An early Cambrian fauna of skeletal fossils from the Emyaksin Formation, northern Siberia

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An assemblage of mineralised skeletal fossils containing molluscs, hyoliths, halkieriids, chancelloriids, tommotiids, lobopodians, paleoscolecids, bradoriids, echinoderms, anabaritids, hyolithelminths, hexactinnelid, and heteractinid sponges is described from the early Cambrian Emyaksin Formation exposed along the Malaya Kuonamka and Bol'shaya Kuonamka rivers, eastern flanks of the Anabar Uplift, northern Siberian Platform. The sampled succession is attributed to the Tommotian–Botoman Stages of Siberia and correlated with Stage 2 of Series 1–Stage 4 of Series 2 of the IUGS chronostratigraphical scheme for the Cambrian. Carbon isotope chemostratigraphy is applied herein for regional correlation. The fauna contains the earliest Siberian and probably global first appearances of lobopodians, paleoscolecids, and echinoderms, and includes elements in common with coeval faunas from Gondwana, Laurentia, and Baltica. For the first time from Siberia, the latest occurrence of anabaritids is documented herein from the Atdabanian Stage. Problematic calcium phosphatic sclerites of *Fengzuella zhejiangensis* have not been previously known from outside China. The sellate sclerites, *Camenella garbowskae* and mitral sclerites, *C. kozlowskii* are unified within one species, *C. garbowskae*. In addition to more common slender sclerites, *Rhombocorniculum insolutum* include broad calcium phosphatic sclerites. A number of fossils described herein demonstrate excellent preservation of fine details of skeletal microstructures. Based on new microstructural data, sclerites of *Rhombocorniculum* are interpreted as chaetae of the type occurring in annelids. A new mollusc *Enigmaconus*? *pyramidalis* Kouchinsky and Vendrasco sp. nov. and a hyolith *Triplicatella papilio* Kouchinsky sp. nov. are described.

Key words: Skeletal fossils, Echinodermata, stratigraphy, Cambrian, Siberia.

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Introduction

The description of "Small Shelly Fossil" faunas of the middle and upper parts of the Emyaksin Formation presented herein continues the chronicle of fossils from the overlying and younger Kuonamka Formation (Gubanov et al. 2004; Kouchinsky et al. 2011), in the same area of the Malaya Kuonamka and Bol'shaya Kuonamka rivers, eastern flanks of the Anabar Uplift of the northern Siberian Platform. Skeletal fauna from the underlying strata of the lower part of the Emyaksin, Medvezhya and Manykay formations of the eastern and western flanks of the Anabar Uplift as well as brachiopods from the middle–upper Emyaksin and Kuonamka Formations are yet under investigation. Among them, a new stem-group brachiopod *Oymurania gravestocki* Ushatinskaya in Kouchinsky et al., in press and paterinid brachiopod *Pelmanotreta neguertchenensis* (Pelman, 1977) have been already reported by Kouchinsky et al. (in press) and Skovsted et al. 2015, respectively. The present material provides additional information for the development of regional and global chronostratigraphy of the Cambrian System, the upper Terreneuvian Series and Cambrian Series 2 (see Babcock and Peng 2007; Landing et al. 2007, 2013; Li et al. 2007). In the present work, we will provisionally correlate the base

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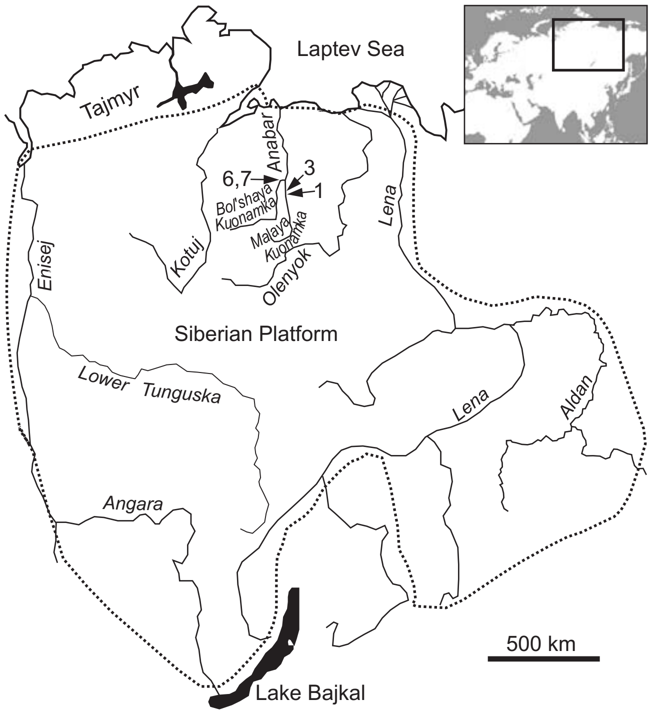


Fig. 1. Map showing location of sections 1, 3, Malaya Kuonamka River; 6, 7, Bol'shaya Kuonamka River.

of Cambrian Stage 2 of the Terreneuvian Series with the lowermost *Watsonella crosbyi* Zone of Avalonia and South China, the base of Cambrian Series 2 and Stage 3 within the lowermost Atdabanian Stage in Siberia (near the appearance of the oldest trilobites) and the base of Cambrian Stage 4 with the lower part of Botoman Stage in Siberia (due to the occurrence of *Bergeroniellus* species).

Institutional abbreviations.—SMNH, Swedish Museum of Natural History, Stockholm, Sweden with prefixes Mo (molluscs), Ar (arthropods), Ec (echinoderms), Sp (sponges), and X (other fossils).

Material and methods

Material described herein was obtained by Artem Kouchinsky and Stefan Bengtson in 1996, during fieldwork along the Malaya Kuonamka and Bol'shaya Kuonamka rivers, on the eastern flanks of the Anabar Uplift, Siberian Platform (Fig. 1). Except for one sample from the upper Botoman limestone concretions (within bituminous shale) of the basal Kuonamka Formation, the fossils described herein derive from Tommotian–lower Botoman limestone rocks of the middle–upper part of the Emyaksin Formation (Fig. 2). Section 1 (70°08.5'N, 114°00'E, the coordinates according to Google Earth) crops out along the left bank of the Malaya Kuonamka River, near and downstream of the village Zhilinda. The lowermost part of the section belongs to the uppermost Emyaksin Formation represented by bioturbated fossiliferous greenish-grey, glauconitic, lime mudstone with wacke- and packstone. Those are interbedded with greenish-grey shale, especially in the uppermost 3 m, and overlain by the Kuonamka Formation (see Kouchinsky et al. 2011). Other sections cut through the bioturbated fossiliferous reddish-maroon and greenish-grey lime mud- and wackestone of the middle–upper parts of the Emyaksin Formation. Section 3 (section A-42 in Val'kov 1975; 70°13'N, 113°42'E) is exposed along the left bank of the Malaya Kuonamka River, 1.5–2 km downstream from the mouth of the Maspaky Brook. Section 6 (section A-53 in Val'kov 1975; 70°43'N, 112°50'E) is exposed along the right bank of the Bol'shaya Kuonamka River, 1–2.5 km downstream from the mouth of the Ulakhan-Tyulen Brook. Section 7 (section A-54 in Val'kov 1975; 70°43'N, 112°52.5'E) 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 were initially extracted from the limestone (1–3 kg samples) using a buffered solution of 10% acetic acid.

Samples for carbon isotope analysis from sections 1, 3, 6, and 7 (Fig. 2) were also collected in 1996 and analysed in Stockholm in 1999–2000. Kouchinsky et al. (2001) describe methods and results of analyses from sections 3 and 6. Results of carbon isotope analysis from sections 1 and 7 are available in Supplementary Online Material: SOM 1 avialable at http://app.pan.pl/SOM/app60-Kouchinsky_etal_SOM.pdf and at the Pangaea database at http://www.pangaea.de/.

Fauna of the middle–upper Emyaksin Formation

The assemblages of skeletal fossils reported herein from the limestone of the middle–upper Emyaksin Formation and carbonate concretions of the basal Kuonamka Formation contain the following groups: shells of molluscs and calcium phosphatic brachiopods, conchs and opercula of hyoliths; sclerites of tommotiids, halkieriids, chancelloriids, *Rhombocorniculum*, protoconodonts, lobopodians, and paleoscolecids; carapace fragments of arthropods, including bradoriids; plates of echinoderms; spicules of hexactinellid and heteractinid sponges; tubes of hyolithelminths and anabaritids; and a few other problematic sclerites and globules (SOM 2 and 3). Polymerid and agnostid trilobites of the Botoman Stage from the uppermost Emyaksin and lower Kuonamka Formation provide the main biostratigraphical context (Korovnikov 2006; Rozanov and Varlamov 2008), whereas carbon isotope chemostratigraphy enables correlation with the lower Cambrian stratotypes of the southeastern Siberian Platform (Kouchinsky et al. 2001).

With the exception of a single sample 7/36.6 from the Atdabanian Stage and samples K1-3B and 7/70 from the lower Botoman Stage, calcium phosphatic internal moulds of molluscan shells extracted from the samples are rare (SOM 2). They are represented by "micromolluscs" (<5 mm). Although the small size of molluscan shells herein may be a taphonomic artifact (Martí Mus et al. 2008), larger mol-

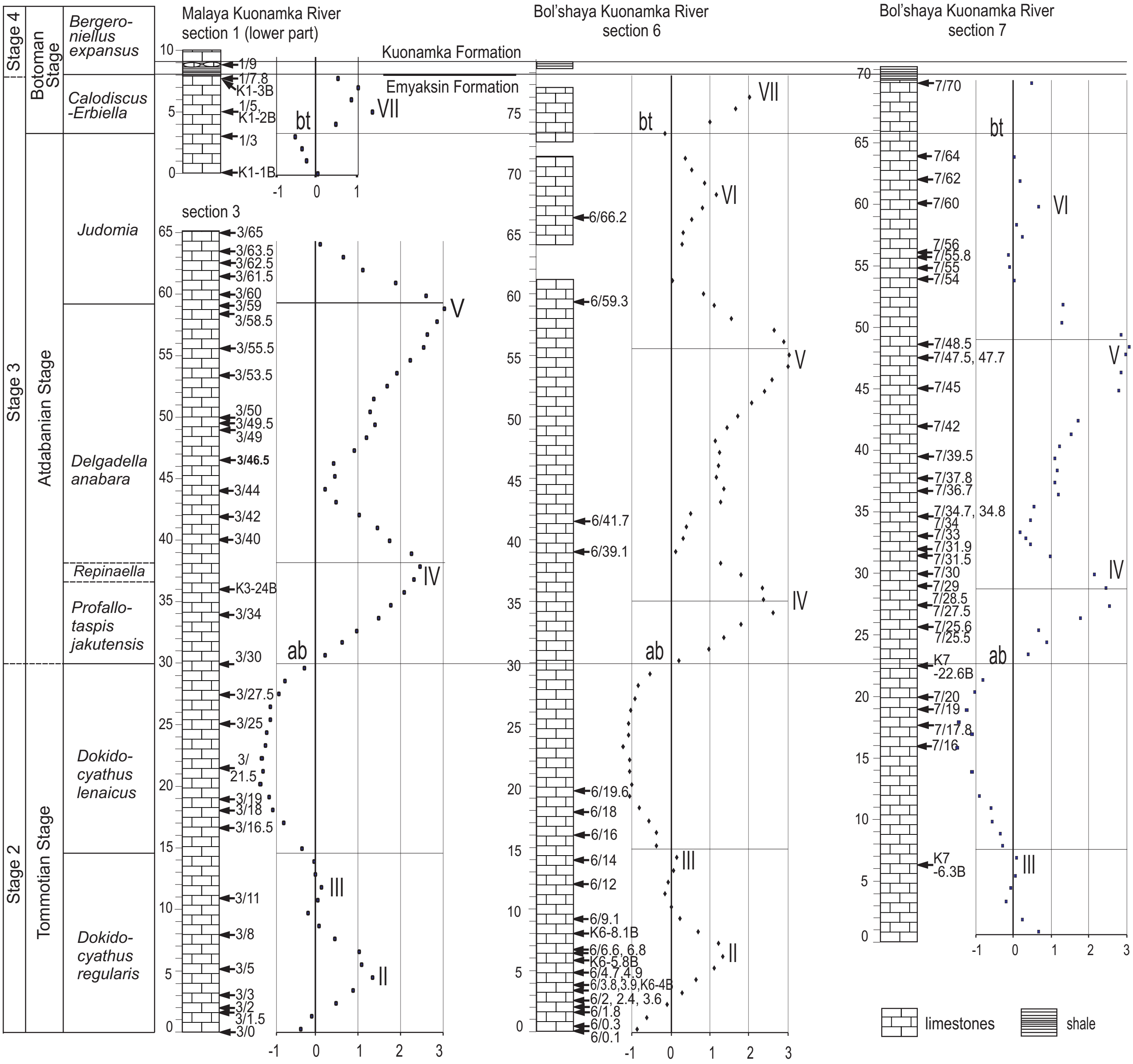


Fig. 2. Derivation of fossiliferous samples (arrows with numbers) and chemostratigraphic correlation of sections 1 and 3 (Malaya Kuonamka River) with sections 6 and 7 (Bol'shaya Kuonamka River). Correlation with carbon isotope features II–VII from stratotypes of south-eastern Siberian Platform (Brasier et al. 1994) according to Kouchinsky et al. (2001). Note that the zero level in all sections corresponds to the water level above which the sections were exposed in 1996. Description of fauna from the lower part of the Emyaksin Formation in complementary outcrops at the Bol'shaya Kuonamka River (below that zero level) will be published elsewhere. Fauna from the overlying Kuonamka Formation is published by Gubanov et al. (2004) and Kouchinsky et al. (2011).

luscan shells, by contrast with hyoliths, were not identified in the outcrops and in the samples available. Some of the molluscs from Bol'shaya Kuonamka and characters of their shell microstructures were also demonstrated by Kouchinsky (2000a) and Vendrasco et al. (2011b). These include *Enigmaconus*? *pyramidalis* Kouchinsky and Vendrasco sp. nov.

Hyoliths from the middle–upper parts of the Emyaksin Formation of the eastern flanks of the Anabar Uplift (Malaya Kuonamka and Bol'shaya Kuonamka) were investigated by Val'kov (1975) and summarised later by Val'kov (1987; see SOM 3 for taxa). Those hyolith conchs were mainly extracted by mechanical preparation and/or known from thin-sections. Most of them are several cm long. The differences in size and preservation prohibit comparison with the micro-sized hyoliths extracted chemically and figured herein. Some of the latter were preliminarily reported by Kouchinsky (2000b). In our material, hyoliths are generally common and locally abundant in thin sections and in rock samples (SOM 2). They can reach several cm in width and length, but their chemical extraction typically fails. Hyoliths described here are represented by calcium phosphatic internal moulds, as well as by phosphatised conchs and opercula, recovered in remarkable diversity from samples 7/36.7, K1-3B, and 7/70, including opeculum *Triplicatella papilio* Kouchinsky sp. nov.

Halkieriids are represented by rare phosphatised sclerites and internal moulds of *Halkieria* sp. from the lower part of the *Delgadella anabara* Zone, Atdabanian Stage (Bol'shaya Kuonamka River). The moulds are more common but poorly preserved in sample 7/30 (SOM 2). Chancelloriid sclerites occur throughout the sections, ranging from the lower *Dokidocyathus regularis* Zone, Tommotian Stage, to the *Bergeroniellus expansus* Zone, Botoman Stage (SOM 2). They occur as numerous calcium phosphatic and glauconitic internal moulds of disarticulated and occasionally articulated sclerites rarely preserving also phosphatised walls. They are generally referred to *Chancelloria* spp., including *Chancelloria* cf. *C. eros*. A single disarticulated sclerite is found in the basal part of section 6, but they become common (tens of specimens), even abundant (hundreds and thousands of sclerites per sample) in the upper Tommotian through Botoman strata.

Calcium phosphatic disarticulated sclerites of tommotiids include *Camenella garbowskae* Missarzhevsky in Rozanov and Missarzhevsky, 1966 and *Lapworthella dentata* Missarzhevsky in Rozanov et al., 1969. The sellate sclerites, *Camenella garbowskae* and mitral sclerites, *C. kozlowskii* are unified within one species, *C. garbowskae*. *Camenella garbowskae* occurs in the Tommotian beds, more commonly in the lower part. In addition to more common slender sclerites, *Rhombocorniculum insolutum* include broad calcium phosphatic sclerites. Rare specimens of *Lapworthella dentata* range from the *Delgadella anabara* Zone, Atdabanian Stage through the *Calodiscus*-*Erbiella* Zone, Botoman Stage, but are relatively more common in the upper *Judomia* Zone, Atdabanian Stage (samples 7/62 and 7/64). Together with common calcium phosphatic brachiopods, such as paterinids, acrotretids, and lingulids, they will be described elsewhere.

Calcium phosphatic problematic sclerites of *Rhombocorniculum insolutum* Missarzhevsky in Missarzhevsky and Mambetov, 1981 occur in strata correlated with the *Dokidocyathus lenaicus* Zone, Tommotian Stage through the lower *Delgadella anabara* Zone, Atdabanian Stage. Sclerites of *R. cancellatum* (Cobbold, 1921) are described herein from beds correlated with the *Judomia* Zone, Atdabanian Stage (most abundant in samples 3/62.5, 6/66.2, and 7/60).

Protoconodonts are represented by *Amphigeisina danica* (Poulsen, 1966), *Gapparodus bisulcatus* (Müller, 1959), and *Hagionella cultrata* (Missarzhevsky, 1977) from calcareous concretions of the basal Kuonamka Formation (sample 1/9), *Bergeroniellus expansus* Zone, upper Botoman Stage. *Hagionella cultrata* (Missarzhevsky, 1977) is also found in the Emyaksin Formation, in beds attributed herein to the *Delgadella anabara* Zone. Protoconodonts, including several unnamed forms, are very rare in the Emyaksin Formation, but become common in the overlying Kuonamka Formation (see also Kouchinsky et al. 2011). The occurrence of *Gapparodus bisulcatus* reported herein from the lower part of Cambrian Stage 4 is the earliest one known from the Siberian Platform, where this form also occurs in the Cambrian Stage 5, Kuonamka Formation (Kouchinsky et al. 2011).

Calcium phosphatic lobopodian sclerites *Microdictyon* cf. *M. rhomboidale* Bengtson, Matthews, and Missarzhevsky, 1986 are found in the middle *Judomia* Zone, Atdabanian Stage. Rare fragments of *Microdictyon* sp. are reported herein from beds correlated with the *Delgadella anabara* Zone, being the earliest occurrence of lobopodians known from Siberia. Disarticulated sclerites of the paleoscolecid *Hadimopanella knappologica* (Bengtson, 1977) occur in the *Judomia* through *Calodiscus-Erbiella* Zone and are abundant in the upper *Judomia* Zone.

Fragments of carapaces and calcium phosphatic cones with tubercles on the external surface, such as *Cambrocassis verrucatus* Missarzhevsky, 1977 and similar sclerites *Nikolarites spasskyi* Vasil'eva, 1994, occur in beds correlated with the uppermost *Delgadella anabara* Zone and overlying strata of the upper Emyaksin Formation. Spines that are probably derived from bradoriid arthropods, such as *Mongolitubulus spinosus* (Hinz, 1987), occur in the *Judomia* Zone and higher, in the Emyaksin Formation, as well as in the upper Botoman carbonate concretions of the basal Kuonamka Formation.

Echinoderm ossicles include brachiolars and brachioliferous thecal plates of eocrinoids, uniserial unbranched (brachitaxial) and bifurcating (axillary) brachial plates of blastozoan echinoderms, edrioasteroid ambulacral and thecal plates, and other thecal plates of enigmatic affinity. The plates occur in the upper part of the *Delgadella anabara* Zone, Atdabanian Stage through the *Calodiscus-Erbiella* Zone of the lower Botoman Stage.

Tubes of hyolithelminths, represented by *Hyolithellus* spp. and *Torellella* cf. *T. laevigata* (Linnarson, 1871), are common in this collection and present in most of the samples studied (SOM 2). Rare calcium phosphatic internal moulds of tubes of anabaritids are recognised herein from the Atdabanian Stage, as well as problematic calcium phosphate sclerites of *Fengzuella zhejiangensis* He and Yu, 1992.

Various siliceous pentactines and hexactines of hexactinellid sponges are abundant in the basal part of section 6, attributed herein to the lower *Dokidocyathus regularis* Zone and in the middle of the *Delgadella anabara* Zone in sections 3 and 7 (SOM 2). Other rare forms, such as monaxonous siliceous spicules, have an uncertain affinity with Hexactinellida. Spicules of heteractinid sponges occur in the uppermost Emyaksin Formation, *Calodiscus-Erbiella* Zone, Botoman Stage. The collection of sponge spicules is represented by megascleres.

Finally, phosphatised globules are found in many samples from the Emyaksin Formation, but their preservation prevents identification of the available globular objects. Among almost featureless and deformed globules, a single well preserved specimen of *Aetholicopalla adnata* Conway Morris in Bengtson et al., 1990, a form with uncertain, probably algal-related higher rank affinity was found in the *Calodiscus-Erbiella* Zone, lower Botoman Stage.

Systematic palaeontology

Phylum Mollusca Cuvier, 1797

Class uncertain

Order Helcionellida Geyer, 1994

Family Yochelcionellidae Runnegar and Jell, 1976

Genus *Yochelcionella* Runnegar and Pojeta, 1974

Type species: *Yochelcionella cyrano* Runnegar and Pojeta, 1974; *Redlichia chinensis* Zone, Ordian Stage; Mootwingee Range, New South Wales, Australia.

Remarks.—*Yochelcionella* is erroneously placed under Family Helcionellidae Wenz, 1938 in Gubanov et al. (2004) and Kouchinsky et al. (2011).

Yochelcionella cf. *Y. greenlandica* Atkins and Peel, 2004

Fig. 3.

Material.—Eight calcium phosphatic internal moulds, including four figured specimens SMNH Mo 160417, 160418, 167648, and 167649 from sample 7/36.7. Emyaksin Formation, Bol'shaya Kuonamka River; correlated with the *Delgadella anabara* Zone, Atdabanian Stage.

Description.—Shell slightly cyrtoconic, laterally somewhat compressed, with a sub-apical tube (snorkel) and overhanging apex inclined towards snorkel. In lateral view, the supra-apical margin is convex near the apex, but straightens towards the aperture. Three to four transverse folds run around the inner shell surface (as reflected by internal moulds), more prominent laterally. The aperture is oval, with a length/width ratio of ca. 1.5. The diameter of bulbous apex varies from 0.2 to 0.3 mm. Snorkel, drop-like or oval in cross-section (Fig. $3A_2$–C_2), narrows distally without apparent flaring and projects upwards at ~45° with respect to the apertural plane.

Remarks.—The fossils herein were described as *Yochelcionella* sp. by Kouchinsky (2000a: 130, fig. 9). Comparison with shells and internal moulds of the same size belonging to twenty known species of *Yochelcionella* shows that the fossils described herein are most similar to the holotype of *Y. greenlandica* Atkins and Peel, 2004 from Stage 4 of Laurentia (Atkins and Peel 2008: fig. 8 A–D), but the latter has a slightly more pronounced overhang of the apex and a relatively slim snorkel.

Family Helcionellidae Wenz, 1938

Genus *Bemella* Missarzhevsky in Rozanov et al., 1969

Type species: *Helcionella jacutica* Missarzhevsky in Rozanov and Missarzhevsky, 1966; *Dokidocyathus regularis* Zone, Tommotian Stage; Tiktirikteekh, near Churan village, middle Lena River, Siberia.

Bemella? sp.

Fig. 4.

Material.—Five calcium phosphatic internal moulds, including four figured specimens SMNH Mo 167650–167653 from sample 7/36.7. Emyaksin Formation, Bol'shaya Kuonamka River; correlated with the *Delgadella anabara* Zone, Atdabanian Stage.

Description.—Low cyrtoconic, laterally somewhat compressed shell. Apertural margin suboval in outline, narrowing towards straight subapical margin, with length/width ratio 1.8 to 2.0. Apex bulbous and somewhat compressed laterally, strongly inclined and projecting beyond the apertural margin. Sub-apical side concave and relatively short. Supra-apical side long and evenly convex. The inner surface of the shell (as reflected by internal moulds) bears concentric folds.

Remarks.—The fossils have diagnostic features of *Bemella*, but their assignment is hampered by incomplete preservation as smooth internal moulds.

Genus *Parailsanella* Zhegallo in Voronova et al., 1987

Type species: *Parailsanella acris* Zhegallo in Voronova et al., 1987; *Fallotaspis* Zone, Montezuman Stage; Mackenzie Mountains, Northwest Territories of Canada.

Remarks.—*Parailsanella* includes bilaterally symmetrical, laterally compressed, slightly cyrtoconic univalves. *Parailsanella* is smaller in general and more laterally compressed than *Ilsanella* Missarzhevsky, 1981. *Ilsanella* is usually represented by larger (>1 cm) forms, with straight apertural margin, whereas in mm-sized *Parailsanella* (sensu Parkhaev in Gravestock et al. 2001) there is a sinus or train, which is not, however, reported from the type species, *P. acris* (Voronova et al. 1987: 45, pl. 20: 1). Lateral compression is not as conspicuous as in stenothecids (see below). *Parailsanella* is most similar to *Mackinnonia* Runnegar in Bengtson et al., 1990 (see below), but the latter can be distinguished by a lower shell, strongly hooked apex and more prominent train with a pegma-like structure. Comparison with generally similar *Anabaroconus* Gubanov, Kouchinsky, Peel, and Bengtson, 2004 (see also Kouchinsky et al. 2011) is hampered by its different mode of preservation as silicified shells. The otherwise similar *Capitoconus* Skovsted, 2004 was originally distinguished from *Parailsanella* only by a larger and more elongated protoconch. The forms described below fit the diagnosis of *Parailsanella*, although without a sinus or train preserved.

Parailsanella sp. 1

Figs. 5, 6.

Material.—Thirty-nine calcium phosphatic internal moulds, including four figured specimens SMNH Mo 160415, 160416, 167655, and 167656 from sample 7/36.7. Emyaksin Formation, Bol'shaya Kuonamka River; correlated with the *Delgadella anabara* Zone, Atdabanian Stage.

Description.—Slightly cyrtoconic, laterally somewhat compressed shells. Supra-apical surface evenly convex; sub-apical surface concave. Aperture broadly oval, with length/width ratio 1.7 to 2.0. Low and broad comarginal folds, faint on small (juvenile) specimens, are situated on the inner shell surface (as reflected by internal moulds). The apex is ~0.3 mm in lateral view, bulbous and pinched at its base.

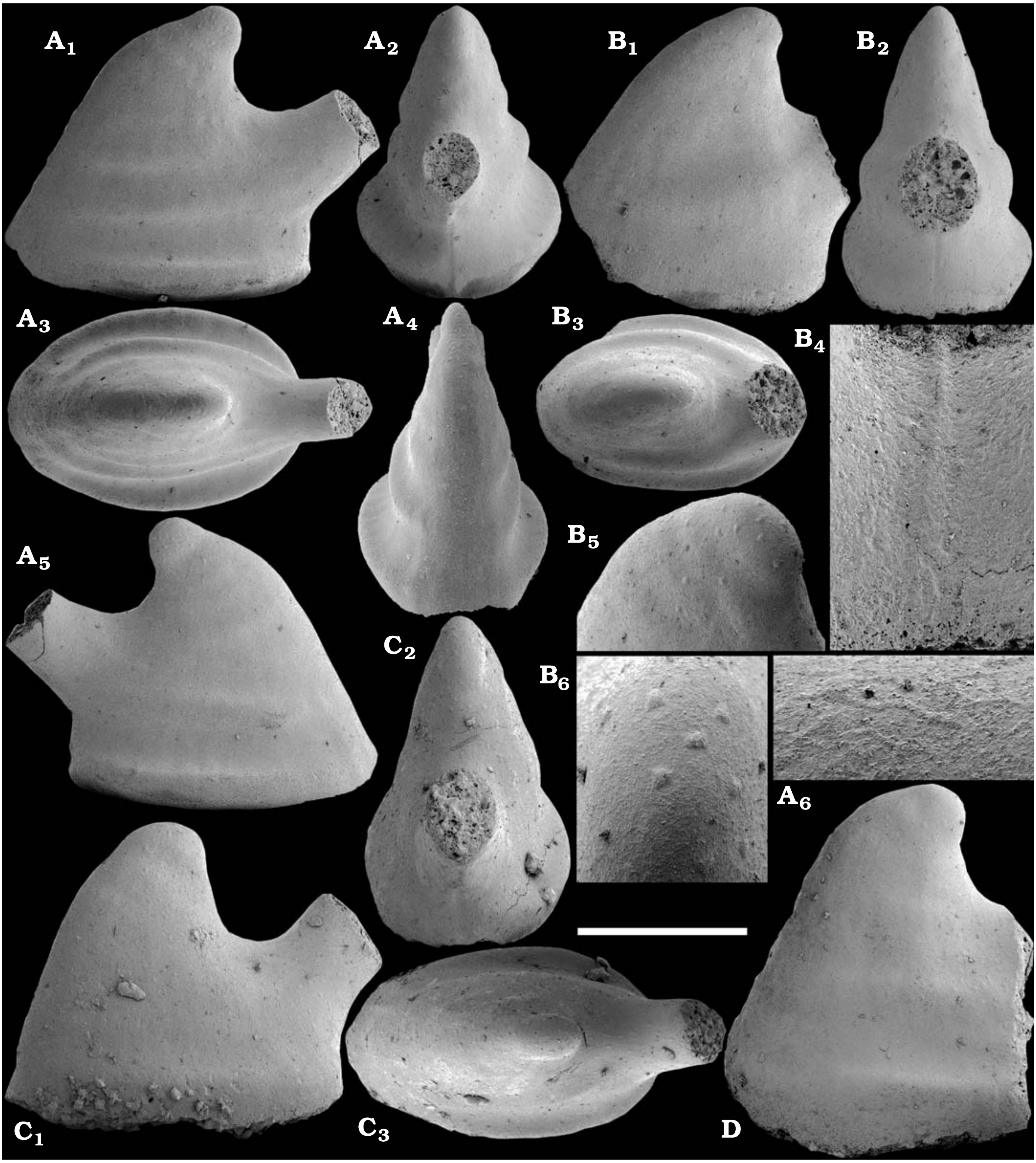


Fig. 3. Helcionellid mollusc *Yochelcionella* cf. *Y. greenlandica* Atkins and Peel, 2004 internal moulds from lower Cambrian Emyaksin Formation, Bol'shaya Kuonamka River, Anabar Uplift, Siberia; sample 7/36.7. **A**. SMNH Mo 160417; lateral ($A_{1,\,A5}$), sub-apical (A_2), upper (A_3), and supra-apical (A_4) views; A_6, polygonal texture on the surface of snorkel mould. **B**. SMNH Mo 160418; lateral (B_1), sub-apical (B_2), and upper (B_3) views; B_4, enlargement of B_2, with a shallow groove between the snorkel and aperture; B_5, apical part of the mould with tubercles; B_6, close-up of B_5. **C**. SMNH Mo 167648; lateral (C_1), sub-apical (C_2), and upper (C_3) views. **D**. SMNH Mo 167649; lateral view. Scale bar 600 µm, except A_6, 60 µm; B_4, 150 µm; B_5, 300 µm; B_6, 120 µm.

Remarks.—The surface of internal moulds, excluding apical area, is commonly covered with pits ~5 µm in diameter and 10–20 µm apart (Fig. 6A). In one case, a juvenile mould preserves a shallow polygonal texture with centres of polygons

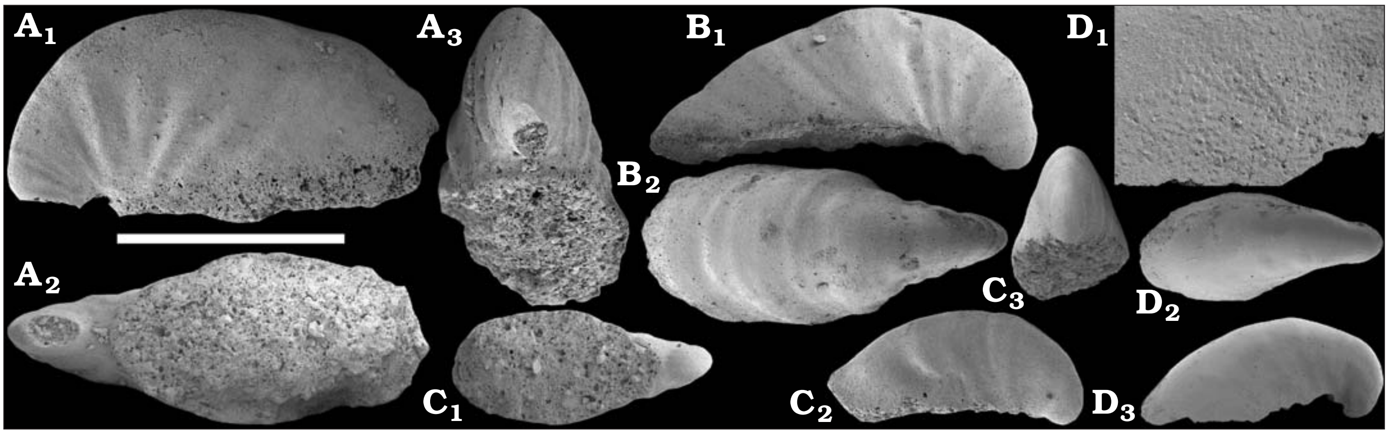


Fig. 4. Helcionellid mollusc *Bemella*? sp. internal moulds from lower Cambrian Emyaksin Formation, Bol'shaya Kuonamka River, Anabar Uplift, Siberia; sample 7/36.7. **A**. SMNH Mo 167650; lateral (A_1), apertural (A_2), and sub-apical (A_3) views. **B**. SMNH Mo 167651; lateral (B_1) and upper (B_2) views. **C**. SMNH Mo 167652; apertural (C_1), lateral (C_2), and sub-apical (C_3) views. **D**. SMNH Mo 167653; D_1, close-up of apertural margin in D_3; upper (D_2) and lateral (D_3) views. Scale bar 1200 μm, except D_1, 300 μm.

10–20 μm apart (Fig. 6B). *Parailsanella* sp. 1 is very similar to *Capitoconus inclinatus* Skovsted, 2004 from Stage 4 of Greenland, but the latter form has a relatively larger globose protoconch and laterally more compressed shell. The fossils described herein are discussed as *Ilsanella* sp. by Kouchinsky (2000a: 130, fig. 8).

Parailsanella sp. 2

Fig. 7.

Material.—Single calcium phosphatic internal mould SMNH Mo 167658 from sample 7/70. Uppermost Emyaksin Formation, Bol'shaya Kuonamka River; *Calodiscus*-*Erbiella* Zone, lower Botoman Stage.

Description.—Slightly cyrtoconic and laterally compressed shell. Aperture is narrow oval, with length/width ratio of 3. The apex is bulbous, ~0.3 mm in lateral view. The inner shell surface (as reflected by internal moulds) is covered with comarginal folds.

Remarks.—The form is similar to *Capitoconus artus* Skovsted, 2004 from Stage 4 of Greenland. The latter is preserved, however, with remains of phosphatised shell, with prominent sharp transverse ribs and a more distinct apex (Skovsted 2004: fig. 5). *Parailsanella* sp. 2 is more compressed laterally and has more distinct narrower comarginal folds than *Parailsanella* sp. 1 herein.

Genus *Figurina* Parkhaev in Gravestock et al., 2001

Type species: Figurina figurina Parkhaev in Gravestock et al., 2001; *Abadiella huoi* Zone, lower Cambrian; Horse Gully section, Yorke Peninsula, Australia.

Figurina cf. *F. nana* (Zhou and Xiao, 1984)

Fig. 8.

Material.—Two phosphatised internal moulds, SMNH Mo167659 and 167660 from sample 7/70. Uppermost Emyaksin Formation, Bol'shaya Kuonamka River; *Calodiscus*-*Erbiella* Zone, lower Botoman Stage.

Description.—Low, slightly cyrtoconic, laterally somewhat compressed shell, 0.8–0.9 mm in width and height and 1.7 mm long, with rounded apex displaced towards the apertural margin and indistinct protoconch. The inner shell surface (as reflected by internal moulds) has faint transversal folds. Subapical surface is very short. Aperture oval, a little flared, with subapical train.

