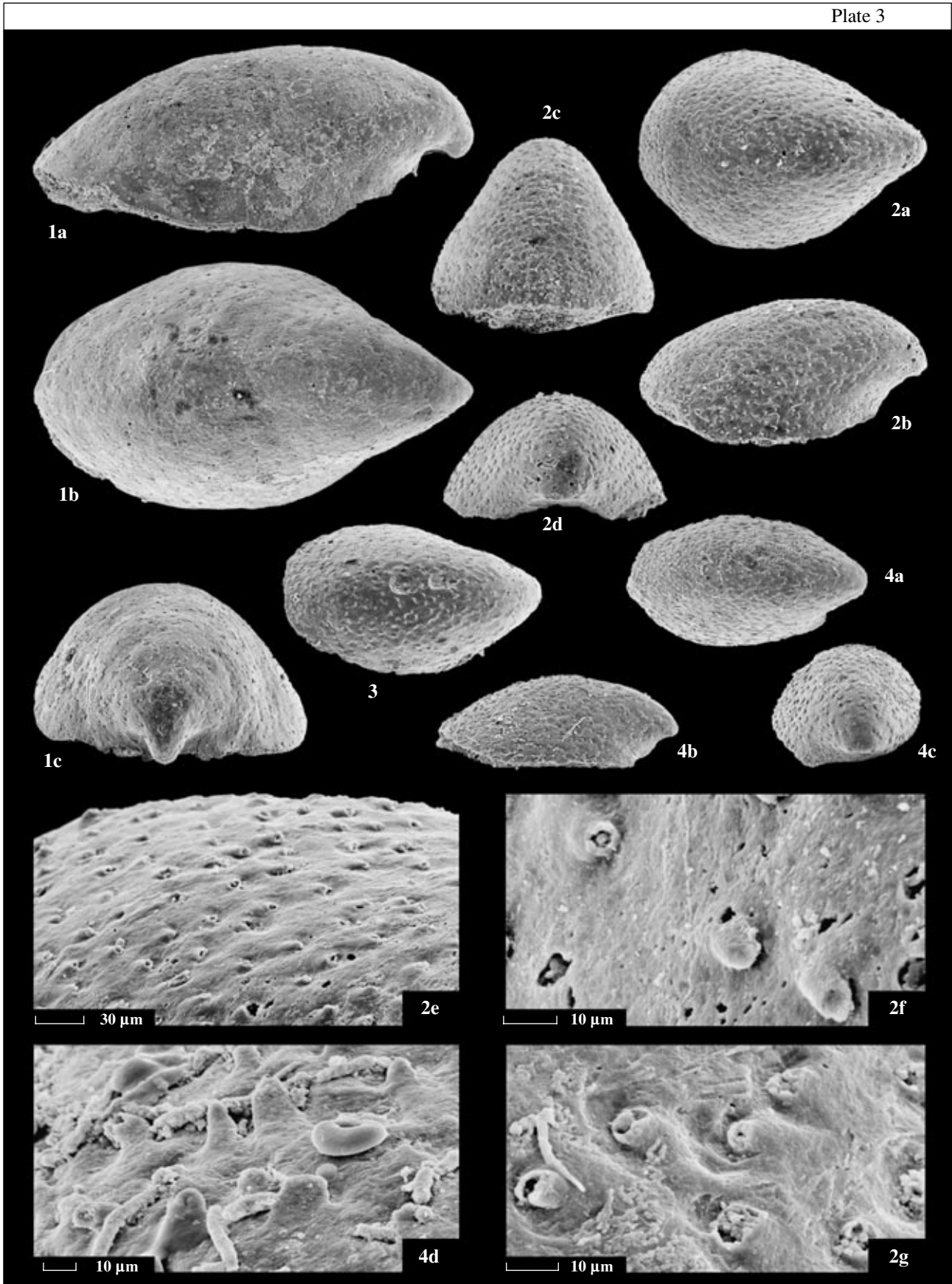
E t y m o l o g y. From the Latin *granulosus* (granulated).

H o l o t y p e. PIN, no. 4664/1640, internal mold; South Australia, Yorke Peninsula, borehole SYC-101, depth 201.45 m; Lower Cambrian, Botomian Stage, *Stenotheca drepanoidea* Beds.

D e s c r i p t i o n. The shell is cap-shaped, evenly and rapidly expanding from the apex towards the aperture, wide (about 0.77 times as wide as long), and rather low (about twice as long as high). The apex is pointed, shifted backwards to extend beyond the posterior shell edge for a distance of one-sixth of the shell length, and slightly bent downwards. The anterior field of the shell is evenly convex and flattens towards the aperture, the lateral fields are slightly convex, the posterior field is short and slightly concave. The aperture is simple, without sinus, widely egg-shaped, with widely rounded anterior and slightly extended posterior margins. The outer ornamentation of the shell is unknown. The protoconch is unknown. The surface of the internal mold has granulated microornamentation represented by small cylindrical granules, about 15 μm in diameter and up to 20 μm long. The axes of the granules are perpendicular to the surface of the mold. The granules may occasionally accumulate in the apical area of the mold (Pl. 4, fig. 2e).

M e a s u r e m e n t s, in μm :

| Specimen no. | Shell length | Shell height | Shell width |
|----------------------|--------------|--------------|-------------|
| 4664/1640 (holotype) | 1260 | 600 | 980 |
| 4664/1529 | 1240 | 585 | (940) |



