

The new stem-group brachiopod *Oymurania* from the lower Cambrian of Siberia

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A stem-group brachiopod, *Oymurania gravestocki* Ushatinskaya gen. et sp. nov. is described herein from the middle Atdabanian–lower Botoman Stages (~Cambrian Stage 3) of the Siberian Platform. The fossils were extracted from limestone beds of the Emyaksin, Perekhod, and Pestrotsvet formations as assemblages of disarticulated orthoconic to cyrtoconic porous shells in apatite preservation. The originally organophosphatic shells of *Oymurania* are externally similar to mitral sclerites (ventral valves) of the stem-group brachiopod *Micrina*, although no sellate-like sclerites, nor differentiated subapical area with apophyses were recognised in our material. The range of *Oymurania* shells with sub-central to posteromarginal apex is similar to that of ventral valves of *Mickwitzia*. *Oymurania* is also characterised by the system of radial and orthogonal canals open in pairs or triplets in small depressions or indentations of growth lamellae in the outer shell surface. The orthogonal (*Micrina*–*Setatella* type) and radial (horizontal setigerous tubes) canals are widespread among the early Cambrian stem-group brachiopods, such as *Micrina*, *Mickwitzia*, and *Setatella*. In addition to these canals, *Oymurania* exhibits a well-developed acrotretoid columnar microstructure, also known from *Setatella*. A broad subapical platform in cyrtoconic shells (presumably ventral valves) of *Oymurania* is interpreted homologous to the deltoid area in mitrals of *Micrina* and pseudointerarea/interarea in ventral valves of *Setatella*/paterinid brachiopods. Except with probable cell imprints and openings of orthogonal canals, no morphological differentiation was, however, reflected by the shell interior of *Oymurania gravestocki*. Being closely related to tannuolinids and mickwitzids, *Oymurania* complements the picture of diversification of the early Cambrian stem-group brachiopods that occurred in parallel with radiation of paterinids and other crown-group brachiopods on the Siberian Platform and worldwide.

Key words: Brachiopoda, *Oymurania*, *Mickwitzia*, *Micrina*, *Setatella*, Cambrian, Siberia.

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Introduction

The “Cambrian explosion” represents the geologically rapid diversification of eukaryotic organisms during the first ca. 25 Ma of the Cambrian Period and is marked in the fossil record by the first appearance of biomineralization in many groups of animals (e.g., Kouchinsky et al. 2012). The first diversification of the crown-group Brachiopoda in the Cambrian Age 3 is preceded by the first major radiation of the Lophotrochozoa in the Terreneuvian Epoch, including organisms interpreted as stem-

group lophophorates and stem-group brachiopods (Holmer et al. 2002, 2008, 2011; Williams and Holmer 2002; Skovsted et al. 2008, 2009a–c, 2011; Balthasar et al. 2009; Murdock et al. 2012). Tommotiids (Cambrian Epochs 1–3) are one of such groups that occupy a basal position in the stem Brachiopoda. Tommotiids are polyphyletic and represented by sedentary and vagrant animals that typically occur in the fossil record as disarticulated organophosphatic external sclerites (Bengtson 1970). Among them, tannuolinids are most advanced and include bivalved brachiopod-like *Micrina* Laurie, 1986 (Cambrian

Epoch 2). The earliest members of the phylum Brachiopoda, class Paterinata (Cambrian–Ordovician), appear by the end of the Terreneuvian Epoch (Cambrian Age 2). Paterinid brachiopods exhibit morphological combinations unusual for other brachiopods: organophosphatic composition characteristic of the subphylum Linguliformea, strophic hinge present in the calcareous subphylum Rhynchonelliformea, and shell structure similar to that in stem-group brachiopods (Williams et al. 1998; Skovsted et al. 2008, 2009c, 2011; Balthasar et al. 2009; Holmer et al. 2009; Topper et al. 2013). In parallel with radiation of the linguliformean and rhynchonelliformean brachiopods during the Cambrian Age 3, such other stem-group brachiopods as mickwitziiids became widespread. The aim of this paper is to report a new genus and species of stem-group brachiopods, *Oymurania gravestocki* Ushatinskaya gen. et sp. nov. from the Cambrian Stage 3 of the Siberian Platform, which shares combination of plesiomorphic brachiopod features with tannuolinids and mickwitziiids.

Institutional abbreviations.— FUB, Freie Universität Berlin, Germany; PIN, Paleontological Institute, Moscow, Russia; SMNH, Museum of Natural History, Stockholm, Sweden.

Material and methods

The material derives from the Atdabanian–lower Botoman limestone beds of the Pestrotsvet, Perekhod (middle reaches of the Lena River) and Emyaksin (Bol’shaya Kuonamka River) formations of the Siberian Platform (Fig. 1). The

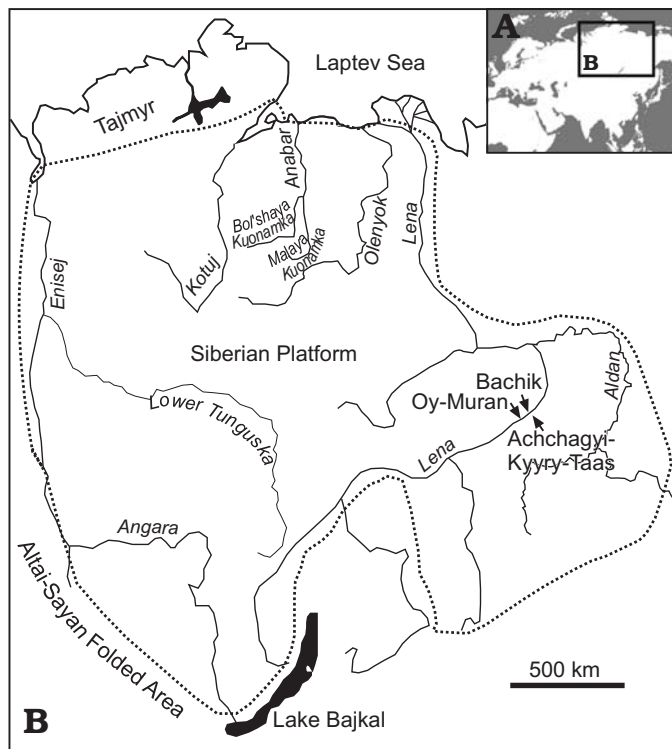


Fig. 1. Location of the studied area (A), map showing sections on the Siberian Platform (B).

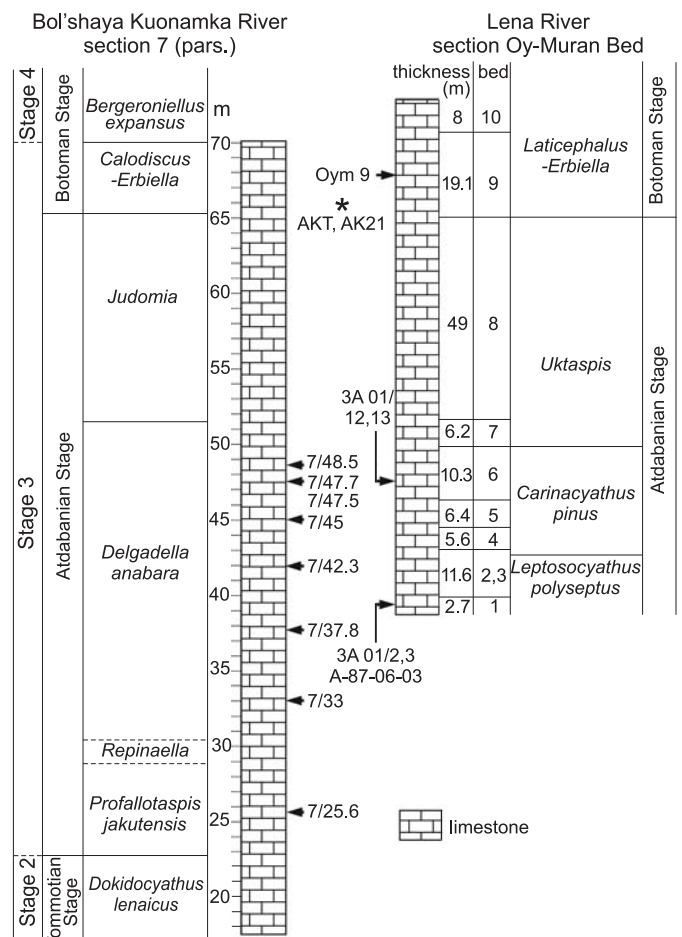


Fig. 2. Derivation of fossiliferous samples (arrows with numbers) from sections Bol’shaya Kuonamka, Oy-Muran, and Achchagyi-Kyyry-Taas. Asterisk indicates stratigraphic position of samples (AKT, AK21) from the top of Achchagyi-Kyyry-Taas section (not shown) with respect to the Oy-Muran and Bol’shaya Kuonamka sections. Bol’shaya Kuonamka section 7 scale in meters continues to the bottom of the section (see Kouchinsky et al. 2015: fig. 2).

fossils described herein range from the *Leptosocyathus polyseptus* Zone (type material) of the Atdabanian Stage to the *Porocyathus squamosus-Botomocyathus zelenovi* Zone (*Laticephalus-Erbiella* Zone) of the lower Botoman Stage (Fig. 2). The Atdabanian fossils were collected by Andrej Zhuravlev in 1981 and 1987 at the Oy-Muran section (61°04’18” N, 126°10’44” E), left bank of the Lena River, 3.2 km upstream from the mouth of the Gostinaya River and in 1981 at section Bachik (61°05’50” N, 126°17’34” E), left bank of the Lena River, 3.8 km downstream from the mouth of the Gostinaya River. A single Botoman specimen was obtained from Bed 9 of the Oy-Muran section by Michael Steiner in 2008. In addition to the type material, an abundant assemblage of shells was collected by AK and MS in 2008 from the top of the Achchagyi-Kyyry-Taas section (61°05’25” N, 126°40’54” E) located at the right bank of the Lena River, near the mouth of the Achchagyi-Kyyry-Taas Brook (Figs. 1 and 2), from the *Bergeroniellus mic-macciformis-Erbiella* Zone limestone beds of the Perekhod Formation (Member 3, bed 21; see Varlamov et al. 2008).