Remarks.—Internal mould is covered with shallow pits, 10 μm in diameter (Fig. 8A_4). The fossils have diagnostic features of *Figurina* Parkhaev in Gravestock et al. 2001. Compared to the type species, *F. figurina* Parkhaev in Gravestock et al. 2001 (Series 2, Australia), *F. capitata* Parkhaev in Gravestock et al. 2001 (Series 2, Australia), *F. groenlandica* Skovsted, 2004 (Stage 4, Laurentia), and *F. nana* (Zhou and Xiao, 1984) (Series 2, North China and Australia), the fossils are most similar to *F. nana* (see Gravestock et al. 2001: pl. 35: 7), but one of the specimens herein (Fig. 8B) appears wider. *Figurina* cf. *F. nana* are also similar to internal moulds of juveniles of *Mackinnonia anabarica* (see below, Figs. 9C, 11C), but are twice as big and have wider and less curved apex.

Genus *Mackinnonia* Runnegar in Bengtson et al., 1990

Type species: Mackinnonia davidi Runnegar in Bengtson et al., 1990; *Abadiella huoi* Zone, lower Cambrian; Horse Gully section, Yorke Peninsula, Australia.

Mackinnonia anabarica Parkhaev, 2005

Figs. 9–11.

Material.—Twenty two calcium phosphatic internal moulds, including six figured specimens SMNH Mo 160419, 160420, 167662–167665 from sample 7/70 and fifteen specimens from sample K1-3B. Uppermost Emyaksin Formation, Bol'shaya Kuonamka and Malaya Kuonamka rivers; *Calodiscus*-*Erbiella* Zone, lower Botoman Stage.

Description.—Cyrtoconic, laterally compressed shell, with length/width ratio 1.8 to 2.5. The apex is displaced to near the apertural margin and hooked. The aperture is drop-like

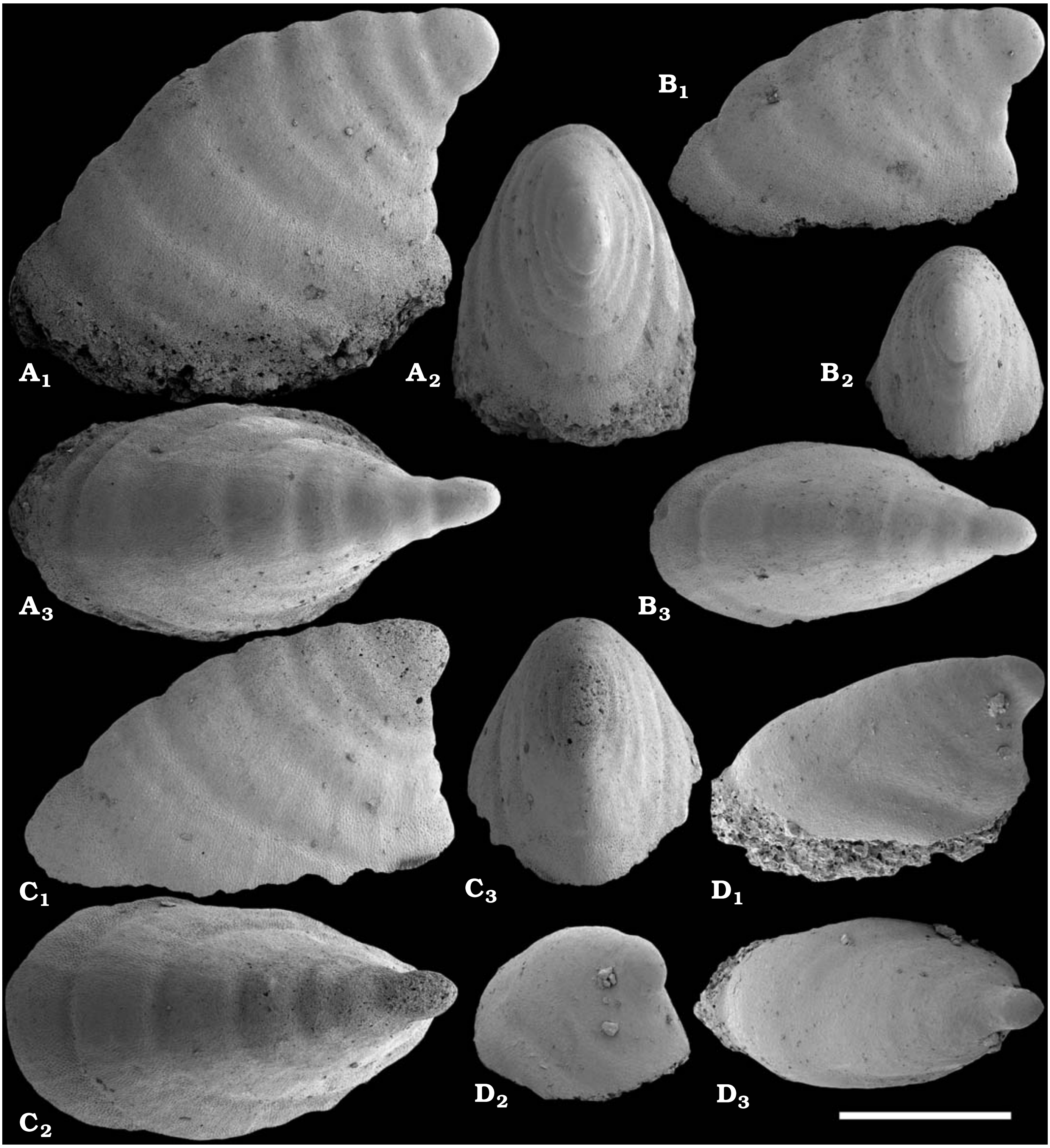


Fig. 5. Helcionellid mollusc *Parailsanella* sp. 1 internal moulds from lower Cambrian Emyaksin Formation, Bol'shaya Kuonamka River, Anabar Uplift, Siberia; sample 7/36.7. **A**. SMNH Mo 160415; lateral (A_1), sub-apical (A_2), and upper (A_3) views. **B**. SMNH Mo 167655; lateral (B_1), sub-apical (B_2), and upper (B_3) views. **C**. SMNH Mo 167656; lateral (C_1), upper (C_2), and sub-apical (C_3) views. **D**. SMNH Mo 160416; lateral (D_1), oblique sub-apical (D_2), and upper (D_3) views. Scale bar 600 μm.

in dorsal profile, narrowing towards the subapical margin. The subapical margin of the aperture curves upwards and forms a train. The protoconch is not distinct on the internal mould. The inner shell surface (as reflected by internal moulds) bears concentric folds, which are most prominent near the apertural margin of larger specimens and tend to disappear in the subapical region. Smaller (juvenile?) shell has only one fold on the inner surface, near the apertural

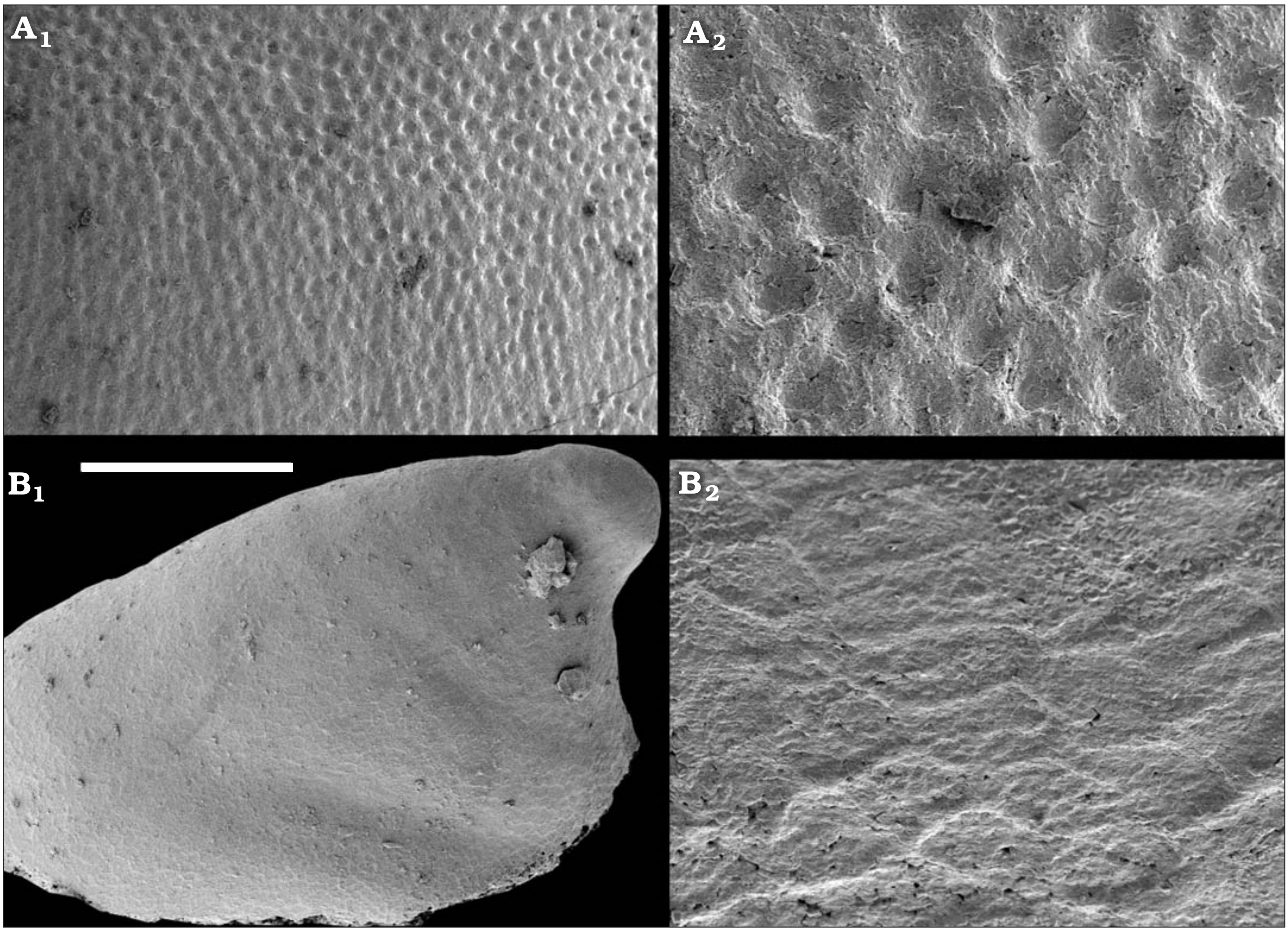


Fig. 6. Helcionellid mollusc *Parailsanella* sp. 1 internal moulds from lower Cambrian Emyaksin Formation, Bol'shaya Kuonamka River, Anabar Uplift, Siberia; sample 7/36.7. **A**. SMNH Mo 167656; close-up of Fig. 5C$_2$; A$_1$, pits on the surface of internal mould; A$_2$, close-up of A$_1$. **B**. SMNH Mo 160416; close-ups of Fig. 5D; B$_1$, lateral view, polygonal texture on the mould; B$_2$, polygons, close-up of B$_1$. Scale bar: A$_1$, 120 µm; A$_2$ and B$_2$, 30 µm; B$_1$, 300 µm.

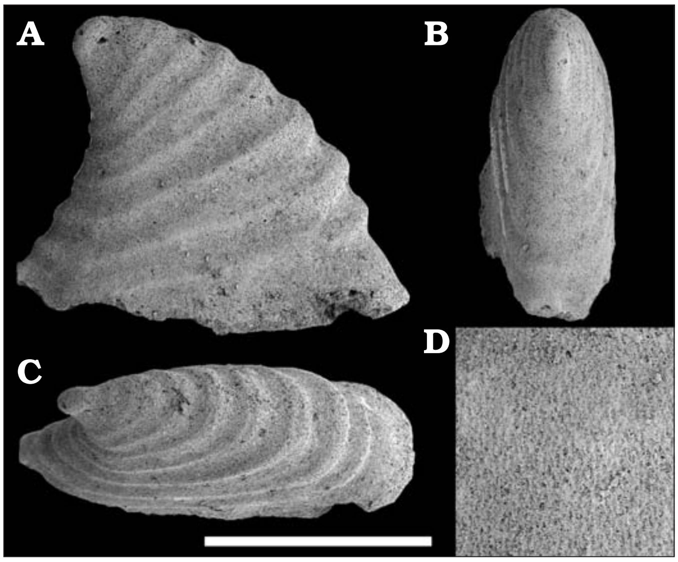


Fig. 7. Helcionellid mollusc *Parailsanella* sp. 2 internal moulds from lower Cambrian Emyaksin Formation, Bol'shaya Kuonamka River, Anabar Uplift, Siberia; SMNH Mo 167658, sample 7/70; lateral (**A**), sub-apical (**B**), and oblique upper (**C**) views. **D**. Close-up of A, showing pits on the surface of internal mould. Scale bar 1200 µm, except D, 300 µm.

margin and continuous with the pegma-like structure (Figs. 9C, 11C).

Remarks.—The surface of the moulds is covered with 10–40 µm wide, blunt tubercles and bears reticulate microornamentation best seen on the convex parts (folds) of the mould. The tubercles tend to be situated in comarginal rows, similar to what occurs in *Mellopegma* (Vendrasco et al. 2011b). Where concentric folds are developed, the tubercles are concentrated along their surface. Reticulation is formed by shallow concave polygons, ca. 20 µm wide. On the surface of concentric folds, the polygons become deeper and more variable in size, with a diameter typically ranging from 2–10 µm (Fig. 10G). The microornamentation flattens out in the subapical area. In addition to the polygonal texture, some specimens of *Mackinnonia* show imprints of a laminar shell microstructure in the concave bands between folds on the internal mould (Fig. 10C, G). As demonstrated by Runnegar (in Bengtson et al. 1990: fig. 159g), the troughs on internal moulds of *Mackinnonia* correspond to areas where the shell was thicker, and where the inner layer of shell microstructure would be preserved, whereas the

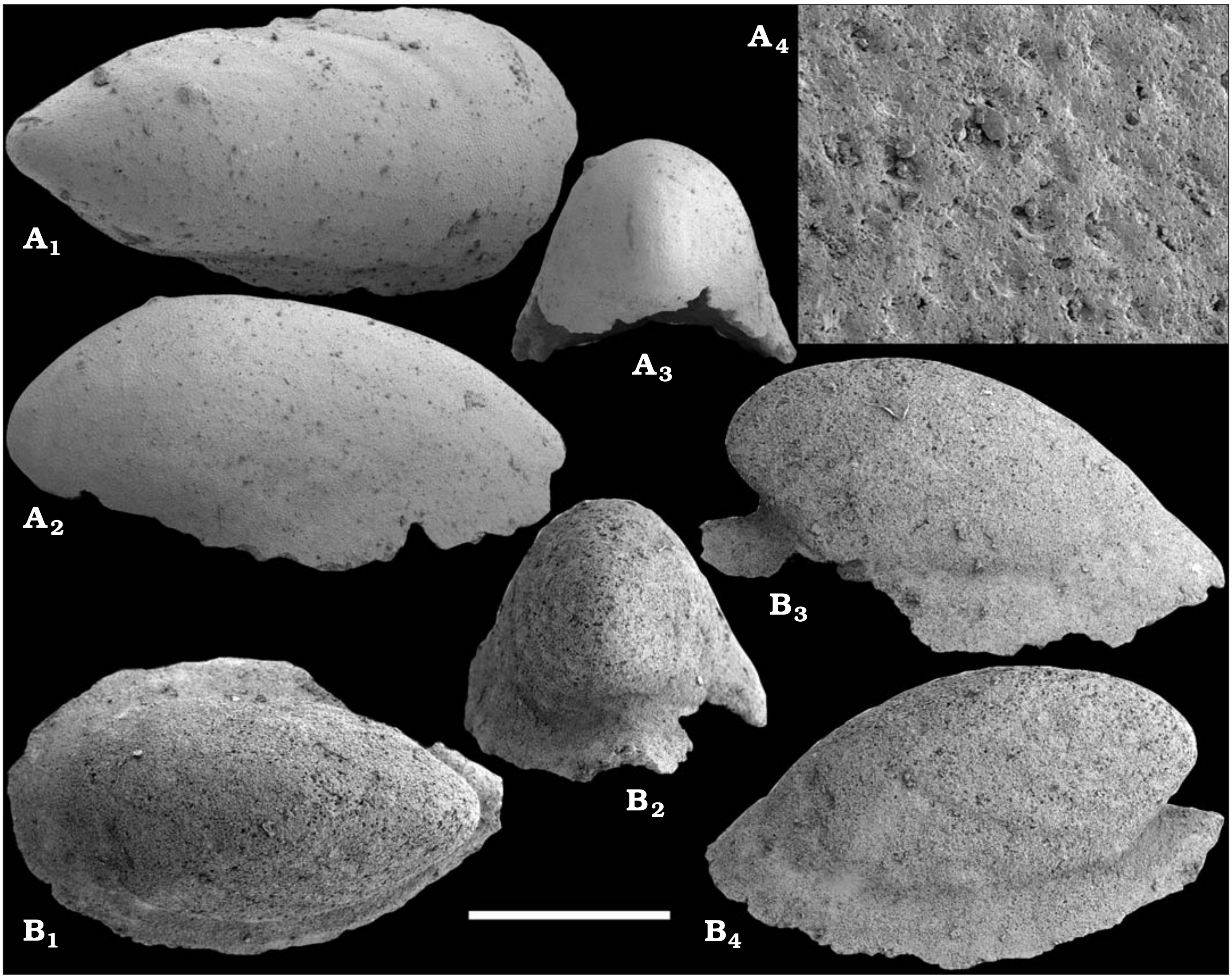


Fig. 8. Helcionellid mollusc *Figurina* cf. *F. nana* (Zhou and Xiao, 1984) internal moulds from lower Cambrian Emyaksin Formation, Bol'shaya Kuonamka River, Anabar Uplift, Siberia; sample 7/70. **A**. SMNH Mo 167659; upper (A_1), lateral (A_2), and sub-apical (A_3) views; A_4, close-up of A_1, pits on the surface of internal mould. **B**. SMNH Mo 167660; upper (B_1), sub-apical (B_2), lateral (B_3, B_4) views. Scale bar 600 µm, except A_4, 30 µm.

convex folds correspond to thin regions of shell where the outer layer of shell microstructure could be preserved. Thus, *Mackinnonia* appears to have had the common molluscan shell microstructure pattern of an outer prismatic shell layer (represented by polygons) and an inner laminar shell layer. This pattern characterises modern monoplacophorans, as well as *Mellopegma* and other stenothecids (Vendrasco et al. 2011b).

Parkhaev (in Gravestock et al. 2001) reassigned *Mellopegma rostratum* Zhou and Xiao, 1984 to *Mackinnonia* Runnegar in Bengtson et al., 1990. According to Parkhaev (in Gravestock et al. 2001) and Parkhaev (2005), *M. obliqua* Landing and Bartowski, 1996 from Stage 4 of Laurentia, as well as *Bemella costa* Zhou and Xiao, 1984 and *B. anhuiensis* Zhou and Xiao, 1984 from North China, should be regarded as junior synonyms of *M. rostrata* (Zhou and Xiao, 1984). However, the illustrations of *M. rostrata* (as well as *B. costa* and *B. anhuiensis*) are not detailed, and it appears that individuals of this species tend to lack the more frequent and prominent internal ridging that characterises *M. davidi*. *M. rostrata* is also curved more than *M. davidi*, and for these reasons we view the synonymy as questionable. The ornamentation of the internal mould of *Mackinnonia anabarica* from the lower Botoman Stage of Siberia with tubercles would be the only reliable difference from otherwise similar *M. davidi* Runnegar in Bengtson et al., 1990 from Cambrian Series 2 of South Australia (Bengtson et al. 1990; Gravestock et al. 2001) and *M. rostrata* from Stage 4 of South and North China (Zhou and Xiao 1984; Feng et al. 1994) and lower Stage 5 of the Mediterranean region (Spain; Wotte 2006). It is, however, hard to confirm or deny the lack of tubercles in the original *M. rostrata* illustrated by Xiao and Zhou (1984) from China. *M. rostrata* and *M. anabarica* appear to share the same higher degree of coiling than that illustrated in *M. davidi* by Bengtson et al. (1990: fig. 159), whereas *M. davidi* has more frequent and prominent internal ridging.

The fossils described herein were discussed as *Mackin-*

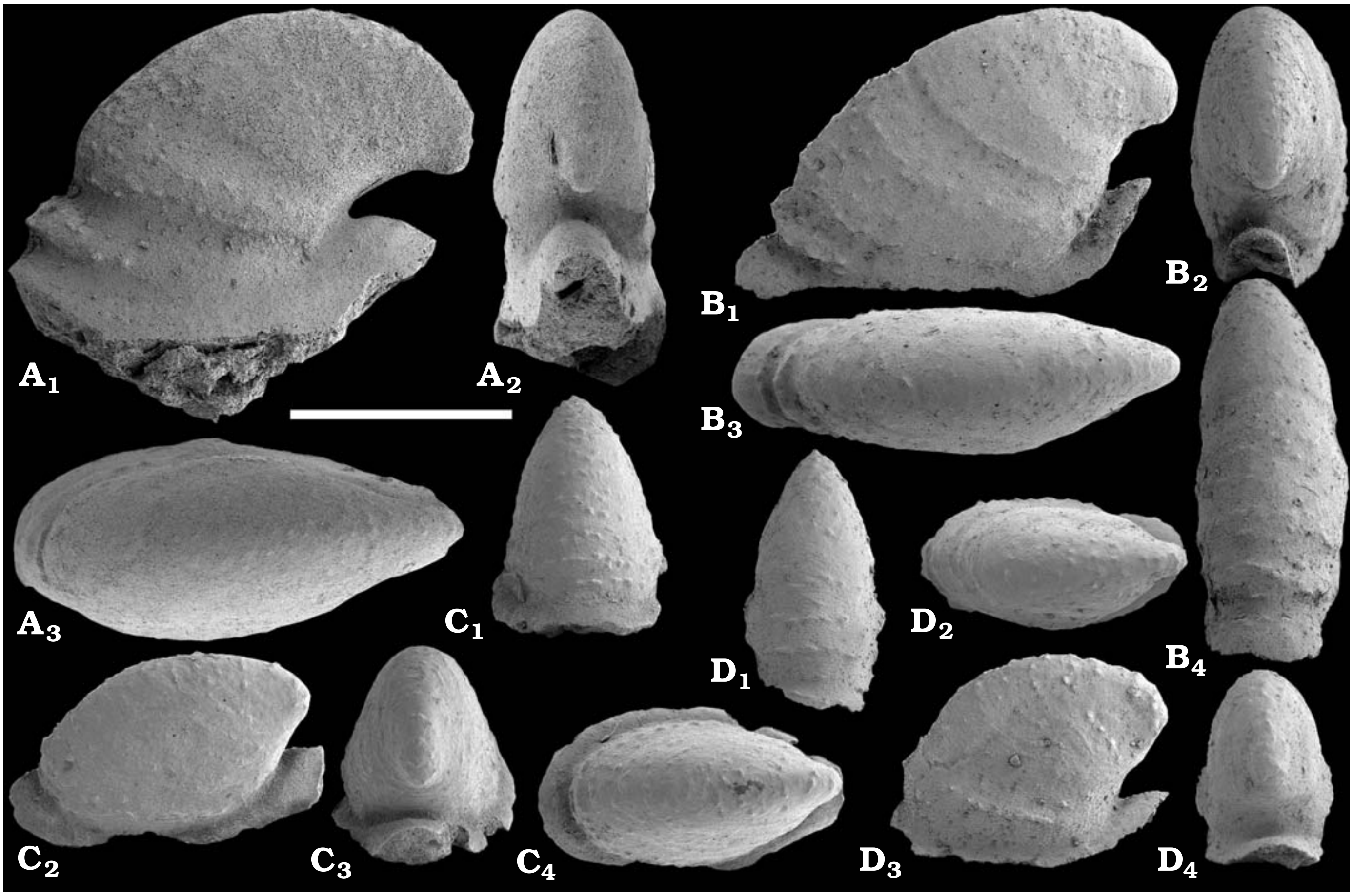


Fig. 9. Helcionellid mollusc *Mackinnonia anabarica* Parkhaev, 2005 internal moulds from lower Cambrian Emyaksin Formation, Bol'shaya Kuonamka River, Anabar Uplift, Siberia; sample 7/70. **A**. SMNH Mo 167662; lateral (A_1), sub-apical (A_2), and upper (A_3) views. **B**. SMNH Mo 167663; lateral (B_1), sub-apical (B_2), upper (B_3), and supra-apical (B_4) views. **C**. SMNH Mo 160419; supra-apical (C_1), lateral (C_2), sub-apical (C_3), and upper (C_4) views. **D**. SMNH Mo 167664; supra-apical (D_1), upper (D_2), lateral (D_3), and sub-apical (D_4) views. Scale bar 600 µm.

nonia sp. by Kouchinsky (2000a: 131, fig. 10). *Mackinnonia anabarica* Parkhaev, 2005 and *Leptostega hyperborea* Parkhaev, 2005 (see below) were originally described from sample B-247, which is from an unknown locality, according to Parkhaev (2005). However, the same sample available in the material of Vladimir V. Missarzhevsky and collected by Larisa G. Voronova derives from near the mouth of the Ulakhan-Tyulen Brook, Bol'shaya Kuonamka River (as written on a label). Thus, it is equivalent to section 6 herein, which should be considered the type locality for those two species.

Stratigraphic and geographic range.—Lower Botoman Stage, Siberian Platform.

Genus *Leptostega* Geyer, 1986

Type species: Leptostega irregularis Geyer, 1986; *Acadoparadoxides mureroensis* Zone, Leonian Stage; Porma, Cantabrian Mountains, Spain.

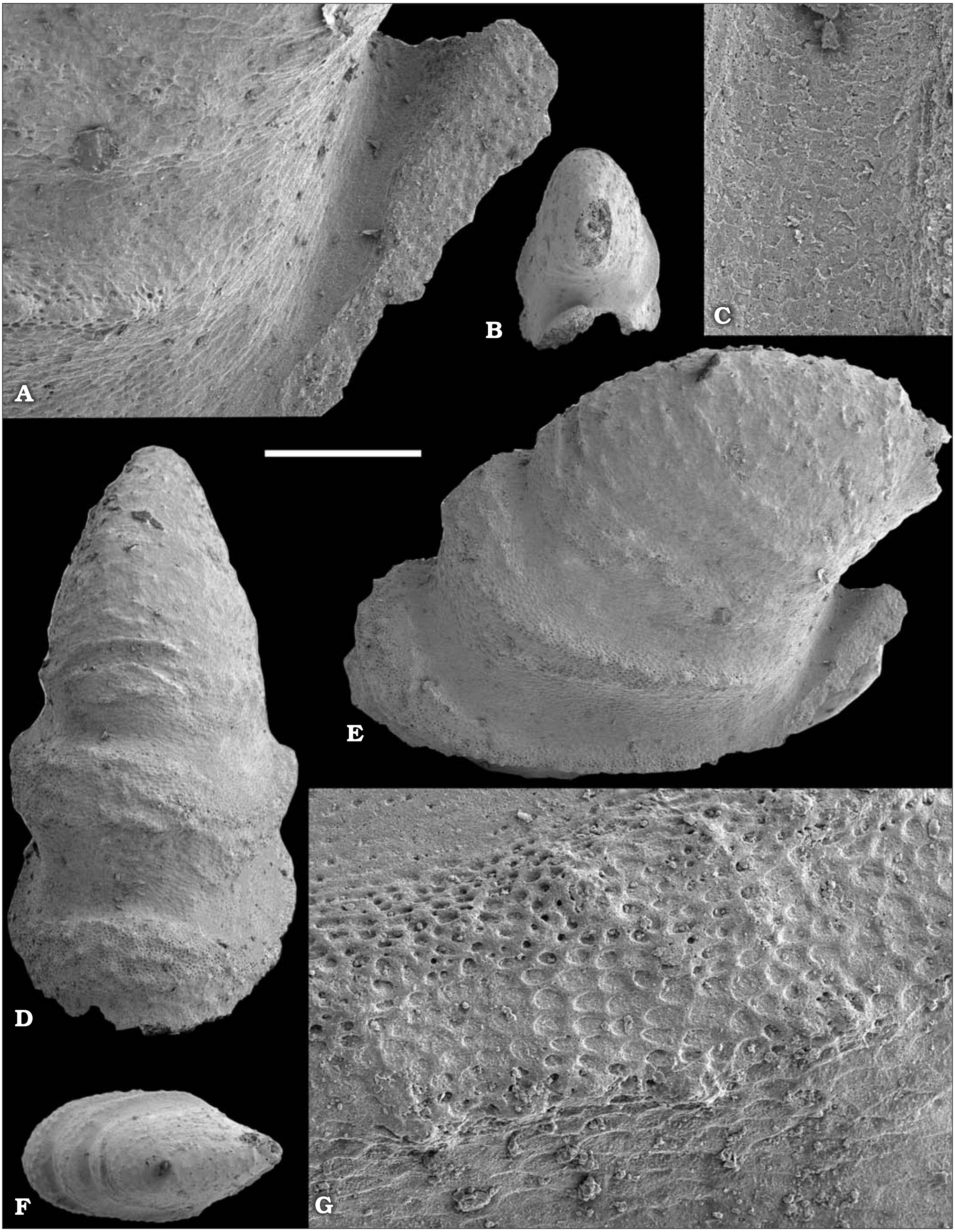
Leptostega hyperborea Parkhaev, 2005

Fig. 12.

Material.—Four incomplete calcium phosphatic internal moulds, including three figured specimens SMNH Mo 167667–167669 from sample 7/70. Uppermost Emyaksin Formation, Bol'shaya Kuonamka River; *Calodiscus-Erbiella* Zone, lower Botoman Stage.

Description.—Laterally compressed shell nearly orthoconic shell, with sub-central or slightly inclined apex (Fig. 12A_1). The length/width ratio at the apertural region is ca. 2.7. The inner shell surface (as reflected by internal moulds) carries strong and broad concentric folds, prominent on the narrow sides of the moulds. The aperture narrows slightly towards the sub-apical side.

Remarks.—The moulds were collected from the type beds of *Leptostega hyperborea* Parkhaev, 2005 (see Remarks for *Mackinnonia anabarica*). *L. hyperborea* is reported from the Botoman and, probably, Amgan Stages (herein and Kouchinsky et al. 2011, respectively), thus, occurs within Stage 4—lower Drumian Stage of Siberia. *Leptostega* Geyer, 1986 was first described from the basal middle Cambrian of Spain (Geyer 1986; see Kouchinsky et al. 2011: 133 for comparison of *L. irregularis* Geyer, 1986 with *L. hyperborea*), *Acadoparadoxides mureroensis* Zone, lower Leonian Stage. The lower part of the zone can be correlated with the upper Toyonian Stage of Siberia (Geyer 1998, 2005; Geyer and Landing 2004) and the Series 2/Series 3 transition.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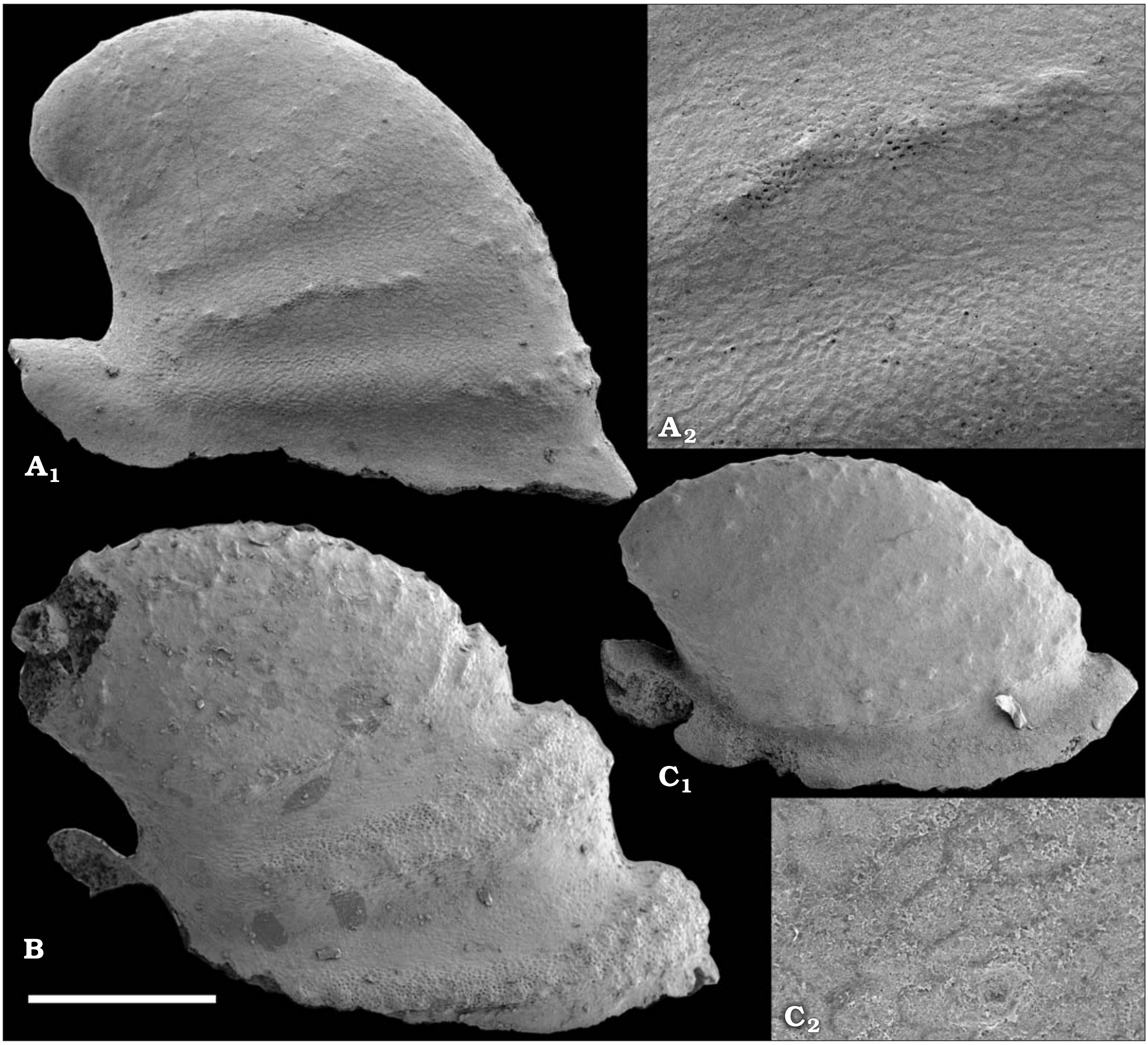

Fig. 11. Helcionellid mollusc *Mackinnonia anabarica* Parkhaev, 2005 internal moulds from lower Cambrian Emyaksin Formation, Bol'shaya Kuonamka River, Anabar Uplift, Siberia; sample 7/70. **A**. SMNH Mo 160420; A_1, lateral view; A_2, close-up of A_1, microtexture on the surface of internal mould, detailed. **B**. SMNH Mo 167665 (see also Fig. 10); lateral view. **C**. SMNH Mo 160419 (see also Fig. 9C); C_1, lateral view; C_2, close-up of C_1, polygons on the surface of internal mould. Scale bar: 300 µm, except A_2, 120 µm; C_2, 60 µm.

Stratigraphic and geographic range.—Lower Botoman Stage and, probably, Amgan Stage, Siberian Platform.

Family ?Helcionellidae Wenz, 1938

Genus *Pararaconus* Runnegar in Bengtson et al., 1990

Type species: *Pararaconus staitorum* Runnegar in Bengtson et al., 1990; *Abadiella huoi* Zone, lower Cambrian; Horse Gully section, Yorke Peninsula, Australia.

Pararaconus sp.

Fig. 13.

Material.—A single phosphatic internal mould SMNH Mo 160421 from sample 7/70. Uppermost Emyaksin Formation,

← Fig. 10. Helcionellid mollusc *Mackinnonia anabarica* Parkhaev, 2005 internal moulds from lower Cambrian Emyaksin Formation, Bol'shaya Kuonamka River, Anabar Uplift, Siberia; SMNH Mo 167665, sample 7/70. **A**. Close-up of E, texture on the surface of internal mould in sub-apical region. **B**. Sub-apical view. **C**. Close-up of A, texture at the base of sub-apical train. **D**. Supra-apical view. **E**. Lateral view. **F**. Upper view. **G**. Texture on the surface of comarginal folds. Scale bar: A, 120 µm; B, F, 600 µm; C, 30 µm; D, E, 300 µm; G, 60 µm.