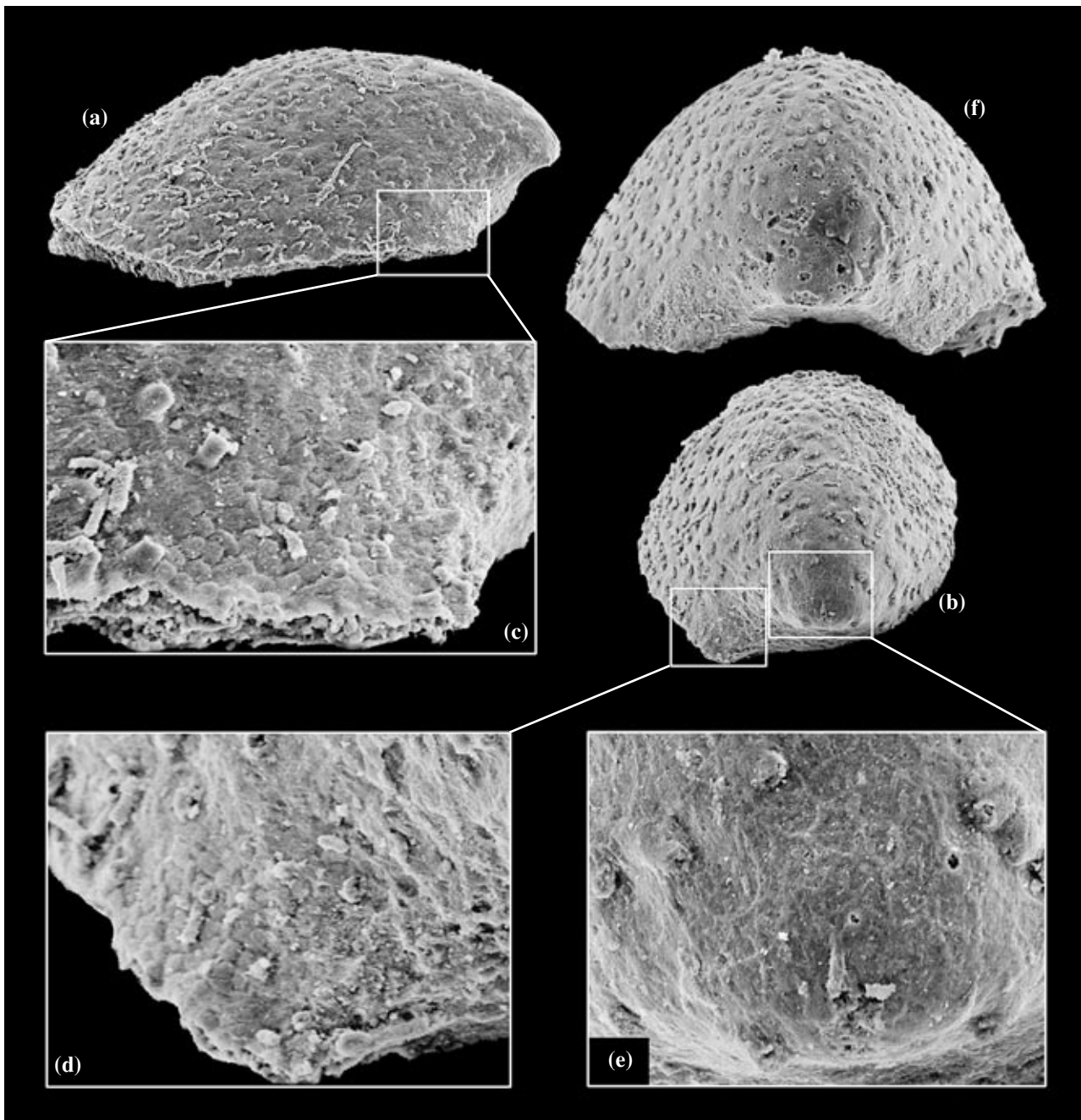
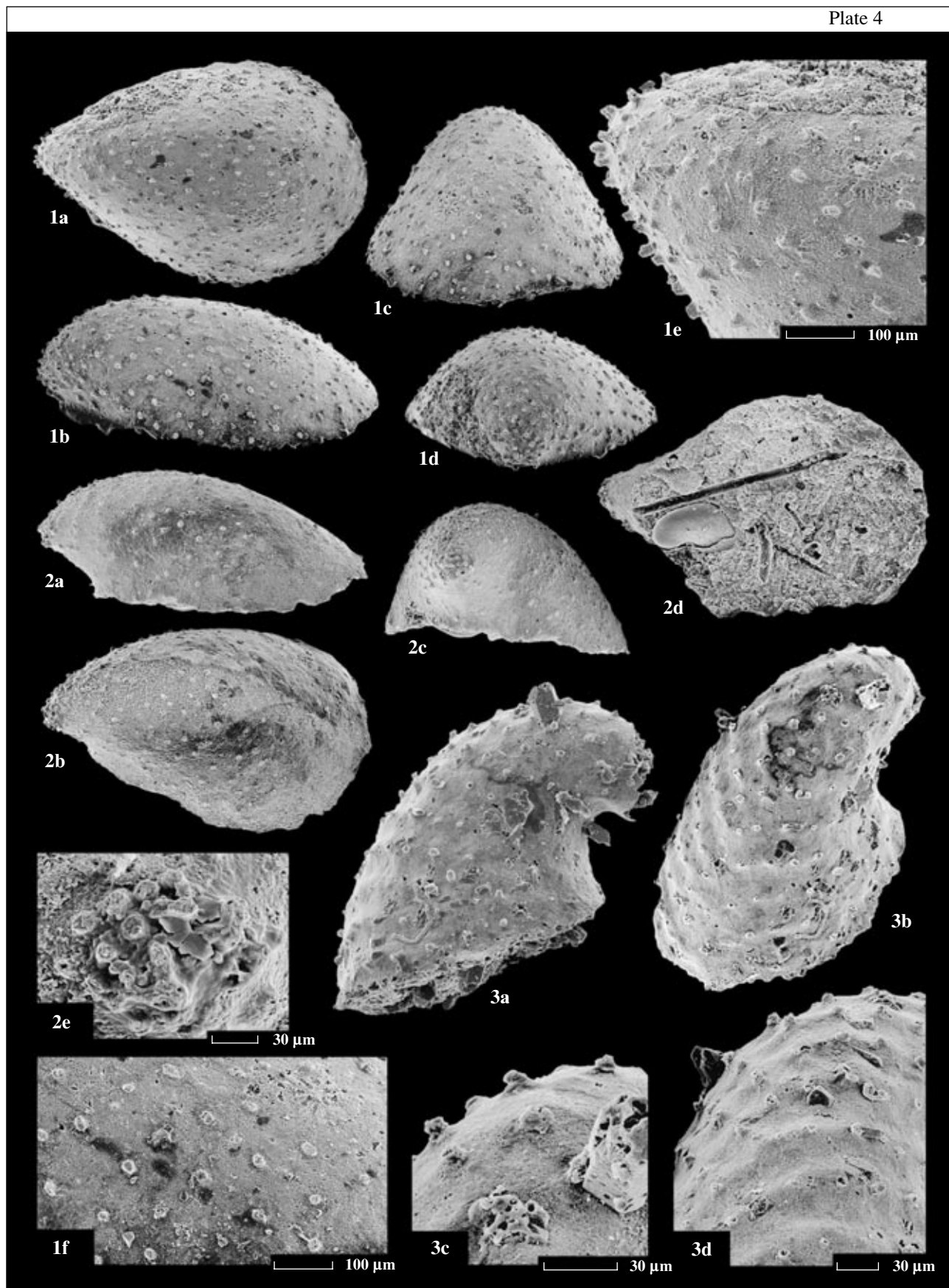


Fig. 1. *Auricullina papulosa* Vassiljeva, 1998; Lower Cambrian, Tommotian Stage, *tortuosa* Subzone; Siberian Platform, middle reaches of the Lena River (Tiktirikteekh Creek, locality M303/2; see Rozanov *et al.*, 1969, text-figs. 5, 6); (a–e) specimen PIN, no. 5083/0039, internal mold: (a) left view, $\times 120$; (b) oblique posterior view, $\times 120$; (c) fragment of the posterolateral mold surface with a distinct polygonal microrelief (supposed imprint of pallial myostracum), $\times 530$; (d) same area, $\times 590$; (e) fragment of the apical area of the mold with smoothed polygonal microrelief (supposed imprint of cells of the mantle epithelium), $\times 530$; (f) specimen PIN, no. 5083/0038, internal mold, posterior view; the posterolateral areas of the mold surface lack mammillated microornamentation and possibly are attachment sites of shell muscles, $\times 120$.