The Emyaksin Formation was sampled by AK and Stefan Bengtson in 1996 in the eastern flanks of the Anabar Uplift, where section 7 (70°43'N, 112°52.5'E; = section A-54 in Val'kov 1975; Fig. 1) crops out along the left bank of the Bol'shaya Kuonamka River, 3.5–4 km downstream from the mouth of the Ulakhan-Tyulen Brook. Fossils from the middle part of the Emyaksin Formation therein are chemostratigraphically correlated with the middle Atdabanian *Delgadella anabara* Zone of south-eastern Siberian Platform (see Kouchinsky et al. 2001 and Kouchinsky et al. 2015, for description of methods and analytical results; Kouchinsky et al. 2015: SOM 2, for distribution of *Oymurania gravestocki* and associated fauna therein).

All the fossils were chemically extracted from limestone rocks with buffered ca. 10% diluted acetic acid and represent shells in apatitic preservation. These were manually sorted from the acid-resistant residues under a binocular microscope, then mounted and coated with gold for examination with scanning electron microscopes CamScan-4 at PIN, Hitachi S4300 at NRM, and Zeiss Supra 40VP at FUB.

Systematic palaeontology

Phylum, class, order, and family uncertain
(stem-group Brachiopoda)

Genus *Oymurania* Ushatinskaya nov.

Etymology: After the Oy-Muran section, type locality.

Type species: *Oymurania gravestocki* Ushatinskaya sp. nov.; see below.

Species included: Type species and probably a new, not yet formally described species from Morocco (*Micrina* sp. in Skovsted et al. 2014).

Diagnosis.—Bilaterally symmetrical presumably biconvex organophosphatic shells with circumferential growth. Valves orthoconic to cyrtoconic, with a broad subapical platform. Walls composed of laminae perforated by tiny canals and interconnected by acrotretoid columns. Two types of thicker canals perforate the wall orthogonally vs. parallel to lamination and open on the shell exterior through the pores situated in a common depression or indentation of growth increments.

Remarks.—*Oymurania* is different from other bivalved stem-group brachiopods and linguliform brachiopods in a unique combination of features, such as the acrotretoid columnar microstructure of its organophosphatic laminated shell, radial and orthogonal systems of canals having external openings associated with each other, and a broad subapical platform. In *Oymurania* sp. described by Skovsted et al. 2014 as *Micrina* sp. from Cambrian Stage 3 of Morocco, a pair of low ridges on the inner surface of the subapical platform is probably homologous to apophyses in mitrals sclerites of *Micrina* (Skovsted et al. 2014).

Stratigraphic and geographic range.—Atdabanian to lower Botoman Stages (~Cambrian Stage 3), Siberian Platform and Gondwana (Morocco).

Oymurania gravestocki Ushatinskaya sp. nov.

Figs. 3–13.

Etymology: In honour of the Australian palaeontologist David Gravestock.

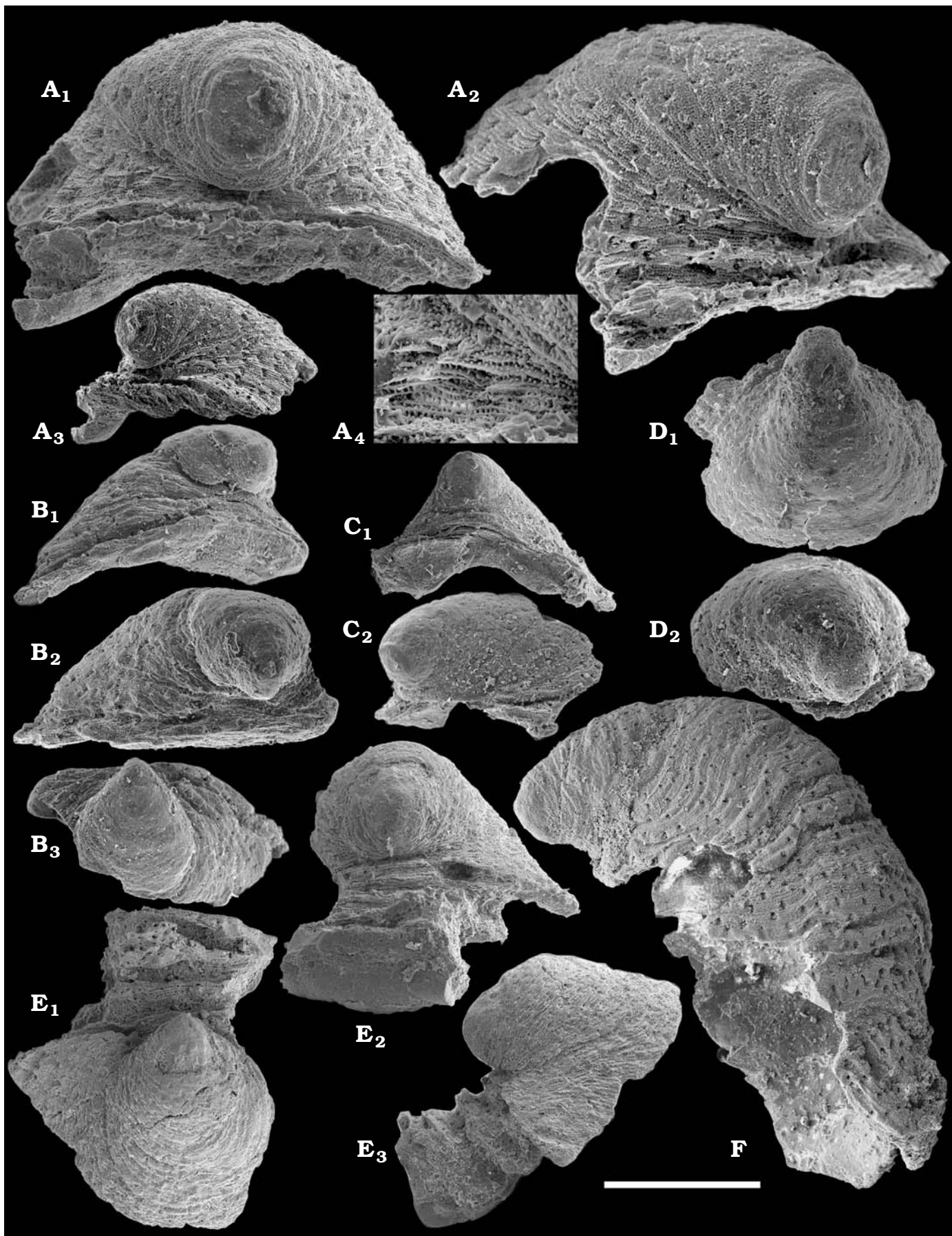
Type material: Holotype: PIN 4194/101 (Fig. 3A). Paratypes: PIN 4194/102, 103, 104 (Fig. 3B, C, D).

Type locality: 61°04'18"N, 126°10'44"E, Oy-Muran section, middle reaches of the Lena River, left bank, 3.2 km upstream of the Gostinaya River, southeastern part of the Siberian Platform (Fig. 1).

Type horizon: Bed 1, Oy-Muran section, Pestrotsvet Formation, *Leptosocyathus polyseptus* Zone, Atdabanian Stage, lower Cambrian.

Material.—In addition to the type material, the following specimens were obtained from the Oy-Muran section: 10 shells and shell fragments from samples 3A 01/2, 3A 01/3 and A-87-06-03 (Fig. 2), including figured PIN 4194/104, 107, from the *Leptosocyathus polyseptus* Zone; 11 shell fragments from samples 3A 01/12 and 3A 01/13, Pestrotsvet Formation, *Carynocyathus pinus* Zone (Bed 6), Atdabanian Stage; and a single cyrtoconic shell fragment, FUB Oym9-09 from the *Porocyathus squamosus-Botomocyathus zelenovi* Zone (*Laticephalus-Erbiella* Zone), Bed 9, lower Botoman Stage (Fig. 3E). Two orthoconic shells *Oymurania ?gravestocki* PIN 4194/105, 106 (Fig. 4), from sample 3A 01/13 are questionably attributed herein to the same species as complementary valves of its bimembrate organophosphatic skeleton (see discussion). Additionally, eight shell fragments are available from section Bachik (Fig. 1), samples 3A 03/62 and 3A 03/73, Perekhod Formation, *Nochoroicyathus kokoulini* Zone, Atdabanian Stage. Assemblages of orthoconic to cyrtoconic calcium phosphate shells attributed to *Oymurania gravestocki* are also described herein from samples 7/42.3, 7/45, 7/47.5, 7/47.7, and 7/48.5, Emyaksin Formation, Bol'shaya Kuonamka River section 7, *Delgadella anabara* Zone, Atdabanian Stage (ca. 30 shells and apical fragments, including SMNH X5285–X5289; Figs. 5, 6) and from Bed 21, Member 3 of the Perekhod Formation, Achchagyi-Kyry-Taas section, *Bergeroniellus micmacciformis-Erbiella* Zone, lower Botoman Stage (ca. 100 shells and apical fragments, including SMNH X5290–X5304 and FUB AK21-001–019; Figs. 7–13).

Description.—Almost orthoconic to cyrtoconic, nearly bilaterally symmetrical, rapidly expanding organophosphatic shells with rounded blunt or tapered and up to 90° inclined apex. Width and length of the aperture are nearly equal. Shell height does not exceed the diameter of aperture. Subapical margin of the aperture bends outward (Fig. 3A₁–A₃, B₁) and forms a prominent platform extended along the subapical margin and consisting of a series of growth increments (Fig. 3E). Subapical side gradually passes into convex lateral sides. Apical part sub-central (Figs. 4A, B, 6, 7A, B) to posteromarginal (Figs. 8–10). Initial part of the shell (Fig. 7) less than 200 µm in diameter, without growth increments and with irregularly folded hemi-spherical surface, indistinctly separated from the mature shell. Outer surface of the mature shell is circumferentially ornamented with co-marginal or undu-