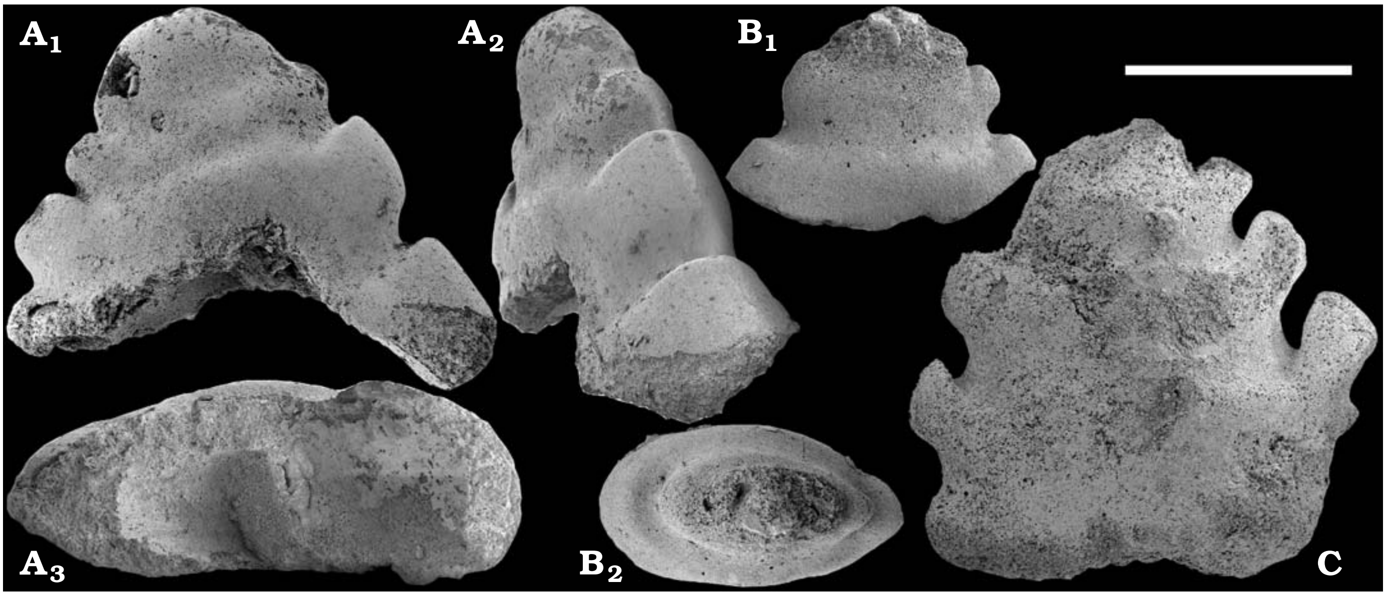

Fig. 12. Helcionellid mollusc *Leptostega hyperborea* Parkhaev, 2005 internal moulds from lower Cambrian Emyaksin Formation, Bol'shaya Kuonamka River, Anabar Uplift, Siberia; sample 7/70. **A**. SMNH Mo 167667; lateral (A_1), oblique supra-apical (A_2), and apertural (A_3) views. **B**. SMNH Mo 167668; lateral (B_1) and upper (B_2) views. **C**. SMNH Mo 167669; lateral view. Scale bar 600 μm, except C, 1200 μm.

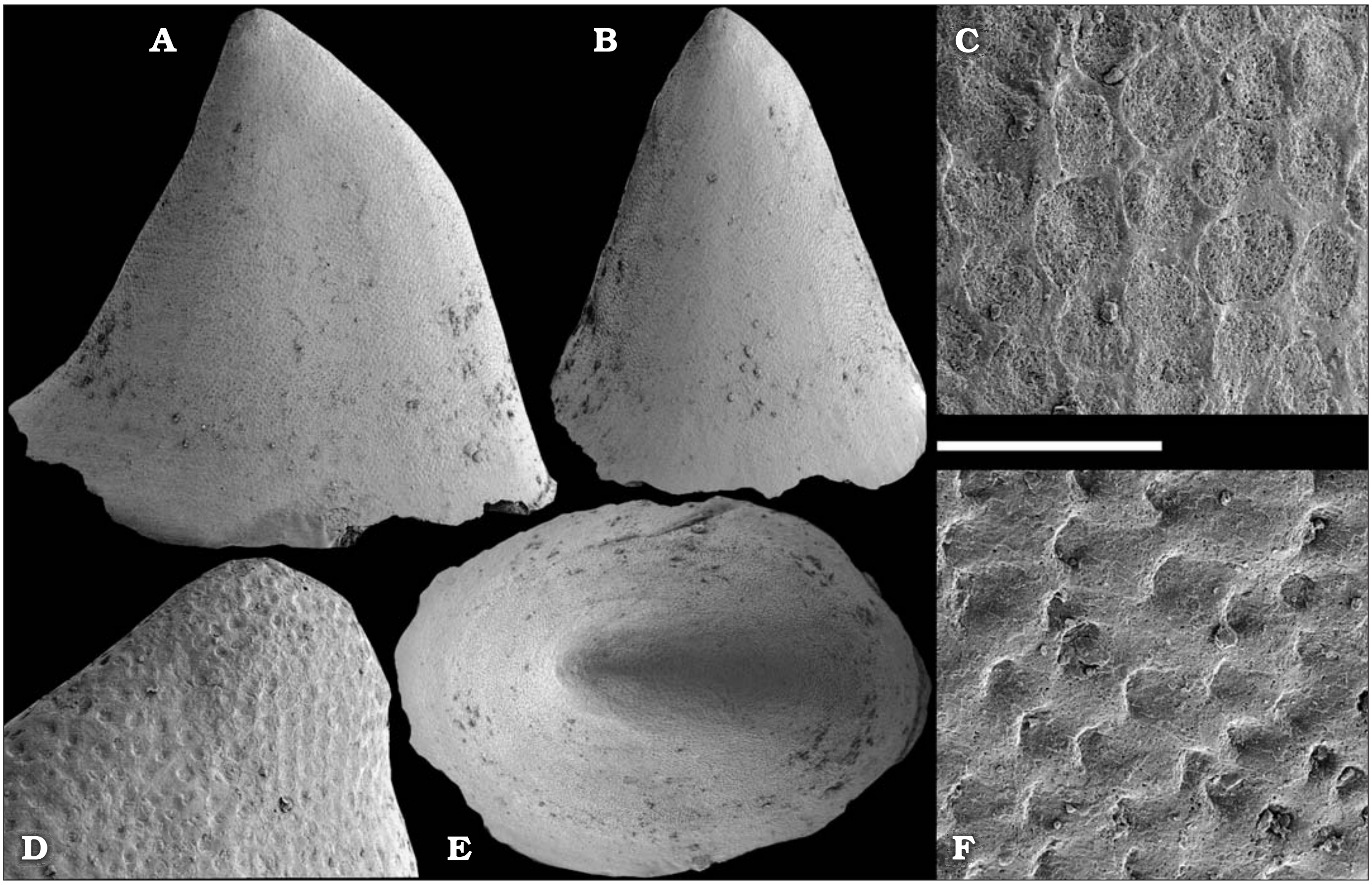

Fig. 13. Helcionellid mollusc *Pararaconus* sp. internal mould from lower Cambrian Emyaksin Formation, Bol'shaya Kuonamka River, Anabar Uplift, Siberia; SMNH Mo 160421, sample 7/70. **A**. Lateral view. **B**. Sub-apical view. **C**. Close-up of D. **D**. Polygonal texture on the apical surface of internal mould. **E**. Upper view. **F**. Pits on the surface of mould near the aperture. Scale bar: A, B, E, 600 μm; D, 120 μm; C, F, 30 μm.

Bol'shaya Kuonamka River; *Calodiscus*-*Erbiella* Zone, lower Botoman Stage.

Remarks.—The fossil represents a slightly laterally compressed (length/width ratio of the aperture ca. 1.4) orthocon-

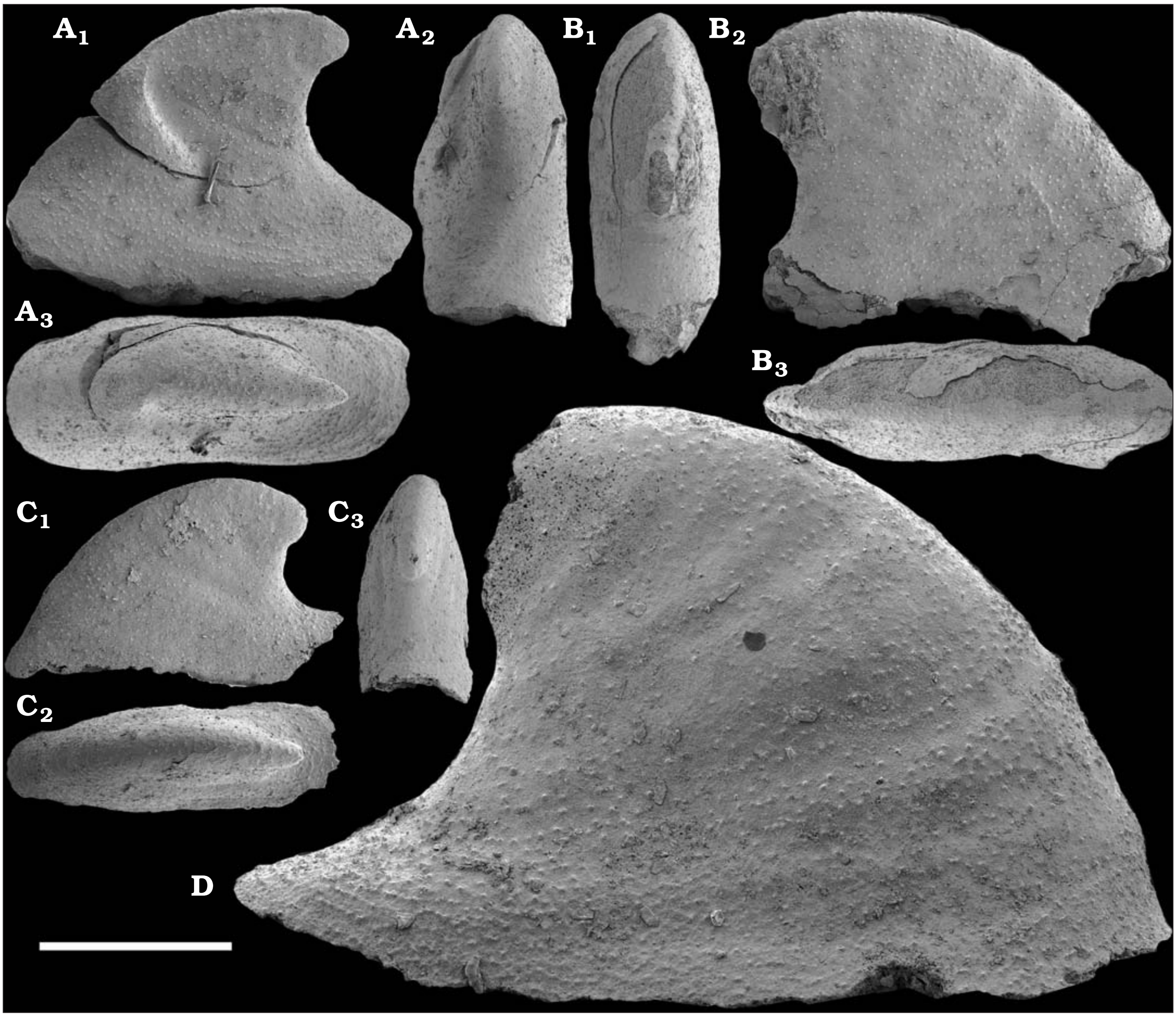

Fig. 14. Helcionellid mollusc *Mellopegma uslonicum* Parkhaev, 2004 internal moulds from lower Cambrian Emyaksin Formation, Bol'shaya Kuonamka River, Anabar Uplift, Siberia; sample B-247 (A), sample 7/70 (B–D). **A**. SMNH Mo 167672; lateral (A_1), sub-apical (A_2), and upper (A_3) views. **B**. SMNH Mo 167671; sub-apical (B_1), lateral (B_2), and upper (B_3) views. **C**. SMNH Mo 160410; lateral (C_1), upper (C_2), and sub-apical (C_3) views. **D**. SMNH Mo 167612; lateral view. Scale bar 600 µm, except D, 300 µm.

ic internal mould with a slightly displaced apex. The surface of the mould is smooth and covered with polygons, 10–20 µm wide (Fig. 13C, D, F; see also description of surface textures in Kouchinsky 2000a). The distinguishing characters of both known species of *Pararaconus*, *P. staitorum* Runnegar in Bengtson et al., 1990 (type species) and *P. paradoxus* Parkhaev in Gravestock et al. 2001 from the *Abadiella huoi* Zone of Australia relate to the presence/absence (respectively) of lateral depressions (buttresses on internal moulds) near the aperture (Parkhaev in Gravestock et al. 2001). The ventral margin of the fossil herein is jagged and the original aperture margin appears to be broken off. Thus without knowing these character states we cannot determine with certainty to which species of *Pararaconus* this fossil belongs. The fossil is discussed as *Obtusoconus* sp. by Kouchinsky (2000a: 131, fig. 11).

Family Stenothecidae Runnegar and Jell, 1980

Genus *Mellopegma* Runnegar and Jell, 1976

Type species: *Mellopegma georginense* Runnegar and Jell, 1976; *Ptychagnostus atavus-Peronopsis opimus* Zone, Floran Stage; eastern Georgina Basin, western Queensland, Australia.

Mellopegma uslonicum Parkhaev, 2004

Fig. 14.

Material.—Seven calcium phosphatic internal moulds, including three SMNH Mo 160410, 167612, and 167671 from sample 7/70 and one internal mould SMNH Mo 167672 from sample B-247 (collected by Larisa G. Voronova and found in the collection of Vladimir V. Missarzhevsky). Uppermost Emyaksin Formation, Bol'shaya Kuonamka River; *Calodiscus-Erbiella* Zone, lower Botoman Stage.

Remarks.—Cyrtoconic, laterally highly compressed shell. The apex projects within the apertural margin. The aperture is elongated oval in outline (length/width ratio 3.0–3.7) and has a slight lateral flaring and subapical train. The surface of the internal mould bears faint concentric folds and is covered with evenly spaced blunt tubercles (Fig. 14D). The fossil is discussed as "Unnamed form 3" by Kouchinsky (2000a: fig. 5M–O). For discussion and comparison with other species see Vendrasco et al. (2011b: 18).

Stratigraphic and geographic range.—Lower Botoman Stage, Siberian Platform (Vendrasco et al. 2011b and herein) and Eastern Transbaikalia (Parkhaev 2004).

Order uncertain

Family Enigmaconidae Mackinnon, 1985

Genus *Enigmaconus* Mackinnon, 1985

Type species: *Enigmaconus parvus* Mackinnon, 1985; *Ptychagnostus cassis* Zone, Boomerangian Stage; Cobb Valley, Nelson Province, South Island, New Zealand.

Remarks.—*Enigmaconus* Mackinnon, 1985 is represented by a similar pegma-bearing, but slightly cyrtoconic whith a more extended apex species *E. parvus* Mackinnon, 1985. Pegma-like structures in the sub-apical part of the shell are also known from several forms of molluscs attributed to different genera. The pegma was first described in ribeirioid rostroconchs (Pojeta and Runnegar 1976). It represents a hard internal plate that connected the left and right sides of the ribeirioid rostroconch shell and is visible as a groove on internal moulds. In some lower–middle Cambrian helcionellids, a similar structure is produced by a sub-apical invagination or internal thickening of the wall. When *Enigmaconus* and *Eurekapegma* were described from the Middle Cambian of New Zealand (Mackinnon 1985), the pegma was known only from the cosmopolitan lower Cambrian mollusc *Watsonella* (= *Heraultipegma*). At that time, *Watsonella* was considered a rostroconch (Pojeta and Runnegar 1976), and Mackinnon (1985) speculated that *Enigmaconus* may have been ancestral to rostroconchs, based on the shared characteristic of the pegma. Since that time, other pegma-bearing species have been reported from the lower Cambrian of France (Kerber 1988) and Mongolia (Esakova and Zhegallo 1996), middle Cambrian of Greenland (Peel 1994) and Australia (Vendrasco et al. 2010). Runnegar (1996) suggested that because of the widespread nature of pegma-like structures in Cambrian molluscs, they likely evolved convergently in different lineages.

Enigmaconus? *pyramidalis* Kouchinsky and Vendrasco sp. nov.

Figs. 15, 16.

Etymology: From pyramid, referring to the shape of the internal moulds.

Type material: Holotype: SMNH Mo 167676, internal mould (Fig. 15). Paratypes: SMNH Mo 160422, 167677 and 167678, internal moulds (Fig. 16).

Type locality: 70°43'N, 112°52.5'E (section 7 herein, or section A-54 in Val'kov 1975), Bol'shaya Kuonamka River, eastern flanks of the Anabar Uplift, northern Siberia.

Type horizon: Uppermost Emyaksin Formation (sample 7/70), *Calodiscus-Erbiella* Zone, lower Botoman Stage.

Material.—Twenty-eight calcium phosphatic internal moulds, including four figured SMNH Mo 160422, 167676–167678 from the type horizon (sample 7/70) and one specimen from sample K1-3B.

Diagnosis.—Bilaterally symmetrical, nearly orthoconic shells with a large centrally placed apex and wide oval aperture with a broad sub-apical sinus. A narrow cleft (cast of pegma-like structure) separates a flattened smooth sub-apical portion from the rest of the mould. The surface of the internal moulds is covered with somewhat inclined and scaly polygons.

Description.—Orthoconic shell, with a broad centrally placed apex and wide oval aperture. A deep narrow pegma-like protrusion (reflected by a cleft on the internal mould) projects ventrally (Fig. 16A_3) and separates a flattened portion from the rest of the shell. Aperture with a broad sub-apical sinus. Almost the entire surface of the internal mould is covered with flattened convex polygons, ca. 20 μm wide, that gradually become smooth towards the top of the mould.

Remarks.—The fossil is discussed as *Enigmaconus* sp. by Kouchinsky (2000a: 133, fig. 12).

Stratigraphic and geographic range.—Known only from its type locality and horizon.

Order Pelagiellida Mackinnon, 1985

Family Pelagiellidae Knight, 1956

Genus *Pelagiella* Matthew, 1895

Type species: *Cyrtolites atlantoides* Matthew, 1894; lower Cambrian, New Brunswik, Canada.

Remarks.—Herein, *Pelagiella* is tentatively merged with *Cambretina* Horný, 1964 and *Costipelagiella* Horný, 1964 (see also Kouchinsky et al. 2011: 136).

Pelagiella sp. 1

Figs. 17, 18, 19A.

Material.—Nine calcium phosphatic internal and external moulds, including figured SMNH Mo 167679–167685 from sample 7/70 and six moulds from sample K1-3B. Uppermost Emyaksin Formation, Bol'shaya Kuonamka and Malaya Kuonamka rivers; *Calodiscus-Erbiella* Zone, lower Botoman Stage.

Description.—Very rapidly expanding shell consisting of up to ¾ whorl. Aperture wide, asymmetrical, with pinched and strongly drawn-out peripheral side (Figs. 17A_3, 19A_2). The peripheral surface of the whorl is rounded and distally extended, separated from the spiral and umbilical surfaces

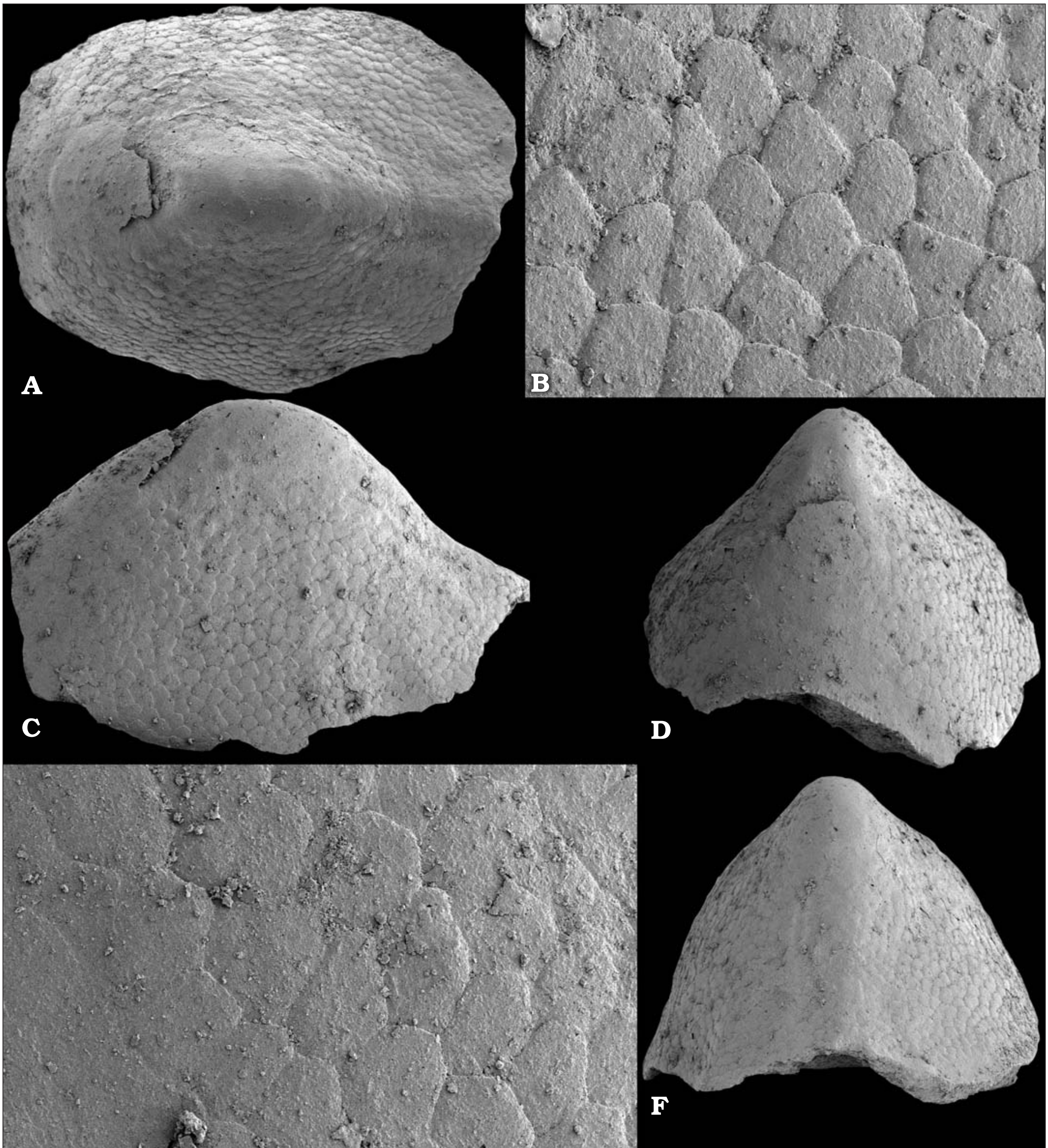

Fig. 15. Mollusc *Enigmaconus*? *pyramidalis* sp. nov., holotype, internal moulds from lower Cambrian Emyaksin Formation, Bol'shaya Kuonamka River, Anabar Uplift, Siberia; SMNH Mo 167676, sample 7/70. **A**. Upper view. **B**. Close-up of A, scaly texture on internal mould. **C**. Lateral view. **D**. View on the pegma-like sub-apical structure. **E**. Close-up of C. **F**. View on the side opposite to D. Scale bar 300 µm, except B, E, 60 µm.

by an angle.The spiral surface of the whorl is depressed and concave, whereas the umbilical surface is convex (Figs. $17A_1$, $19A_1$). Ornamentation of the shell exterior consists of fine radial striations, 1–3 µm wide, and transversal, narrow ribs. Distance between ribs up to ~50 µm (Fig. 18). The ornamentation of ribs fades out towards the periphery of the

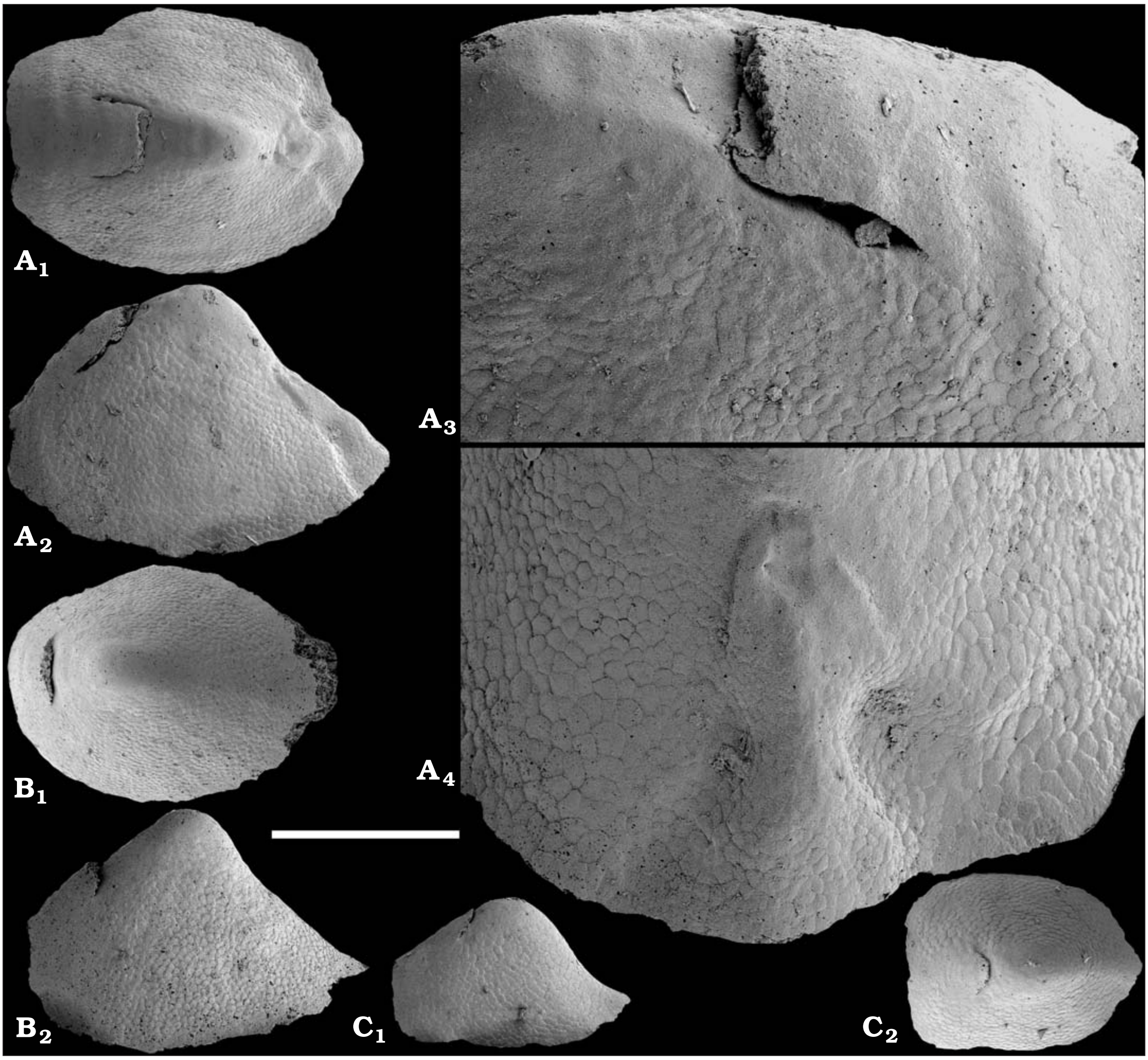

Fig. 16. Mollusc *Enigmaconus*? *pyramidalis* sp. nov., paratypes, internal moulds from lower Cambrian Emyaksin Formation, Bol'shaya Kuonamka River, Anabar Uplift, Siberia; sample 7/70. **A**. SMNH Mo 160422; upper (A_1) and lateral (A_2) views; A_3, view on the pegma-like structure; A_4, view on the side opposite to the pegma-like structure with shell deformation reflected on the internal mould. **B**. SMNH Mo 167677; upper (B_1) and lateral (B_2) views. **C**. SMNH Mo 167678; lateral (C_1) and upper (C_2) views. Scale bar 600 µm, except A_3, A_4, 200 µm.

whorl (Fig. 18B). A sinusoidal course of ribbing follows the relief of the umbilical and upper spiral surfaces.

Remarks.—The fossils described here are generally most similar to *Pelagiella madianensis* (Zhou and Xiao, 1984) illustrated in Gravestock et al. (2001: pl. 46), but the ornamentation of *P. madianensis* consists of granules arranged in spiral rows (Parkhaev in Gravestock et al. 2001). The ornamentation of *Pelagiella* sp. 1 herein consists of comarginal ribs similarly spaced as in the middle Cambrian *Pelagiella* sp. cf. *Costipelagiella zazvorkai* from the overlying Kuonamka Formation (Kouchinsky et al. 2011), but they do not appear to extend to the periferal portion of the whorl. *Pelagiella* sp. 1 differ from *Pelagiella* sp. 2 described below in having a strongly extended peripheral part of the aperture and whorl, a more depressed spiral side and more rapidly expanding whorl. Unlike other species of *Pelagiella*, *Pelagiella* sp. 1 has a strongly extended peripheral part of the aperture.

Pelagiella sp. 2

Figs. 19B, C, 20.

Material.—One calcium phosphatic internal mould, SMNH Mo 160429 and one fragmentary external mould, SMNH

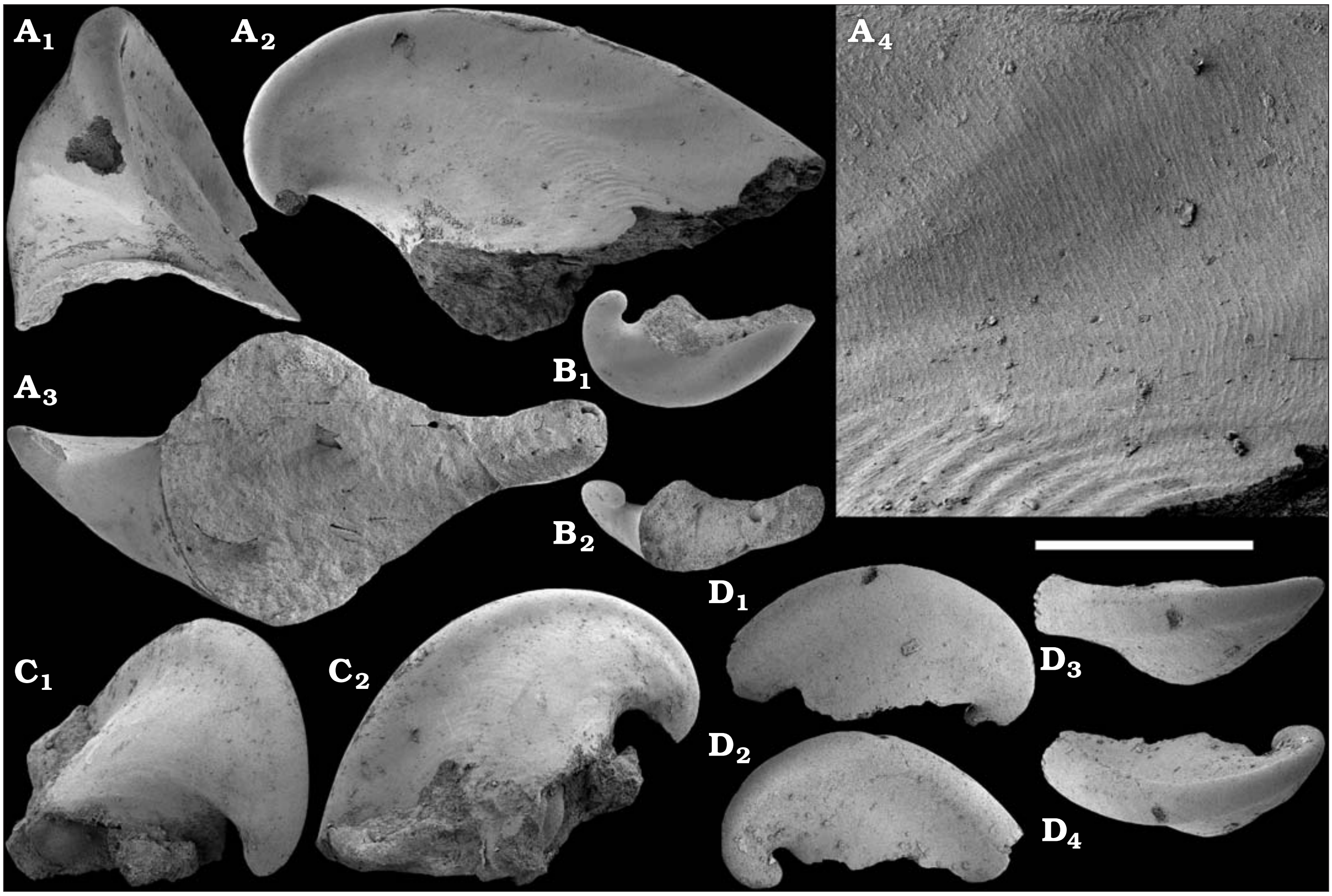

Fig. 17. Pelagiellid mollusc *Pelagiella* sp. 1 internal moulds from lower Cambrian Emyaksin Formation, Bol'shaya Kuonamka River, Anabar Uplift, Siberia; sample 7/70. **A**. SMNH Mo 167679; sub-apical (A_1), spiral side (A_2), and apertural (A_3) views; A_4, close-up of A_2, striation on the surface of internal mould. **B**. SMNH Mo 167680; umbilical side (B_1) and apertural (B_2) views. **C**. SMNH Mo 167681; oblique umbilical (C_1) and umbilical side (C_2) views. **D**. SMNH Mo 167682; umbilical side (D_1), spiral side (D_2), abapertural (D_3), and oblique abapertural (D_4) views. Scale bar 1200 μm, except A_4, 300 μm.

Mo 167688 of the same specimen, from sample K1-3B. Two internal moulds SMNH Mo 167686–167687 from sample 7/70. Uppermost Emyaksin Formation, Malaya Kuonamka and Bol'shaya Kuonamka rivers; *Calodiscus*-*Erbiella* Zone, lower Botoman Stage.

Description.—Rapidly expanding shell consisting of ¾ whorl. Aperture is asymmetrical oval (Figs. $19B_2$, C_3, $20A_2$). The peripheral surface of the whorl is rounded and passes without angulation into convex spiral and umbilical surfaces of the whorl. Ornamentation of the shell exterior (Fig. 20B) consists of fine radial striations, 1–3 μm wide, and transversal narrow ribs that appear on the surface from ca. ½ revolution. Distance between ribs increases with growth and towards periphery of the whorl, up to ~25 μm.

Remarks.—The fossils are discussed as *Pelagiella* cf. *subangulata* by Kouchinsky (2000a: 135, fig. 14). On one of the internal moulds, a low polygonal texture is developed unilaterally as a radially extended area transitional between the peripheral and spiral surfaces of the whorl (Fig. $20A_4$, A_5; Kouchinsky 2000a: fig. 14A, arrow E). The texture consists of polygons, up to 50 μm in width, with tubercles, 5–10 μm in diameter, at their centres (Fig. $20A_4$, A_5).

Among other pelagiellids, the forms described herein are distinguished by the ornamentation of the shell exterior with comarginal ribs thought to be diagnostic of *Costipelagiella* Horný, 1964. The ribs are twice as densely spaced as in the middle Cambrian *C. zazvorkai* Horný, 1964 and *Pelagiella* sp. cf. *Costipelagiella zazvorkai* from Siberia (Kouchinsky et al. 2011), although the shell exterior was apparently similarly smooth over the initial half revolution. *C. nevadense* Skovsted, 2006 from Laurentia and *Costipelagiella* sp. cf. *C. zazvorkai* from the middle Cambrian of New Zealand (MacKinnon 1985) are more laterally compressed, but have similarly spaced ribs, which do not extend, however, to the peripheral portion of the whorl in the former form.

Class Bivalvia Linnaeus, 1758

Order uncertain

Family Fordillidae Pojeta, 1975

Genus *Fordilla* Barrande, 1881

Type species: *Fordilla troyensis* Barrande, 1881; lower Cambrian, New York State, USA.