Explanation of Plate 3

Figs. 1–4. *Auricullina papulosa* Vassiljeva, 1998; specimen, no. 5083/0335, internal mold: (1a) left view, $\times 44$; (1b) dorsal view, $\times 44$; (1c) posterior view, $\times 44$; Siberian Platform, Aldan River, sample no. 3121/9 (coll. N.P. Meshkova); (2) specimen PIN, no. 5083/0038, internal mold: (2a) dorsal view, $\times 67$; (2b) oblique left view, $\times 67$; (2c) oblique anterior view, $\times 67$; (2d) posterior view, $\times 67$; (2e–2g) fragments of mold surface with mammillated microornamentation; Siberian Platform, middle reaches of the Lena River, Tiktirikteekh Creek, locality M303/2 (see Rozanov *et al.*, 1969, text-figs. 5, 6); Lower Cambrian, Tommotian Stage, *tortuosa* Subzone; (3) specimen PIN, no. 5083/0039, internal mold, dorsal view, $\times 67$; same age and locality; (4) specimen PIN, no. 5083/0040, internal mold: (4a) dorsal view, $\times 67$; (4b) left view, $\times 67$; (4c) oblique posterior view, $\times 67$; (4d) fragment of mold surface with mammillated microornamentation; same age and locality.



Comparison. See description of *A. papulosa*.

Remarks. A similar unnamed brachiopod-like form was described and illustrated by Zhong from the Lower Cambrian of South China (Zhong, 1977, p. 122, pl. 4, figs. 3, 5). It is difficult to determine the exact age of this find because the fossil assemblage as a whole has a Tommotian appearance; however, such forms as *Pelagiella* sp. (Zhong, 1977, pl. 2, figs. 12, 13) suggest a younger, possibly Atdabanian–Botomian, age of the assemblage or, at least, of part of it.

Occurrence. Lower Cambrian, Botomian Stage of South Australia, and probably, the middle part of the Lower Cambrian of South China.

Material. Two specimens from the type locality.

SHELL PORES OF CAMBRIAN MOLLUSKS

The character of the internal mold ornamentation in the species just described, *A. papulosa* and *A. granulosa*, allows me to assume that papillae of mammillated microornamentation and cylindrical granules of granulate microornamentation replicate the pore structures of the shell wall in these species. The presence of pores within the shell wall of ancient mollusks was already reported by Kouchinsky (2000). He briefly described the “tuberculated” microornamentation of the internal mold, which possibly represents a replica of the shell pores of the following forms from the Tommotian–Botomian of the northern Siberian Platform: Unnamed form 1 [= *Auricullina papulosa* Vass.], Unnamed form 2 [= *Postacanthella* sp.], Unnamed form 3 [= *Mellopegma uslonica* Parkhaev, 2004], and *Mackinnonia* sp. [= *M. anabarica* Parkhaev, 2005]. In the table the list of species with similar microornamentation of the internal mold is considerably extended both taxonomically and in respect to the morphological diversity of sculptural elements as well.

The pores in the mineralized layer of shell are known in almost all classes of recent mollusks. Schröder (1907) was the first to describe them in freshwater clams of the family Sphaeriidae. Later similar pores or channels, which were referred to as tubuli or caecae, were found in other groups of freshwater and marine bivalves (Rosso, 1954; Omori *et al.*, 1962; Omori and Kobayasi, 1963; Oberling, 1964; Hudson, 1969; Waller, 1980; Tiu and Prezant, 1989; Kirichuk

and Stadnichenko, 1997), monoplacophorans (Warén, 1988; Warén and Bouchet, 1990), and scaphopods (Ivanov and Memmi, 1989). The pores in gastropod shells are common mainly in members of primitive groups, i.e., Cyclobranchia [= Docoglossa] (Haszprunar, 1988), Scissurellidae and Fissurellidae (Reindl and Haszprunar, 1994), and in so-called “hot-vent groups,” Neomphalidae, Peltospiridae, and Lepetodrilidae from deep-sea hot vents (Kiel, 2004; Sasaki, 1998; Sasaki *et al.*, 2004).

Similar structures of polyplacophorans, aesthetes (microaesthetes and megaesthetes), penetrate the entire wall of the valves (Boyle, 1976; Sirenko, 1992) and are closed on the outer valve surface by perforated apical caps (Currie, 1989).

In spite of the morphological similarity of channels in shells of different taxonomic groups of mollusks, cytological and ontogenetic studies revealed their heterogeneity and, consequently, nonhomologous nature (Reindl and Haszprunar, 1996). However, the morphological similarity of these structures suggests their functional similarity. Thus, we can admit that channels and pores in shells of the earliest members of the phylum Mollusca performed a function analogous to that performed by these structures in modern organisms.

The functional significance of aesthetes, tubuli, and caecae of recent mollusks is not yet known in detail (Hudson, 1969; Togo *et al.*, 1993; Kouchinsky, 2000). It was suggested that they are important in metabolism (respiration and synthesis, transportation, and storage of high-molecular compounds) and biomineralization and can perform sensory, protective (against boring organisms), and/or mechanical functions (Reindl and Haszprunar, 1996). For some groups it was proposed that the shell pores of an animal are used to repair a damaged periostracum (Baxter *et al.*, 1987). This assumption is confirmed by observations on polyplacophorans, the aesthetes of which are more closely spaced in those species that are exposed to more intense wave abrasion (Currie, 1989).

The arrangement of pores over the internal shell surface is rather peculiar in some recent mollusks. The highest density of pores occurs in the umbonal area of bivalves, whereas the pores are seldom in muscle scar regions and always absent near the valve edge below the pallial line (Kirichuk and Stadnichenko, 1997).

Explanation of Plate 4

Figs. 1 and 2. *Auricullina granulosa* sp. nov.; South Australia, Yorke Peninsula; Lower Cambrian, Botomian Stage, Parara Limestone; (1) holotype no. 4664/1640, internal mold: (1a) dorsal view, $\times 50$; (1b) oblique right view, $\times 50$; (1c) oblique anterior view, $\times 50$; (1d) oblique posterior view, $\times 50$; (1e, 1f) fragments of mold surface with granulate microornamentation; borehole SYC-101, depth 201.45 m, *Stenotheca drepanoidea* Zone (see Gravestock *et al.*, 2001, text-figs. 11, 16); (2) specimen PIN, no. 4664/1529, internal mold: (2a) right view, $\times 50$; (2b) oblique dorsal view, $\times 50$; (2c) oblique posterior view, $\times 50$; (2d) apertural view, $\times 50$; (2e) granules in the apical area; Curramuka Quarry, sample no. Cur-10, *Bemella communis* Zone (see Gravestock *et al.*, 2001, text-figs. 10, 16).

Fig. 3. *Daedalia daedala* Parkhaev in Gravestock *et al.*, 2001; holotype, no. 4664/0511, internal mold: (3a) left view, $\times 150$; (3b) oblique left view, $\times 150$; (3c, 3d) fragments of mold surface with granulate microornamentation; South Australia, Yorke Peninsula; Lower Cambrian, Botomian Stage, Parara Limestone, Horse Gully section, sample no. HG6, *Bemella communis* Zone (see Gravestock *et al.*, 2001, text-figs. 7, 16).