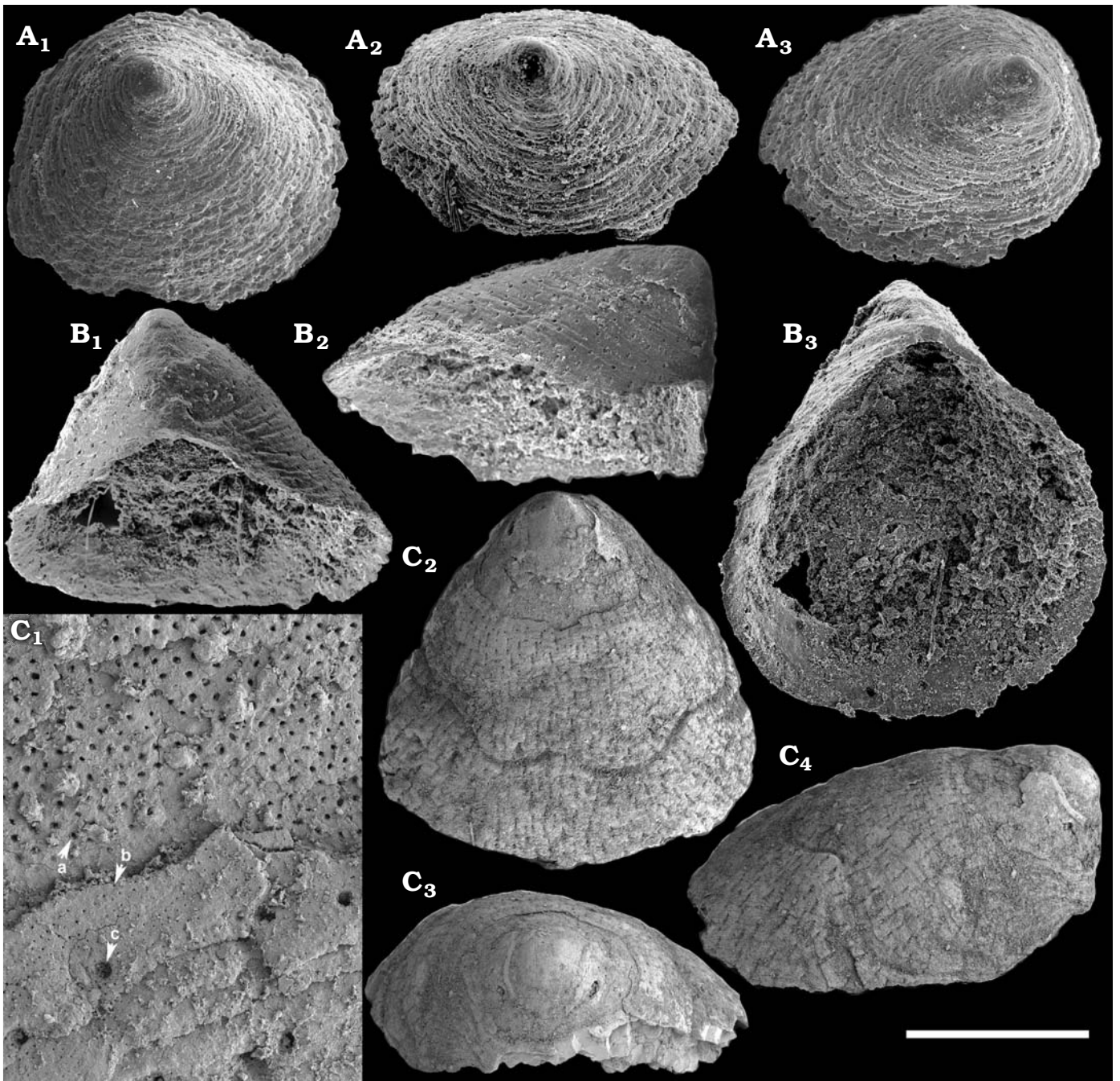


Fig. 4. Stem group-brachiopod *Oymurania ?gravestockii* Ushatinskaya gen. et sp. nov., orthoconic (presumably dorsal) valves, from the lower Cambrian Pestrotsvet Formation, Oy-Muran section, Siberia. **A.** PIN 4194/105; upper (A₁), subapical (A₂), and oblique side (A₃) views. **B.** PIN 4194/106; subapical (B₁), lateral (B₂), and apertural (B₃) views. **C.** SMNH X 5305; upper (C₂), subapical (C₃), and lateral (C₄) views; close-up of C₂, showing fine and coarser pores in the apical part of the shell wall (C₁), the openings of axial canals on exfoliated shell surface (arrow a), presumably on the surface of primary shell layer (arrow b); an opening of an orthogonal canal (arrow c). Scale bar A, B, 600 μm; C₂–C₄, 1200 μm; C₁, 120 μm.

← Fig. 3. Stem group-brachiopod *Oymurania gravestockii* Ushatinskaya gen. et sp. nov., cyrtoconic (presumably ventral) valves, from the lower Cambrian Pestrotsvet Formation, Oy-Muran section, Siberia. **A.** PIN 4194/101, holotype; subapical side (A₁), oblique subapical (A₂, A₃) views, close-up of A₂ showing columnar microstructure (A₄). **B–D.** PIN 4194/102, 103, 104, paratypes; oblique subapical (B₁, B₂, C₂, D₂), upper (B₃, D₁), and subapical (C₁) views. **E.** FUB Oym9-09, shell with a fragment of a broad subapical platform attached; upper (E₁), subapical (E₂), and lateral (E₃) views. **F.** PIN 4194/107, lateral view. Scale bar 600 μm, except A₁, A₂, 300 μm; A₄, 120 μm.

lating folds of growth increments. The inner shell surface is generally smooth, with growth lines, fine tuberculation and polygonal ornamentation (Figs. 6C₃, 9B, 11A₂, A₃, A₆, B).

Microstructure.—Shell wall (up to 0.25 mm thick) has a laminated structure (Figs. 3A₄, 12C₂, 13B). In the outer portion of the wall, lamination is obliquely arranged towards