Remarks.—Elicki and Gürsu (2009) noted a high degree of

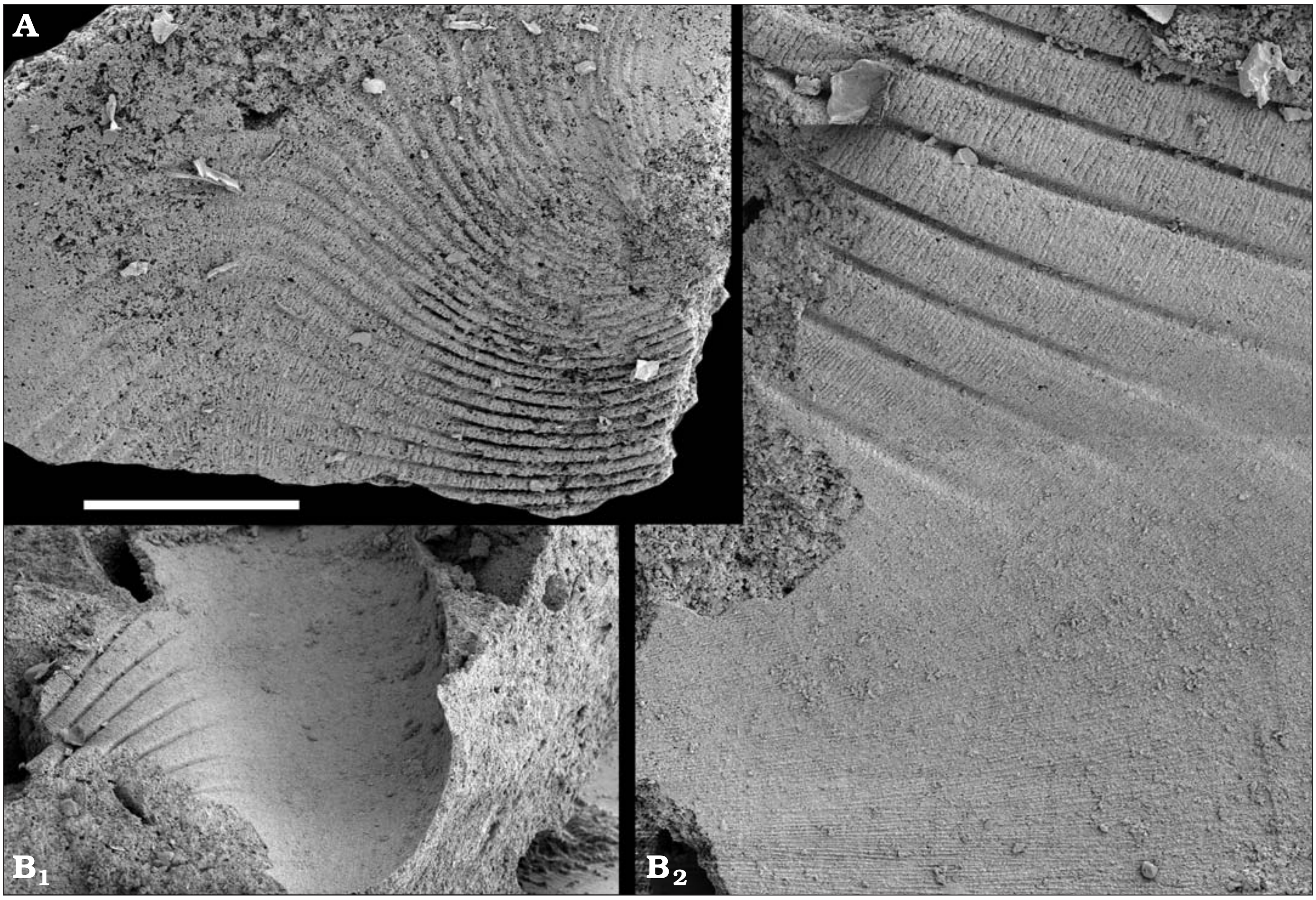

Fig. 18. Pelagiellid mollusc *Pelagiella* sp. 1, external mould of the outer shell surface, from lower Cambrian Emyaksin Formation, Bol'shaya Kuonamka River, Anabar Uplift, Siberia; sample 7/70. **A**. SMNH Mo 167683, sinusoidal course of transverse ribs of the shell exterior. **B**. SMNH Mo 167684; B_1, transversal ribs fade out distally; B_2, close-up of B_1. Scale bar: A, B_1, 300 µm; B_2, 120 µm.

intraspecific and intrageneric variation in the very similar Cambrian bivalves *Fordilla* Barrande, 1881 and *Pojetaia* Jell, 1980. In addition to the extensive variation within lower-level taxa, many of the proposed distinguishing characteristics such as muscle scar placement and dentition are not preserved in many fossils. Thus the most useful diagnostic character between these two genera appear to be shell shape, with the umbo typically more anteriorly placed in *Fordilla* (Jell 1980; Runnegar and Bentley 1983). Elicki and Gürsu (2009) argued that *Pojetaia* and *Fordilla* can be reliably distinguished by total size (*Fordilla* is larger) and the ratio of anterior length to total length. In the fossil described herein (Fig. 21A), the umbo is distinctly shifted towards the anterior margin in a way more reminiscent of *Fordilla troyensis*, the type species of that genus. The smaller specimen (Fig. 21B) may be a poorly preserved juvenile, but its more centrally placed umbo, ration of anterior length to total length (ca. 45%) and total length (ca. 1 mm) are similar to *Pojetaia* Jell, 1980 (see Elicki and Gürsu 2009).

Fordilla cf. *F. sibirica* Krasilova, 1977

Fig. 21.

Material.—One calcium phosphatic internal mould, SMNH Mo 167690 (Fig. 21A) and, probably, SMNH Mo 167692 (Fig. 21C, larger fragment), from sample 7/70. Uppermost Emyaksin Formation, Bol'shaya Kuonamka River; *Calodiscus*-*Erbiella* Zone, lower Botoman Stage.

Description.—Shell ca. 2.5 mm in length (Fig. 21A), equivalved, with valves suboval in lateral outline and anteriorly located umbones (Fig. $21A_1$). Dentition is represented by casts of a single weakly impressed tooth and corresponding socket on each valve (Fig. $21A_2$, A_3). Ligament area elongated, straight, opisthodetic, occupying more than half of the dorsal margin. In lateral view, the angle between dorsal and posterior margins is ~135° (Fig. $21A_1$). The ration of anterior length (horizontal distance between anterior margin and the center of the umbo) to total length is ca. 36% (see Elicki and Gürsu 2009).

Remarks.—The fossil in Fig. 21A is most similar to *F. sibirica* in general morphology, but the definitive assignment is hampered by the lack of muscular imprints preserved. Krasilova (1977) described *F. sibirica* based on twenty internal moulds from the Atdabanian of Siberia. Runnegar and Pojeta (1992) listed *F. sibirica* as a junior synonym of *F. troyensis*, but Elicki

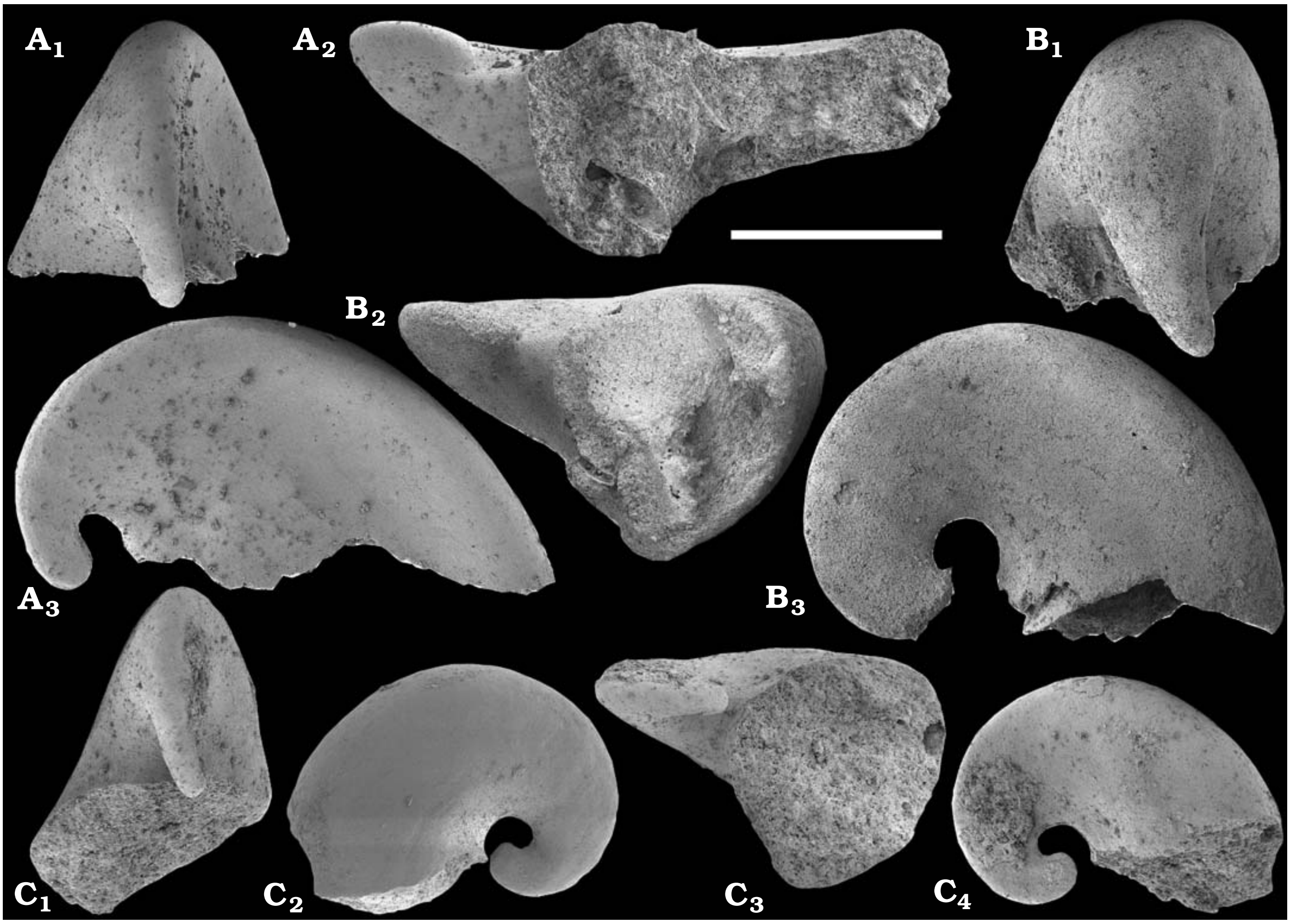

Fig. 19. Comparison of internal moulds of two pelagiellid molluscs *Pelagiella* sp. 1 (A) and *Pelagiella* sp. 2 (B, C) from lower Cambrian Emyaksin Formation, Bol'shaya Kuonamka River, Anabar Uplift, Siberia; sample 7/70. **A**. SMNH Mo 167685; sub-apical (A_1), apertural (A_2), and spiral side (A_3) views. **B**. SMNH Mo 167686; sub-apical (B_1), apertural (B_2), and spiral side (B_3) views. **C**. SMNH Mo 167687; sub-apical (C_1), umbilical side (C_2), apertural (C_3), and spiral side (C_4) views. Scale bar 600 μm.

and Gürsu (2009) argued that these species can be differentiated by features such as a straight dorsal margin, smaller size, less concavity, and a different pattern of shell microstructure. We concur with Elicki and Gürsu. The fossil here differs from *F. troyensis* in having a straighter dorsal margin and lacking a dorsoventral expansion in the posterior region of the valves. *F. germanica* Elicki, 1994 has a more elongated shape.

Imprints of shell microstructure are visible at the posterior margin (Fig. 21A_4). As with *Pojetaia* the inner shell microstructure near the margin of *Fordilla* consists of laminae whose growth direction parallels the closest region of the valve margin (Fig. 21A_4). Elsewhere the shell microstructure is less well organised (Runnegar and Pojeta 1992; Vendrasco et al. 2011a). This pattern has been described in *Pojetaia runnegari*, *Fordilla troyensis*, and now *Fordilla* cf. *F. sibirica.* The occurrence of this pattern of microstructure in *Fordilla* cf. *F. sibirica* supports the arguments that it is a diagnostic character of the Family Fordillidae and that this was the primitive type of shell microstructure in bivalves, which may have been a precursor to nacre (Vendrasco et al. 2011a).

Phylum uncertain

Class Hyolitha Marek, 1963

Order Orthothecida Marek, 1966

Family uncertain

Genus *Majatheca* Missarzhevsky in Rozanov et al., 1969

Type species: *Majatheca tumefacta* Missarzhevsky in Rozanov et al., 1969; upper Tommotian Stage, lower Cambrian; Tiktirikteekh, near Churan village, middle Lena River, Siberian Platform.

Majatheca tumefacta Missarzhevsky in Rozanov et al., 1969

Figs. 22A–E, 23A, B, 24.

Material.—Twenty phosphatised internal moulds and conchs from sample 7/25.5 (correlated with the *Profallotaspis jakutensis* Zone), sample 7/27.5 (correlated with the *Repinaella* Zone), samples 7/28.5, 7/29, 7/31.5, and 7/34 (correlated with the *Delgadella anabara* Zone); twenty-three phosphatised conchs, including SMNH X 4600–4604, from sample

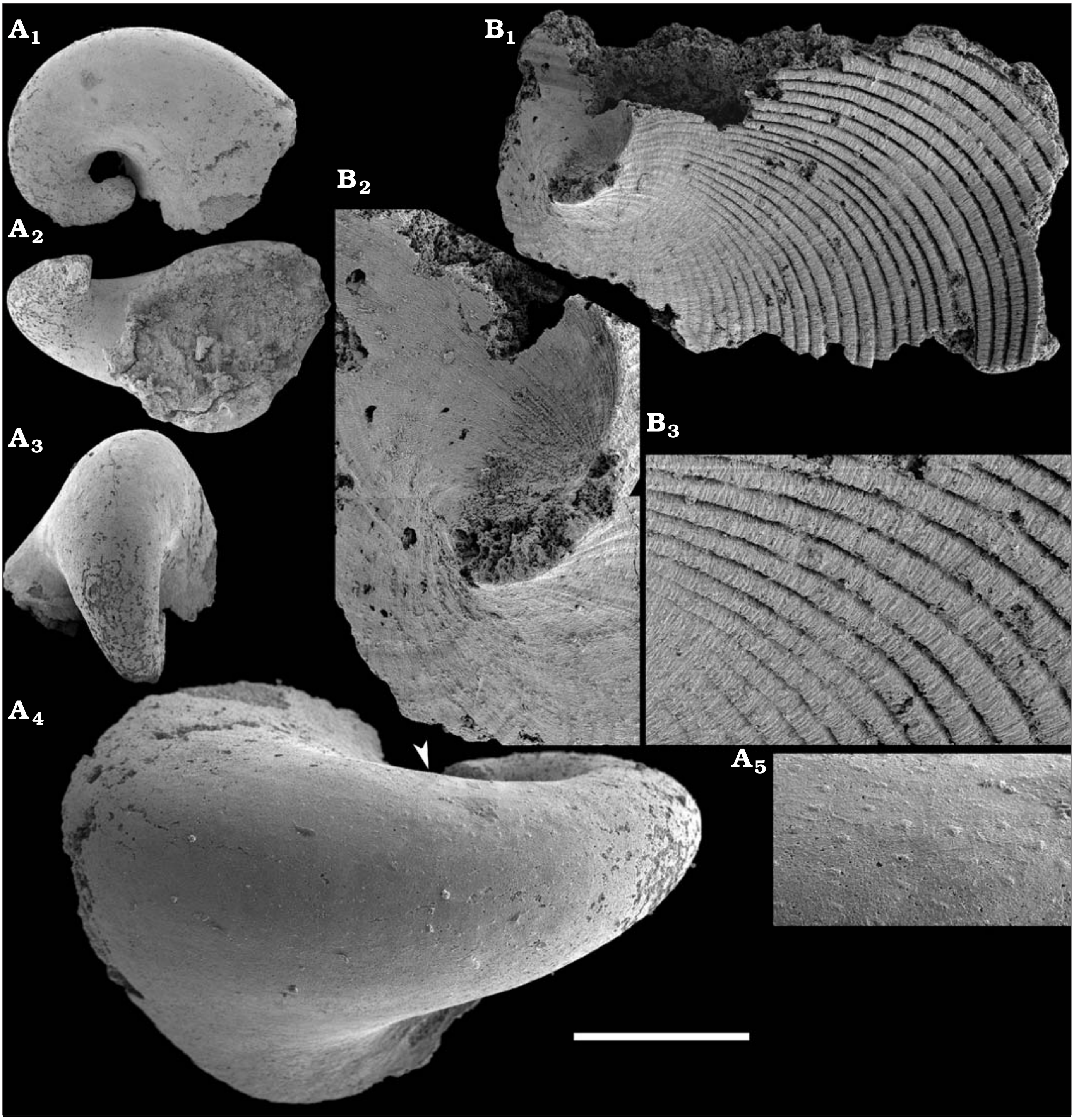

Fig. 20. Pelagiellid mollusc *Pelagiella* sp. 2 from lower Cambrian Emyaksin Formation, Malaya Kuonamka River, Anabar Uplift, Siberia; sample K1-3B. **A**. SMNH Mo 160429, internal mould; spiral side (A_1), apertural (A_2), sub-apical (A_3), and abapical (A_4) views; A_5, polygonal network on the spiral side (arrowed in A_4). **B**. SMNH Mo 167688; B_1–B_3, external mould of the outer shell surface. Scale bar: A_1–A_3, 600 μm; A_4, B_1, 300 μm; and A_5, B_2–B_3, 120 μm.

7/36.7, correlated with the *Delgadella anabara* Zone, Atdabanian Stage; Emyaksin Formation, Bol'shaya Kuonamka River. Seven phosphatised conchs, including SMNH X 4605 and 4606, from sample 7/70 and several additional conchs from sample K1-3B; several phosphatised opercula, including SMNH X 4607 and 4608, from samples 1/7.8 and K1-3B (respectively); Uppermost Emyaksin Formation, Malaya Kuonamka and Bol'shaya Kuonamka rivers; *Calodiscus*-*Erbiella* Zone, lower Botoman Stage.

Description.—Conch gently curved dorsally at the initial part, with broadly oval aperture. Ventral and dorsal margins of the aperture protrude slightly. Apical angle is ca. 25°. The initial part is rounded and separated from the main conch by a septum. The wall consists of two layers of fibrous bundles. In the outer one, the bundles are inclined longitudinally towards the conch apex and contain pore canals. The bundles of the inner layer run transversely around the conch.

Operculum outline is oval. On the inner surface of operculum, a well-developed circular ridge delimits a rounded triangular or rounded trapezoidal depression in the middle. The ridge and medial depression carry radial folds and expose radially oriented fibres in places (Kouchinsky 2000b: fig. 7A, D). The marginal part of the operculum is about one-third of the opercular radius in width and is formed of stacked growth laminae penetrated by pores (Fig. 24; see description of these porous opercula in Kouchinsky 2000b).

Remarks.—The fossils are described by Kouchinsky (2000b: 69, fig. 3) as Allathecid? hyolith, microstructural type A, forms 1 and 2. Missarzhevsky (in Rozanov et al. 1969: 119) noted that the wall of *Majatheca tumefacta* is built of acicular units (“crystals”) perpendicular to the surface. Opercula, illustrated as *Allatheca* sp. in Rozanov et al. (1969: pl. 11: 4, 8) and attributed to *M. tumefacta* in Sokolov and Zhuravleva (1983: pl. 22: 7), as well as *Allatheca* sp. 2 (Meshkova 1974: pl. 11: 12) are very similar to those in Fig. 24A herein. Conchs and opercula herein attributed to *M. tumefacta* co-occur in sample K1-3B. Sample K1-3B from the Malaya Kuonamka section contains a variety of often well-preserved hyolith opercula, in contrast to the coeval sample 7/70 from Bol’shaya Kuonamka that contains only poorly preserved opercula but well-preserved hyolith conchs. The general disparities in the numbers of hyolith opercula versus conchs from the same level is probably explained by local differences in hydrodynamic sorting (see Malinky and Skovsted 2004).

Stratigraphic and geographic range.—Upper Tommotian–lower Botoman Stages, Siberian Platform.

Genus *Allatheca* Missarzhevsky in Rozanov et al., 1969

Type species: *Allatheca corrugata* Missarzhevsky in Rozanov et al., 1969; *Dokidocyathus regularis* Zone, Tommotian Stage, lower Cambrian; Tiktirikteekh, near Churan village, middle Lena River, Siberian Platform.

Allatheca? cf. *A. corrugata* Missarzhevsky in Rozanov et al., 1969

Fig. 22F–I.

Material.—Eleven phosphatised conchs and internal moulds, including SMNH X 4609–4612, from sample 7/36.7. Emyaksin Formation, Bol’shaya Kuonamka; correlated with the *Delgadella anabara* Zone, Atdabanian Stage.

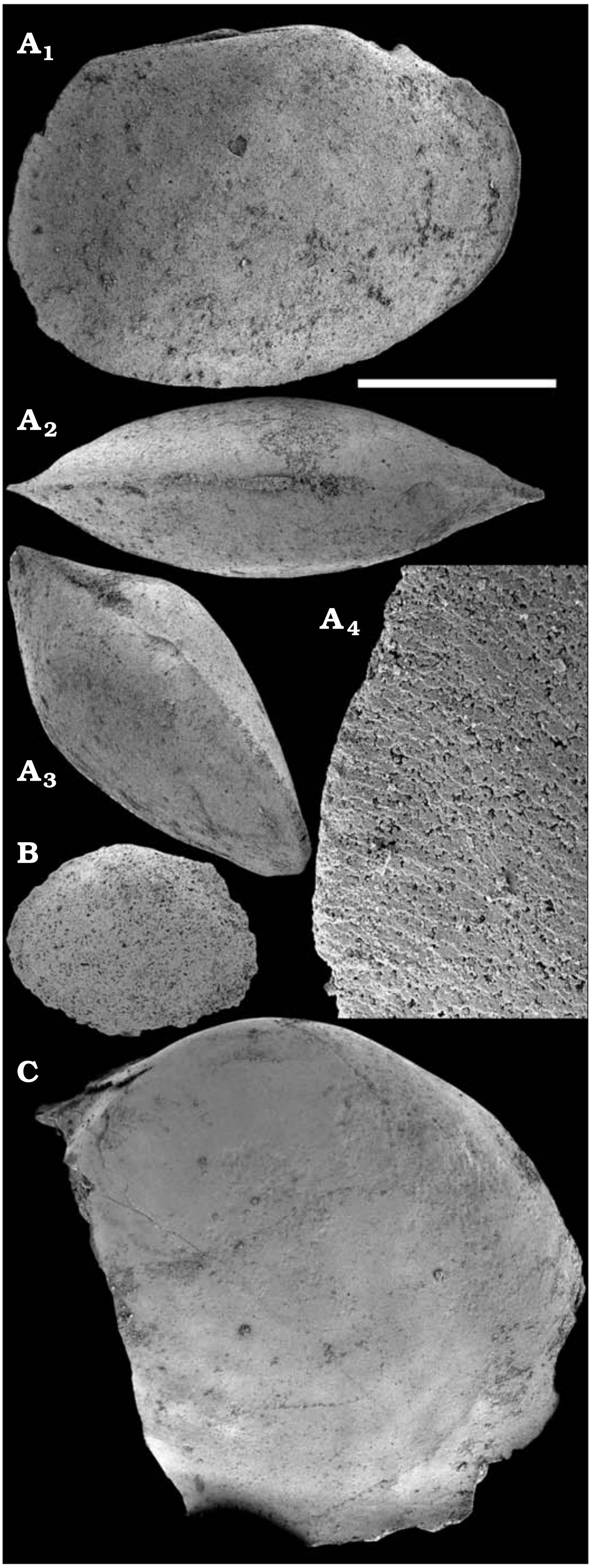

Fig. 21. Internal moulds of bivalved molluscs from lower Cambrian Emyaksin Formation, Bol’shaya Kuonamka River, Anabar Uplift, Siberia; sample 7/70. **A**. *Fordilla* cf. *F. sibirica* Krasilova, 1977, SMNH Mo 167690; right lateral (A_1), dorsal (A_2), and oblique dorsal (A_3) views; A_4, close-up of A_1. **B**. Undetermined fordillid bivalve, SMNH Mo 167691, left lateral view. **C**. Fragment of a larger specimen, interpreted herein as *Fordilla* cf. *F. sibirica*, SMNH Mo 167692, lateral view. Scale bar 1000 µm, except A_4, 100 µm.

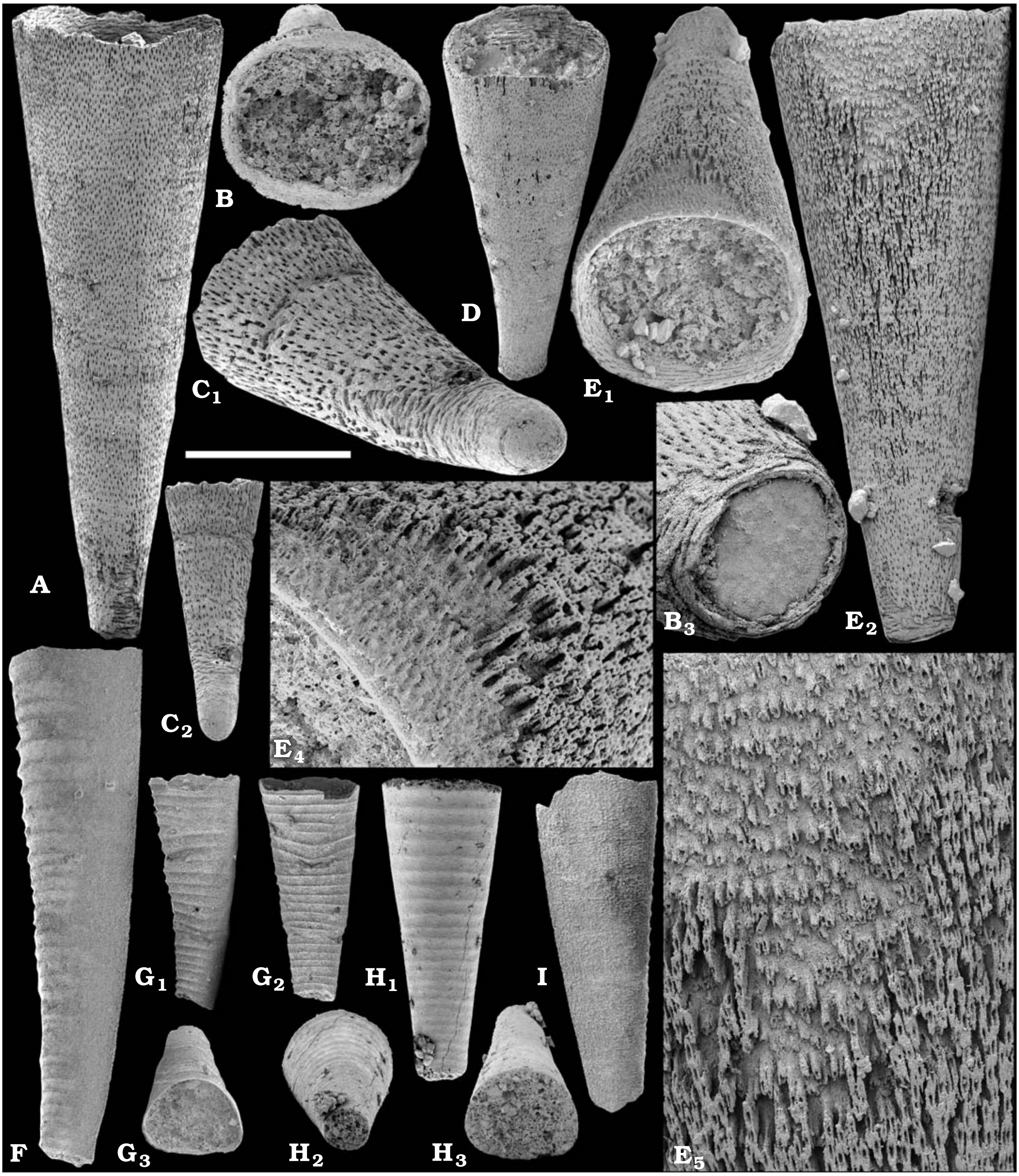

Fig. 22. Hyolith conchs from lower Cambrian Emyaksin Formation, Bol'shaya Kuonamka River, Anabar Uplift, Siberia; sample 7/36.7. **A**–**E**. *Majatheca tumefacta* Missarzhevsky in Rozanov et al., 1969, conchs with phosphatised microstructure of the walls. **A**. SMNH X 4600 (Mo 160442 in Kouchinsky 2000b: fig. 3); dorsal view. **B**. SMNH X 4601; apertural view. **C**. SMNH X 4602 (Mo 160441 in Kouchinsky 2000b: fig. 3); oblique lateral (C_1) and dorsal (C_2) views. **D**. SMNH X 4603; dorsal view. **E**. SMNH X 4604; apertural (E_1) and dorsal (E_2) views; E_3, septum in the apical part; E_4 and E_5, phosphatised fibrous bundles near the aperture. **F**–**I**. *Allatheca*? cf. *A. corrugata* Missarzhevsky in Rozanov et al., 1969. **F**. SMNH X 4609; lateral view. **G**. SMNH X 4610; lateral (G_1), dorsal (G_2), and apertural (G_3) views. **H**. SMNH X 4611; dorsal (H_1), apical (H_2), and apertural (H_3) views. **I**. SMNH X 4612; ventral view. Scale bar 600 μm, except C_1, 300 μm; E_3–E_5, 200 μm.

Description.—Slightly dorso-ventrally curved conch, 1–2 mm long, with convex dorsal and flattened ventral sides. Dorso-lateral part is semi-circular in transverse section, and passes via rounded margins into a slightly convex ventral part. In dorsal view, the apical angle is ca. 20°. The aperture has an apparently straight dorsal margin. The conch is ornamented dorso-laterally with distinct narrow transverse ribs. The ventral surface is smooth.

Remarks.—The cross-section and ornamentation of the conchs are typical of *Allatheca corrugata* Missarzhevsky in Rozanov et al., 1969 (tentatively synonymised herein with *A. anabarica* Val'kov, 1975). The illustrated individuals are therefore interpreted as probable juveniles of typically larger, several cm-sized *Allatheca corrugata*, which are reported from the middle part of Emyaksin Formation (Val'kov 1975, 1987).

Genus *Conotheca* Missarzhevsky in Rozanov et al., 1969

Type species: *Conotheca mammilata* Missarzhevsky in Rozanov et al., 1969; upper Tommotian Stage, lower Cambrian; Tiktirikteekh, near Churan village, middle Lena River, Siberian Platform.

Conotheca cf. *C. mammilata* Missarzhevsky in Rozanov et al., 1969

Figs. 25E–G, 26K, 27A–E, H.

Material.—Six specimens from sample 3/42; three specimens, including SMNH X 4620, from sample 3/65; five, including SMNH X 4621 and 4622, from sample 7/27.5; two from sample 7/28.5; five, including SMNH X 4623, from sample 7/29; SMNH X 4663 from sample 7/30, eight from sample 7/31.5, including SMNH X 4624; one from sample 7/33; one from sample 7/34; nine phosphatised conchs with internal moulds, including SMNH X 4625–4627, from sample 7/36.7; several specimens from sample 7/55; one specimen, SMNH X 4628, from sample 7/70, five from sample K1-3B and five from sample 1/7.8. Emyaksin Formation, Malaya Kuonamka and Bol'shaya Kuonamka rivers; correlated with the *Repinaella* Zone, Atdabanian Stage–*Calodiscus*-*Erbiella* Zone, lower Botoman Stage.

Description.—Slightly dorso-ventrally curved conch, with a straight aperture and circular cross-section. The surface is covered with straight transverse growth lines. Apical angle is up to 15°. Juvenile conch is blunt and bulbous. Wall microstructure consists of inner layer of transverse fibres running around the conch, and the outer layer composed of longitudinally oriented fibres (Fig. 27A, B).

Remarks.—*Conotheca mammilata* Missarzhevsky in Rozanov et al., 1969 is known from the Tommotian and Atdabanian Stages of Siberia. In the type material, the apical angle ranges from 8–20° and the presence of both robust and gracile forms was indicated in the original description of *C. mammilata* by Missarzhevsky (in Rozanov et al. 1969: 113). Specimens with better-preserved phosphatised walls show microstructure similar to that of some other hyoliths described herein (Fig. 27A–D; see also Kouchinsky 2000b).

Conotheca circumflexa Missarzhevsky in Rozanov et al., 1969

Fig. 27F.

Material.—One phosphatised conch, SMNH X 4629, from sample 7/55; Emyaksin Formation, Bol'shaya Kuonamka River; correlated with the *Judomia* Zone, upper Atdabanian Stage.

Description.—Conch helically curved about a half revolution clockwise towards the direction of growth. The aperture is straight and rounded, slightly oval. The surface of conch is covered with straight, faint, transverse lines. The apical angle is ca. 20°. Wall microstructure is similar to that of other hyoliths (see also Kouchinsky et al. 2009: fig. 45).

Stratigraphic and geographic range.—Lower Cambrian, Atdabanian Stage, Siberian Platform.

Conotheca spp.

Fig. 28.

Material.—Several phosphatised opercula with cardinal processes, including SMNH X 4630–4632, from sample K1-3B; uppermost Emyaksin Formation, Malaya Kuonamka; *Calodiscus*-*Erbiella* Zone, lower Botoman Stage. One operculum, SMNH X 4633, from sample 7/31.5; Emyaksin Formation, Bol'shaya Kuonamka; correlated with the *Delgadella anabara* Zone, Atdabanian Stage.

Remarks.—Circular opercula from sample K1-3B with two prominent cardinal processes, nearly perpendicular to the surface of the operculum (Fig. 28A–C). The processes diverge at ca. 30º. The inner surface has a smooth distal ridge at the margin, low rounded polygonal pattern in the middle and faint radial striation laterally. The margin thins out gradually. Conchs with circular cross-section are not found in sample K1-3B, but occur in the coeval sample 7/70 from Bol'shaya Kuonamka.

The operculum from sample 7/31.5 has weakly developed cardinal processes and radially oriented lateral folds of the circular distal ridge (Fig. 28D). The ridge slopes abruptly towards the margin of the operculum. Radial folds developed laterally on the distal ridge are reminiscent of those described as tubular clavicles (Malinky and Skovsted 2004) in *Conotheca australiensis* Bengtson in Bengtson et al., 1990, of which the interior surface morphology is otherwise different. Several straight fragments of conchs with circular cross-section (Fig. 27H) co-occur with the operculum in sample 7/31.5.

Genus *Loculitheca* Sysoev, 1968

Type species: *Circotheca anulata* Sysoev, 1959; lower Cambrian; Kotuj River, left bank, 6 km downstream of the mouth of Kotujkan River, Siberian Platform.

Loculitheca? sp.

Fig. 25D.

Material.—Several tens of fragments of phosphatised internal moulds, including SMNH X 4634, from sample 7/36.7. Emyaksin Formation, Bol'shaya Kuonamka; correlated with the *Delgadella anabara* Zone, Atdabanian Stage.


A1
A2
A3
B1
B2
G1
B3
C
D
E
F1
F2
G2
F3
F4
F5
H
I1
I2
B4

Remarks.—The moulds are straight, 1–2 mm long, slightly diverging (<5°) and covered with faint thin transversal growth lines. Oval septae with straight margins are perpendicular to the wall and concave towards the conch aperture. The fossils are most similar morphologically to *Loculitheca* Sysoev, 1968. *Turcutheca* Missarzhevsky in Rozanov et al., 1969 and *Ovalitheca* Sysoev, 1968 are also similar but have laterally curved conchs; no such curvature is recognised in the fragments available.

Genus *Tetratheca* Sysoev, 1968

Type species: *Quadrotheca clinisepta* Sysoev, 1960; upper Atdabanian Stage, lower Cambrian; mouth of the Sinyaya River, middle reaches of the Lena River, Siberian Platform.

Tetratheca clinisepta (Sysoev, 1960)

Fig. 26F–H.