The species of Cambrian mollusks with internal mold microornamentation that can be interpreted as a cast of shell pores

| Species | Family | Locality | Age | Reference | Type of microornamentation |
|---|-----------------|---|-------------------------|---|---|
| <i>Auricullina papulosa</i> Vassiljeva, 1998 | Helcionellidae | Siberian Platform: Anabar Region, Aldan-Lena and Uchur-Maya regions; China: Shaanxi, uppermost Dengying Formation | Tommotian Stage | Kouchinsky, 2000, text-figs. 5A–5F (Unnamed form 1); Steiner <i>et al.</i> , 2004, fig. 4.12; this paper, Pl. 3, figs. 1–4, Fig. 1 | Conical papillae 7–15 µm in diameter and 20 µm long |
| <i>Auricullina granulosa</i> sp. nov. | Helcionellidae | South Australia, Yorke Peninsula, Parara Limestone | Botomian Stage | This paper, Pl. 4, figs. 1, 2 | cylindrical granules up to 15 µm in diameter and up to 20 µm long |
| <i>Postacanthella elegans</i> Yue, 1984 | Helcionellidae | China: Shaanxi, uppermost Dengying Formation | Tommotian Stage | Xing <i>et al.</i> , 1984, p. 164, pl. 26, figs. 1, 2 | Conical papillae about 30 µm in diameter |
| <i>Postacanthella</i> sp. | Helcionellidae | Siberian Platform: Anabar Region | Tommotian Stage | Kouchinsky, 2000, text-figs. 5G–5K (Unnamed form 2) | Conical papillae 10–15 µm in diameter |
| <i>Tuberoconus paucipalillae</i> Yue, 1984 | Helcionellidae | China: Shaanxi, uppermost Dengying Formation | Tommotian Stage | Xing <i>et al.</i> , 1984, p. 160, pl. 26, figs. 8, 9 | Hemispheric granules about 15–20 µm in diameter |
| <i>Daedalia daedala</i> Parkhaev, 2001 | Helcionellidae | South Australia, Yorke Peninsula, Parara Limestone | Botomian Stage | Gravestock <i>et al.</i> , 2001, p. 147, pl. 27, figs. 4, 5; present paper, Pl. 4, fig. 3 | Conical tubercles with spherical granules 10–12 µm in diameter |
| <i>Anhuiconus microtubens</i> Zhou et Xiao, 1984 | Coreospiridae | China: Henan and Anhui; South Australia: Yorke Peninsula, Parara Limestone | Atdaban-Botomian stages | Zhou and Xiao, 1984, p. 128, pl. 1, figs. 1–6; Feng <i>et al.</i> , 1994, p. 4, pl. 4, figs. 1, 2; Gravestock <i>et al.</i> , 2001, p. 164, pl. 30, figs. 1–7; present paper, Figs. 6d–6g | Small granules 2–3 µm in diameter |
| <i>Mackinnonia anabarica</i> Parkhaev, 2005 | Trenellidae | Siberian Platform: Anabar Region | Botomian Stage | Parkhaev, 2005, p. 44, pl. 2, figs. 2a and 2e; Kouchinsky, 2000, text-figs. 5L–5O (<i>Mackinnonia</i> sp.) | Conical tubercles with a blunt top, diameter 10–20 µm |
| <i>Leptostega hyperborea</i> Parkhaev, 2005 | Trenellidae | Siberian Platform: Anabar Region | Botomian Stage | Parkhaev, 2005, p. 45, pl. 2, fig. 1f | Small granules about 3 µm in diameter |
| <i>Mellopegma uslonica</i> Parkhaev, 2004 | Stenotheceidae | East Transbaikalia and Siberian Platform: Anabar Region | Botomian Stage | Kouchinsky, 2000, text-figs. 5L–5O (Unnamed form 3); Parkhaev, 2004, p. 19, pl. 2, figs. 5–9; present paper, Fig. 2 | Spherical granules about 8–10 µm in diameter |
| <i>Philoxenella spiralis</i> Vostokova, 1962 | Khairkhaniiidae | Siberian Platform: Anabar Region and Aldan-Lena Region | Tommotian Stage | Present paper, Fig. 4 | Small granules about 3–6 µm in diameter |
| <i>Khairkhania rotata</i> Missarzhevsky, 1981 | Khairkhaniiidae | Mongolia and Siberian Platform | Tommotian Stage | Present paper, Fig. 3 | Columns 3–6 µm in diameter and about 20 µm long |
| <i>Barskovia hemisymmetrica</i> Golubev, 1976 | Khairkhaniiidae | Mongolia and Siberian Platform | Tommotian Stage | Present paper, Fig. 5 | Small granules about 3–5 µm in diameter |
| <i>Nongoliella australiensis</i> Parkhaev, 2001 | Aldanellidae | South Australia: Yorke Peninsula, Parara Limestone and Flinders Range, Mermerna Formation | Botomian Stage | Gravestock <i>et al.</i> , 2001, p. 197, pl. 48, figs. 1–5; present paper, Figs. 6a–6c | Granules 5–7 µm in diameter |