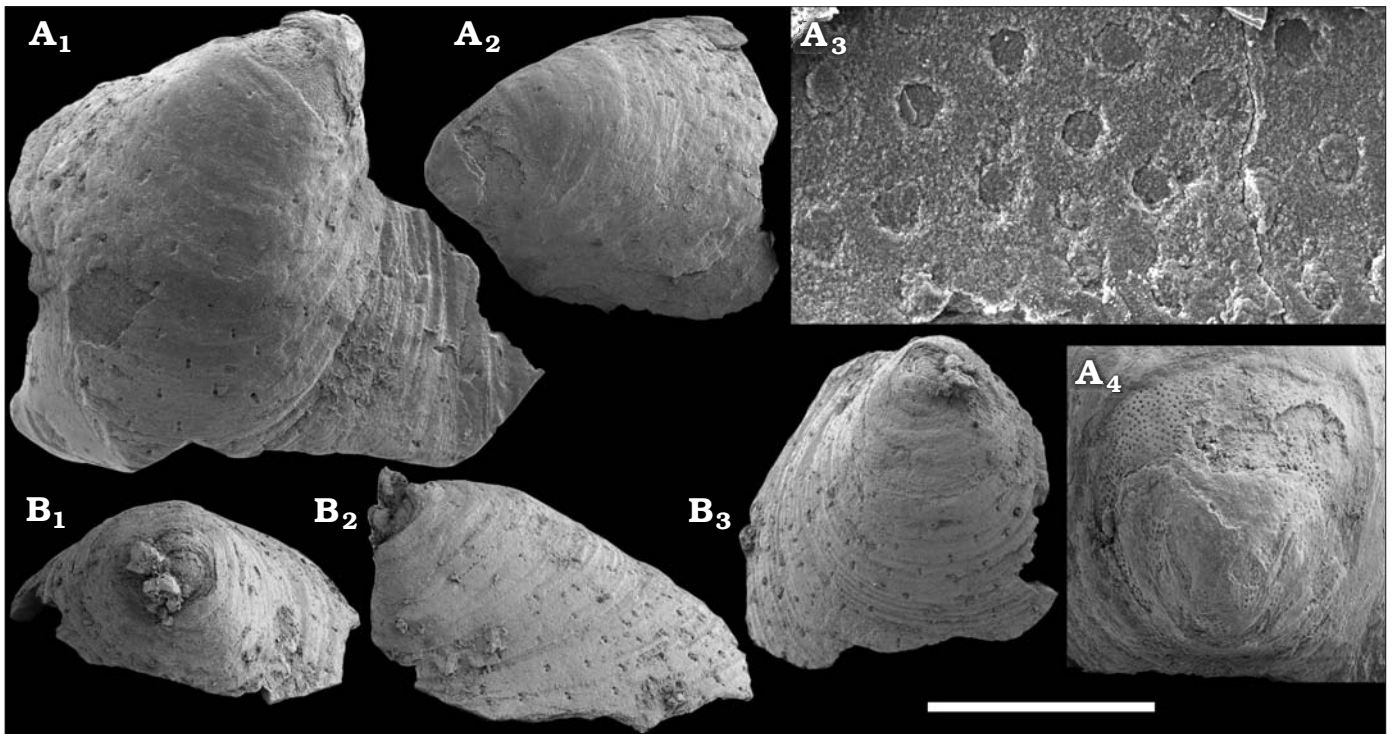


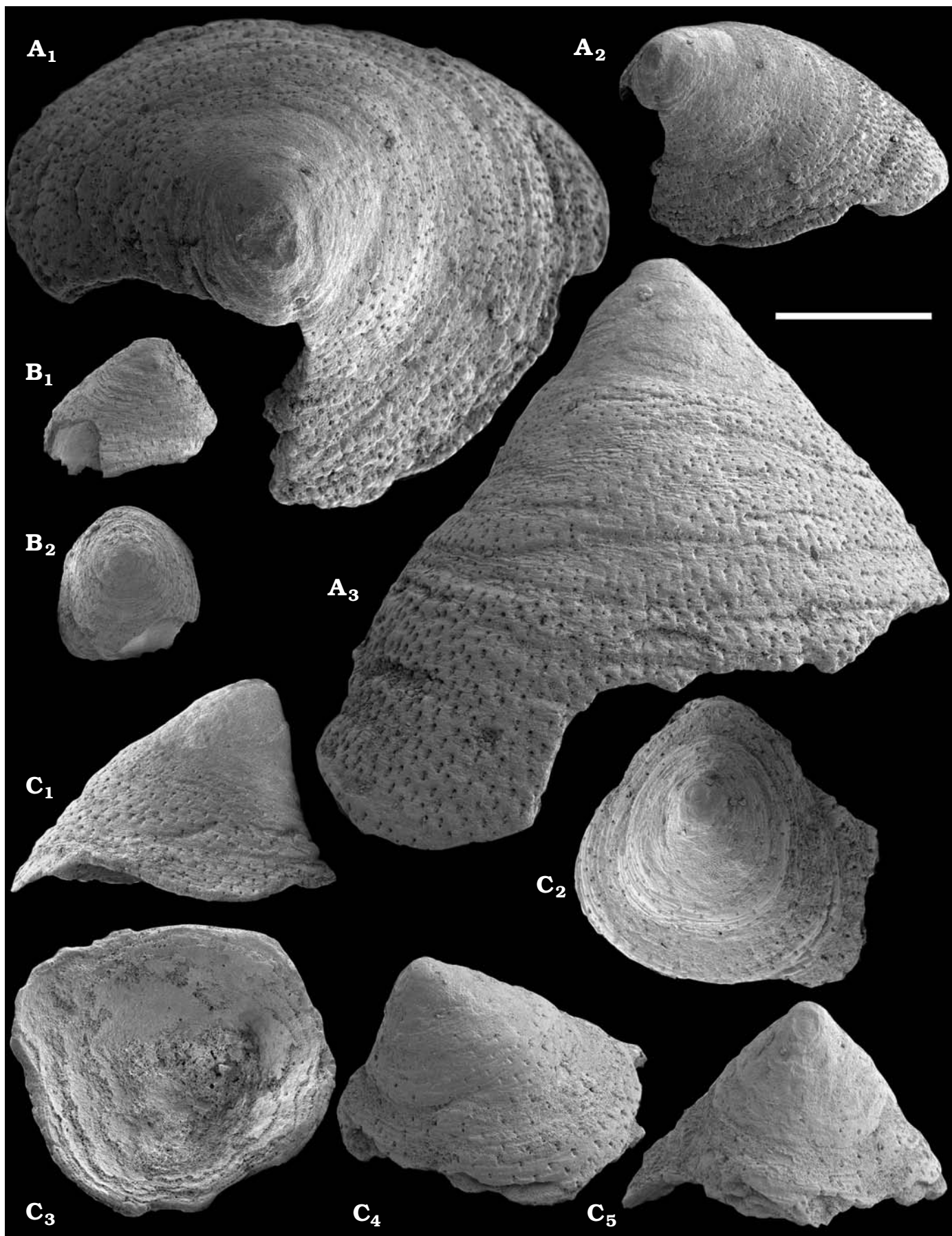
Fig. 5. Stem group-brachiopod *Oymurania gravestocki* Ushatinskaya gen. et sp. nov., cyrtocoelic (presumably ventral) valves, from the lower Cambrian Emyaksin Formation, Bol'shaya Kuonamka section 7, Siberia. **A.** SMNH X5285, sample 7/33; upper (A_1), oblique lateral (A_2), and apical (A_3) views; close-up of A_3 , showing fine pores (A_4). **B.** SMNH X5286, sample 7/47.7; subapical (B_1), lateral (B_2), and upper (B_3) views. Scale bar 600 μm , except A_3 , 15 μm , A_4 , 300 μm .

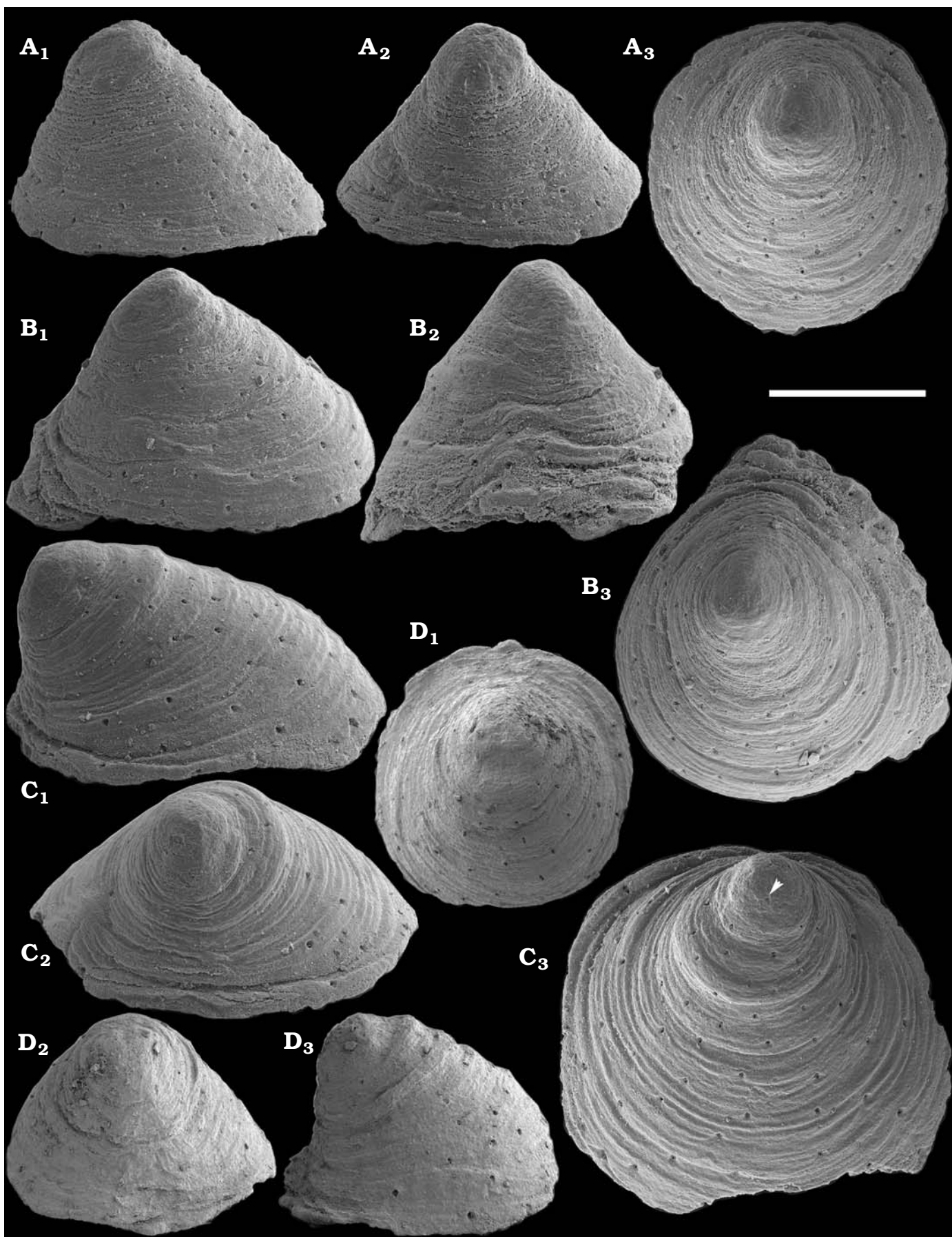
the outer shell surface and consists of sparsely arranged laminae (Fig. 10E–H). The inner portion of the wall is more compact and less distinctly laminated more or less parallel to the inner shell surface (Figs. 10H, 13A). Compact and more spacious types of lamination co-occur in the wall (Figs. 10E–H; 11B: arrows b and c). The laminae (ca. 5 μm thick) are perforated by thin open canals (2–4 μm in diameter), as observed on exfoliated apical (Figs. 4C₁: arrow a; 5A₃, A₄) and distal (Fig. 13B, F) parts of the shell. The canals continue through several successive laminae in perpendicular direction (Figs. 10F, 13B). The canals are often filled (Fig. 5A₃) and/or encrusted by apatite and are represented by columns (2–5 μm in diameter) that traverse spaces between laminae (Fig. 3A₄, 10F). These spaces are up to 10 μm thick (Figs. 10E, F, 13A), partly or completely filled with apatite. The ends of columns commonly produce tuberculation on the entire outer shell surface (Figs. 3A₂, A₄, 7A, 12A₅, A₆, A₈), 100–300 tubercles per 0.01 mm^2 .

The edges of growth increments are indented with depressions containing openings of two types of coarser canals (10–20 μm in diameter). Canals of the first type (radial) run obliquely or parallel to the surface of growth lamellae in radial direction with respect to the shell surface and open at the edges of growth increments (Figs. 10G, 12A₃, B₁, C₂).

Canals of the second type (orthogonal) penetrate through the shell wall nearly perpendicular to the growth lamellae (Figs. 10G arrowed, 12A₅, A₆, A₈ arrowed, B₁) and open on the inner shell surface (Figs. 10E arrowed; 11B: arrow a). Openings of radial and orthogonal canals are both observed on the shell exterior where they are located in groups of two or three within the same depression or indentation in the wall (Fig. 12A₃, A₅, A₆, A₈, B₁). The aperture of the radial canal always occupies a more proximal position in the group, where one or two orthogonal canals open distally. In smaller specimens (Fig. 7) or in the proximal part of larger shells (Fig. 12A₆), one radial and one orthogonal canal open close to each other within the same radially extended depression or pit (2–3 such depressions/pits per 0.01 mm^2 on the outer surface of 1–2 mm sized specimens). Rare small pits of that kind occur on the juvenile shells (Fig. 7C₃ arrowed) and early mature shell (Figs. 4C₁: arrow c, 7). The depressions become more extended radially at later growth stages (Fig. 12A₁–A₄, A₇). In most distal locations, the canals open in indentations of the edges of growth increments. These indentations have a deltoid shape extended radially and pointed proximally (Fig. 12A₅, A₈, B₁). Each of the deltoids contains a single opening of a radial canal at the narrow end and usually two openings of orthogonal canals in the broader external part.

Fig. 6. Orthocoelic (presumably dorsal) valves of stem group-brachiopod *Oymurania gravestocki* Ushatinskaya gen. et sp. nov. from the lower Cambrian Emyaksin Formation, Bol'shaya Kuonamka section 7, Siberia. **A.** SMNH X5287, sample 7/48.5; upper (A_1), oblique lateral (A_2), and supra-apical (A_3) views. **B.** SMNH X5288, sample 7/48.5; lateral (B_1) and upper (B_2) views. **C.** SMNH X5289, sample 7/47.7; lateral (C_1 , C_4), upper (C_2), apertural (C_3), and subapical (C_5) views. Scale bar 600 μm , except A_3 , 1200 μm .