Material.—Nineteen phosphatised conchs and internal moulds, including SMNH X 4641 and 4642, from sample 7/70 and one additional internal mould, SMNH X 4643, from sample B-247. Uppermost Emyaksin Formation, Bol’shaya Kuonamka River; *Calodiscus*-*Erbiella* Zone, lower Botoman Stage.

Description.—Straight conch, rectangular in cross-section and covered with faint straight transversal growth lines. The four sides of the conch are slightly depressed and separated from each other by a longitudinal keel. The apical angle is <5°. A smooth septum, concave towards the apex, is preserved in one of the fragments (Fig. $26G_2$).

Remarks.—In one of the internal moulds, the apertural end is a little flared (Fig. 26F). Phosphatised casts of pore channels perpendicular to the wall are preserved between inner and outer phosphatic crust delimiting the now-dissolved wall (Fig. 26G, H).

Stratigraphic and geographic range.—Atdabanian and lower Botoman Stages, Siberian Platform.

← Fig. 23. Hyolith conchs from lower Cambrian Emyaksin Formation, Bol’shaya Kuonamka River, Anabar Uplift, Siberia. **A**, **B**. *Majatheca tumefacta* Missarzhevsky in Rozanov et al., 1969, conchs with phosphatised microstructure of the walls; sample 7/70. **A**. SMNH X 4605 (Mo 160444 in Kouchinsky 2000b: fig. 3); A_1, close-up of the ventral inner surface at the aperture; A_2, close-up of the dorsal outer surface at the aperture; A_3, dorsal view. **B**. SMNH X 4606 (Mo 160445 in Kouchinsky 2000b: fig. 3); apertural (B_1), dorsal (B_3), and lateral (B_4) views; B_2, close-up of the dorsal surface with longitudinal striae. **C**–**G**. Orthothecida? sp. indet. 1, conchs with phosphatised microstructure of the walls; sample 7/70. **C**. SMNH X 4613; ventral view. **D**. SMNH X 4614; dorsal view. **E**. SMNH X 4615; dorsal view. **F**. SMNH X 4616 (Mo 160448 in Kouchinsky 2000b: fig. 4); dorsal (F_1) and lateral (F_2) views. **G**. SMNH X 4617; apertural (G_1) and ventral (G_2) views. **H**, **I**. Conchs of apparently the same species, Orthothecida? sp. indet. 1, with phosphatised microstructure of the walls; sample 7/33. **H**. SMNH X 4618 (Mo 160449 in Kouchinsky 2000b: fig. 4); ventral inner surface. **I**. SMNH X 4619 (Mo 160447 in Kouchinsky 2000b: fig. 4); lateral (I_1) and dorsal (I_2) views. Scale bar: A_1, A_2, B_2, 150 μm; A_3, B_1, B_3, B_4, H, I, 600 μm; C–G, 1200 μm.

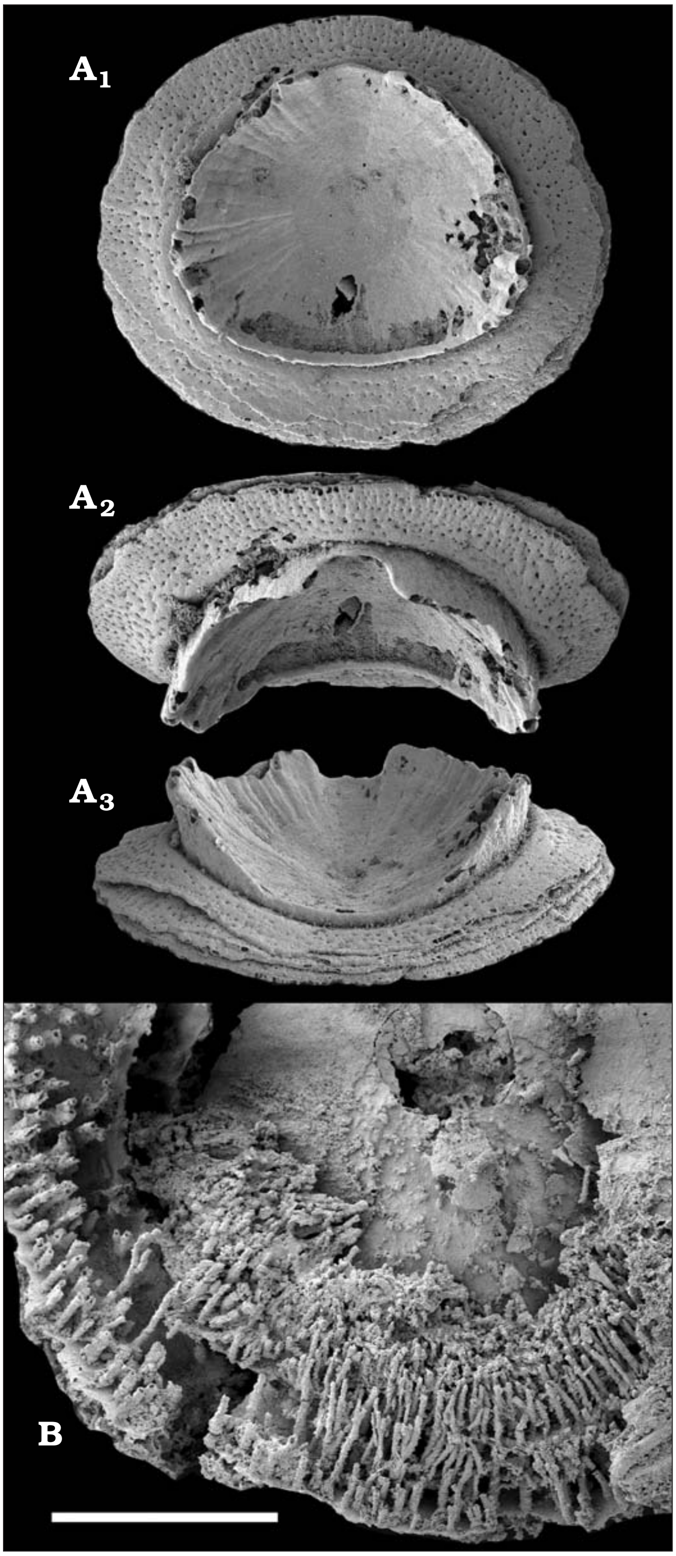

Fig. 24. Opercula of hyoliths *Majatheca tumefacta* Missarzhevsky in Rozanov et al., 1969 with phosphatised microstructure of the walls from lower Cambrian Emyaksin Formation, Malaya Kuonamka River, Anabar Uplift, Siberia. **A**. SMNH X 4607 (Mo 160465 in Kouchinsky 2000b: fig. 7), sample 1/7.8; inner (A_1), dorsal (A_2), and ventral (A_3) views. **B**. SMNH X 4608 (Mo 160467 in Kouchinsky 2000b: fig. 7), sample K1-3B; broken operculum with phosphatised canals preserved. Scale bar: A, 600 μm; B, 300 μm.

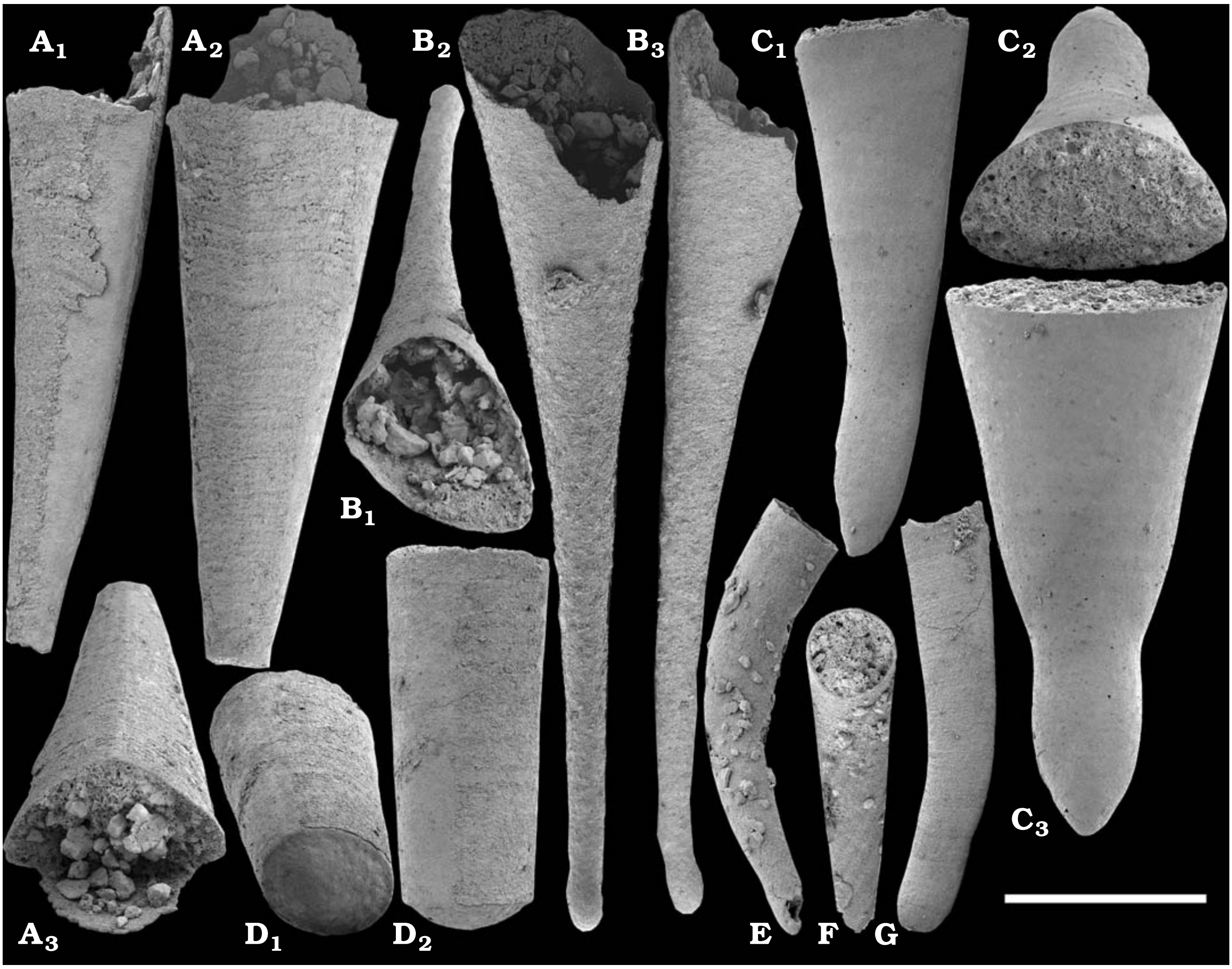

Fig. 25. Hyolith conchs from lower Cambrian Emyaksin Formation, Bol'shaya Kuonamka River, Anabar Uplift, Siberia; sample 7/36.7. **A**. Hyolithida sp. indet. 1, SMNH X 4656; lateral (A_1), dorsal (A_2), and apertural (A_3) views. **B**. "*Lenatheca groenlandica* (Poulsen, 1932)"?, initial part, SMNH X 4640; apertural (B_1), dorsal (B_2), and lateral (B_3) views. **C**. *Microcornus*? sp., SMNH X 4655; lateral (C_1), apertural (C_2), and dorsal (C_3) views. **D**. *Loculitheca*? sp., SMNH X 4634; D_1, oblique apical view, septum; D_2, plan view of the conch. **E**–**G**. *Conotheca* cf. *C. mammilata* Missarzhevsky in Rozanov et al., 1969. **E**. SMNH X 4625; lateral view. **F**. SMNH X 4626; dorsal view. **G**. SMNH X 4627; lateral view. Scale bar 600 μm.

Genus *Lenatheca* Missarzhevsky in Rozanov et al., 1969

Type species: *Hyolithus* (*Orthotheca*) *bayonet* var. *groenlandicus* Poulsen, 1932; lower Cambrian, northeast Greenland.

Remarks.—According to Malinky and Skovsted (2004), the genus name *Lenatheca* is inadequately founded by Missarzhevsky (in Rozanov et al., 1969) on poorly preserved type material of *Hyolithus* (*Orthotheca*) *bayonet* var. *groelandicus* Poulsen, 1932. Investigation by Malinky and Skovsted (2004) revealed difference between Poulsen's type material and available Siberian specimens from Missarzhevsky's collection. Val'kov (1975: 77) attributed, however, such forms found by him in the uppermost Emyaksin Formation to *Lenatheca*

Fig. 26. Hyolith conchs from lower Cambrian Emyaksin Formation, Bol'shaya Kuonamka River, Anabar Uplift, Siberia; sample B-247 (F) and sample 7/70 (A–E, G–L). **A**–**E**. "*Lenatheca groenlandica* (Poulsen, 1932)", internal moulds. **A**. SMNH X 4635; apical (A_1), ventral (A_2), and lateral (A_3) views. **B**. SMNH X 4636; apical (B_1) and dorsal (B_2) views. **C**. SMNH X 4637; dorsal (C_1), apertural (C_3), and lateral (C_4) views; C_2, cross-section of apical part. **D**. Internal mould with septum, SMNH X 4638; transversal view from the apical end. **E**. Internal mould with septum, SMNH X 4639; transversal view from the apical end. **F**–**H**. *Tetratheca clinisepta* (Sysoev, 1960). **F**. Internal mould with flared apertural end, SMNH X 4643; oblique apertural view. **G**, **H**. Partly phosphatised conchs. **G**. SMNH X 4641; G_1, longitudinal view; G_2, oblique transversal view on the septum from the apical end. **H**. SMNH X 4642; H_1, longitudinal view; H_2, oblique transversal view from the apertural end. **I**, **J**. Orthothecida? sp. indet. 2. **I**. SMNH X 4644; lateral (I_1), dorsal (I_2), apical (I_3), and apertural (I_4) views. **J**. SMNH X 4645; dorsal view of a smaller mould. **K**. *Conotheca* cf. *C. mammilata*, SMNH X 4628; apertural (K_1), lateral (K_2), and dorsal (K_3) views. **L**. Internal mould of a hyolith conch with septa (not discussed in the text), SMNH X 4662; L_1, transversal view of the septa; L_2, oblique view of a septum. Scale bar: A, B, C_1, C_3, C_4, 2 mm; D–H, 600 μm; I–L, 1200 μm.

→


A1
A3
C1
C4
F
G2
G1
C2
H1
C3
H2
A2
B1
D
B2
E
I1
I2
K1
K2
K3
L1
L2
I3
I4
J

Fig. 27. Hyolith conchs from lower Cambrian Emyaksin Formation, Bol'shaya Kuonamka River and basal Kuonamka Formation, Malaya Kuonamka River, Anabar Uplift, Siberia. **A**–**E**, **H**. *Conotheca* cf. C. *mammilata* Missarzhevsky in Rozanov et al., 1969. **A**. SMNH X 4623, sample 7/29; longitudinal view on presumably dorsal side. **B**. SMNH X 4621, sample 7/27.5; longitudinal view on presumably dorsal side. **C**. SMNH X 4622, sample 7/27.5; longitudinal view. **D**. SMNH X 4663, sample 7/30; D_1, transversal view from the apertural end; D_2, longitudinal view. **E**. SMNH X 4620, sample 3/65; lateral (E_1) and dorsal (E_2) views. **H**. SMNH X 4624, sample 7/31.5; longitudinal view. **F**. *Conotheca circumflexa* Missarzhevsky in Rozanov et al., 1969, SMNH X 4629; F_1, oblique longitudinal view showing transversal section; F_2, longitudinal view. **G**, **J**. *Linevitus*? *minutus* Missarzhevsky in Rozanov and Missarzhevsky, 1966. **G**. SMNH X 4657, sample 7/31.5; lateral (G_1), dorsal (G_2), and apertural (G_3) views. **J**. SMNH X 4658, sample 7/70; ventral side with growth increments. →

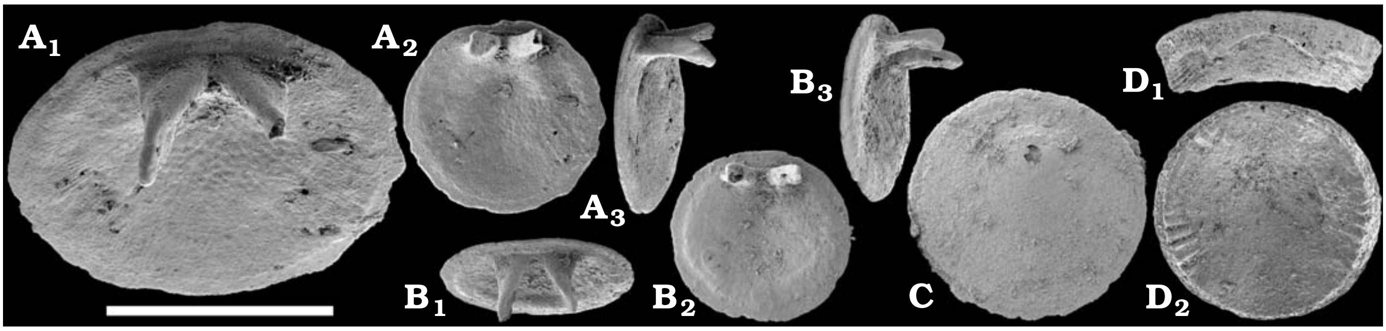

Fig. 28. Hyolith opercula *Conotheca* spp. from lower Cambrian Emyaksin Formation, Malaya Kuonamka River and Bol'shaya Kuonamka River, Anabar Uplift, Siberia. **A**–**C**. Opercula with long processes, sample K1-3B. **A**. SMNH X 4630; oblique dorsal (A_1), inner (A_2), and lateral (A_3) views. **B**. SMNH X 4631; dorsal (B_1), inner (B_2), and lateral (B_3) views. **C**. SMNH X 4632; outer view. **D**. Operculum without processes, SMNH X 4633, sample 7/31.5; dorsal (D_1) and inner (D_2) views. Scale bar 600 µm, except A_1, 300 µm.

groenlandica (Poulsen, 1932). Taking into account inappropriate designation to the genus and species, the fossils are described herein under "*Lenatheca groenlandica* (Poulsen, 1932)" to refer to their definition by Val'kov (1975).

"*Lenatheca groenlandica* (Poulsen, 1932)"

Figs. 25B, 26A–E.

Material.—Twenty phosphatised internal moulds, including SMNH X 4635–4639, from sample 7/70 and probably six more, including SMNH X 4640, from sample 7/36.7. Emyaksin Formation, Bol'shaya Kuonamka River; *Calodiscus*-*Erbiella* Zone, lower Botoman Stage and *Delgadella anabara* Zone, Atdabanian Stage (respectively).

Description.—Conch straight (Fig. 26A) or slightly curved laterally (Fig. 26C). In dorsal view the apical angle is ca. 30°. Cross-section drop-shaped (Fig. 26C_2) or rounded triangular at the juvenile conch (Fig. 26A_1), acquiring ventral invagination at later stages (Fig. 26B_1, C_3, E). Arched dorsal side with median longitudinal ridge on top and inflated flanks. Antero-lateral edges bluntly rounded. Ventral side contains a broad median depression with a flattened bottom. Septa are oval in outline, with two radial folds diverging at ca. 40º on the dorsal portion (Fig. 26D, E).

Orthothecida? sp. indet. 1

Fig. 23C–I.

Material.—Twenty-five phosphatised conchs, including SMNH X 4613–4617, from sample 7/70, fourteen from sample K1-3B and three from sample 1/7.8; uppermost Emyaksin Formation, Bol'shaya Kuonamka and Malaya Kuonamka rivers; *Calodiscus*-*Erbiella* Zone, lower Botoman Stage. Several conch fragments, including SMNH X 4618 and 4619, from samples 7/33 and 7/31.9; Emyaksin Formation, Bol'shaya Kuonamka River; correlated with the *Delgadella anabara* Zone, Atdabanian Stage.

Description.—Almost straight or slightly dorso-ventrally curved conchs, up to several mm long. The dorso-lateral part is semi-circular in transverse section, passing via rounded margins into a flattened ventral part. In dorsal view, the apical angle is ca. 15°. The conch wall includes two horizontal layers of fibres (microstructure is described in detail by Kouchinsky 2000b). Fibres in the inner layer run transversely on the dorsal side and branch towards the aperture laterally (Fig. 23F, H). The fibres may branch and anastomose intensively and are less regularly arranged on the ventral side of the conch, although their typical orientation there is transverse. The outer layer consists of longitudinally oriented fibres on the dorsal side (Fig. 23I).

Remarks.—The hyoliths are discussed as allathecid(?) hyolith, microstructural type B, forms 1 and 2 by Kouchinsky (2000b: 70, figs. 4, 5).

Orthothecida? sp. indet. 2

Fig. 26I, J.

Material.—Ten internal moulds, including SMNH X 4644 and 4645, from sample 7/70 and eight from sample K1-3B; uppermost Emyaksin Formation, Bol'shaya Kuonamka and Malaya Kuonamka rivers (respectively); *Calodiscus*-*Erbiella* Zone, lower Botoman Stage. Several internal moulds from sample 7/54; Emyaksin Formation, Bol'shaya Kuonamka River; correlated with the *Judomia* Zone, upper Atdabanian Stage.

Description.—Conchs, 2–4 mm long, slightly curved dorso-ventrally, with apical angle ca. 10º. Initial part gradually narrows towards the apex (Fig. 26J). Cross-section rounded triangular (Fig. 26I_3, I_4). Apertural part expands in a funnel-like fashion. Surface of internal mould is smooth, covered with faint discontinuous transversal striae.

Order and family uncertain

Genus *Triplicatella* Conway Morris in Bengtson et al., 1990

Type species: *Triplicatella disdoma* Conway Morris in Bengtson et al., 1990; *Abadiella huoi* Zone, lower Cambrian; Curramulka, Yorke Peninsula, Australia.

I. Fragment of a hyolith conch with phosphatised microstructure, SMNH X 4664, sample 6/18; dorsal (I_1), lateral (I_2), and apertural (I_3) views; I_4, close-up of the apical end. **K**. Hyolithida sp. indet. 2, pyritised conch, with operculum attached, SMNH X 4659, sample 1/9; oblique apertural (K_1) and lateral (K_2) views. Scale bar 600 µm, except A, B, I_4, 300 µm; I_1–I_3, J, 1200 µm.

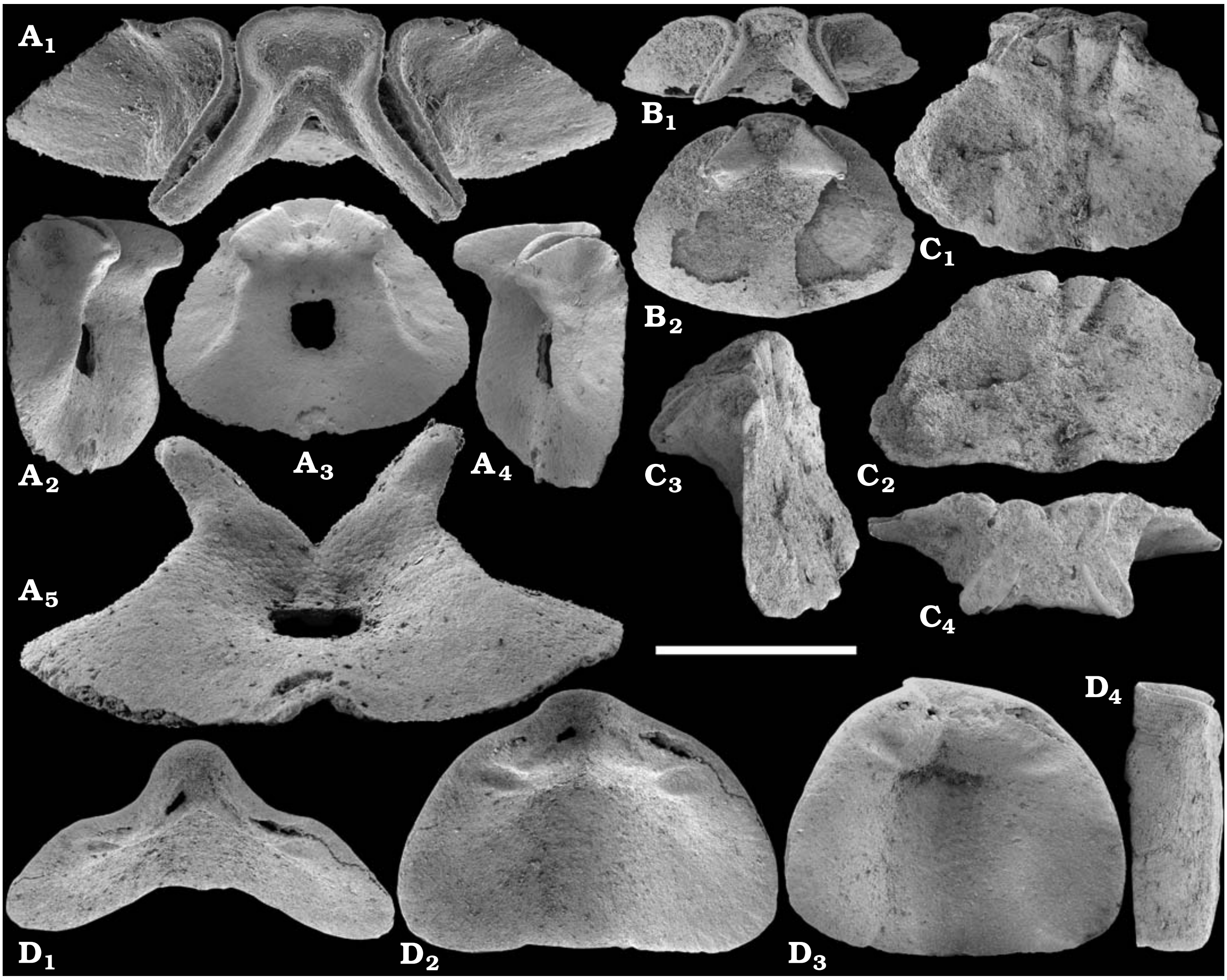

Fig. 29. Hyolith opercula *Triplicatella* spp. from lower Cambrian Emyaksin Formation, Malaya Kuonamka River and Bol'shaya Kuonamka River, Anabar Uplift, Siberia. **A**, **B**. *Triplicatella papilio* sp. nov. **A**. SMNH X 4646, holotype, sample K1-3B; dorsal (A_1), lateral (A_2, A_4), inner (A_3), and ventral (A_5, note flattened rounded polygons at the base of the dorsal folds) views. **B**. SMNH X 4647, paratype, sample 7/70; dorsal (B_1) and inner (B_2) views. **C**. *Triplicatella sinuosa* Skovsted, Peel, and Atkins, 2004; SMNH X 4648, sample B-247; outer (C_1), oblique ventral (C_2), lateral (C_3), and dorsal (C_4) views. **D**. *Triplicatella* cf. *T. peltata* Skovsted, Peel, and Atkins, 2004; SMNH X 4649, sample 7/70; dorsal (D_1), inner (D_2), oblique inner (D_3), and lateral (D_4) views. Scale bar 600 μm, except A_1, A_5, 300 μm.

Triplicatella papilio Kouchinsky sp. nov.

Fig. 29A, B.

Ethymology: From Latin *papilio*, butterfly; for the butterfly-like appearance of the operculum.

Type material: Holotype: SMNH X 4646 (Fig. 29A). Paratype: SMNH X 4647 (Fig. 29B).

Type locality: 70°08.5'N, 114°00'E, Malaya Kuonamka River, left bank at the village Zhilinda, eastern flanks of the Anabar Uplift, northern Siberian Platform.

Type horizon: Uppermost Emyaksin Formation, *Calodiscus-Erbiella* Zone, lower Botoman Stage, lower Cambrian.

Material.—Several phosphatised opercula, including holotype SMNH X 4646, from sample K1-3B and paratype SMNH X 4647, from sample 7/70; uppermost Emyaksin Formation, Malaya Kuonamka and Bol'shaya Kuonamka rivers (respectively); *Calodiscus-Erbiella* Zone, lower Botoman Stage.

Diagnosis.—Species of *Triplicatella* with the operculum rounded trapezoidal in plan view and with two prominent folds on the dorsal margin.

Description.—Operculum rounded trapezoidal in plan view, 0.8–1 mm wide, with flattened outer surface. Two prominent and laterally flattened blade-like radial folds of the dorsal surface diverge at ca. 80°, but their bases are perpendicular to the dorsal margin of the operculum (Fig. 29A_1, $_{B1}$). Invagination of the dorsal margin produces three distinct folds on the outer surface. The folds continue ventrally as two low ridges, which level off towards the margin of the operculum. The ventral part of the operculum has two broad and shallow folds.

Remarks.—*Triplicatella* Conway Morris in Bengtson et al., 1990 includes three described species, *T. disdoma* Conway Morris in Bengtson et al., 1990 (type species), *T. sinuosa* Skovsted, Peel, and Atkins, 2004, and *T. peltata* Skovsted, Peel, and Atkins, 2004. There are also four forms in open nomenclature (Skovsted et al. 2004). *T. papilio* sp. nov. is different from other known forms of *Triplicatella* in having only two inner prominent folds of the dorsal margin.

Stratigraphic and geographic range.—Known only from its type locality and horizon.

Triplicatella sinuosa Skovsted, Peel, and Atkins, 2004

Fig. 29C.

Material.—Single phosphatised operculum, SMNH X 4648, from sample B-247 and a single fragment from sample 7/70; uppermost Emyaksin Formation, Bol'shaya Kuonamka River; *Calodiscus*-*Erbiella* Zone, lower Botoman Stage.

Remarks.—The fossil is very similar to *Triplicatella sinuosa* from Cambrian Stage 4 of Laurentia (Skovsted et al. 2004) in having three strongly developed inner folds of the dorsal margin. Two weak ventral folds are recognizable. The lateral margins of the operculum are not completely preserved, but the operculum was presumably elliptical in outline.

Stratigraphic and geographic range.—*Bonnia*-*Olenellus* Zone, Dyeran Stage of Greenland and lower Botoman Stage of the Siberian Platform.

Triplicatella cf. *T. peltata* Skovsted, Peel, and Atkins, 2004

Fig. 29D.

Material.—Single phosphatised operculum, SMNH X 4649, from sample 7/70; uppermost Emyaksin Formation, Bol'shaya Kuonamka River; *Calodiscus*-*Erbiella* Zone, lower Botoman Stage.

Description.—The operculum has a rounded trapezoidal shape in plan view, ca. 1 mm wide, convex, with a single and prominent fold on the dorsal margin. In lateral view, the crest of the fold reaches the apex (Fig. 29D_4). The internal surface is smooth, with a deep median depression in the sub-central part. Two short and rounded converging lateral ridges are situated near the dorsal margin.

Remarks.—Specimens of *Triplicatella peltata* Skovsted, Peel, and Atkins, 2004 from the Cambrian Stage 4 of Laurentia are similar in outline, number of folds and structure of the inner surface, although the dorsal fold is broader and more prominent than in the fossil herein.

Operculum type 1

Fig. 30A.

Material.—Single phosphatised operculum SMNH X 4650, from sample K1-3B; uppermost Emyaksin Formation, Malaya Kuonamka River; *Calodiscus*-*Erbiella* Zone, lower Botoman Stage.

Description.—The operculum has a circular outline, but is partly broken in the middle. Two massive, laterally flattened cardinal processes are directed at ca. 90º from the inner surface of the operculum. Ridges directed ventrally represent the continuation of the processes. The distal side of the ridges dip steeply towards the margin of the operculum.

Operculum type 2

Fig. 30B, F.

Material.—Three phosphatised opercula, including SMNH X 4651 and 4652, from sample K1-3B; uppermost Emyaksin Formation, Malaya Kuonamka River; *Calodiscus*-*Erbiella* Zone, lower Botoman Stage.

Description.—The operculum has a circular outline. Prominent cardinal processes diverge at ca. 40°. They are higher than the clavicles, which extend in the ventral direction from the cardinal processes. The processes are broken off in one of the specimens (Fig. 30F). The distal ridge dips steeply towards the margin of the operculum, and more gently towards the interior.

Operculum type 3

Fig. 30C–E.

Material.—Several phosphatised opercula, including SMNH X 4653 and 4654, from sample K1-3B; uppermost Emyaksin Formation, Malaya Kuonamka River; *Calodiscus*-*Erbiella* Zone, lower Botoman Stage.

Description.—The operculum have a rounded trapezoidal outline. Cardinal processes are short, whereas the blade-like clavicles are higher. In a larger specimen (Fig. 30C), the clavicles include a series of radial folds. The distal ridge facing the margin dips steeply, whereas more gently towards the interior.

Order Hyolithida Sysoev, 1957

Family uncertain

Genus *Microcornus* Mambetov, 1972

Type species: Microcornus parvulus Mambetov, 1972; *Rhombocorniculum cancellatum* Zone, lower Cambrian; Geres Member of the Shabakty Group, Ushbas River, Lesser Karatau, Kazakhstan.

Microcornus? sp.

Fig. 25C.

Material.—Several tens of calcium phosphatic internal moulds, including SMNH X 4655, from sample 7/36.7; several additional moulds from samples 7/27.5, 7/31.5, 3/59, and 3/65; Emyaksin Formation, Bol'shaya Kuonamka and Malaya Kuonamka rivers; correlated with the interval of *Repinaella*–*Judomia* zones, Atdabanian Stage.

Description.—Short conchs, gently curved dorso-ventrally, expand fast from a relatively thick bulbous protoconch. The dorsal side is arched without angulations and passes into a convex, but more flattened ventral side. In dorsal view, the apical angle is ca. 30°. The bulbous juvenile conch with a small tip is

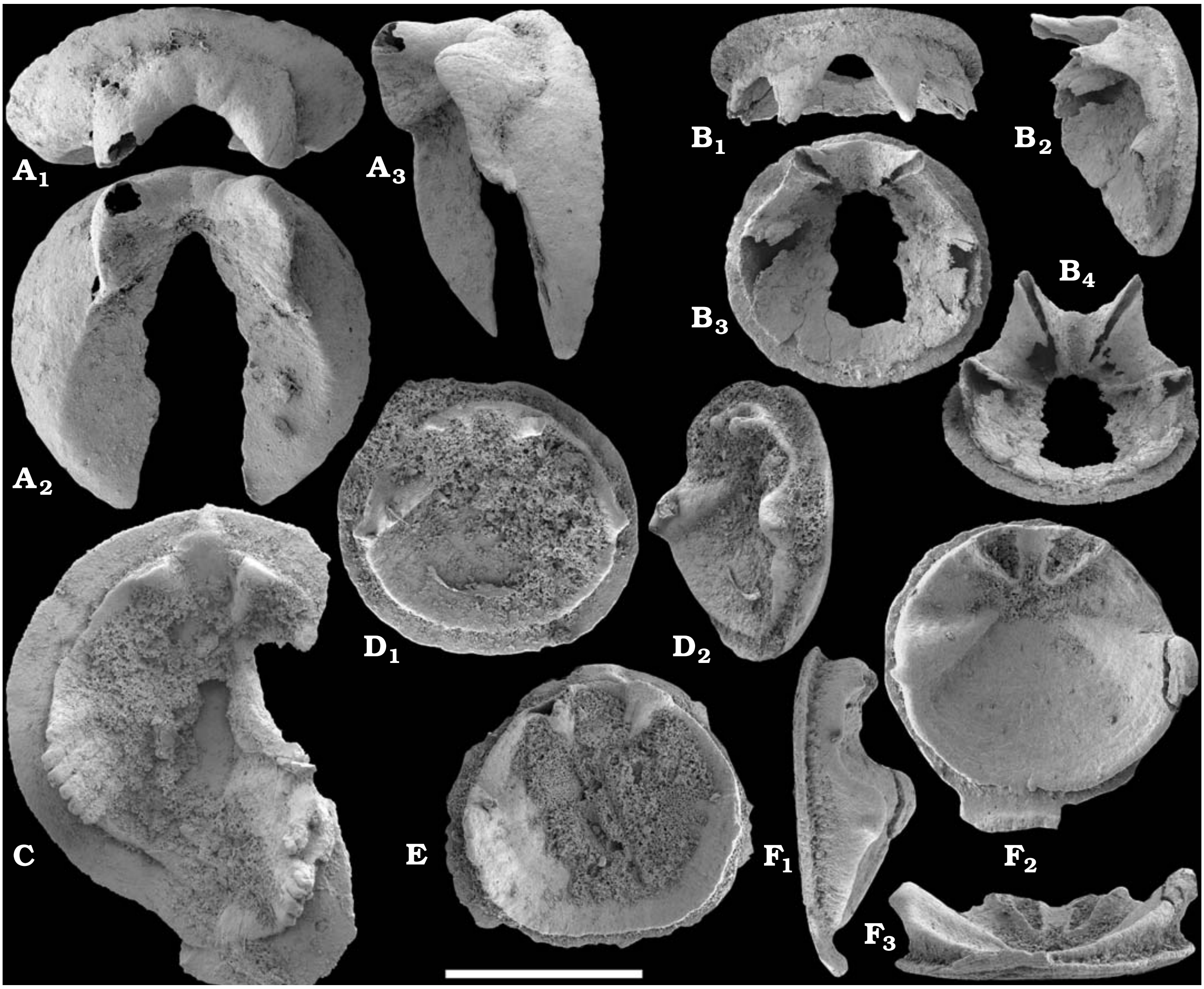

Fig. 30. Hyolith opercula from lower Cambrian Emyaksin Formation, Malaya Kuonamka River, Anabar Uplift, Siberia; sample K1-3B. **A**. Operculum type 1, SMNH X 4650; dorsal (A_1), inner (A_2), and lateral (A_3) views. **B**, **F**. Operculum type 2. **B**. SMNH X 4651; dorsal (B_1), lateral (B_2), inner (B_3), and oblique ventral (B_4) views. **F**. SMNH X 4652; lateral (F_1), inner (F_2), and ventral (F_3) views. **C**–**E**. Operculum type 3, SMNH X 4653 (**C**), SMNH X 4654 (**D**), and SMNH X 4668 (**E**); inner (C, D_1, E) and oblique lateral (D_2) views. Scale bar 600 μm.

somewhat dorso-ventrally flattened and shifted dorsally (Fig. 25C_1), separated from the main part by a constriction.