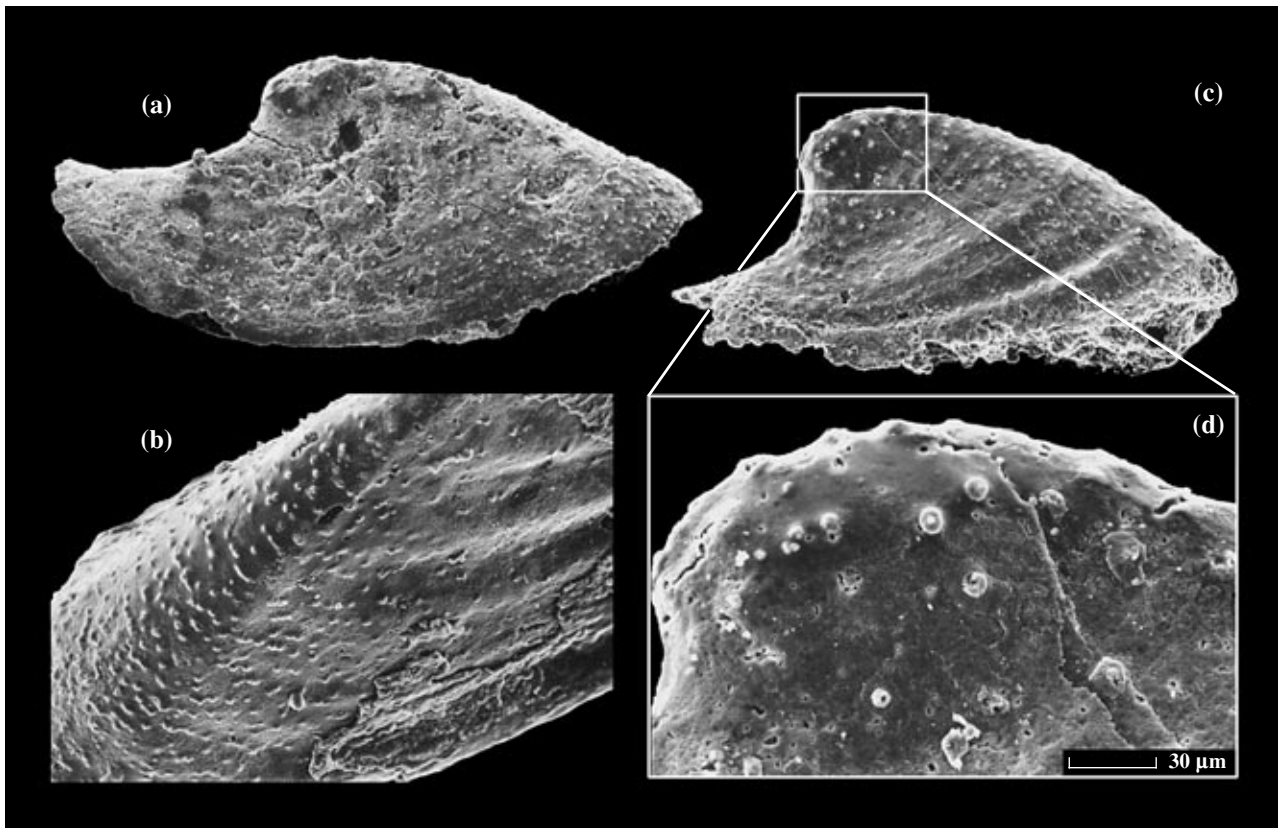


Fig. 2. *Mellopegma uslonica* Parkhaev, 2004; Lower Cambrian, Botomian Stage, Uslon Section, village of Georgievka, eastern Transbaikalia: (a) specimen PIN, no. 2019/1047, internal mold, right view, $\times 85$; (b) holotype, no. 2019/1051, fragment of the anterolateral surface of a mold with granulate microornamentation, $\times 155$; (c, d) specimen PIN, no. 2019/1125, internal mold: (c) right view, $\times 85$; (d) fragment of the apical area of a mold with granulate microornamentation.

Similar data were obtained by other authors, except for observation that pores are completely absent from the attachment areas of adductors (Togo *et al.*, 1993). This pattern of pore distribution in the shell can be explained as follows. The channels host the appendages of the outer mantle epithelium, which fasten the mantle to the shell. The necessity of such fixation disappears in areas of adductor scars, where the muscle fibers are attached to the prismatic pallial myostracum, and near the shell edge, where the mantle retains mobility.

It is noteworthy that in some species of Cambrian gastropods (i.e., *Auricullina papulosa*, Fig. 1) the areas of supposed muscle attachment (posterolateral regions of the shell with a prismatic wall structure) also lack channels. This conformity of paleontological data to observations on recent forms supports the assumption that mammillated microornamentation of the internal mold of these species is a replica of the pore system of the shell wall, while the prominent areas of the mold with polygonal microornamentation (Figs. 1c, 1d) are an imprint of the pallial myostracum.

The aesthetes of recent polyplacophorans perform a photoreceptive function (Smith, 1960), i.e., they act as photoreceptive “eyes” on the animal dorsum. This is supported by the pronounced photonegative response to

irritation by direct light (Arey and Crozier, 1919; Currie, 1989). A photoreceptive function for the mantle appendages in blind channels (covered by an outer organic layer, periostracum) of pelecypod shells is also supposed (Togo *et al.*, 1993). A similar function of shell channels cannot be excluded for some ancient mollusks. If this is true, the spherical structures on the internal molds of *Mellopegma* (Fig. 2) and *Daedalia* (Pl. 4, fig. 3) can be interpreted as molds of microcavities within a wall that may have hosted photoreceptive cells.

A fairly distinctive structure is present in a few specimens of the species *Khairkhanina rotata* Missarzhevsky, 1981 (Fig. 3). Long, thin phosphate columns (3–6 μm in diameter and about 20 μm long) remain in place when the carbonate shell substance was dissolved by treatment with acetic acid. The columns connect the internal mold surface with a thin phosphate envelope that coated the exterior of the shell. The internal mold surface has imprints of the cross-lamellar microstructure of the shell (Fig. 3f) or, more rarely, phosphatized fragments of its elements, i.e., aggregates of fibers (Figs. 3g, 3h). A similar structure was described in brachiopods (Ushatinskaya, 1995, photographs 75, 80, 83a) and was referred to as the “columnar type of microstructure” (Holmer, 1989; Ushatinskaya, 1996). The