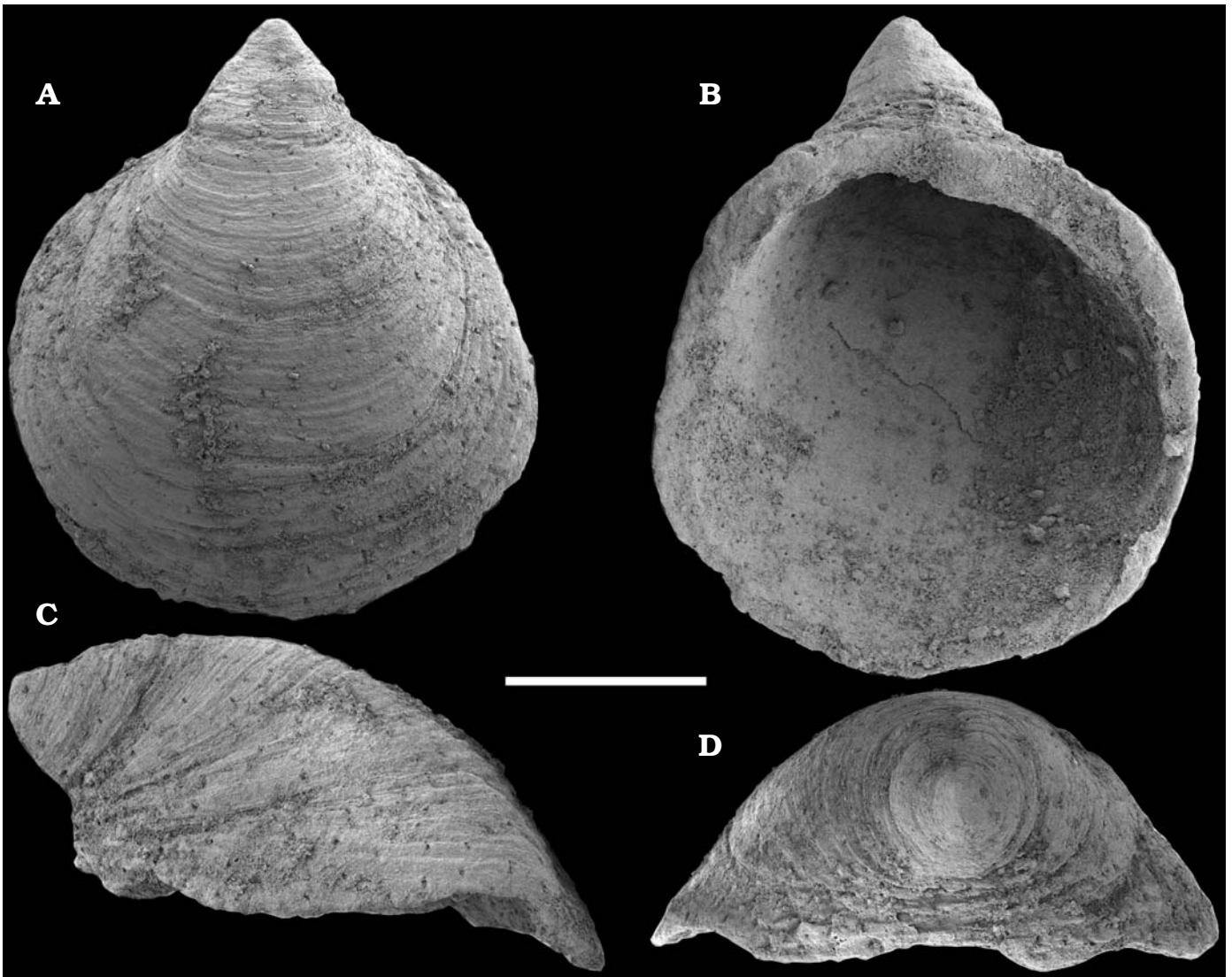


Fig. 8. Stem group-brachiopod *Oymurania gravestocki* Ushatinskaya gen. et sp. nov. from the lower Cambrian Perekhod Formation, Achchagyi-Kyyry-Taas section, Siberia. Cyrtococonic (presumably ventral) valve (SMNH X5296); upper (A), apertural (B), lateral (C), and subapical (D) views. Scale bar 600 μ m.

Remarks.—The general morphology of the shell varies from nearly orthoconic with sub-central apex to cyrtococonic with postero-marginal apex. The Achchagyi-Kyyry-Taas assemblage contains almost orthoconic (Fig. 7A, B) as well as slightly cyrtococonic (Fig. 7C, D) but otherwise very similar relatively small forms. Larger specimens from that assemblage are represented by shells with up to 90° curved apices (Figs. 8–10). Shells with blunt wider apices with evidence of erosion (Figs. 10A–D, 12C,) co-occur with those having tapered and narrower apices (Figs. 8, 9). The same variants of preservation of cyrtococonic and almost orthoconic shells from other localities are observed (Figs. 3–6). The subapically stacked growth lamellae are also susceptible to erosion and poorly preserved in larger specimens. In a single case,

however, a broad and probably complete series of subapical lamellae is found attached to an apical fragment of a cyrtococonic shell (Fig. 3E).

Fragmented shells described by Vasil’eva (1998: pls. 48–50) from the Atdabanian Stage of the Lena-Aldan area of the Siberian platform as problematic *Stratosia* exhibit a similar acrotretoid columnar microstructure and canals penetrating the wall subparallel to lamination (Vasil’eva 1998: 117). Without access to the original material it is difficult, however, to conclude on the affinity of *Stratosia* with *Oymurania*.

A single ventral valve of *Oymurania* sp. described by Skovsted et al. 2014 from Cambrian Stage 3 of Morocco as mitral sclerite of *Micrina* sp. probably represents a new species of *Oymurania*. It has a less inclined apex and low

← Fig. 7. Stem group-brachiopod *Oymurania gravestocki* Ushatinskaya gen. et sp. nov., small specimens from the lower Cambrian Perekhod Formation, Achchagyi-Kyyry-Taas section, Siberia. A, B. Orthoconic (presumably dorsal) valves, FUB AK21-006 (A) and AK21-015 (B). C, D. Cyrtococonic (presumably ventral) valves, FUB AK21-004 (C) and SMNH X5290 (D); arrow in C₃ points to a single opening of canal on the juvenile shell. Lateral (A₁–D₁), subapical (A₂–D₂), and upper (A₃–D₃) views. Scale bar 300 μ m.

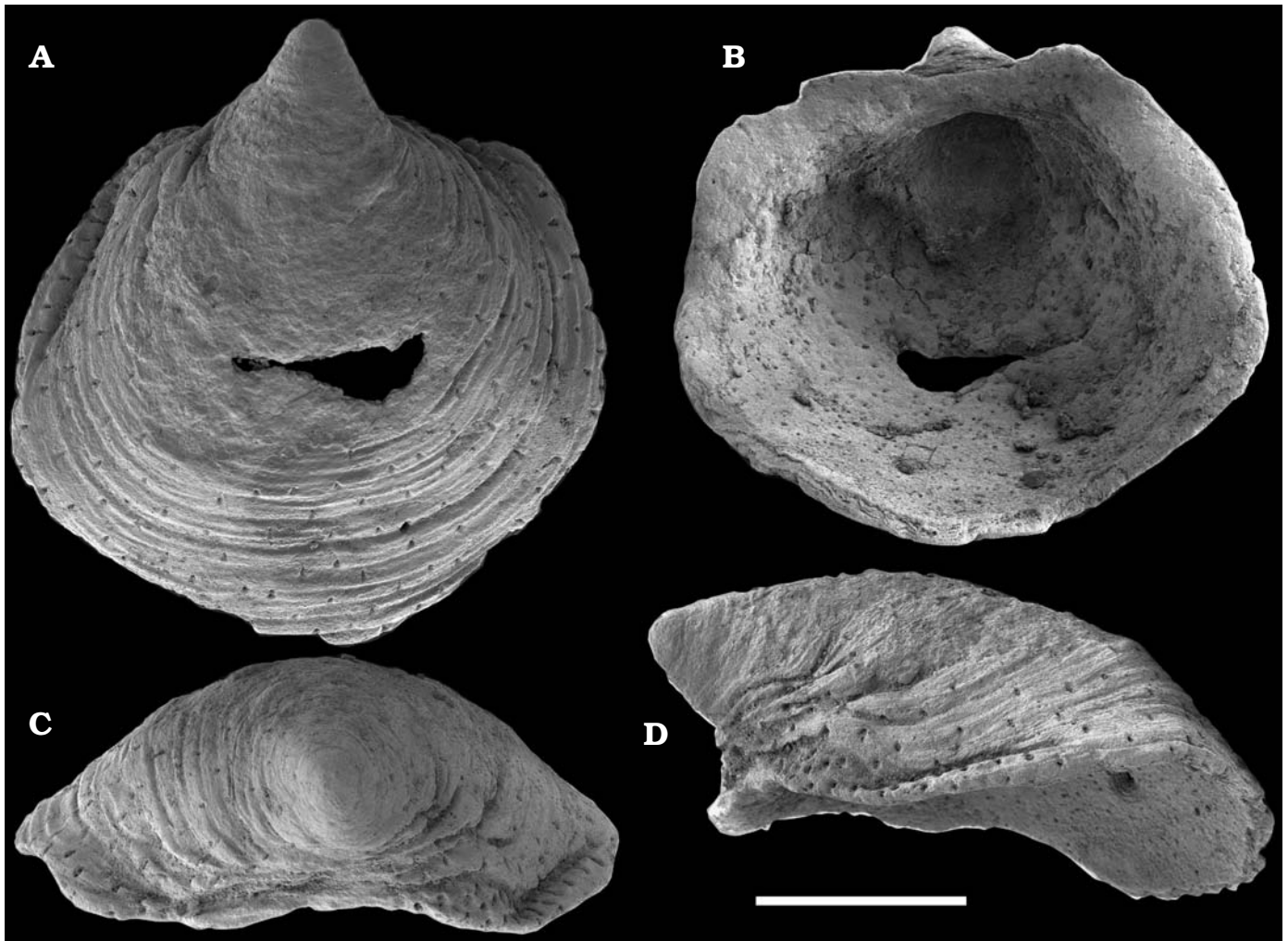


Fig. 9. Stem group-brachiopod *Oymurania gravestocki* Ushatinskaya gen. et sp. nov. from the lower Cambrian Perekhod Formation, Achchagyi-Kyyry-Taas section, Siberia. Cyrtoconic (presumably ventral) valve (SMNH X5297); upper (A), apertural (B), subapical (C), and lateral (D) views. Scale bar 600 μ m.

ridges situated on the inner side of the subapical platform and apparently lacks the triplets of pores in distal parts of the shell (Skovsted et al. 2014: fig. 10).