Remarks.—This material is generally similar to *Microcornus* Mambetov, 1972, described from Stages 3–5 of the Siberian Platform, Kazakhstan, Mongolia, Australia, Avalonia (Britain), and South China (Bengtson et al. 1990), but preservation as smooth internal moulds with a straight aperture precludes more detailed assignement.

Genus *Linevitus* Sysoev, 1958

Type species: Hyolithus obscurus Holm, 1893; *Lejopyge laevigata* Zone, middle Cambrian; Sweden.

Remarks.—Placement of the following Siberian species under *Linevitus* Sysoev, 1958 is questioned by Berg-Madsen and Malinky (1999), because the type material is represented by much larger fossils. Moreover, since the genus is not established on a firm morphological ground, the name *Linevitus* appears to be justified only for the type species (Berg-Madsen and Malinky 1999).

Linevitus? *minutus* Missarzhevsky in Rozanov and Missarzhevsky, 1966

Fig. 27G, J.

Material.—Single specimen from sample 7/30, three specimens, including SMNH X 4657, from sample 7/31.5 and four specimens from sample 7/31.9; correlated with the *Delgadella anabara* Zone, Atdabanian Stage. One specimen, SMNH X 4658, from sample 7/70; *Calodiscus*-*Erbiella* Zone, lower Botoman Stage. Emyaksin Formation, Bol'shaya Kuonamka River.

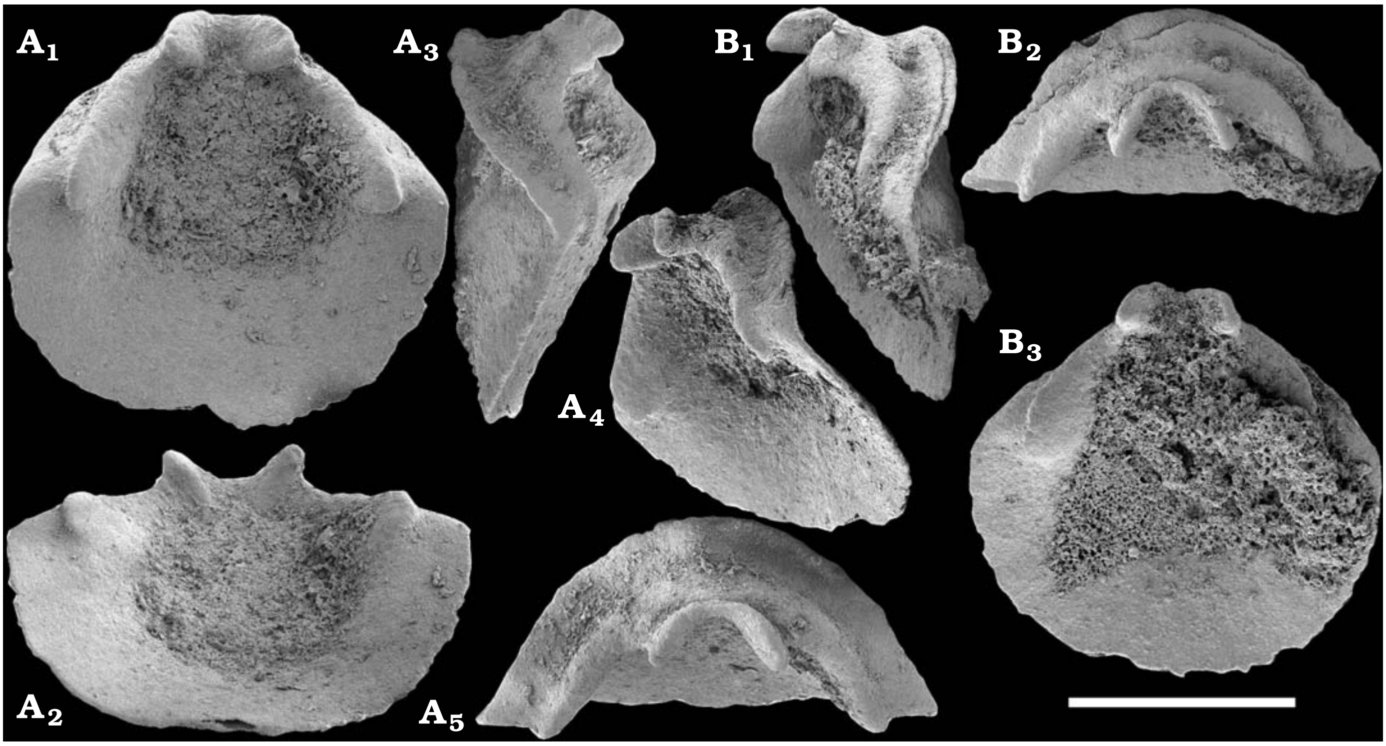

Fig. 31. Hyolith opercula *Parkula* cf. P. *esmeraldina* Skovsted, 2006 from lower Cambrian Emyaksin Formation, Malaya Kuonamka River, Anabar Uplift, Siberia; sample K1-3B. **A**. SMNH X 4660; inner (A_1), oblique ventral (A_2), lateral (A_3, A_4), and dorsal (A_5) views. **B**. SMNH X 4661; lateral (B_1), dorsal (B_2), and inner (B_3) views. Scale bar 300 µm.

Description.—Conch straight sided, with a sub-triangular cross-section. Dorsal surface rounded in the middle, with flanks dipping towards rounded lateral longitudinal ridges, grading into a slightly convex ventral surface. In dorsal view, the apical angle is ca. 30°. The conch is covered with transverse growth lines slightly curved towards the apex on dorsum. On venter, the growth lines are strongly curved towards the aperture and parallel with the edge of a long semi-circular ligula. Growth lines produce small lateral sinuses. Apical end not preserved.

Remarks.—This is very similar to the holotype of *Linevitus minutus* Missarzhevsky illustrated by Rozanov and Missarzhevsky (1966: 108, pl. 11: 7, 8; John Malinky, personnal communication in 2008), from the Tommotian Stage of Siberia. The curvature towards dorsum seen in the species is not apparent in the fragments available. The fossils are also similar to Hyolithida indet. 3 (Kouchinsky et al. 2011: fig. 11G–I).

Genus *Parkula* Bengtson in Bengtson et al., 1990

Type species: Parkula bounites Bengtson in Bengtson et al., 1990; *Abadiella huoi* Zone, lower Cambrian; Kulpara, Yorke Peninsula, Australia.

Parkula cf. *P. esmeraldina* Skovsted, 2006

Fig. 31.

Material.—Two phosphatised opercula, SMNH X 4660 and 4661, from sample K1-3B. Uppermost Emyaksin Formation, Malaya Kuonamka River; *Calodiscus*-*Erbiella* Zone, lower Botoman Stage.

Description.—The operculum has a crescent-shaped dorsal lobe and a strongly convex semi-circular ventral lobe. The dorsal margin is inclined at ca. 90° with respect to the ventral lobe. The dorsal lobe bears blade-like clavicles situated along the margin between two lobes. Cardinal processes diverge at ca. 90º.

Remarks.—The operculum is most similar to *Parkula esmeraldina* Skovsted, 2006, which is also different from *P. bounites* Bengtson in Bengtson et al., 1990 in having more diverged, longer and more dorsally situated cardinal processes. No conchs attributable to *Parkula* have been found associated with the opercula in our material. *Parkula* spp. are known from Cambrian Series 2 of Australia (Bengtson et al. 1990; Gravestock et al. 2001), Antarctica (Wrona 2003), and Laurentia (Malinky and Skovsted 2004; Skovsted 2006; Skovsted and Peel 2007).

Hyolithida sp. indet. 1

Fig. 25A.

Material.—Over twenty internal moulds, including SMNH X 4656, from sample 7/36.7 and several additional moulds from samples 7/54 and 7/55. Emyaksin Formation, Bol'shaya Kuonamka River; correlated with the *Delgadella anabara* and *Judomia* zones, Atdabanian Stage.

Description.—Conch slightly dorso-ventrally curved, with convex, arched dorsal and slightly convex ventral sides and lateral longitudinal ridge between them. Cross-section is rounded triangular. The aperture has a slight dorsal sinus and a protruding prominent ventral lip. Shallow dorsal sinus just inside aperture. Apical angle ca. 20º.

Hyolithida sp. indet. 2

Fig. 27K.

Material.—Two pyritised conchs, including SMNH X 4659, from sample 1/9. The last specimen represents an almost complete but unsatisfactorily preserved conch with operculum attached to the aperture. Carbonate concretions of the basal Kuonamka Formation, Malaya Kuonamka River; *Bergeroniellus expansus* Zone, upper Botoman Stage.

Description.—The conch is gently curved dorso-ventrally at its initial part and has a convex, arched dorsal surface with 8–9 low longitudinal folds and a flattened ventral surface. In dorsal view, the apical angle is ca. 15°. The juvenile conch is elongated, tapered, slightly curved dorsally with respect to the main conch.

Hyolithid helen?

Fig. 32.

Material.—Single phosphatised fragment SMNH X 4665, from sample 7/70. Uppermost Emyaksin Formation, Bol'shaya Kuonamka River; *Calodiscus*-*Erbiella* Zone, lower Botoman Stage.

Discussion.—The fragment of an elongated blade-like fossil. The external surface (seen in the upper part of the images in Fig. 32) is ornamented with continuous transverse terraces. The fossil contains longitudinally oriented fibres reminiscent to those in hyoliths described herein. The fossil can be tentatively interpreted as a fragment of a hyolithid helen, oriented in Fig. 32 with its more proximal portion to the right.

Phylum and class uncertain

Remarks.—Halkieriids are loosely placed within the lophotrochozoan phylogeny, ranging from stem-group Lophotrochozoa/Mollusca (Conway Morris and Caron 2007) to subclass Diplacophora Vinther and Nielsen, 2005 of the class Polyplacophora De Blainville, 1816 (Parkhaev and Demidenko 2010: 955).

Order Sachitida He in Yin et al., 1980

Family Halkieriidae Poulsen, 1967

Genus *Halkieria* Poulsen, 1967

Type species: Halkieria obliqua Poulsen, 1967; lower Cambrian, Bornholm.

Halkieria sp.

Fig. 33.

Material.—Single phosphatised sclerites from samples 7/25.6 (SMNH X 4666), 7/27.5, and 7/36.7 (SMNH X 4667). Emyaksin Formation, Bol'shaya Kuonamka River; correlated with the interval of *Profallotaspis jakutensis*–*Delgadella anabara* zones, Atdabanian Stage.

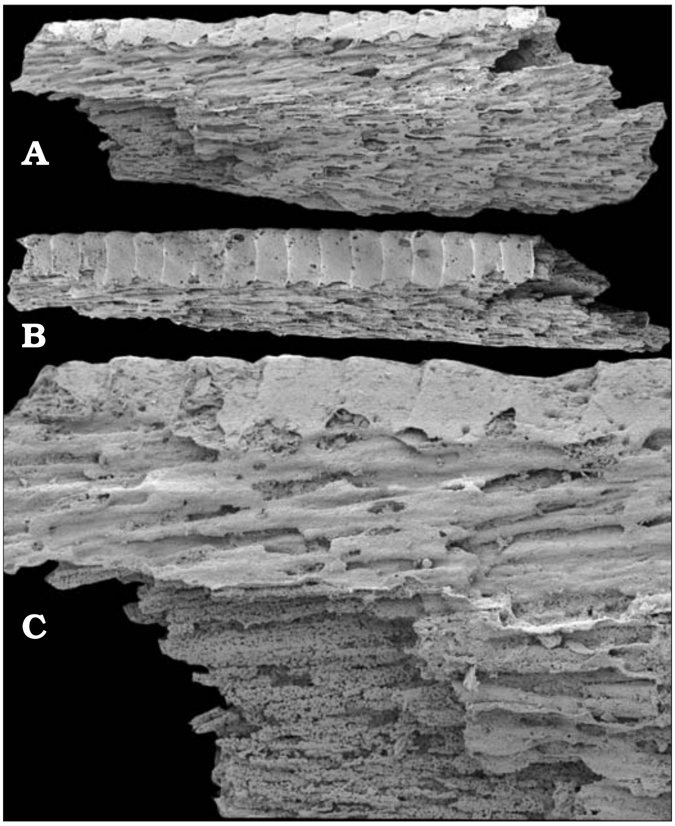

Fig. 32. Phosphatised fragment of presumably hyolithid helen with fibrous internal structure preserved, from lower Cambrian Emyaksin Formation, Bol'shaya Kuonamka River, Anabar Uplift, Siberia; SMNH X 4665, sample 7/70. **A**. Plan view on the broader side of the fragment. **B**. View on the narrower side. **C**. Enlargement of A. Scale bar 600 μm, except C, 200 μm.

Description.—Asymmetrical, elongated, blade-like and curved sclerites with transversely convex lower and upper sides. The base of sclerites has a rounded triangular, broad (Fig. 33A$_1$) or extended narrower (Fig. 33B$_2$) aperture surrounded by undulating walls with auricules. Wall microstructure consists of aciculate elements assembled in broad laths, arranged in transversal rows (Fig. 33A$_3$; see also Bengtson et al. 1990; Porter 2008).

Phylum and class uncertain

Order Chancelloriida Walcott, 1920

Family Chancelloriidae Walcott, 1920

Genus *Chancelloria* Walcott, 1920

Type species: Chancelloria eros Walcott, 1920; middle Cambrian; Burgess Shale, British Columbia, Canada.

Chancelloria spp.

Fig. 34.

Material.—Thousands of disarticulated sclerites from many samples ranging in age from the lower *Dokidocyathus regularis* Zone of the Tommotian Stage to the *Bergeroniellus ex-*

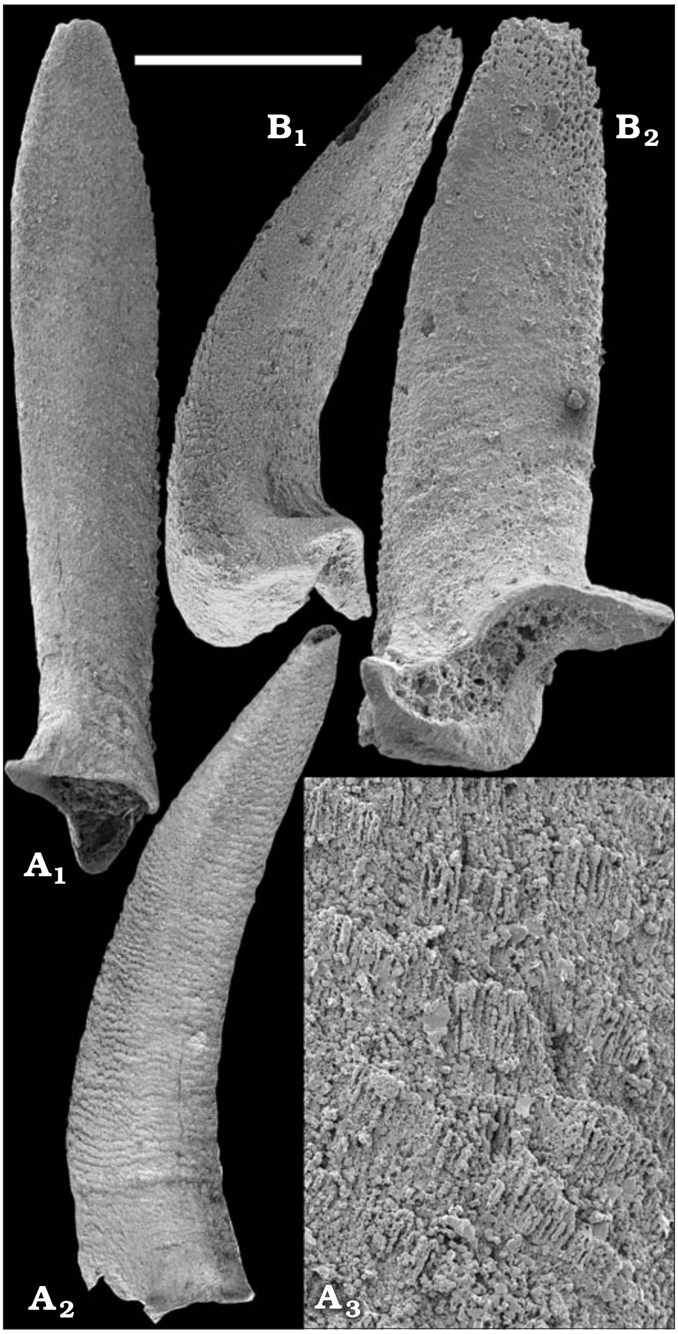

Fig. 33. Halkieriid *Halkieria* sp. from lower Cambrian Emyaksin Formation, Bol'shaya Kuonamka River, Anabar Uplift, Siberia. **A**. SMNH X 4667, sample 7/36.7; A_1, plan view on the lower side of sclerite and its aperture; A_2, oblique lateral view; A_3, close-up of A_2, fibrous microstructure. **B**. SMNH X 4666, sample 7/25.6; B_1, lateral view; B_2, plan view on the lower side of sclerite and its aperture. Scale bar 300 μm, except A_3, 30 μm.

pansus Zone of the upper Botoman Stage, Malaya Kuonamka and Bol'shaya Kuonamka rivers (SOM 2). In addition, over twenty articulated or partially articulated sclerites of 6+1 and 7+1 types from samples 3/42, 7/17.8, 7/36.7, 7/70, and K1-3B; single forms 3+0 from sample 3/42, 4+0 from samples 7/70 and K1-3B, 5+0 from samples 7/34.7 and K1-3B, and 9+0 from sample 7/70. Figured specimens are SMNH X 3416, 4669–4681. After the chemical dissolution of the rock, disarticulated sclerites mostly represent internal moulds composed partly of phosphate, and partly of fine-grained limestone matrix. The moulds are rarely glauconised in section 3, but more often glauconitic in other sections. Articulated and some disarticulated sclerites from samples 7/36.7, 7/70, and K1-3B preserve phosphatised walls.

Remarks.—The majority of sclerites have six to seven lateral rays with one central ray (6–7+1), with lateral rays gently curved away from the plane of the basal facet and sometimes laterally, while the slender central ray is almost perpendicular to the base of the rosette (Fig. 34B, G, H). Forms composed of three, four, or five lateral rays (3–5+0) are relatively rare (Fig. 34F, K–M). Several species of *Chancelloria* may be present, although 6–7+1 types of sclerites are similar to those of *Chancelloria eros* Walcott, 1920, the lectotype of which has common 6–7+1 and rare 4–5+0 sclerites in the scleritome (Bengtson et al. 1990). Sclerites of 3+0 type may derive from *Allonnia* sp. (Bengtson et al. 1990). Phosphatised internal moulds of much larger disarticulated sclerites co-occur with smaller sclerites in sample 7/70. A single disarticulated sclerite from sample 6/66.2 demonstrates a composition of aciculate laths (Fig. 34A; see also Kouchinsky 2000a). This microstructure may reflect the original structure of the mineralised wall, and it has also been observed in middle Cambrian chancelloriid sclerites of 4+0 and 6–7+1 types from Greenland (AK and John Peel, personal observations 2012).

Phylum and class uncertain (?stem-group Brachiopoda)

Order Tommotiida Missarzhevsky, 1970

Family Tommotiidae Bengtson, 1970

Genus *Camenella* Missarzhevsky in Rozanov and Missarzhevsky, 1966

Type species: Camenella garbowskae Missarzhevsky in Rozanov and Missarzhevsky, 1966; *Dokidocyathus regularis* Zone, Tommotian Stage, lower Cambrian; Chekurovka village, lower Lena River, Siberia.

Remarks.—See Bengtson (1986a) and Skovsted et al. (2009) for emended diagnosis of the genus, synonymics and discussion of the nominal species included in *Camenella*. The sellate sclerites, *Camenella garbowskae* Missarzhevsky in Rozanov and Missarzhevsky, 1966 and mitral sclerites, *C. kozlowskii* Missarzhevsky in Rozanov and Missarzhevsky, 1966 are unified herein within one species, *C. garbowskae* Missarzhevsky in Rozanov and Missarzhevsky, 1966. As in other species of *Camenella* described with a bimembrate scleritome model (see Skovsted et al. 2009), sinistral and dextral symmetry variants (D- and L-forms sensu Bengtson 1970) of both types of sclerites co-occur. The sclerites are of the same size range and share similar surface ornamentation with radial and comarginal folds.

Camenella garbowskae Missarzhevsky in Rozanov and Missarzhevsky, 1966

Figs. 35–38.

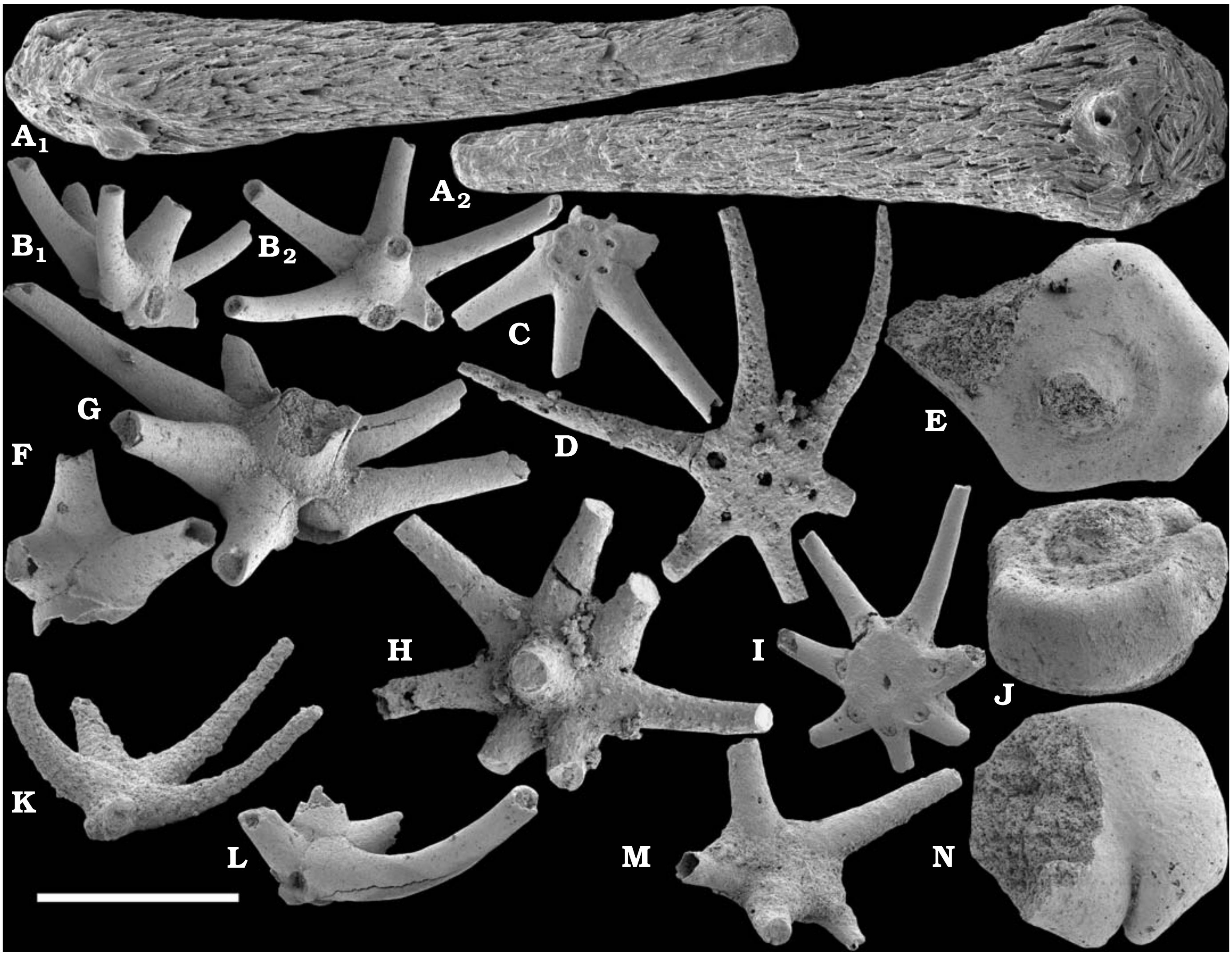

Fig. 34. Chancelloriids *Chancelloria* spp. from lower Cambrian Emyaksin Formation, Bol'shaya Kuonamka River and Malaya Kuonamka River, Anabar Uplift, Siberia. **A**. SMNH X 3416, sample 6/66.2, internal mould of a disarticulated ray with aciculate remains of presumably original microstructure of the wall; lateral (A_1) and basal (A_2) views. **B–D**. Articulated sclerites of 6+1 type. **B**. SMNH X 4672, sample 7/70; lateral (B_1) and external (B_2) views. **C**. SMNH X 4673, sample 7/70; basal view. **D**. SMNH X 4674, sample K1-3B; basal view. **E**, **J**, **N**. Internal moulds of basal parts of larger disarticulated sclerites; sample 7/70. **E**. SMNH X 4669; basal view. **J**. SMNH X 4670; oblique basal view. **N**. SMNH X 4671; external view. **F**. Articulated sclerites of 4+0 type, SMNH X 4681, sample 7/70; external view. **G–I**. Articulated sclerites of 7+1 type. **G**. SMNH X 4675, sample 7/70; lateral view. **H**. SMNH X 4676, sample K1-3B; external view. **I**. SMNH X 4677, sample K1-3B; basal view. **K–M**. Articulated sclerites of 5+0 type. **K**. SMNH X 4678, sample 7/34.7; lateral view. **L.** SMNH X 4679, sample K1-3B; lateral view. **M**. SMNH X 4680, sample K1-3B; external view. Scale bar 600 μm, except A, 300 μm.

Holotype: Sellate sclerite GIN 3470/73 (Rozanov and Missarzhevsky 1966: pl. 11: 4).

Type locality: Near Chekurovka village, lower reaches of Lena River, northern Siberia.

Type horizon: Lower Tyuser Formation, *Dokidocyathus regularis* Zone, Tommotian Stage.

Material.—Over one hundred calcium phosphatic sellate and mitral sclerites, including SMNH X 4682–4699, from samples 3/0, 3/1.5, 3/5, 3/21.5, 6/0.3, 6/1.8, 6/2, 6/3.9, K6-4B, 6/4.9, K6-5.8B, 6/6.6, 6/6.8, 6/9.1, 6/14, 6/18, 7/16, and 7/19. Emyaksin Formation, Malaya Kuonamka and Bol'shaya Kuonamka rivers; Tommotian Stage. Identifiable in the collection are 46 sellates (45%) and 57 mitrals (55%), of which 59% of sellates and 51% of mitrals are of the dextral variant.

Emended diagnosis.—Species of *Camenella* with sellate and mitral sclerites having well-developed co-marginal ribs. Sellate sclerites asymmetrical, with distinct sella separating larger and smaller lobes. Larger lobe with several radial ridges. Apex slightly coiled, up to 1/2 whorls. Duplicature in large sclerites adpressed to the inner surface laterally and near the apex. Mitral sclerites pyramidal, with well developed obplicate and accrescent sides. Plicate side with usually four pronounced radial ridges separated by deep folds. Obplicate side with several faint radial ridges and striation. Accrescent and decrescent sides without radial ridges.

Description.—Sellate sclerites (Figs. 35, 36) are asymmetrical, up to 5 mm long and 3.5 mm wide (after Missarzhevsky in Rozanov and Missarzhevsky 1966) in plan view, with a

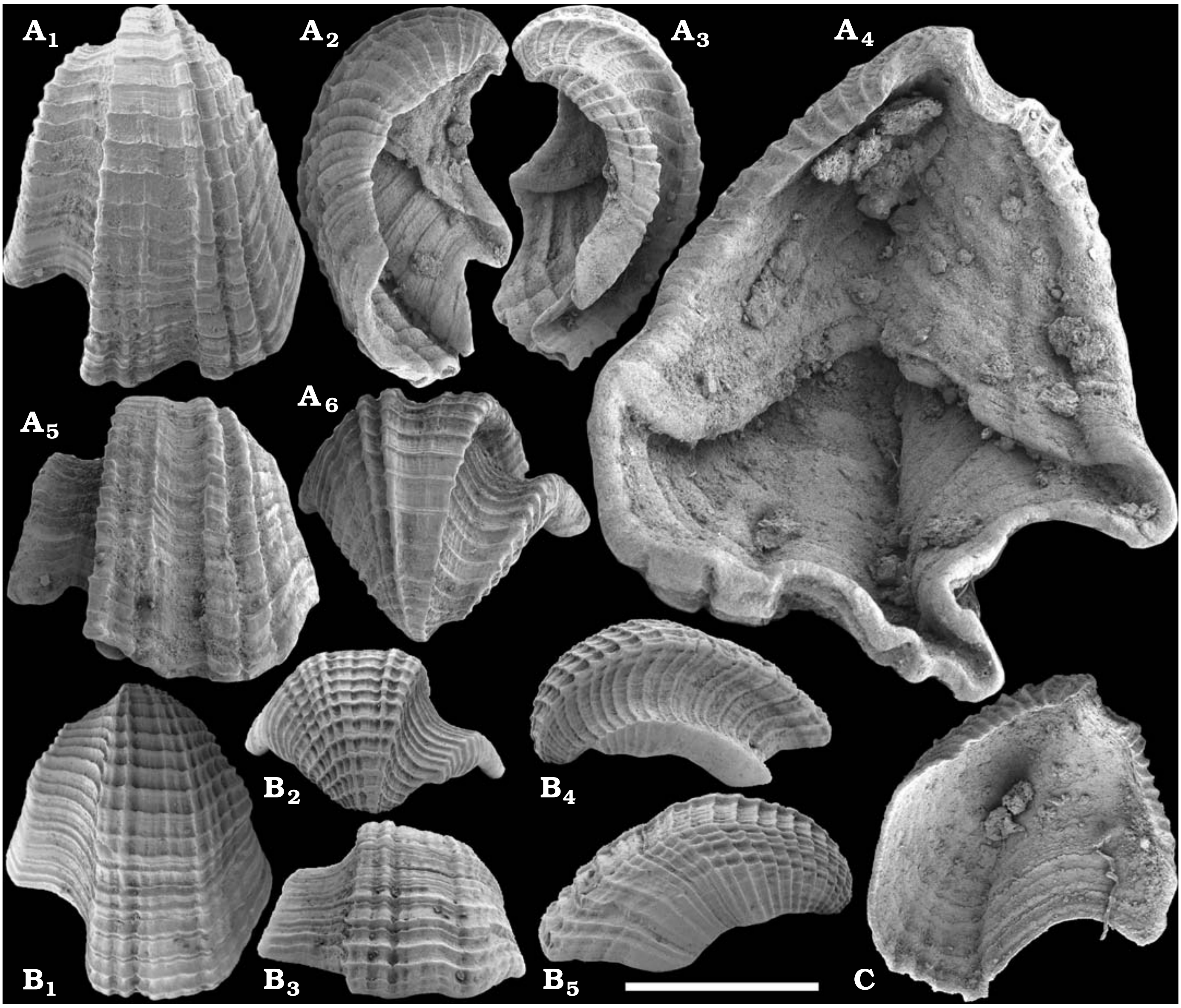

Fig. 35. Tommotiid *Camenella garbowskae* Missarzhevsky in Rozanov and Missarzhevsky, 1966 from lower Cambrian Emyaksin Formation, Bol'shaya Kuonamka River, Anabar Uplift, Siberia; sellate sclerites, L-forms. **A**. SMNH X 4682, sample 6/14; A_1, plan view; A_2, lateral view on the larger lobe; A_3, lateral view on the smaller lobe; A_4, view on the duplicature; A_5, view on the margin of sclerite; A_6, apical view. **B**. SMNH X 4683, sample 6/3.9; plan (B_1), apical (B_2), and marginal (B_3) views; B_4, lateral view on the smaller lobe; B_5, lateral view on the larger lobe. **C**. SMNH X 4684, sample 6/3.9; view on the inner side. Scale bar 1200 µm, except A_4, C, 600 µm.

sella dividing the sclerite into larger and smaller lobes (e.g., Figs. 35A_1, B_1, 36B_1, C_1). The sella occupies 1/4 to 1/2 of the sclerite width. It represents a deep longitudinal depression with each side marked by a ridge. With the apical angle ~30°, the ridges diverge greater in smaller specimens. The ridge situated on the larger lobe may slightly overhang the floor of the sella (e.g., Figs. 35A_6, 36B_3). With respect to the smaller one, the larger lobe is higher, approximately twice as long and more than four times wider. The larger lobe carries several (up to 15 in available specimens) variously expressed radial ridges and striations. The smaller lobe is ornamented with longitudinal striations. Co-marginal folds are usually well expressed on the entire dorsal surface of sclerites. The ventral surface of the sclerite generally reproduces the relief of the dorsal surface, but is only weakly ornamented with smooth longitudinal and co-marginal folds. A duplicature strongly adpressed to the opposing wall occupies apical and lateral parts of larger specimens (Fig. 35A_4). The apex is coiled through less than half a whorl.

Pyramidal mitral sclerites (Figs. 37, 38) represent asymmetrical and slightly helically twisted cones, up to 3 mm long (measured from apex to the apertural margin) and up to 2.5 mm wide (after Missarzhevsky in Rozanov and Missarzhevsky 1966). The aperture is plicated subquadrate (in smaller specimens) or subrectangular in outline (compare e.g., Figs. 37E, 38D with Figs. 37D_1, 38C_1). The apex is slightly curved over the decrescent side of the sclerites (see explanation of morphological terms in comments to Fig.