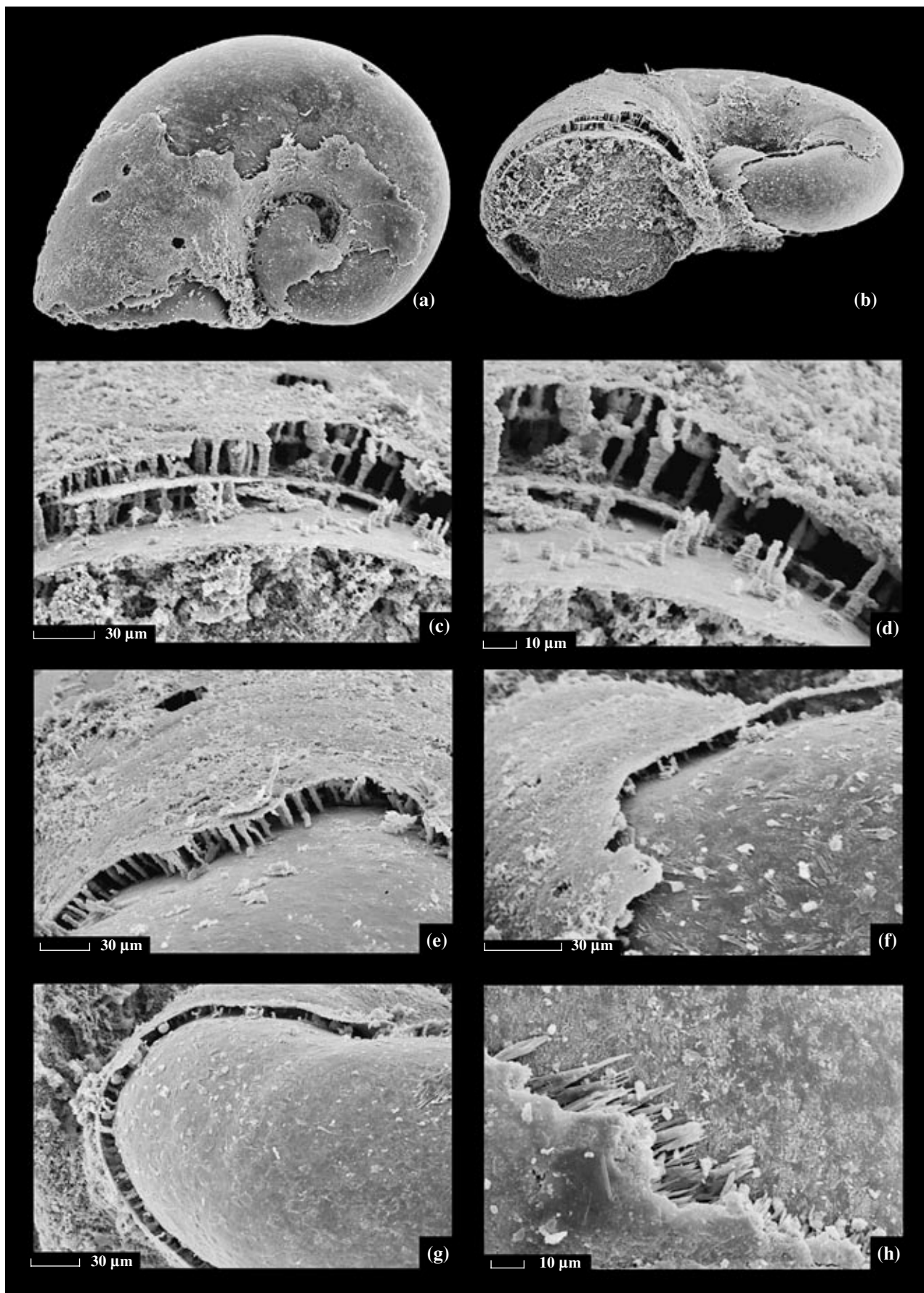


Fig. 3. *Khairkhanina rotata* Missarzhevsky, 1981; Tommotian Stage, Rassokha River, sample 152a (coll. V.E. Savitskii), Siberian Platform; specimen PIN, no. 5083/0153; internal mold with fragments of shell: (a) left view, $\times 78$; (b) apertural view, $\times 78$, (c–e) secondary columnar microstructure of the shell (secondary phosphatization of the organic matter that filled the tubuli); (f) imprint of the original cross-lamellar microstructure of the shell on the surface of internal mold; (g) secondary columnar microstructure of the shell, imprint of the original cross-lamellar microstructure of the shell on the surface of internal mold, and phosphatized fragments of fibers (top right); and (h) phosphatized fragments of fibers that formed the original cross-lamellar microstructure of the shell.

origin of this microstructure is connected with the diagenetic repartition of calcium phosphate within the brachiopod shell, which is accompanied by phosphatization of organic layers of the valves and soft animal tissues (Ushatinskaya, 1995). It has been shown in lingulate brachiopods that the phosphate columns connecting the horizontal lamellae are a result of post-mortem phosphatization of organic threads, which entered the pores penetrating the wall of the shell.

The morphology and chemical composition of the columnar microstructure of *Khairkhanina rotata* suggest that the shell of this species underwent a similar process, with the only difference being that the original composition of the shell substance is carbonate rather than phosphate. Thus, one can assume that columns are phosphatized contents of tubuli, which penetrated the calcareous wall of the mollusk shell. Possibly, the thin external phosphate envelope is a phosphatized perios-

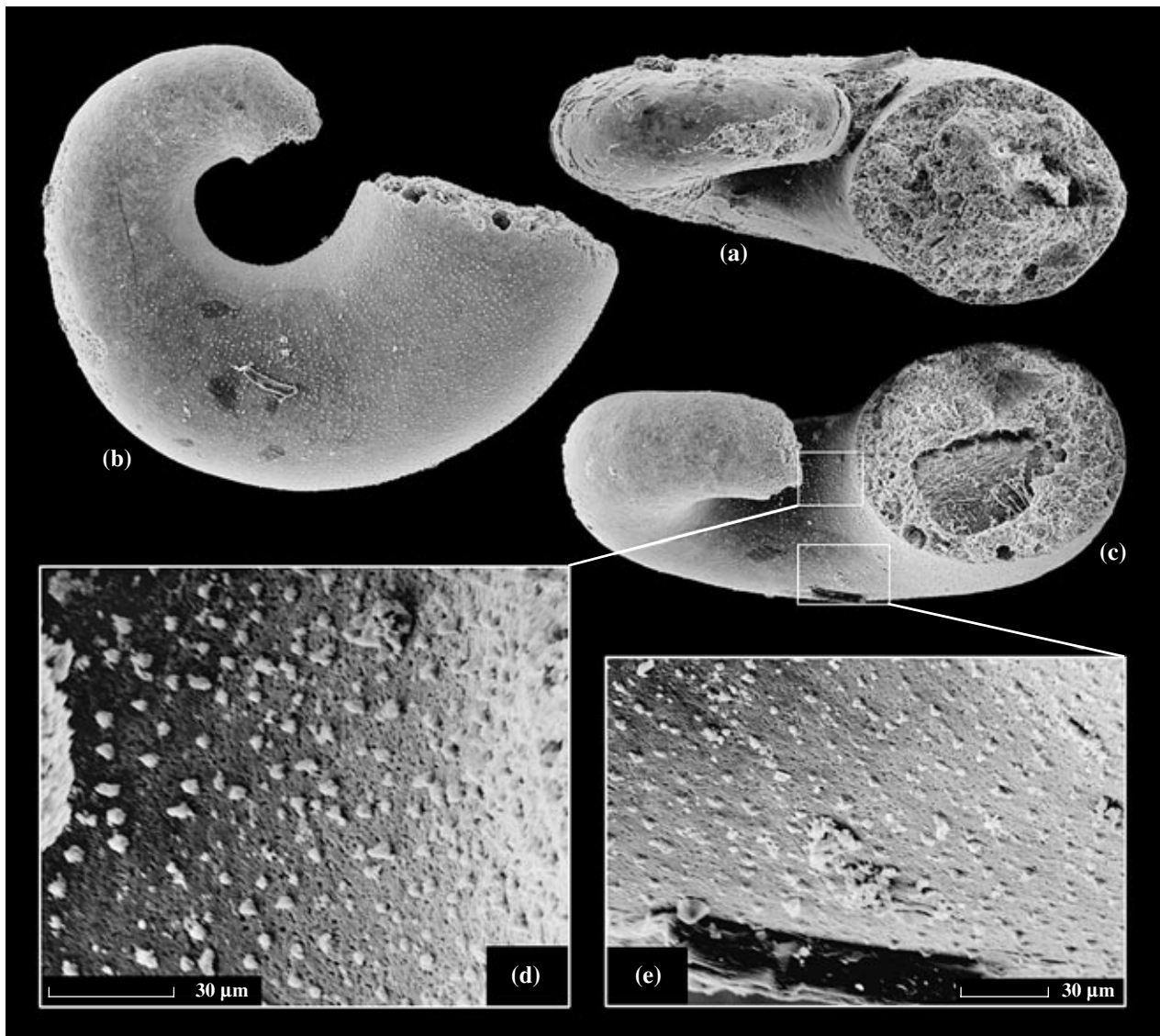


Fig. 4. *Philoxenella spiralis* Vostokova, 1962; Tommotian Stage, Aldan River, sample no. 3121/9 (coll. N.P. Meshkova), Siberian Platform: (a) specimen PIN, no. 5083/0346, internal mold, apertural view, $\times 71$; (b–e) specimen PIN, no. 5083/0345, internal mold: (b) basal view, $\times 71$; (c) oblique apertural view, $\times 71$; (d, e) granular microornamentation of the internal mold.