Another species of stem-group brachiopods, *Tannuolina pavlovi* Kouchinsky, Bengtson, and Murdock, 2010 known from the lowermost Tommotian Stage of northeastern margin of the Siberian Platform (Kouchinsky et al. 2010) was first described under the name *Tannuolina sibirica* Sipin (nomen nudum) by Sipin (2001) in his yet unpublished Doctoral candidate thesis. Kouchinsky et al. (2010) were unaware of the description of *T. sibirica* therein, since the thesis was inaccessible to them at the time of publication. The sellate and mitral sclerites of the species were collected from the top 0.2 m of the Sukharikha Formation and the lowermost 1.7 m of the Krasnoporog Formation, from three localities along the Sukharikha River, among which section 1 (Sipin 2001) corresponds to the type locality of *T. pavlovi*. These

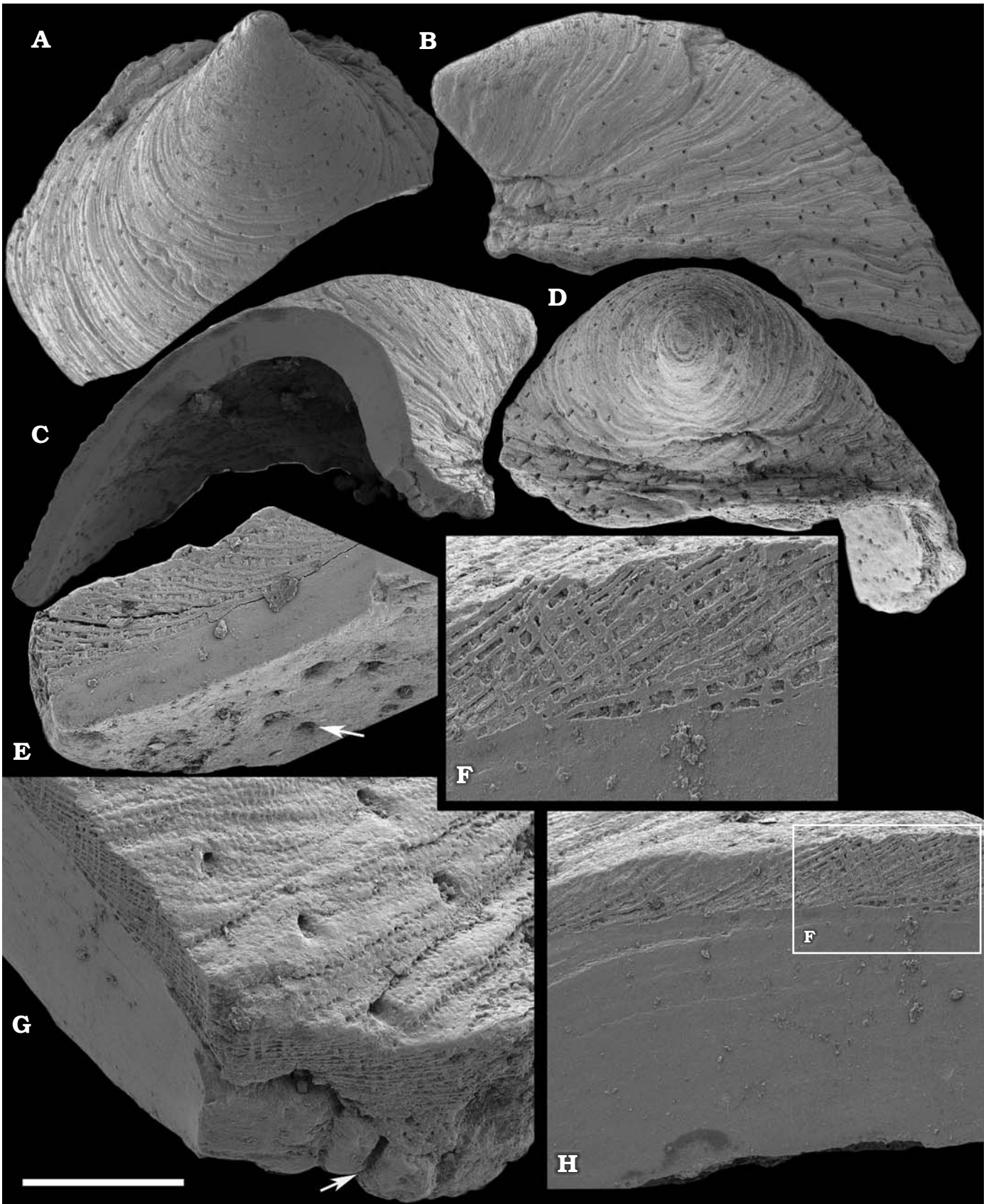
beds were attributed by Sipin (2001) to the *Spinulitheca billingsi*–*Tannuolina sibirica* Zone and correlated with the *Nochoroicyathus sunnaginicus* Zone of the Tommotian Stage.

Stratigraphic and geographic range.—Atdabanian and lower Botoman Stages (~Cambrian Stage 3), Siberian Platform.

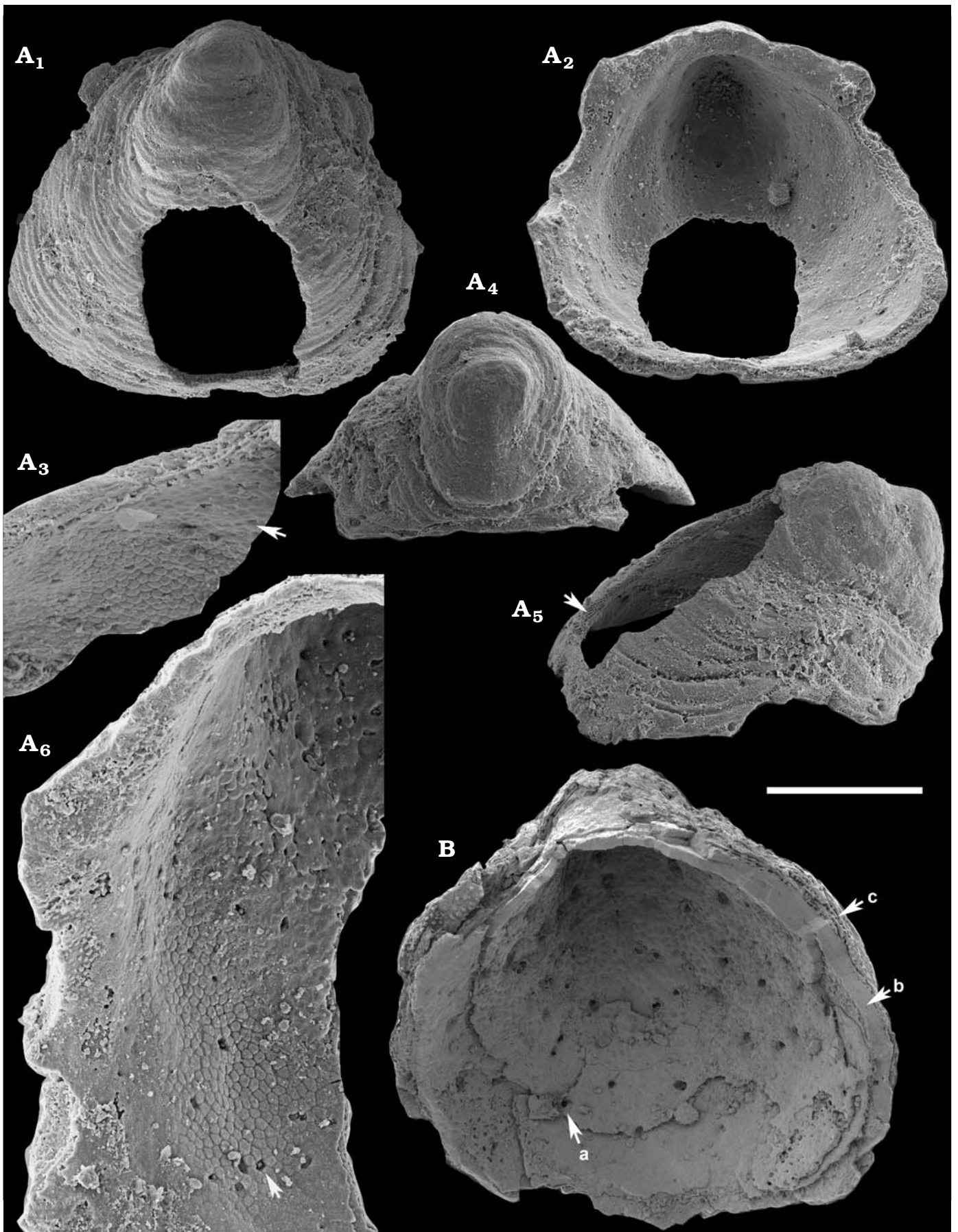
Discussion

The disarticulated orthoconic (with sub-central apex) to cyrtoconic (marginal and postero-marginal apex) apatitic shells described herein presumably belong to the same species of a brachiopod-like organism, because of their generally similar morphology, identical surface sculpture, columnar acrotretoid microstructure in combination with the radial and orthogonal

Fig. 10. Stem group-brachiopod *Oymurania gravestocki* Ushatinskaya gen. et sp. nov. (SMNH X5299) from the lower Cambrian Perekhod Formation, Achchagyi-Kyyry-Taas section, Siberia. A–D. Cyrtoconic shell; upper (A), lateral (B, C), and subapical (D) views. E. The outer part of the wall with obliquely oriented lamination and a more compact structure of the inner wall (arrowed is one of the openings of the orthogonal canals through the wall). →



F, H. Laminae arranged with spaces filled with apatite and traversed by acrotretoid columns (upper part of the figure) and transition to the inner compact portion of the wall (lower part of the figure). **G.** The outer portion of the wall with sparsely arranged laminae showing growth increments and openings of radial canals, as well as a compact portion of the inner wall penetrated by radial pores (arrowed). Scale bar A–D, 600 μm ; E, G, H, 120 μm ; and F, 60 μm .



canals, and the range of shells with more or less marginally displaced and curved apices. Although the orthoconic shells of *Oymurania ?gravestocki* (Fig. 4) from Oy-Muran may belong to a separate species, such shells co-occur with the cyrtoconic ones in the Bol'shaya Kuonamka (Fig. 6). In the Achchagyi-Kyyry-Taas material, cyrtoconic shells generally predominate, whereas the orthoconic ones tend to be represented by relatively small specimens (Fig. 7A, B). The range of variation is similar to that among ventral valves of *Mickwitzia*, where rare and more flattened dorsal valves exhibit a sub-central position of the apex (Balthasar 2004). Highly variable disproportional occurrence of ventral and dorsal valves in fossil assemblages is not unusual and can be explained by their hydrodynamic sorting (Holmer et al. 2008) and differences in fragility. Hence, two interpretations may be put forward. One of them implies that the available assemblage of *Oymurania* shells contains presumably ventral valves, whereas the opposite valve, being originally weakly mineralized and/or highly fragile, is not preserved or not yet identified among fragments. The alternative is that both valves of *Oymurania* are similar, although presumably ventral (more cyrtoconic) valves differ from dorsal (always nearly orthoconic) valves in having a more curved apex and a broad subapical platform formed of successive growth lamellae of the posterior margin.