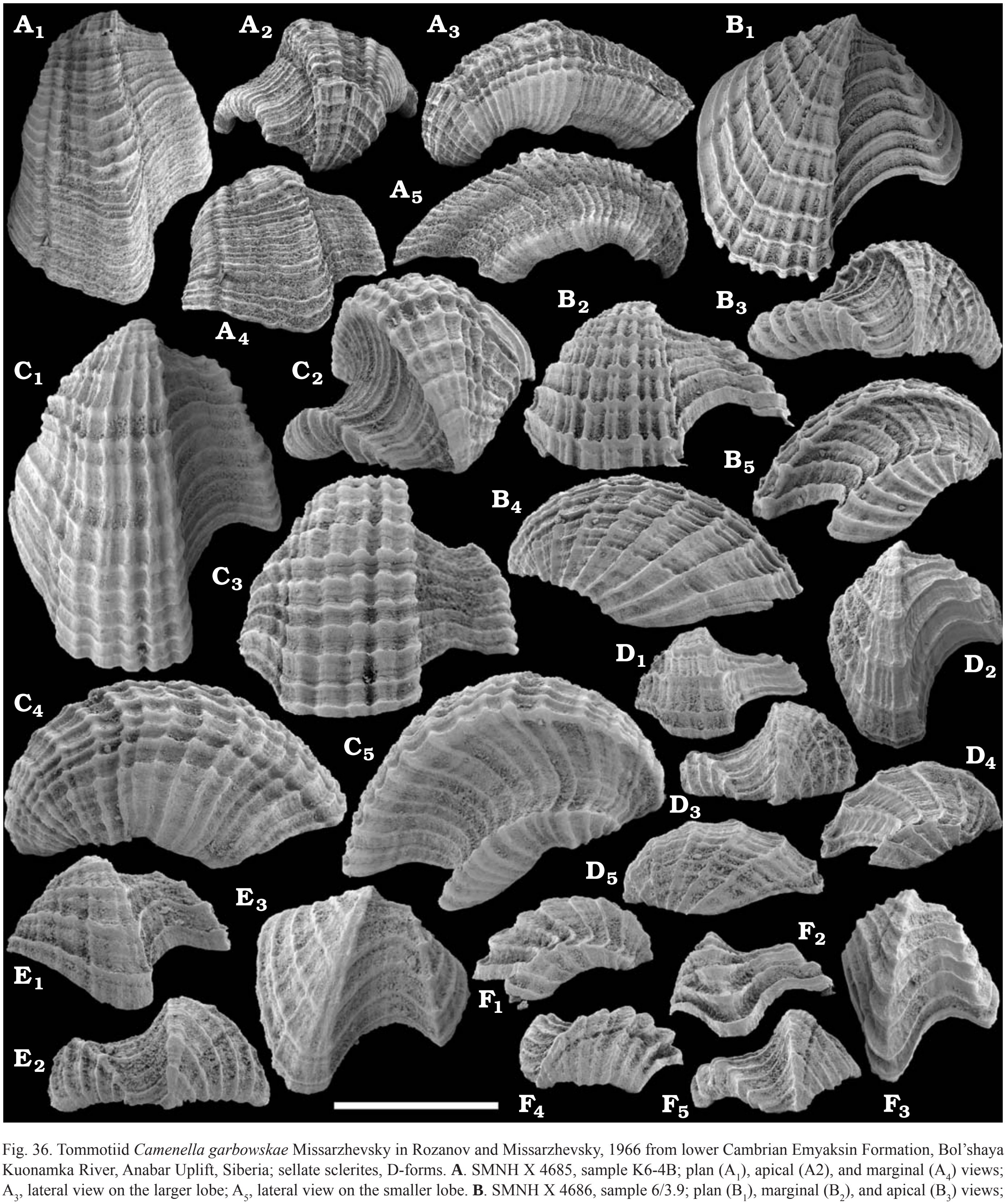

Fig. 36. Tommotiid *Camenella garbowskae* Missarzhevsky in Rozanov and Missarzhevsky, 1966 from lower Cambrian Emyaksin Formation, Bol'shaya Kuonamka River, Anabar Uplift, Siberia; sellate sclerites, D-forms. **A**. SMNH X 4685, sample K6-4B; plan (A_1), apical (A2), and marginal (A_4) views; A_3, lateral view on the larger lobe; A_5, lateral view on the smaller lobe. **B**. SMNH X 4686, sample 6/3.9; plan (B_1), marginal (B_2), and apical (B_3) views; B_4, lateral view on the larger lobe; B_5, lateral view on the smaller lobe. **C**. SMNH X 4687, sample 6/0.3; plan (C_1), apical (C_2), and marginal (C_3) views; C_4, lateral view on the larger lobe; C_5, lateral view on the smaller lobe. **D**. SMNH X 4689, sample 6/1.8; marginal (D_1), plan (D_2), and apical (D_3) views; D_4, lateral view on the smaller lobe; D_5, lateral view on the larger lobe. **E**. SMNH X 4688, sample 6/0.3; marginal (E_1), apical (E_2), and plan (E_3) views. **F**. SMNH X 4690, sample 6/1.8; F_1, lateral view on the smaller lobe; F_4, lateral view on the larger lobe; marginal (F_2), plan (F_3), and apical (F_5) views. Scale bar 600 μm, except A, 1200 μm.

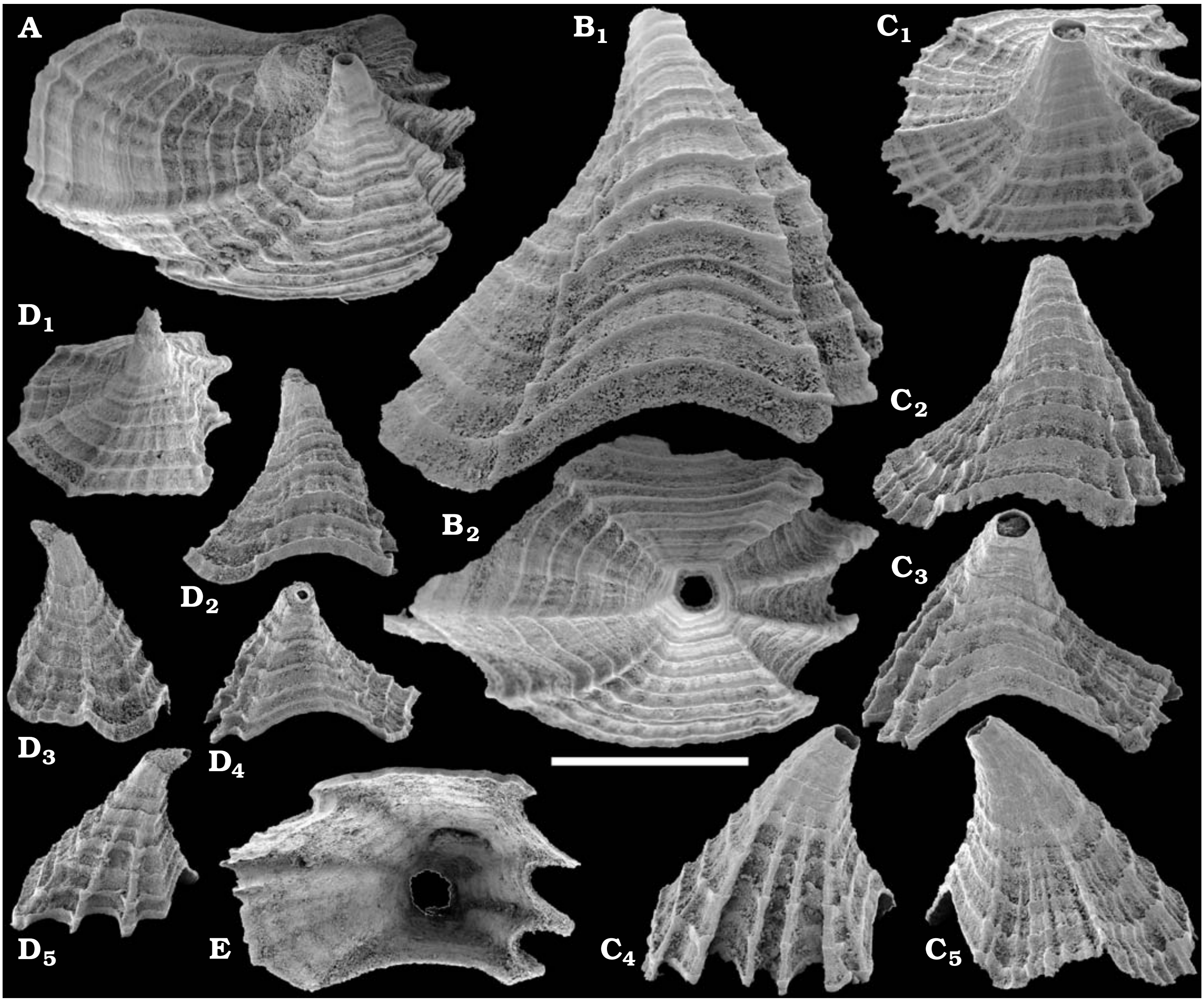

Fig. 37. Tommotiid *Camenella garbowskae* Missarzhevsky in Rozanov and Missarzhevsky, 1966 from lower Cambrian Emyaksin Formation, Bol'shaya Kuonamka River, Anabar Uplift, Siberia; mitral sclerites, L-forms. **A**. SMNH X 4691, sample K6-4B; apical view, with the decrescent, accrescent, plicate, and obplicate sides up, down, right, and left (respectively). **B**. SMNH X 4692, sample 6/0.3; B_1, view on the accrescent side; B_2, apical view. **C**. SMNH X 4693, sample 6/1.8; C_1, apical view; accrescent (C_2), decrescent (C_3), plicate (C_4), and obplicate (C_5) sides views. **D**. SMNH X 4694, sample 6/1.8; D_1, apical view; accrescent (D_2), obplicate (D_3), decrescent (D_4), and plicate (D_5) sides views. **E**. SMNH X 4695; sample 6/3.9; view on the inner surface of sclerite. Scale bar 600 μm.

37A). The plicate and obplicate sides bear several radial ridges, better developed on the plicate side. The ridges increase relief from the apex towards the aperture. The plicate side usually carries four well-defined radial ridges, two of which mark the boundaries with the accrescent and decrescent sides, respectively. The ridges are separated from each other by deep, narrow troughs (e.g., Fig. 37A). By contrast, the accrescent and decrescent sides lack strong radial ridges and are covered with longitudinal striation (Fig. 37A). Continuous co-marginal folds cover the entire surface of sclerite. They curve towards the apex on the accrescent and decrescent sides. The internal surface is covered with smooth radial and co-marginal folds reflecting those on the exterior surface of sclerites (Fig. 37E). The tapering apex is circular in cross-section and exhibit a perforation, 20–100 μm in diameter (e.g., Fig. 37B_2).

Remarks.—*Camenella reticulosa* Conway Morris in Bengtson et al., 1990 is distinguished by very strong co-marginal ribs with superimposed reticulation, strong coiling and wider sella of the sellate sclerites, as well as pronounced radial ribs and intermittent folds on both plicate and obplicate sides of the mitral sclerites. The sellate sclerites in *C. parilobata* differ in having lobes of similar size. The mitral sclerites of *Camenella garbowskae* are distinguished from those of *C. baltica* and *C. parilobata* by more expressed helical twist.

Vladimir V. Missarzhevsky (Rozanov and Missarzhevsky 1966: 96) first noted the similarity between *Camenella gar-*

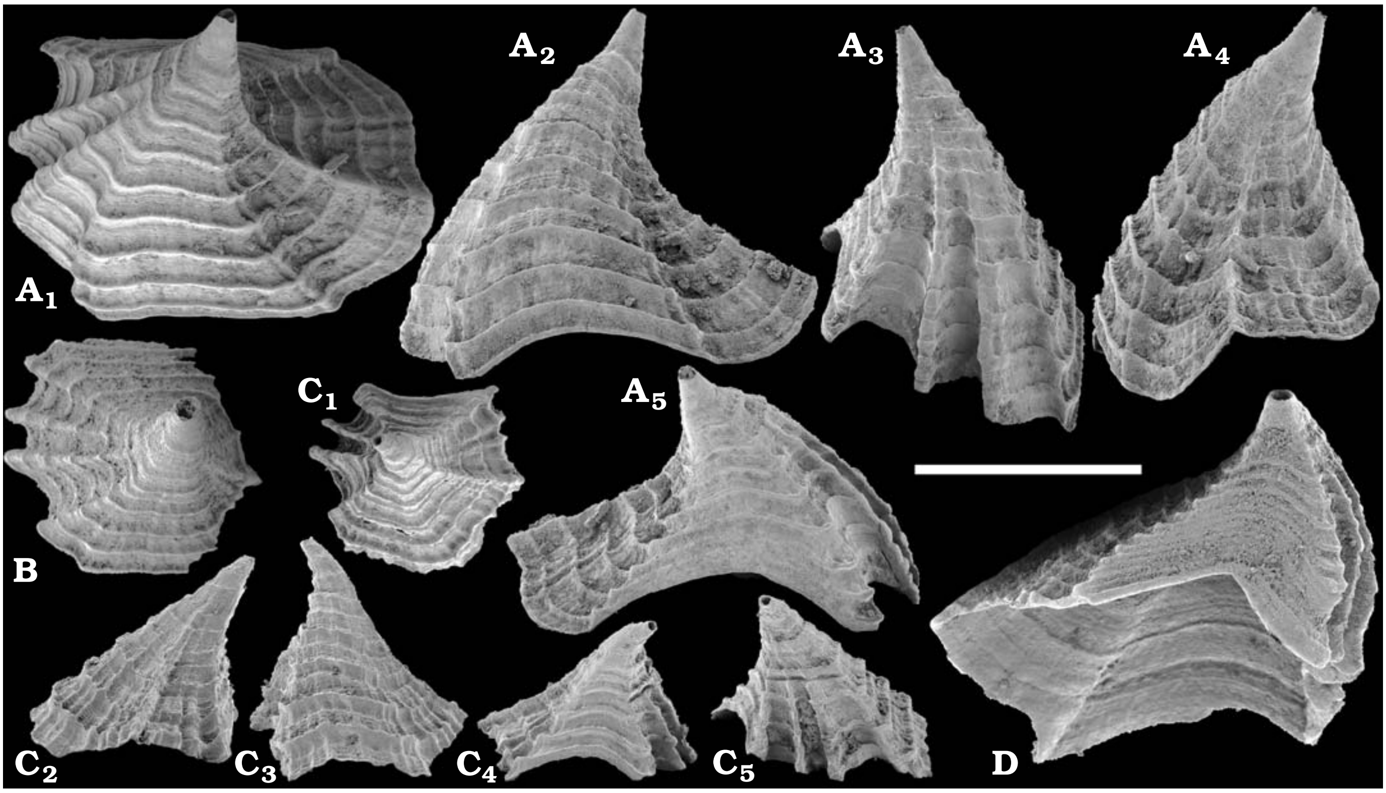

Fig. 38. Tommotiid *Camenella garbowskae* Missarzhevsky in Rozanov and Missarzhevsky, 1966 from lower Cambrian Emyaksin Formation, Bol'shaya Kuonamka River, Anabar Uplift, Siberia; mitral sclerites, D-forms. **A**. SMNH X 4696, sample 6/2; A_1, apical view; accrescent (A_2), plicate (A_3), obplicate (A_4), and decrescent (A_5) sides views. **B**. SMNH X 4697, sample 6/0.3; apical view. **C**. SMNH X 4698, sample K6-4B; C_1, apical view; obplicate (C_2), accrescent (C_3), decrescent (C_4), and plicate (C_5) sides views. **D**. SMNH X 4699, sample K6-4B; view on the aperture and decrescent side. Scale bar 600 μm.

bowskae Missarzhevsky in Rozanov and Missarzhevsky, 1966 and *Camena kozlowskii* Missarzhevsky in Rozanov and Missarzhevsky, 1966 and suggested that they might represent disarticulated skeletal parts of the same organism. Further developments of terminology and taxonomy of tommotiids proposed by Bengtson (1970, 1977, 1986a) are followed here.

Less common, small sellate sclerites (both sinistral and dextral symmetry variants) with a flared margin may well also belong to the *C. garbowskae* scleritome (see *Camenella* cf. *C. garbowskae* in Fig. 39). Rare simplified, laterally compressed mitral sclerites, named "planiform" by Bengtson (1986a) after *Camenella plana* (Missarzhevsky in Rozanov et al., 1969), are described from *Camenella baltica* and *C. parilobata* scleritomes. Several planiform mitrals, attributed herein to *Camenella plana* (see Fig. 40), co-occur with

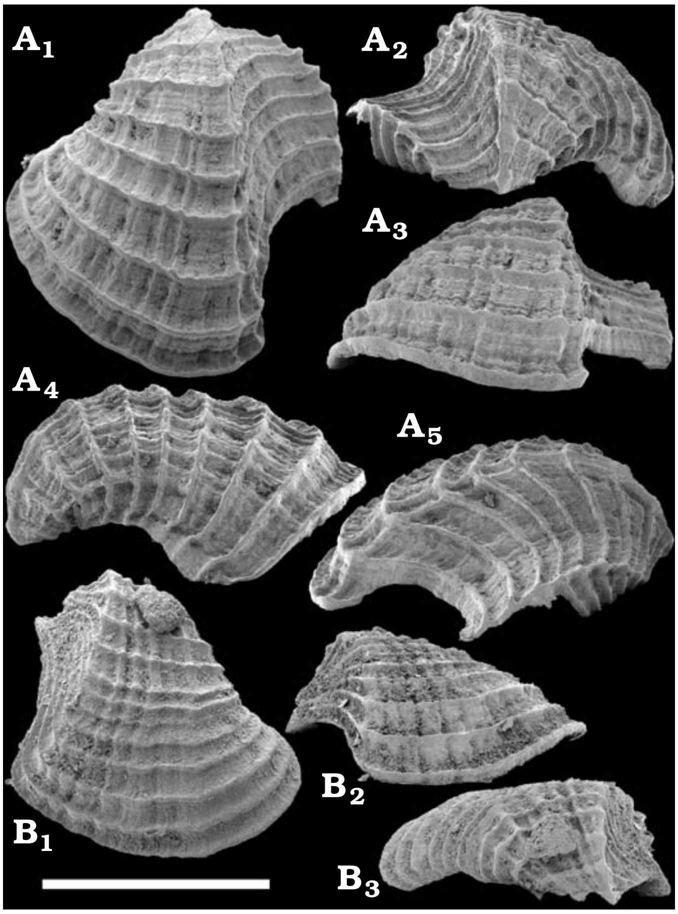

Fig. 39. Tommotiid *Camenella* cf. C. *garbowskae* Missarzhevsky in Rozanov and Missarzhevsky, 1966 from lower Cambrian Emyaksin Formation, Bol'shaya Kuonamka River, Anabar Uplift, Siberia; sellate sclerites. **A**. D-form, SMNH X 4700, sample 6/2; plan (A_1), apical (A_2), and marginal (A_3) views; A_4, lateral view on the larger lobe; A_5, lateral view on the smaller lobe. **B**. L-form, SMNH X 4701, sample 6/3.9; plan (B_1), marginal (B_2), and apical (B_3) views. Scale bar 600 μm.

Fig. 40. Tommotiid *Camenella plana* (Missarzhevsky in Rozanov et al., 1969) from lower Cambrian Emyaksin Formation, Bol'shaya Kuonamka River, Anabar Uplift, Siberia; mitral sclerites. **A**. D-form, SMNH X 4702, sample 6/2; A_1, apical view; A_2, view on the obplicate and decrescent sides; A_3, view on the decrescent and plicate sides. **B**. L-form, SMNH X 4703, sample 6/2; B_1, apical view; B_2, oblique apical view; B_3, view on the obplicate side; B_4, view on the accrescent side. **C**. L-form, SMNH X 4704, sample 6/6.6; C_1, oblique apical view; C_2, accrescent side view; C_3, oblique view on the basal aperture and plicate side; C_4, oblique view on the accrescent and plicate sides. **D**. L-form, SMNH X 4705, sample 6/3.9; D_1, oblique apical view on the accrescent side; D_2, view on the obplicate side; D_3, view on the accrescent side. **E**. D-form, SMNH X 4706, sample 6/6.8; E_1, oblique view on the accrecent and obplicate sides; E_2, oblique view on the obplicate and decrescent sides; E_3, view on the accrescent side; E_4, view on the decrescent side; E_5, oblique apical view; E_6, oblique apical view on the plicate side. Scale bar 600 μm.

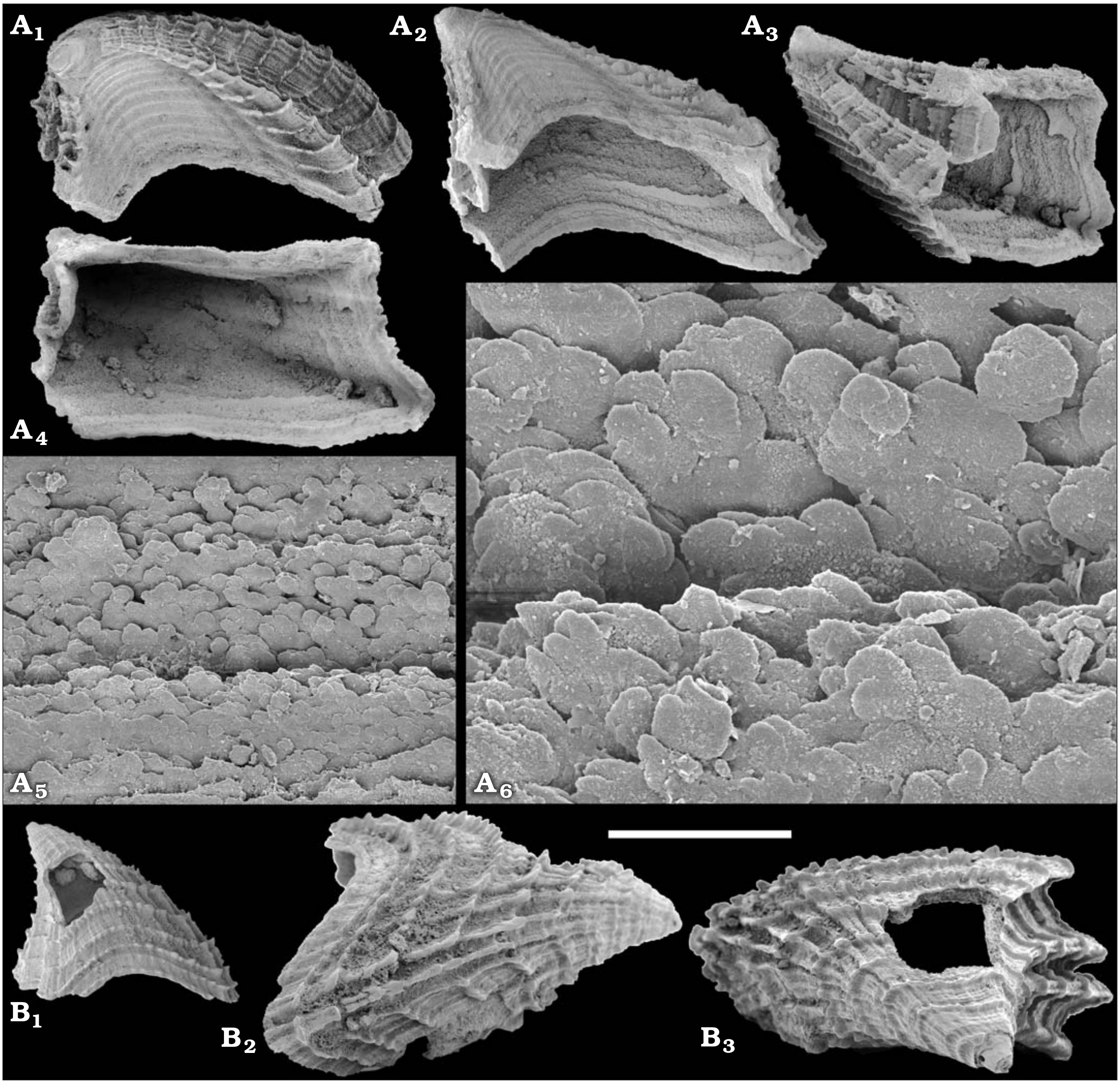

Fig. 41. Tommotiid *Camenella* sp. from lower Cambrian Emyaksin Formation, Bol'shaya Kuonamka River, Anabar Uplift, Siberia; mitral sclerites, sample 6/3.9. **A**. L-form, SMNH X 4707; A_1, oblique apical view; A_2, decrescent side; A_3, plicate side; A_4, aperture; A_5, microstructure of the wall; A_6, close-up of A_5. **B**. D-form, SMNH X 4708; accrescent side (B_1) and apical (B_3) views; B_2, oblique view on the accrescent and obplicate side. Scale bar: A_1–A_4, B_1, 1200 μm; A_5, 120 μm; A_6, 30 μm; B_2, B_3, 600 μm.

more common pyramidal mitral sclerites of *C. garbowskae*. The presence of planiform mitrals in the assemblage supports the suggestion by Bengtson (1986a) that such sclerites may have formed an integral part of the *Camenella* scleritome, but a more abundant collection of sclerites is needed to confirm this. Planiform mitrals occur in both sinistral and dextral symmetry variants. They are strongly flattened in accrescent-decrescent direction and curved with slight to considerable helical twist towards the descrescent side. Their plicate side carries two to three prominent radial ridges and intervening deep folds. *Camenella* cf. *C. plana* is similar to sclerites of *C. garbowskae* in ornamentation. The former, however, are more variable than the pyramidal mitrals of *C. garbowskae* and may include a different species.

The wall of *Camenella* sclerites consists of calcium phosphatic growth laminae. As demonstrated by the inner surface of several well-preserved mitrals of *Camenella* sp. from sample 6/3.9 (Fig. 41), the alternating laminae are composed of more

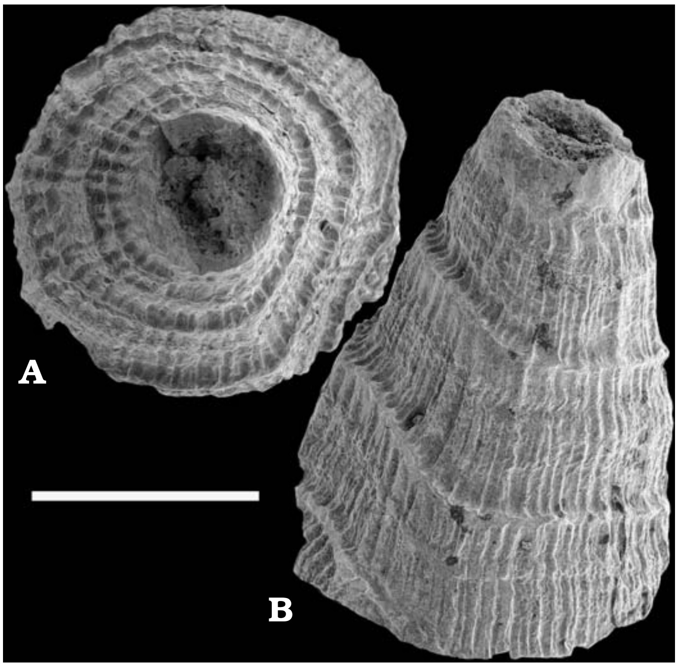

Fig. 42. Tommotiid *Camenella admiranda* (Missarzhevsky in Rozanov and Missarzhevsky, 1966) from lower Cambrian Emyaksin Formation, Bol'shaya Kuonamka River, Anabar Uplift, Siberia; fragment of mitral sclerite, SMNH X 4709, sample K6-5.8B; apical (**A**) and lateral (**B**) views. Scale bar 600 μm.

or less integrated flattened tablet-like aggregates of calcium phosphate. The tablets are not observed in other *Camenella* sclerites available in the collection. The mitrals of *Camenella* sp. are curved and more flattened in accrescent-decrescent direction than pyramidal mitrals of *C. garbowskae*, although less flattened than mitrals of *C. plana*. The ornamentation of the outer surface is also different. Nodes at intersections of radial and co-marginal ridges on all but decrescent sides produce prominent outgrowths in the apical direction. *Camenella* sp. occurs in dextral and sinistral symmetry variants.

Camenella admiranda (Missarzhevsky in Rozanov and Missarzhevsky, 1966) is represented by a single apical fragment of a large mitral sclerite with regularly spaced low radial ridges and distinct comarginal folds (Fig. 42). Sellate sclerites of *C. admiranda* are not known.

Stratigraphic and geographic range.—Tommotian Stage, Siberia.

Camenella aff. *C. garbowskae* Missarzhevsky in Rozanov and Missarzhevsky, 1966

Fig. 43.

Material.—Sellate sclerites: one (dextral), SMNH X 4711, from sample 6/18 and two sclerites (dextral and sinistral), SMNH X 4712 and 4713, from sample 7/16; correlated with the *Dokidocyathus lenaicus* Zone, Tommotian Stage. One (sinistral), SMNH X 4710, from sample 7/31.9; correlated with *Delgadella anabara* Zone, Atdabanian Stage. Emyaksin Formation, Bol'shaya Kuonamka River.

Description.—The sellate sclerites are asymmetrical, up to 2 mm long and 1.6 mm wide in plan view, with a sella dividing the sclerite into larger and smaller lobes. The sella occupies up to 1/3 of the sclerite width between a ridge situated on the larger lobe and a strong angulation of the margin of the smaller lobe. The ridge slightly overhangs the floor of the sella (Fig. $43D_1$). The larger lobe carries five very prominent radial ridges, and the entire dorsal surface of the sclerite is ornamented with distinct comarginal folds. The larger lobe is much higher than the smaller one, longer, and up to 10 times wider in plan view (Fig. $43A_1$, A_2). The apex is coiled through up to 3/4 whorl (Fig. $43C_4$, D_2).

Remarks.—The sclerites differ from *Camenella garbowskae* in having less numerous and stronger radial ribs and intervening deep folds on the larger lobe, and in a more coiled apex.

Camenella reticulosa Conway Morris in Bengtson et al., 1990 is distinguished by a superimposed reticulation of co-marginal ribs, even stronger coiling and wider sella of the sellate sclerites. The sellate sclerites in *C. parilobata* differ in having lateral lobes nearly equal in width. Missarzhevsky (in Rozanov et al. 1969: 169) noted morphological variability of *Camenella* and described forms with prominent acute radial ridges from the lower reaches of Lena River as *C. garbowskae* (Rozanov and Missarzhevsky 1966: pl. 13: 11–12).

Family Lapworthellidae Missarzhevsky in Rozanov and Missarzhevsky, 1966

Genus *Lapworthella* Cobbold, 1921

Type species: Lapworthella nigra Cobbold, 1921; *Callavia* Zone, lower Cambrian; Comley, Shropshire, Britain.

Lapworthella dentata Missarzhevsky in Rozanov et al., 1969

Fig. 44C–H.

Material.—Single sclerites from samples 3/53.5, 3/55.5, 6/41.7 (correlated with the *Delgadella anabara* Zone, Atdabanian Stage), and 1/5 (*Calodiscus*-*Erbiella* Zone, lower Botoman Stage), but more common in samples 7/60, 7/62, and 7/64 (correlated with the upper *Judomia* Zone, upper Atdabanian Stage); SMNH X 4716–4721. Emyaksin Formation, Malaya Kuonamka and Bol'shaya Kuonamka rivers.

Description.—Pyramidal, asymmetrically coiled sclerites (broken off fragments up to 1 mm long, but can be somewhat longer), with oval or subrectangular slightly undulating aperture (up to 1 mm wide), commonly elongated transversely to direction of coiling. Apex represents a simple smooth cone with circular cross-section. Apical angle varies between ca. 15° and 45°. External ornamentation consists of distinct transversal ridges bearing short, apically oriented tubercles (denticles). The density of denticles is 35–40 per mm.

Remarks.—*L. dentata* Missarzhevsky in Rozanov et al., 1969 from Stage 3 of Siberia is most similar to *L. schodackensis* (Lochman, 1956) from Laurentia (Landing, 1984) and *L. cornu* (Wiman, 1903) from Baltica and Avalonia, from Cambrian Series 2, Stage 4. Each of these species is represented by

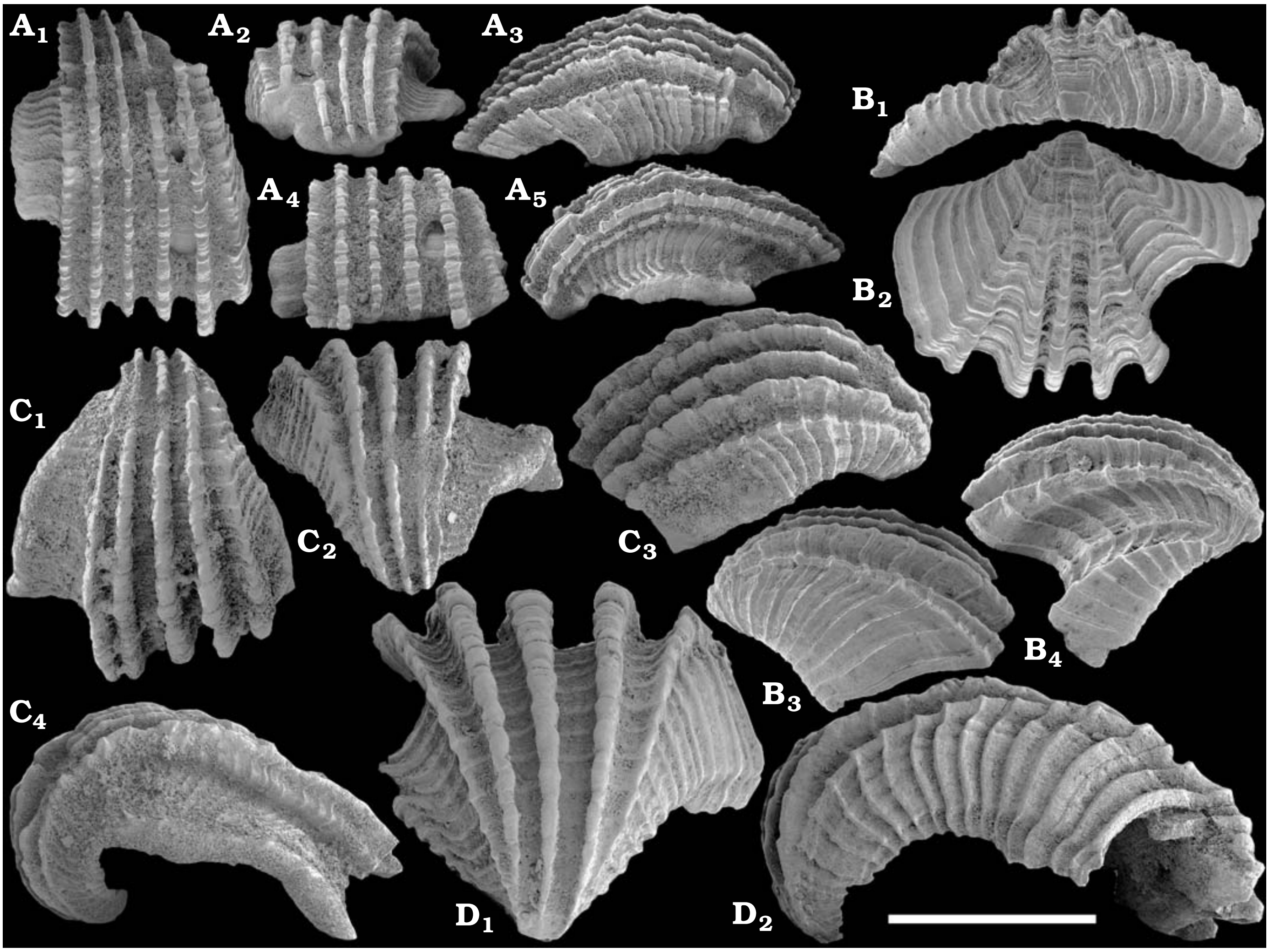

Fig. 43. Tommotiid *Camenella* aff. *C. garbowskae* Missarzhevsky in Rozanov and Missarzhevsky, 1966, sellate sclerites from lower Cambrian Emyaksin Formation, Bol'shaya Kuonamka River, Anabar Uplift, Siberia. **A**. L-form, SMNH X 4710, sample 7/31.9; plan (A_1), apical (A_2), and marginal (A_4) views; A_3, lateral view on the larger lobe; A_5, lateral view on the smaller lobe. **B**. D-form, SMNH X 4711, sample 6/18; apical (B_1) and plan (B_2) views; B_3, lateral view on the larger lobe; B_4, lateral view on the smaller lobe. **C**. L-form, SMNH X 4712, sample 7/16; plan (C_1) and apical (C_2) views; C_3, lateral view on the larger lobe; C_4, lateral view on the smaller lobe. **D**. D-form, SMNH X 4713, sample 7/16; D_1, apical view; D_2, lateral view on the larger lobe. Scale bar: A, C, 1200 μm; B, D, 600 μm.

diverse morphologies with variable apical angle, apertural cross-section (circular to compressed oval or rectangular), axial curvature and spacing of growth ridges (Bengtson 1980; Landing 1984). Missarzhevsky (in Rozanov et al. 1969: 164) indicated denticles as the only difference between *L. dentata* and *L. schodackensis*. The denticles are present, however, in *L. schodackensis* (35–144 per mm, after Landing 1984). Landing (1984) also showed that this feature may be obscured by diagenesis and/or preparation in some specimens. Specimens of *L. cornu* (Wiman, 1903) from Sweden typically carry 10–20 denticles per mm, whereas *L. dentata* has an intermediate number of denticles, 25–45 per mm (Bengtson 1980). Landing (1984) suggested that *L. schodackensis* should be synonymised with *L. dentata* and *L. cornu*. This synonymisation would be acceptable if only the presence or absence of denticles is considered, with *L. cornu* (Wiman 1903) the oldest available name. Otherwise, they are different in the relative density of denticulation. Poorly preserved single specimens of *Lapworthella* cf. *L. tortuosa* Missarzhevsky in Rozanov and Missarzhevsky, 1966 and *Lapworthella* sp. are also available in our material (Fig. 44A, B).