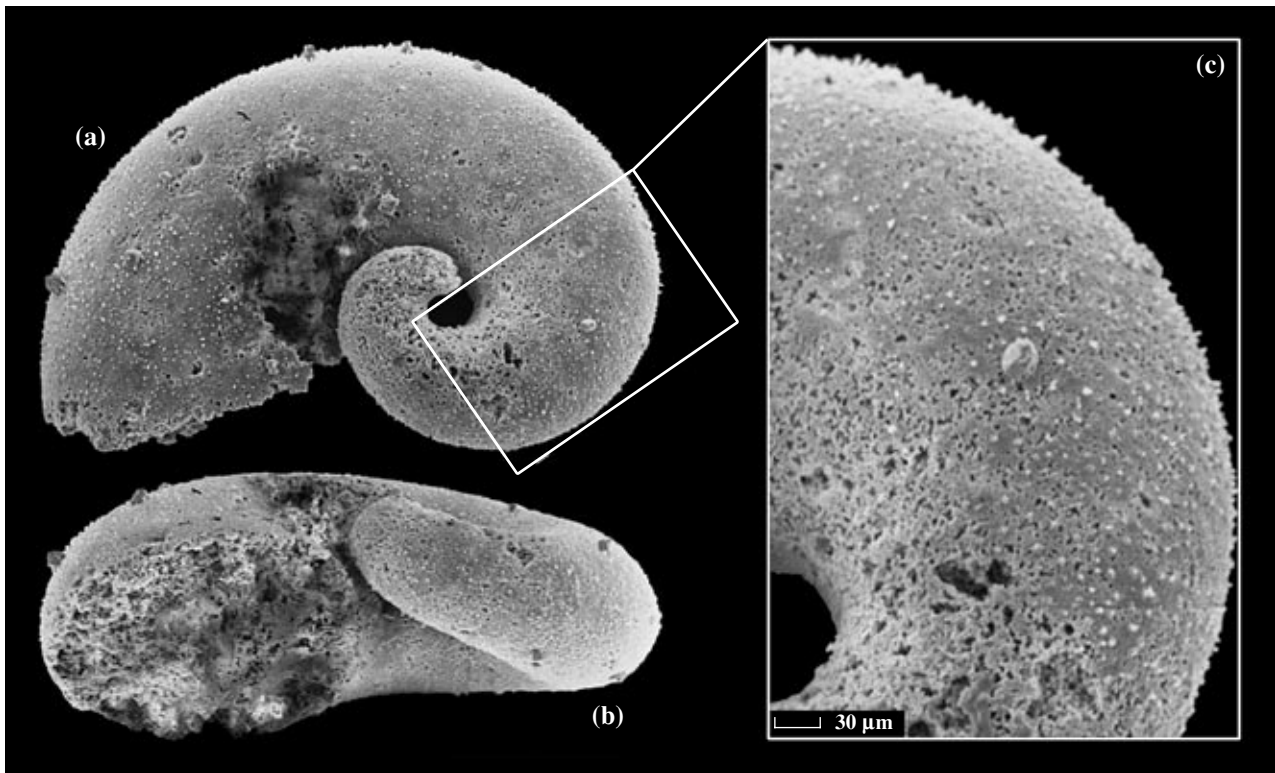


Fig. 5. *Barskovia hemisymmetrica* Golubev, 1976; Tommotian Stage, right bank of the Yenisey River, 6 km downstream from Plakhino Island (Korovnikov *et al.*, 2002; section no. 3, bed no. 6), Siberian Platform; internal mold (specimen from collection of D.P. Sipin, Joint Institute of Geology and Geophysics, Novosibirsk): (a) apical view, $\times 74$; (b) apertural view, $\times 74$; (c) granular microornamentation of the internal mold.

tracum, while the horizontal lamellae (Figs. 3c, 3d) are a phosphatized organic membrane that divided the mineral layers of the shell. If this structure is broken during preparation, the internal mold retains only small granules, i.e., the basal parts of phosphate columns (Fig. 3d). The surface of the internal mold appears to be microgranulated in this type of preservation (Figs. 4, 5). The internal molds of *Philoxenella spiralis* Vostokova, 1962 and *Barskovia hemisymmetrica* Golubev, 1976 with granulated microornamentation are illustrated in Figs. 4 and 5. Most likely, this microornamentation is a result of the destruction of the phosphate envelope and columns that filled the tubuli. The size and arrangement of granules coincide with the size and arrangement of columns in *Khairkhanian rotata* (see Fig. 3d).

A similar pattern is present on the internal molds of *Anhuiconus microtuberus* Zhou et Xiao, 1984 (Figs. 6d–6g) and, especially, in *Nomgoliella australiensis* Parkhaev, 2001 (Figs. 6a–6c), suggesting a similar origin of the granulated relief of the internal molds in these species.

Thus, three general types of microornamental elements on the surface of the internal molds of Cambrian mollusks that are related to shell pores can be distinguished. Each of the morphological types has its own distinct mechanism of origin. The first type (Figs. 7a–7e)

is present in the species *Auricullina papulosa*, *A. granulosa*, *Postacanthella elegans*, *Postacanthella* sp., *Mackinnonia anabarica*, and *Tuberoconus paucipapillae* and is represented by relatively large (on average 15–30 μm) conical or cylindrical papillae or granules. Structurally, these elements are integral to the entire mold surface and, probably, are no more than molds of large pores in the wall of the shell. Possibly, these pores performed a mechanical function, i.e., they hosted the appendages of the outer mantle epithelium that fixed its position in respect to the shell wall.

The second type of microornamental elements (Figs. 7f, 7g) occurs in *Daedalia daedala* and *Mellopegma uslonica* and is represented by regular spherical granules, 8–12 μm in diameter. As previously mentioned, this type of spherical cavities in the shell wall may have served a photoreceptive function.

The third type of microornamental elements (Figs. 7h–7l) is found in *Philoxenella spiralis*, *Khairkhanian rotata*, *Barskovia hemisymmetrica*, *Nomgoliella australiensis*, *Anhuiconus microtuberus*, and, probably, in *Leptostega hyperborea*. Usually, it is represented by small (2–7 μm) granules on the mold surface; however, when better preserved, this type is composed of thin and long columns penetrating the shell wall and reaching (?) the periostracum. The gran-