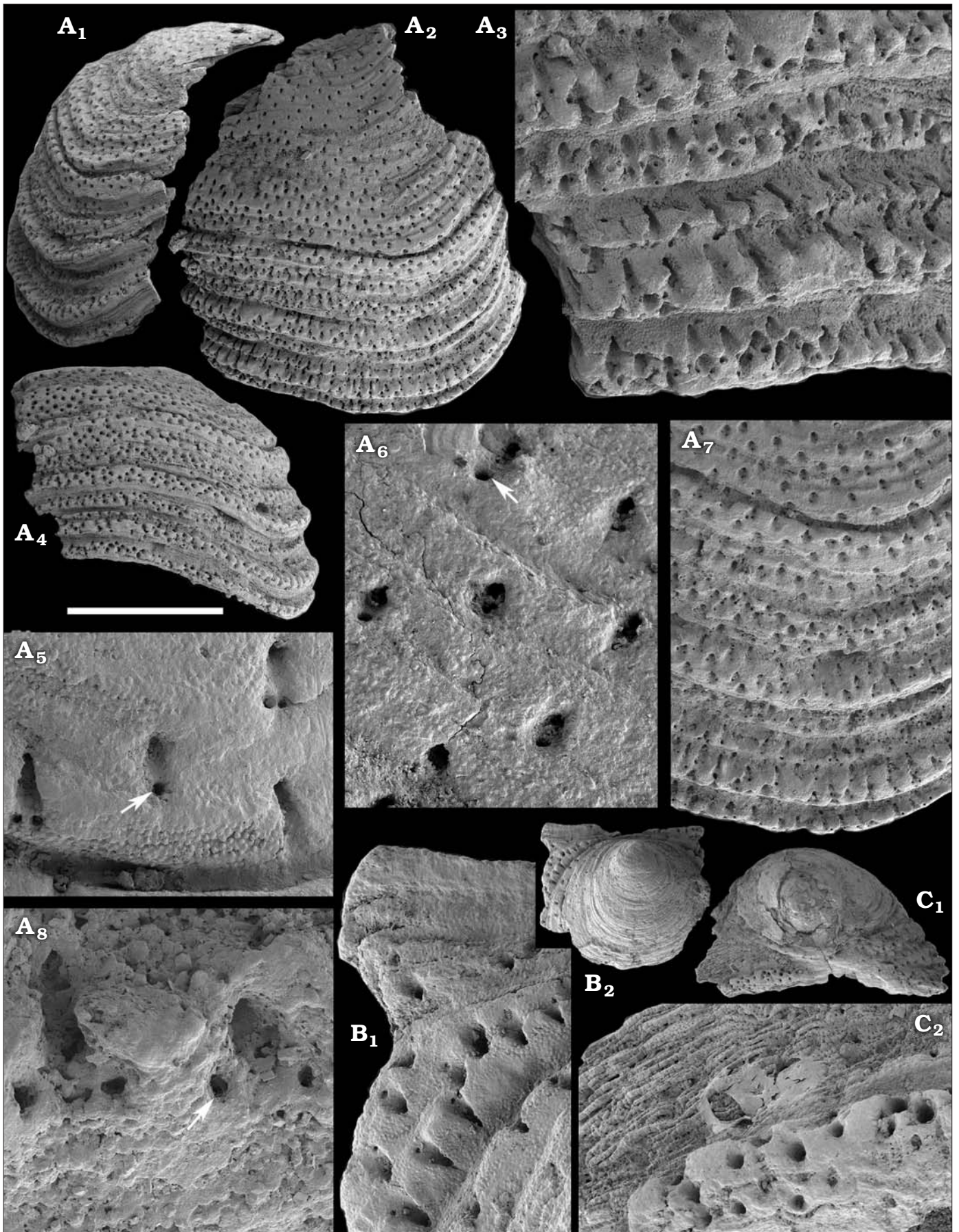
By contrast with *Micrina*, where the medial zone of mitral sclerites is up to four times thinner than the wall at the margin of the sclerite (Williams and Holmer 2002), the shell margin of *Oymurania* is thinner than more proximal parts of the shell (Figs. 10C, 13C). In *Oymurania*, growth of the shell was circumferential. The subapical platform probably allowed for the shell attached to a substrate to grow posteriorly. The presumably dorsal orthoconic valve did not have a prominent subapical platform, but grew more uniformly along the entire margin. There are no signs of a pedicle structure or attachment by cementation in *Oymurania*. Its plausible way of attachment would be by a cuticular pad (Williams et al. 1998), mucus or filaments that is similar to *Mickwitzia* and *Micrina*, but different from pedicle-bearing *Setatella* (Skovsted and Holmer 2003, Skovsted et al. 2010). By contrast with *Oymurania*, both valves in *Setatella* have a pseudointerarea and exhibit a hemiperipheral growth (Skovsted et al. 2010). The morphology of the internal surface of the subapical platform in *Oymurania gravestocki* is unknown, because it is incompletely preserved in all of the specimens. The broad and long subapical platform in *Oymurania* might have had a function of muscle attachment. This is corroborated by presence of a pair of radiating low ridges in *Oymurania* sp. from Morocco, in the area where the apophyses are developed in *Micrina* (Skovsted et al. 2014; fig. 10). The inner surface of the *Oymurania* shell is gener-

ally smooth, and with the exception of scattered openings of orthogonal pores and polygonal ornamentation (Fig. 10E, 11A₆, B) no distinct morphological features are observed. Williams and Holmer (2002) interpreted similar polygonal shell markings in *Micrina* as reflection of soft tissues adjacent to the shell interior, such as mantle epithelium cells and muscle imprints.

The acrotretoid columnar microstructure consists of stratified paired sets of compact laminae delimiting chambers perpendicularly traversed by thin columns (Holmer et al. 2008). Adjacent laminae of contiguous sets are separated by a slot. As known from the organophosphatic brachiopods, such a slot was occupied by an organic membrane onto which the apatite deposited (e.g., Holmer et al. 2009). The axial canals in *Oymurania* (ca. 2 μm in diameter) may continue through several successive sets of laminae (Fig. 13B), whereas the acrotretoid columns probably represent encrustation of apatite along the originally organic fabric that constituted axial canals. The axial canals of the acrotretoid columns in *Oymurania* are equivalent to those canals (2–4 μm) perforating successive laminae in the shell wall. These canals probably penetrate through the primary shell layer to have tiny openings (less than 1 μm) scattered on the shell exterior (Fig. 4C₁; arrow b). In brachiopods, the primary shell layer represents a thin (several μm) sheet consisting of platy apatite deposited underneath the surface of periostracum (Williams and Holmer 2002). Similarly to *Setatella*, the putative primary layer in *Oymurania* is not clearly separated from the underlying laminar secondary layer owing to recrystallization. The outer shell surface is commonly covered by minute tubercles probably reflecting ends of acrotretoid columns (Figs. 7, 10, 12, 13). The acrotretoid columnar microstructure known from the linguliform brachiopods (Williams and Holmer 1992; Cusack et al. 1999; Williams and Cusack 1999) is also present in stem-group brachiopods, such as *Setatella* (Holmer et al. 2002, 2008; Skovsted and Holmer 2003; Skovsted et al. 2010). *Oymurania* has a relatively higher distribution density of canals and respectively acrotretoid columns through the surface of laminae (10000–30000 per mm^2) than that reported from *Setatella* (6000 per mm^2 ; Skovsted and Holmer 2003). In more basal representatives of the stem-group, such as tannuolinids *Tannuolina* Fonin and Smirnova, 1967 and *Micrina*, the acrotretoid columns are not reported. Tannuolinids (Cambrian Stages 2 and 3) are organophosphatic shells (sclerites) perforated by tubular pores and usually consisting of laminae. Recent reconstructions as sessile animals suggest that their sclerites were homologous to shell valves of the linguliform brachiopods (Ushatinskaya 2002; Williams and Holmer 2002; Li and Xiao 2004; Holmer et al. 2008).

Compact and spacious laminar sets co-occur in the wall of *Oymurania* (Figs. 10E–H, 11B, 13A). The laminar sets

← Fig. 11. Stem group-brachiopod *Oymurania gravestocki* Ushatinskaya gen. et sp. nov. from the lower Cambrian Perekhod Formation, Achchagyi-Kyyry-Taas section, Siberia. A. FUB AK21-011; upper (A₁), apertural (A₂), subapical (A₄), and lateral (A₅, oblique lamination of the wall arrowed) views. Close-ups of the inner shell surface with polygonal texture (A₃, A₄) indicates area with shallow concave polygons (A₃, arrowed); openings of the orthogonal canals (A₆, arrowed). B. SMNH X5301, inner surface of a small specimen with shallow concave polygons and openings of orthogonal canals (arrow a); compact (arrow b) and more spacious (arrow c) lamination co-occur in the wall. Scale bar A₁, A₂, A₄, A₅, B, 300 μm ; A₃, A₆, 120 μm .



with acrotretoid columns are distinct in the outer part of the shell wall, where the laminae deflect in accordance with the marginal accretionary growth of the shell and the wedge-shaped laminae with a well-developed columnar microstructure form imbricating growth increments. The inner portion of the wall commonly has a more massive appearance being less distinctly laminated subparallel to the shell surface (Figs. 10H, 13A). Thin insertions of columnar lamination into the compact wall occur (Fig. 13A arrowed). Compact stratified growth lamination in the wall devoid of acrotretoid columnar microstructure is also known from tommotiids (Balthasar et al. 2009; Skovsted et al. 2011). It appears that co-occurrence of the compact layers and the acrotretoid columnar microstructure in *Oymurania* represents an original rather than diagenetic feature (Stefan Bengtson and AK unpublished material). Such a microstructural arrangement is supported taphonomically, by the evidence of erosion of the outer portion of the shell with columnar laminar sets and preservation of more compact portions of the wall underneath. Flattened eroded apices and exfoliated outer shell layer can be explained by reworking of the fossils prior to diagenesis. The outer layer was more susceptible to mechanical degradation than the inner one, notably in the apical part (Figs. 4, 5, 10, 11B, 12C₁). Thus, erosion of the outer shell was facilitated by its relatively loose stratified columnar microstructure in comparison with a denser and more compact inner portion of the secondary shell layer.