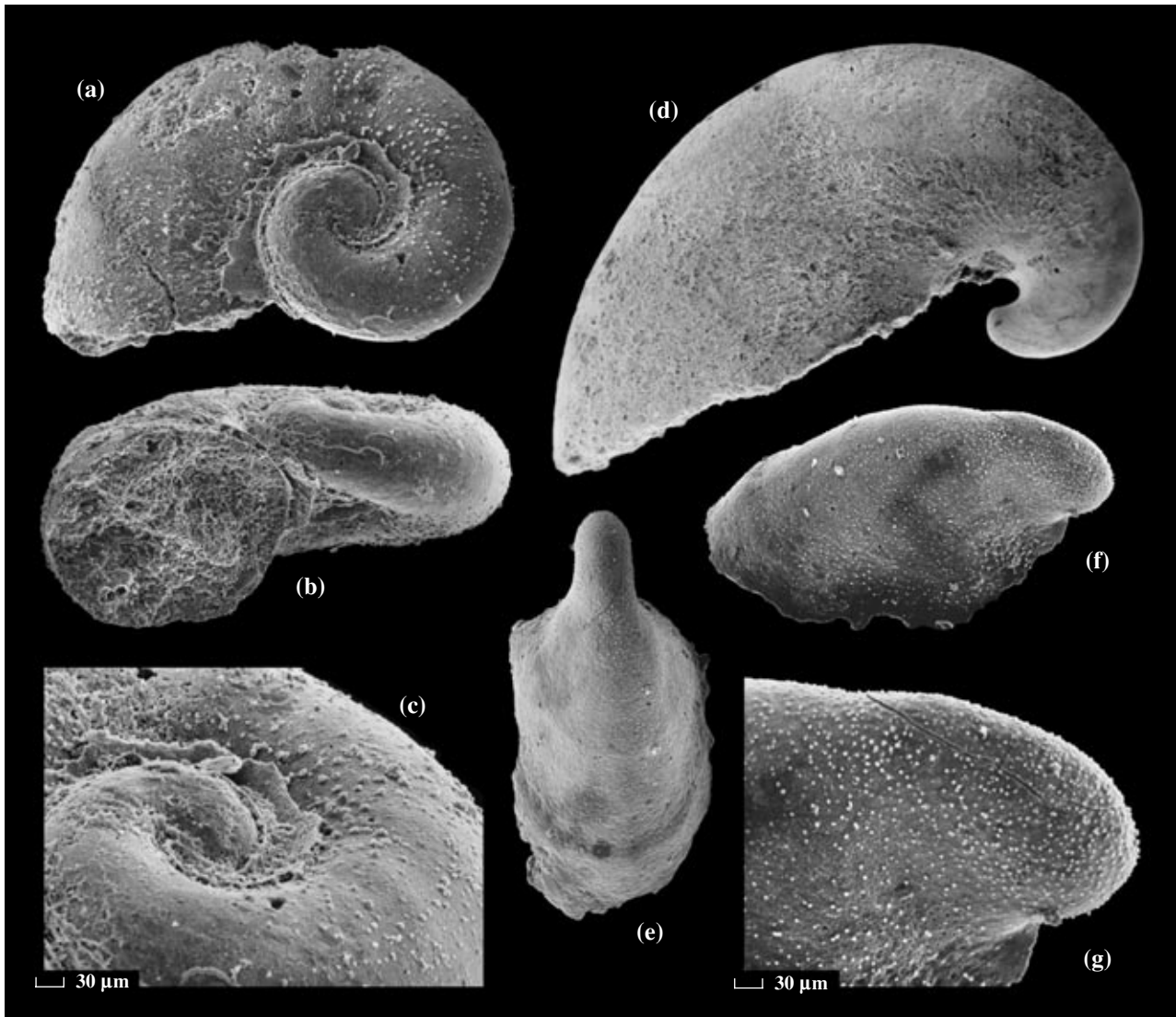


Fig. 6. Granular microornamentation of internal molds of mollusk species from the Botomian Stage of South Australia (Yorke Peninsula, Parara Limestone): (a–c) *Nomgoliella australiensis* Parkhaev, 2001; holotype PIN, no. 4664/1823, internal mold with fragments of shell; Horse Gully locality (sample HG no. 0): (a) apical view, $\times 78$; (b) apertural view, $\times 78$; (c) granular microornamentation preserved on the upper part of the whorl; (d–g) *Anhuiconus microtuberus* Zhou et Xiao, 1984; (d) specimen PIN, no. 4664/1867, internal mold; Horse Gully locality (sample HG no. 0), left view, $\times 28$; (e–g) specimen PIN, no. 4664/1734, internal mold; borehole SYC-101 (depth 167.87 m): (e) dorsal view, $\times 45$; (f) oblique left view, $\times 45$; (g) granular microornamentation preserved on the apical part of the mold.

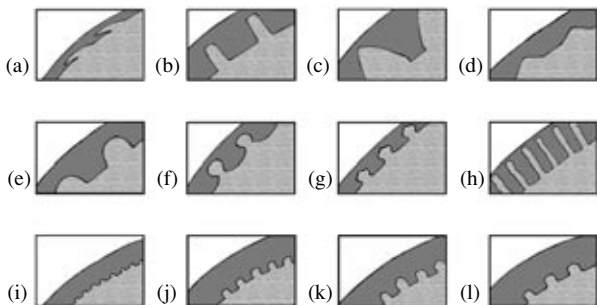


Fig. 7. Schematic structure of shell pores in different species of Cambrian mollusks, $\times 200$: (a) *Auricullina papulosa* Vassiljeva, 1998; (b) *A. granulosa* sp. nov.; (c) *Postacanthella elegans* Yue, 1984; (d) *Mackimmonia anabarica* Parkhaev, 2005; (e) *Tuberoconus paucipalillae* Yue, 1984; (f) *Daedalia daedala* Parkhaev, 2001; (g) *Mellopegma uslonica* Parkhaev, 2004; (h) *Khairkhanina rotata* Missarzhevsky, 1981; (i) *Anhuiconus microtuberus* Zhou et Xiao, 1984 and *Leptostega hyperborea* Parkhaev, 2005; (j) *Barskovia hemisymmetrica* Golubev, 1976; (k) *Philoxenella spiralis* Vostokova, 1962; and (l) *Nomgoliella australiensis* Parkhaev, 2001.

ules (bases of columns) differ structurally from the rest of the mold surface. It is supposed that the columns are a result of the rapid postmortem phosphatization of the appendages of epithelial tissue that filled the tubuli. Possibly, these appendages played some part in the process of biomineralization or restoration of the damaged areas of periostracum.

CONCLUSIONS

The internal molds of Cambrian mollusks display microornamentation that can be interpreted as molds of shell pores or as secondary mineralization of shell pores. The morphology of pores and their arrangement are very similar to those of recent mollusks, suggesting that they serve a similar function. To date, the taxonomic significance of shell pores is difficult to define. At the present it was found among members of several families, i.e., Helcionellidae, Coreospiridae, Trenellidae, Stenothecidae, Khairkhaniidae, and Aldanelidae; i.e., among virtually all main groups of helcionelloid mollusks (Parkhaev, 2002, text-fig. 1). Nowadays, its taxonomic significance is obvious for the lower hierarchical levels since similar species of a genus can be easily distinguished by microornamentation of the mold. For instance, this is true for the genera *Auricullina*, *Mackinnonia*, and *Mellopegma*. In addition, the identical microornamentation of khairkhaniids *Khairkhania rotata*, *Philoxenella spiralis*, and *Barskovia hemysimetrica* (Figs. 3–5) supports the closest relation of these species, which differ only in the type of coiling, i.e., the shell of *Khairkhania* is planispiral, the shell of *Philoxenella* is slightly dextral, and the shell of *Barskovia* is slightly sinistral. Probably, a special study of these genera will reveal that they are synonyms.

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