Different from the acrotretoid columns and their axial canals, the thicker columns or vertical canals (ca. 10 μm in diameter) orthogonally penetrating through the laminar shell wall were first described from *Micrina* and *Setatella* as *Micrina*–*Mickwitzia* columnar structure (Williams and Holmer 2002; Holmer et al. 2002; Skovsted and Holmer 2003). In accordance with revision of mickwitziiids by Skovsted et al. (2010), such a structure is termed herein *Micrina*–*Setatella* columnar structure. Horizontal canals represent longitudinally striated setal tubes that are also known from *Micrina* (Williams and Holmer 2002). Similar striated canals parallel to the shell lamination and open on the ventral pseudointerarea are also available in *Mickwitzia* and *Setatella* (Holmer et al. 2002; Skovsted and Holmer 2003). In *Micrina*, the openings of vertical canals are associated with nick-points and are located in the vicinity of larger openings of horizontal setal canals (Williams and Holmer 2002). The systems of orthogonal and radial canals present in shells of *Oymurania* are apparently homologous with the *Micrina*–*Setatella* columnar structure and the penetrative striated setal columns respectively (Holmer et al. 2008). In *Oymurania*, their external openings are, however, distinctly grouped together within the same indentation or depression

in the outer wall (Fig. 12). The orthogonal canals penetrate through the entire shell nearly perpendicular to the lamination and parallel to the acrotretoid columns (Fig. 10G). In *Setatella*, the orthogonal tubes with walls (2–3 μm thick) contain a central canal up to 5 μm in diameter (open or filled with phosphatic material) or may be preserved as cylindroids without canal, ca. 10 μm in diameter (Skovsted and Holmer 2003; Skovsted et al. 2010). Horizontal setigerous tubes in *Setatella* lay sub-parallel to lamination on the ventral pseudointerarea, within a cylindrical depression and are somewhat thicker (up to 13 μm in diameter) than the vertical tubes. In *Oymurania gravestocki*, the radial canals open at the edges of growth lamellae, notably along the margin of the subapical field. In *Setatella*, density of the vertical canal openings is reported 134 per mm^2 (Skovsted and Holmer 2003), whereas in *Oymurania* the number is 200–300 per mm^2 (equal to the density of depressions with two openings per mm^2). In *Setatella* and *Mickwitzia*, the boundary between the juvenile and mature shell is marked by the appearance of the first canal openings (Balthasar 2004). By comparison with *Mickwitzia*, where the early mature shell is not penetrated by the *Micrina*–*Setatella* or setal canals, openings of those canals appear relatively early in *Micrina* and *Oymurania*, already in the juvenile shell (Holmer et al. 2011; Fig. 7).

Conclusions

Oymurania Ushatinskaya gen. et sp. nov. is widespread on the Siberian Platform where it ranges through the Atdabanian to lower Botoman Stages. It also occurs in Cambrian Stage 3 of Gondwana (Morocco). *Oymurania* is interpreted herein as a stem-group brachiopod with organophosphatic shell consisting of ventral and dorsal valves with rounded anterior margins. *Oymurania* demonstrates a combination of features known from tannuolinids and mickwitziiids as well as linguiform brachiopods. Among the organophosphatic bivalved stem-group brachiopods, *Oymurania gravestocki* is externally most similar to mitral-type sclerites of a tannuolinid *Micrina*. By contrast with the latter, there is no similarity in morphological differentiation of the inner shell surface (i.e., no distinct apophyses present) and no clear difference in general morphology of ventral and dorsal valves (shells that would be similar to sellate sclerites of *Micrina* are missing). The presumably ventral (cyrtocoenic) valve of *Oymurania* differs from putative dorsal (nearly orthocoenic) valve in a more curved apex and a broader subapical platform. Other important differences from *Micrina* are the well-developed acrotretoid columnar microstructure of the wall, as well as the

← Fig. 12. Stem group-brachiopod *Oymurania gravestocki* Ushatinskaya gen. et sp. nov. from the lower Cambrian Perekhod Formation, Achchagyi-Kyyry-Taas section, Siberia. **A.** SMNH X5302, fragment of a large specimen; general views (A_1 , A_2 , A_4); close-up of A_4 showing deltooid pore openings in the distal part of the fragment (A_3); close-ups of A_7 showing deltooid pore openings (A_5 , A_8); close-up of A_7 showing twinned pores in a more proximal area of the shell fragment (A_6 , arrows point to openings of the orthogonal canals); close-up of A_2 (A_7). **B.** SMNH X5292; B_2 , upper view; B_1 , close-up of B_2 showing deltooid pore openings at the subapical margin (B_3). **C.** SMNH X5294; subapical view (C_1); close-up of C_1 showing openings of radial canals and lamination of the wall (C_2). Scale bar A_1 , A_2 , A_4 , B_2 , C_1 , 1200 μm ; A_7 , 600 μm ; A_3 , 300 μm ; B_1 , C_2 , 200 μm ; A_5 , A_6 , 120 μm ; A_8 , 60 μm .

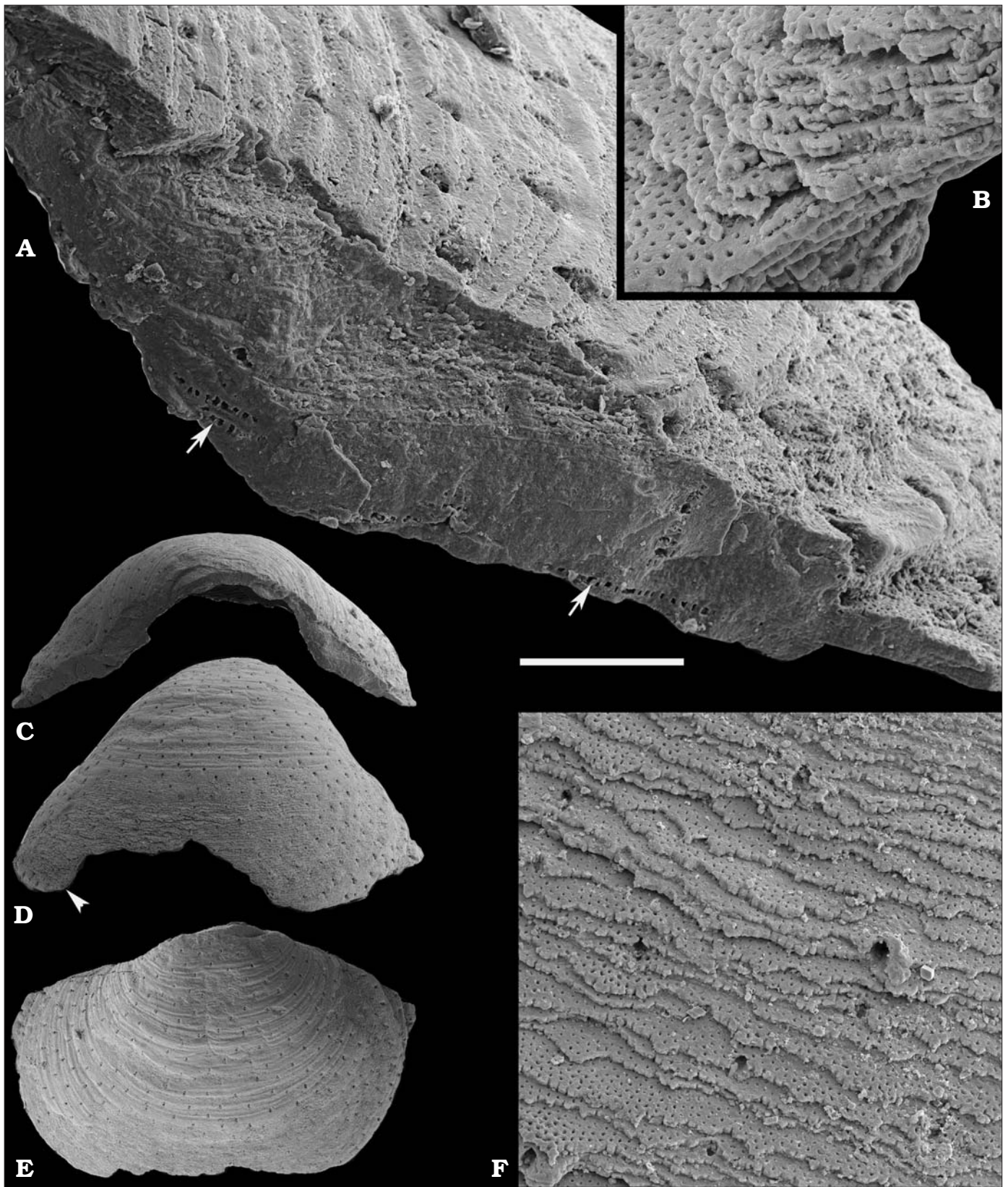


Fig. 13. Stem group-brachiopod *Oymurania gravestocki* Ushatinskaya gen. et sp. nov. from lower Cambrian Perekhod Formation, Achchagyi-Kyyry-Taas section, Siberia. Fragmentary shell with exfoliated surface (FUB AK21-018); apical (C), supra-apical (D), and upper (E) views; close-up of C showing lamellar wall (A), arrowed single chambers with acrotretoid columns situated within otherwise compact portion of the wall; close-up of D showing lamellae of the wall perforated by fine canals (B); close-up of D showing fine and coarser pores on the outer surface (F). Scale bar C–E, 1200 μm ; A, 150 μm ; F, 120 μm ; B, 60 μm .

system of radial and orthogonal canals open on the external shell surface in association with each other in pairs or triplets. More important are similarities to mickwitziiids, such as *Setatella significans* (Skovsted et al. 2010). *Oymurania* and *Setatella* have similar microstructures composed of laminae and acrotretoid columns, but the laminar wall in *Oymurania* exhibits partly compact arrangement where the columnar structures are obscured. Radial canals in *Oymurania* are probably homologous to horizontal setigerous tubes in tannuolinids and mickwitziiids. The orthogonal canals are identical to the *Micrina*–*Setatella* type vertical canals.

Oymurania is less derived morphologically and thus probably more basal in the stem-group Brachiopoda by comparison with *Setatella*, where the latter demonstrates relatively more derived morphological features such as pseudo-interarea, hemiperipheral growth, and ventral pedicle notch (Skovsted et al. 2010). *Oymurania* is more similar in general morphology and distribution of the horizontal setigerous and *Micrina*–*Setatella* type orthogonal canals to such more basal representatives of the stem-group as *Micrina*, but possesses in addition a relatively more derived acrotretoid columnar shell microstructure. Such a new combination of features demonstrates a wider range of their variation in the stem-group Brachiopoda whose evolution occurred in parallel with radiation of the crown-group Brachiopoda in the early Cambrian.

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