Stratigraphic and geographic range.—Lower Cambrian, Atdabanian and lower Botoman Stages, Siberian Platform.

Problematic cones

Fig. 45.

Material.—Two conical sclerites, SMNH X 4722–4723, from sample 6/3.9. Emyaksin Formation, Bol'shaya Kuonamka; correlated with the lower *Dokidocyathus regularis* Zone, Tommotian Stage.

Description.—Two calcium phosphatic cones are of uncertain affinity. The larger cone (Fig. 45A) has a truncated apex, multilayered wall, smooth eroded external surface and pre-

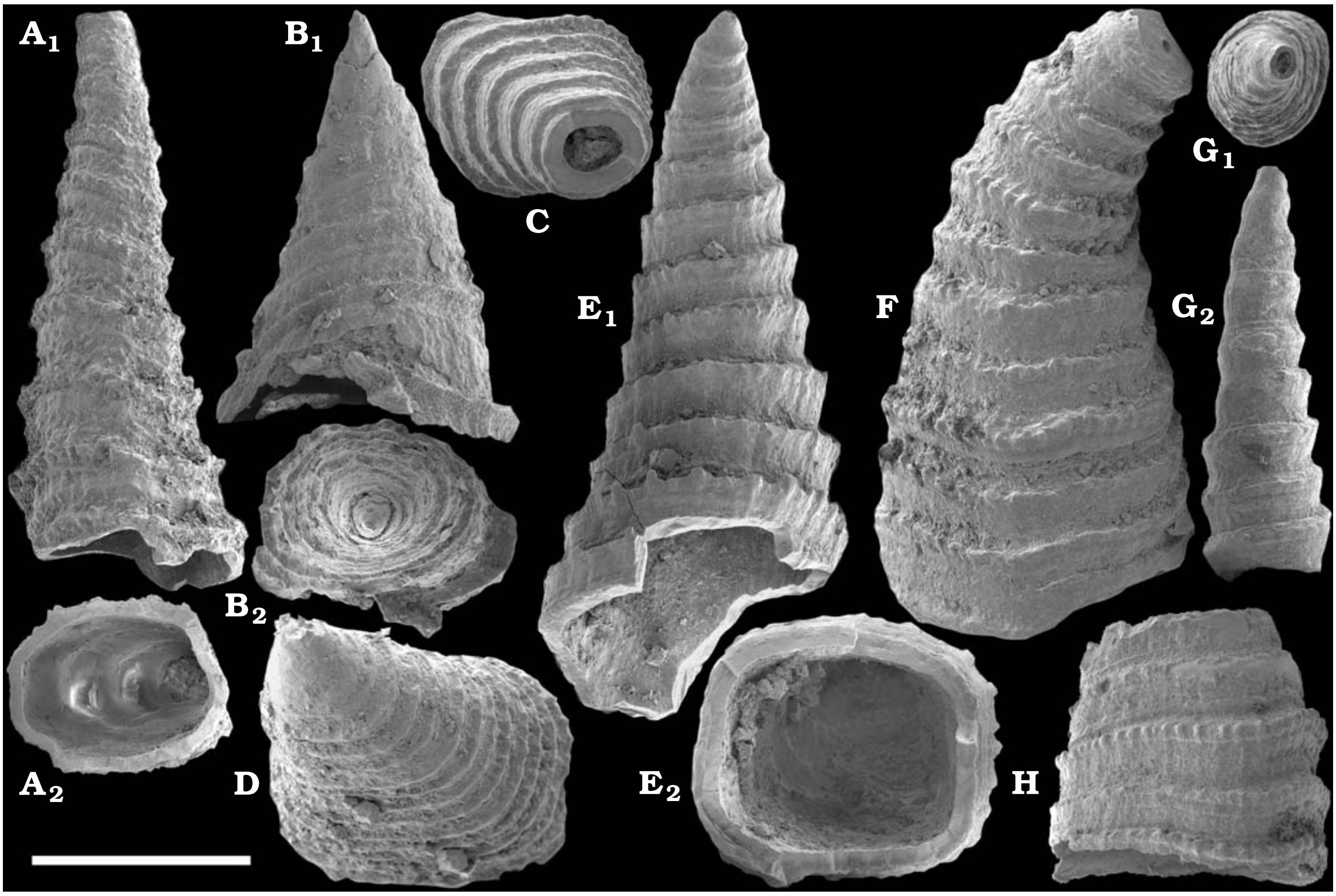

Fig. 44. Tommotiids *Lapworthella* spp. from lower Cambrian Emyaksin Formation, Bol'shaya Kuonamka River and Malaya Kuonamka River, Anabar Uplift, Siberia. **A**. *Lapworthella* cf. *L. tortuosa* Missarzhevsky in Rozanov and Missarzhevsky, 1966, SMNH X 4714, sample K6-8.1B; lateral (A_1) and basal (A_2) views. **B**. *Lapworthella* sp., SMNH X 4715, sample 6/4.9; lateral (B_1) and apical (B_2) views. **C**–**H**. *Lapworthella dentata* Missarzhevsky in Rozanov et al., 1969. **C.** SMNH X 4716, sample 7/60; apical view. **D**. SMNH X 4717, sample 7/60; oblique apical view. **E**. SMNH X 4719, sample 7/62; lateral (E_1) and basal (E_2) views. **F**. SMNH X 4718, sample 7/60; lateral view. **G**. SMNH X 4720, sample 7/64; apical (G_1) and lateral (G_2) views. **H**. SMNH X 4721, sample 1/5; lateral view on the fragment. Scale bar 300 µm, except H, 600 µm.

sumed growth increments preserved inside. In the smaller cone (Fig. 45B), the outer surface has a longitudinal striation that passes into a cancellate and tuberculated ornament at the flared basal part of scerite (Fig. 45B_4).

Phylum, class, order, and family uncertain

Genus *Rhombocorniculum* Walliser, 1958

Type species: Helenia cancellata Cobbold, 1921; *Callavia* Zone, lower Cambrian; Comley, Shropshire, Britain.

Emended diagnosis.—Calcium phosphatic elongated sclerites with a cancellate external ornament, thick wall and a central lumen. The wall is composed of thin parallel hollow tubules arranged obliquely to the surface.

Remarks.—Two species are recognised here, *R. cancellatum* (Cobbold, 1921) and *R. insolutum* Missarzhevsky in Missarzhevsky and Mambetov, 1981. Other described species of *Rhombocorniculum* are synonymised herein with *R. cancellatum*, following the synonymy list in Esakova and Zhegallo (1996: 102), because they fall within the range of variation for the latter species. For that reason, morphological distinction of *R. ungulatum* Missarzhevsky (1989: 214, pl. 25: 11), originally described as *R. cancellatum* by Missarzhevsky (1977: pl. 1: 3–6; see also remarks discussing variability on p. 13 therein), is considered not sufficient to recognise a separate species (but see Esakova and Zhegallo 1996: 103).

Rhombocorniculum is similar in external ornamentation to some bradoriid spines from the same beds as the type material and described under the name *Rushtonites* Hinz, 1987, which is probably a junior synonym of *Mongolitubulus* Missarzhevsky, 1977 (Skovsted and Peel 2001; Topper et al. 2007; see also description of *Mongolitubulus* spines below).

Rhombocorniculum cancellatum (Cobbold, 1921)

Figs. 46–48.

Material.—About two hundred sclerites are available from the Emyaksin Formation of the Malaya Kuonamka and Bol'shaya Kuonamka rivers; correlated with the *Judomia* Zone, Atdabanian Stage. Several tens of sclerites from sample 3/62.5 and a single one from sample 3/65; over twenty five sclerites,

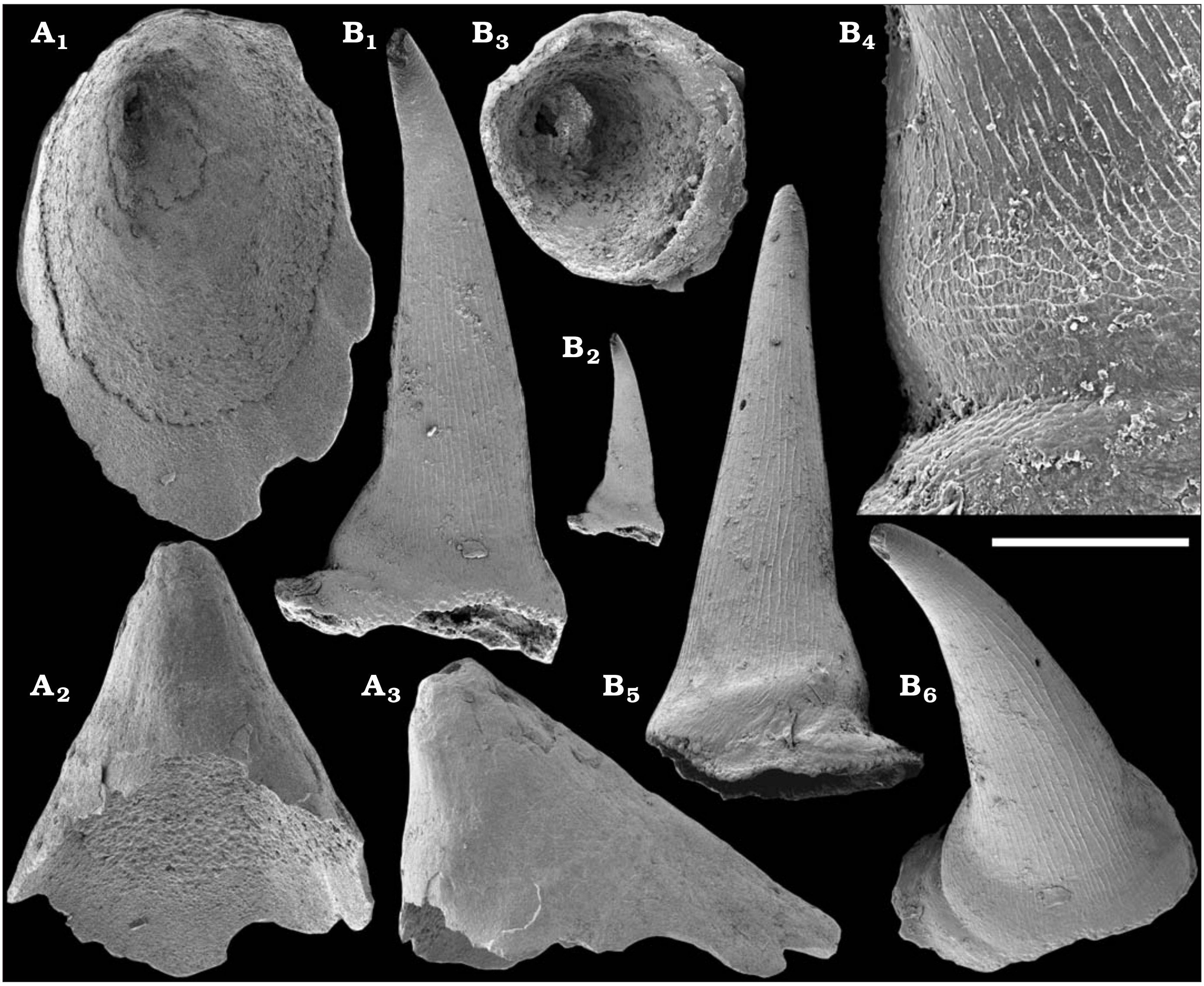

Fig. 45. Problematic cones from lower Cambrian Emyaksin Formation, Bol'shaya Kuonamka River, Anabar Uplift, Siberia; sample 6/3.9. **A**. SMNH X 4722; A_1, view on the inner surface; A_2 and A_3, lateral views. **B**. SMNH X 4723; B_1, B_2, B_5, and B_6, lateral views; B_3, view on the inner surface; B_4, close-up of B_1 showing ornamentation. Scale bar: A, B_2, 600 µm; B_1, B_3, B_5, B_6, 200 µm; B_4, 60 µm.

including six figured specimens SMNH X 4742–4747 from sample 6/66.2; eighteen sclerites, including SMNH X 4748–4753, from sample 7/55, twelve sclerites, including SMNH X 4754 and 4755, from sample 7/55.8, twenty sclerites, including SMNH X 4756–4760, from sample 7/60, ten sclerites, including SMNH X 4761 and 4762, from sample 7/62.

Description.—Sclerites demonstrate a range of variation between slender narrow and broad flattened ones, commonly associated with transitional forms (as in the type strata; see Hinz 1987).

The slender sclerites are elongated and narrow (up to 1.5 mm long and 0.2 mm wide). They can be curved up to 90° and twisted up to 90° clock- or anticlockwise (R-, dextral, and L-, sinistral, forms, respectively). One of the lateral margins of the sclerites is thicker than the other one, which can be blade-like, thus producing an asymmetric drop-like cross-section which is better expressed in the basal part of the sclerites.The sclerite tip is straight and acute. A central simple lumen produces a relatively narrow rounded or oval opening at the basal end of the sclerite. The proximal part,

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Fig. 46. Problematicum *Rhombocorniculum cancellatum* (Cobbold, 1921) from lower Cambrian Emyaksin Formation, Bol'shaya Kuonamka River, Anabar Uplift, Siberia; sample 6/66.2. **A**, **E**, **F**. Slender sclerites. **A**. SMNH X 4742; A_1, close-up of the proximal end of A_2. **E**. SMNH X 4743; lateral view. **F**. SMNH X 4744; F_1 and F_2, lateral views. **D**. Sclerite of a transitional morphology, SMNH 4745; D_1 and D_2, lateral views; D_3, proximal end of sclerite; D_4, D_5, close-up showing longitudinal striation on the external surface of sclerite. **B**, **C**. Broad sclerites. **B**. SMNH X 4746; B_1, close-up of the proximal end with openings of tubules of B_2. **C**. SMNH X 4747; C_2, proximal end with central lumen of specimen in C_1. Scale bar 300 µm, except A_1, 60 µm; B_1, 15 µm; C_2, 120 µm; D_3, D_4, 30 µm; D_5, 3 µm.

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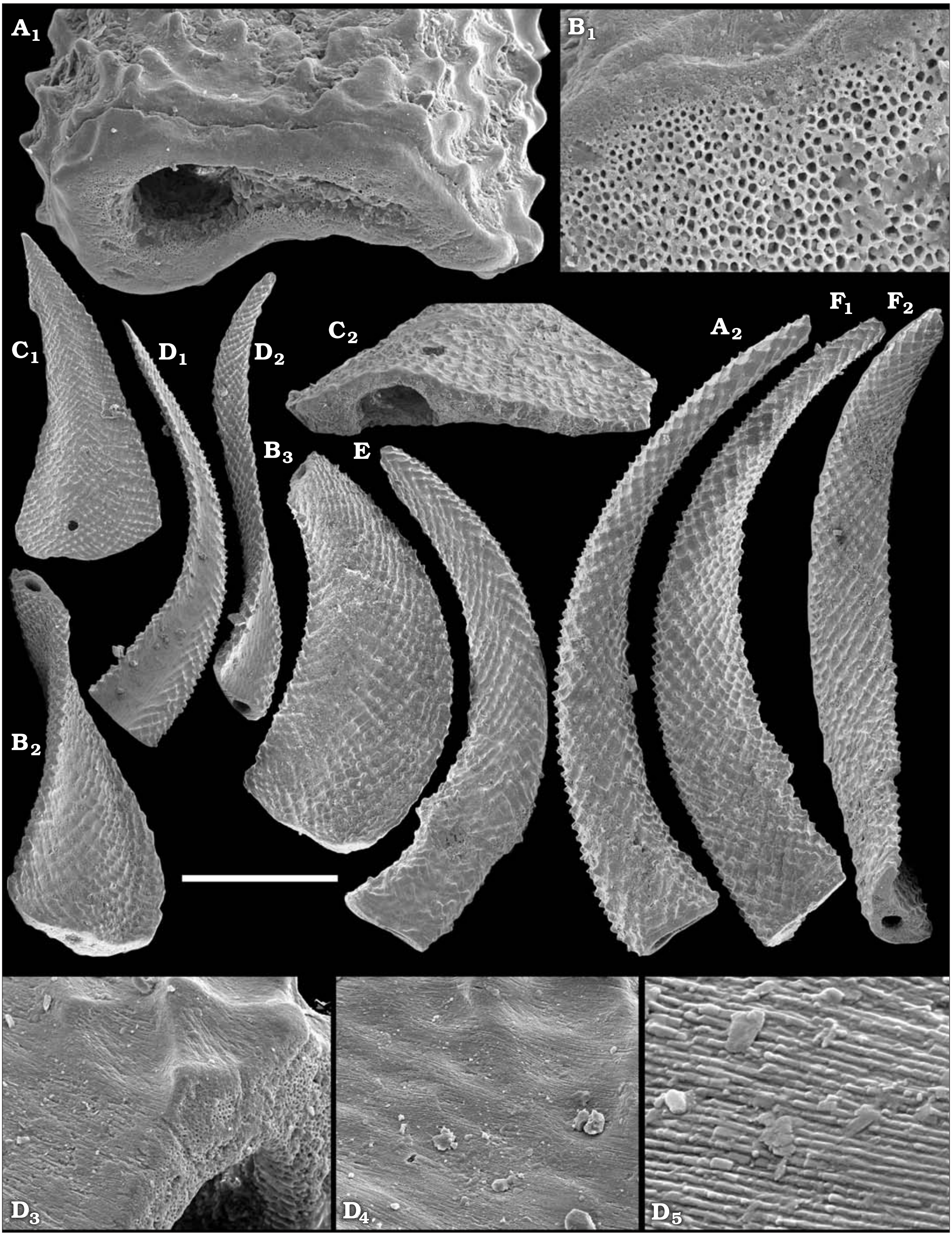

A_1
B_1
C_1
D_1
D_2
C_2
A_2
F_1
F_2
B_3
E
B_2
D_3
D_4
D_5

Fig. 47. Problematicum *Rhombocorniculum cancellatum* (Cobbold, 1921) from lower Cambrian Emyaksin Formation, Bol'shaya Kuonamka River, Anabar Uplift, Siberia. **A**, **C**, **F**. Slender sclerites, sample 7/55. **A**. SMNH X 4748; A_2, proximal end of sclerite in A_1. **C**. SMNH X 4749; C_2, proximal end of sclerite in C_1. **F**. SMNH X 4750; lateral view. **B**, **D**, **E**. Sclerites of transitional morphology, sample 7/55. **B**. SMNH X 4751; B_2, proximal end of sclerite in B_1. **D**. SMNH X 4752; lateral view. **E**. SMNH X 4753; lateral view. **G**, **H**. Sclerites, sample 7/55.8. **G**. Broad sclerite, SMNH X 4754; G_1, view on the broader side; G_2, lateral view. **H**. Basal part of sclerite, SMNH X 4755. Scale bar: 300 µm, except A_2, B_1, C_2, 60 µm; H, 120 µm.

usually somewhat narrowing towards its base, can bear one or several stacked rounded structures (Fig. 48A), similar to growth increments. These rounded structures can either be smooth or carry a smoothened sculpture. The exterior surface of the sclerite is covered with a cancellate sculpture, similar to that described for *R. insolutum* (see above). In many cases, however, the tubercles are nearly perpendicular to the wall (Figs. 46A_1, A_2, 47A_2, C_2, H). The lumen is surrounded by relatively thick walls. The wall contributes to at least half of the sclerite width between the broader sides and significantly

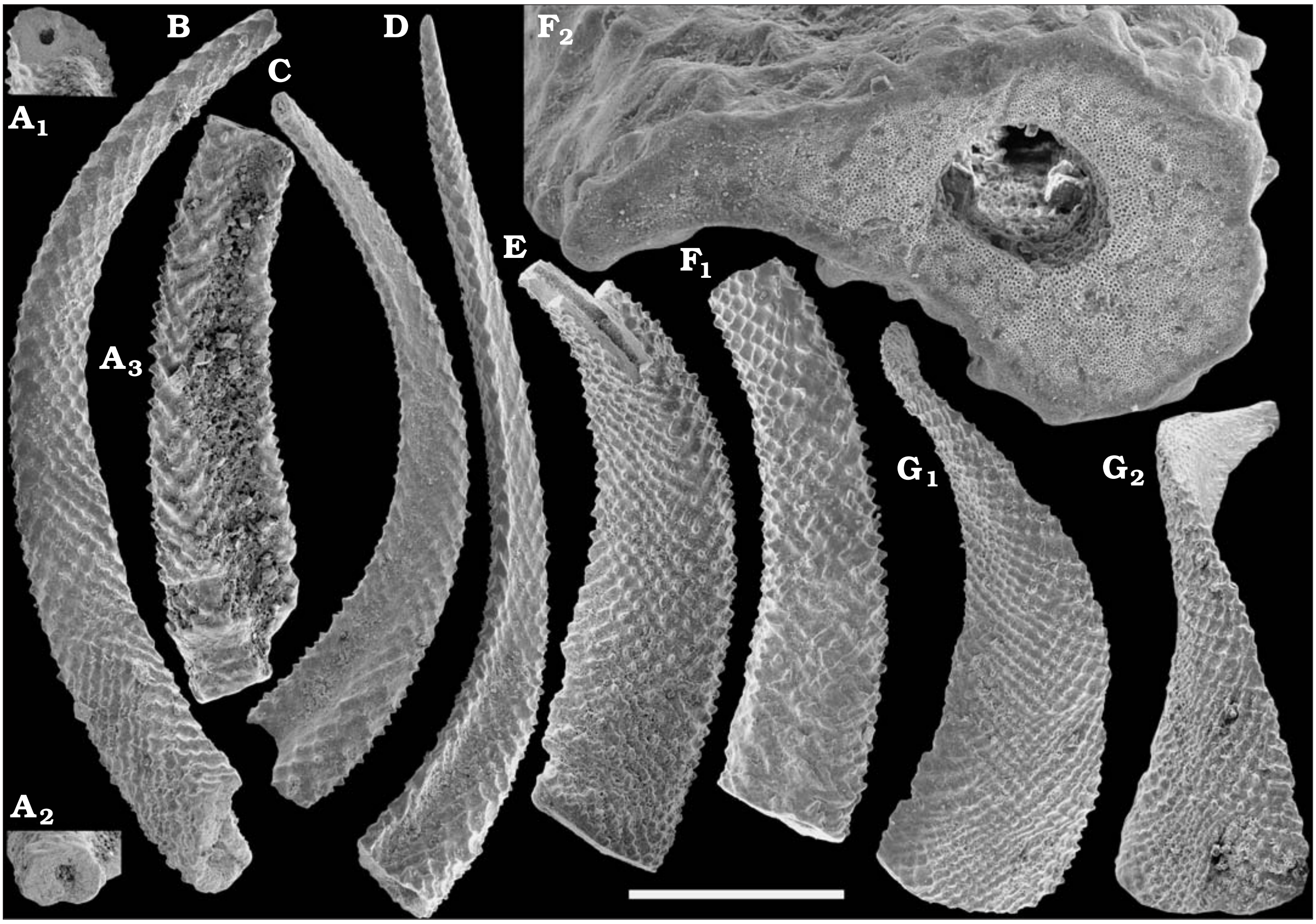


Fig. 48. Problematicum *Rhombocorniculum cancellatum* (Cobbold, 1921) from lower Cambrian Emyaksin Formation, Bol'shaya Kuonamka River, Anabar Uplift, Siberia. **A**–**C**, **E**, **F**. Slender sclerites, sample 7/60. **A**. SMNH X 4756; A$_1$, distal end of sclerite; A$_2$, proximal end of sclerite; A$_3$, lateral view. **B**. SMNH X 4757; lateral view. **C**. SMNH X 4758; lateral view. **E**. SMNH X 4759; lateral view. **F**. SMNH X 4760; F$_1$, lateral view; F$_2$, close-up of basal end showing microstructure. **D**, **G**. Sclerites, sample 7/62. **D**. Slender sclerite, SMNH X 4761; lateral view. **G**. Broad sclerite, SMNH X 4762; G$_1$ and G$_2$, lateral views. Scale bar 300 μm, except F$_2$, 60 μm.

more laterally (Figs. 47B$_1$, C$_2$, 48F$_2$). Similarly to *R. insolutum* (see above), the wall is composed of narrow tubules, 0.1–0.2 μm in diameter (Figs. 46B$_1$, D$_3$–D$_5$, 47B$_1$, C$_2$, 48F$_2$).

The broader sclerites are found in association with the slender ones, but are relatively less common. The broader sclerites share the same general morphology, being flattened, curved up to 90°, and twisted longitudinally up to one revolution, with L- and R-forms also recognised among them (Hinz 1987; Li et al. 2003). The sclerites are narrower and blade-like towards one of the lateral sides. One of the broad sides is slightly concave, whereas the opposite one is convex (e.g., Fig. 47B$_1$). The sculpture is similar to the one described above for slender sclerites. The sclerites have a tapering apical tip and extended basal end with an asymmetrically placed rounded opening of the central lumen. The wall contains tubules, whereas the outer surface exhibits fine longitudinal striation, just as in the slender forms. For comparisons see remarks to *R. insolutum* below.

Stratigraphic and geographic range.—Distributed worldwide in the Cambrian Stage 3, upper Atdabanian–lower Botoman equivalent strata. In the material from the Malaya and Bol'shaya Kuonamka rivers, *R. cancellatum* occurs within the *Judomia* Zone of the Atdabanian Stage. *R. cancellatum* occur in Series 2 of Kazakhstan (Missarzhevsky and Mambetov 1981), South and North China (Li et al. 2003; Steiner et al. 2007), Australia (Gravestock et al. 2001), Avalonia (Landing et al. 1980; Hinz 1987), and the Mediterranean region (Elicki 2005, 2007).

Rhombocorniculum insolutum Missarzhevsky in Missarzhevsky and Mambetov, 1981

Figs. 49–52.

Type material: Holotype: GIN 4296/31 from sample 897/1 (Fig. 49D); paratypes: SMNH X 4724–4726 from sample 897/3 (Fig. 49A–C).

Type locality: Right bank of the Yudoma River, upstream of the mouth of Tyallaakh Rivulet, southeastern Siberian Platform

Type horizon: Exposed top of the Pestrotsvet Formation, early Atdabanian age.

Material.—Among 62 sclerites available from the Emyaksin Formation of Malaya Kuonamka and Bol'shaya Kuonamka, only three (ca. 5%) are clearly originally leaf-like, broad morphotypes, although another two to three appear transitional in morphology (see below). The following specimens from the Anabar Uplift are described in stratigraphically ascending order.

Four slender morphotypes, including two proximally compressed (probably diagenetically) sclerites SMNH X 4728–4730 (Fig. 50B–D) and a bifurcated apical part of another relatively broader sclerite or a twinned sclerite SMNH X 4727 (Fig. 50A) from sample 7/19; one fragment of a slender sclerite from sample 3/27.5; both samples from the same level correlated herein with the upper *Dokidocyathus lenaicus* Zone, upper Tommotian Stage.

One slender morphotype from sample 3/34 and one from sample 7/25.5; one broad sclerite SMNH X 4740 (Fig. 51I), four slender ones SMNH X 4731–4734 (Fig. 51A–D) and six additional slender morphotypes from sample 7/25.6; six slender sclerites from sample K7/22.6B; the samples derive from beds correlated with the *Profallotaspis jakutensis* Zone, lowermost Atdabanian Stage.

Three slender sclerites SMNH X 4735–4737 (Fig. 51F, G_1, H_1), one broad sclerite SMNH X 4738 (Fig. 51J) and one sclerite of transitional morphology SMNH X 4739 (Fig. 51E), as well as sixteen other slender sclerites from sample 7/27.5; seven slender sclerites from sample 7/28.5 and two from sample 7/29; the three samples derive from strata ranging through the *Repinaella* Zone, Atdabanian Stage.

Fifteen slender morphotypes from sample 3/40, one figured broad sclerite SMNH X 4741 (Fig. 52) and one slender from sample 3/42, five slender sclerites from sample 6/39.1; correlated with the lower *Delgadella anabara* Zone, Atdabanian Stage.

Additionally, the holotype from sample 897/3 (Fig. 49D) and three slender sclerites SMNH X 4724–4726 from sample 897/1 (Fig. 49A–C) collected by Stanislav N. Serebryakov and Mikhail A. Semikhatov and included among paratypes by Vladimir V. Missarzhevsky (in Missarzhevsky and Mambetov 1981: 69) are figured herein for comparison. They derive from the exposed top of the Pestrotsvet Formation, cropping out at the right bank of the Yudoma River, upstream of the mouth of Tyallaakh Rivulet, southeastern Siberian Platform, and like the holotype have reportedly an early Atdabanian age.

Description.—Two morphotypes of calcium phosphatic sclerites are herein included within the species, slender stick-like and broad leaf-like ones.

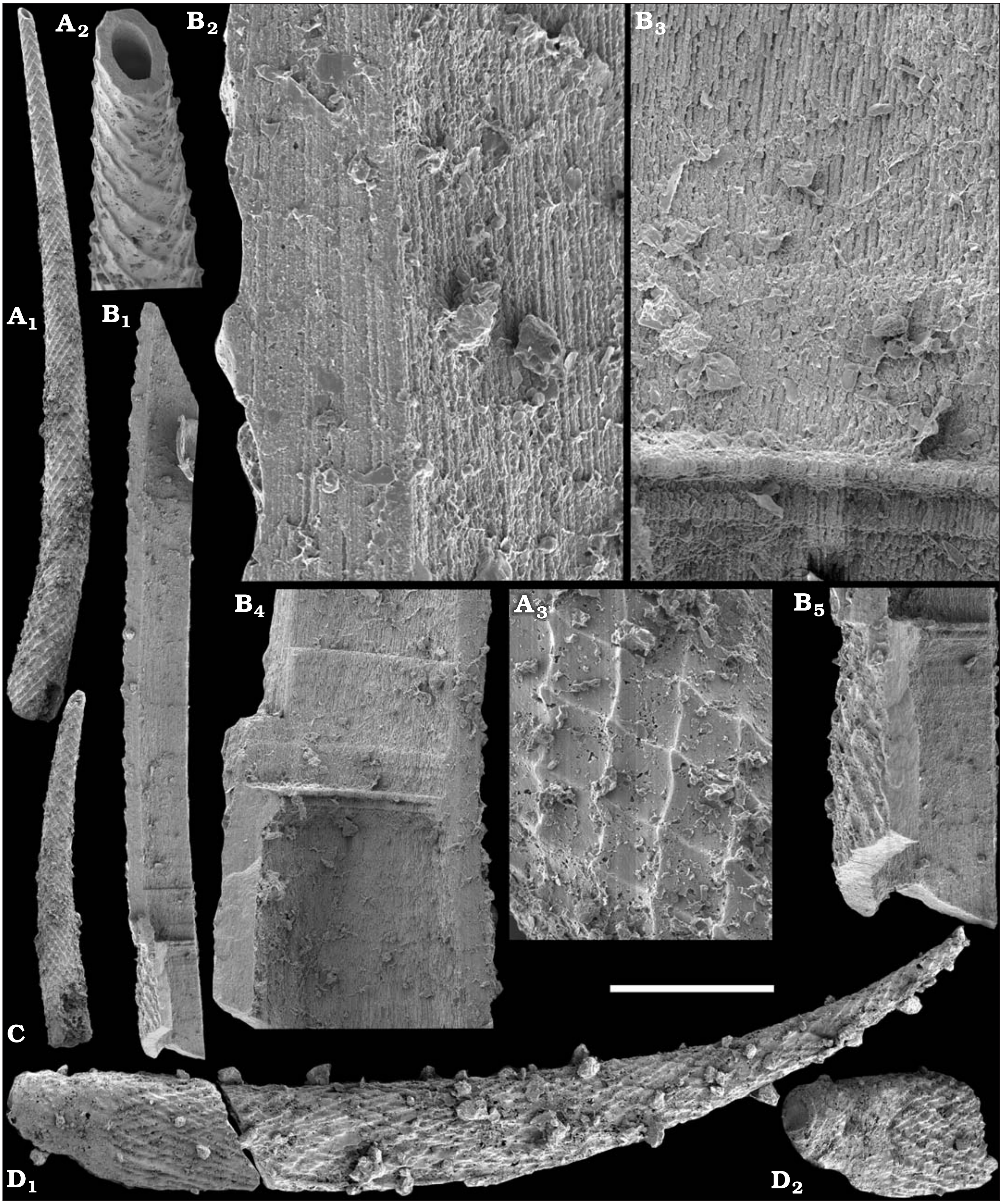
The slender morphotype (representing the type material) comprises elongated narrow (up to 2.5 mm long and 0.2 mm wide) conical sclerites. They are gently curved in one plane, rounded, nearly oval in cross section. The tip of the sclerite is straight and acute. The proximal part usually narrows somewhat towards the base and can bear several circular terraces or a few circular narrow and shallow depressions (clitella). These circular structures usually carry a more smooth sculpture, compared to the ornamentation of the other exterior surface of the sclerite covered with a cancellate sculpture. The sculpture is formed of tessellated tubercles oriented obliquely to the surface towards the apex while rows of tubercles form a rhombic pattern oblique to the longitudinal axis. The sclerites have a central simple longitudinally oriented lumen rounded or oval in cross-section, often open at the proximal end of sclerite. The lumen is surrounded by relatively thick walls. The wall contributes to at least one quarter of the sclerite width. The proximal end of the sclerites can be closed, with no lumen visible. Although some diagenetic compression of the sclerites is possible, the forms with an extended oval cross-section are interpreted herein as transitional in morphology between the broad and typical slender morphotypes (Fig. 51E). The distinction is not that clear, however, and therefore these transitional forms are generally attributed to the slender morphotype.

The broad sclerites associated with the slender ones are rare, and so are forms of transitional morphology, more closely resembling the slender sclerites (see the foregoing section Material). The broad sclerites share the same general morphology, being flattened, not twisted longitudinally, but the apical part is shifted (to the right in the specimens available), having concave and convex opposite broad sides. The sclerites have an apical tip and extended lenticular basal end. The margin of the lumen is not well preserved at the basal part but is probably elongated towards the lateral sides of the sclerite (Fig. $51I_2$, 52C). The sculpture is very similar to what is usually observed on the surface of the slender sclerites. The wall contains tubules, whereas the outer surface exhibits fine longitudinal striation, same as in slender forms (Fig. 52E, F). One sclerite, probably of the broad morphotype, shows bifurcation of its apical part (Fig. 50A). The sclerite is unusual among those attributed to *R. insolutum* and interpreted as aberrant. Other specimens available from that sample (Fig. 50B–D) are similar to slender forms, but proximally compressed.

The wall of all sclerites is essentially composed of narrow tubules, 0.1–0.2 μm in diameter (Figs. 52D, 51G, H). The tubules run parallel to each other and the surface of the wall but tend to dip slightly towards the apex of the sclerite (Fig. $49B_2$). The tubules situated near the outer surface apparently have a smaller diameter. The outer surface of the wall exhibits a fine longitudinal striation. Individual striae, ca. 0.1 μm in diameter (Fig. $51G_3$), represent the outermost casts of tubules. They follow the wall surface, run parallel to each other and do not appear to bifurcate or anastomose.

Remarks.—The type material described by Missarzhevsky and Mambetov (1981) includes only slender sclerites (see Fig. 49), but those co-occur with broad forms in the Kuonamka collection. Since broad morphotypes and transitional forms are also known from *R. cancellatum* (see above), we conclude that, by analogy with the latter, the broad sclerites described herein can be attributed to *R. insolutum*. In contrast, broad sclerites of *R. cancellatum* are longitudinally twisted. The slender sclerites

Fig. 49. Problematicum *Rhombocorniculum insolutum* Missarzhevsky in Missarzhevsky and Mambetov, 1981 from lower Cambrian Pestrotsvet Formation, Yudoma River, Siberia. **A**–**C**. Paratypes, sample 897/3. **A**. SMNH X 4724; A_1, general view; A_2, view on the brocken off tip; A_3, close-up of ornamentation. **B**. SMNH X 4725; B_1, fragmentary sclerite; B_2, close-up →



showing fibrous composition of the wall; B_3, close-up of B_4; B_4, surface of the lumen of sclerite with fragments of transversal ridges, probably representing growth stages; B_5, view showing ornamentation of the outer and inner surfaces of the wall. **C**. SMNH X 4726; lateral view. **D**. Holotype, GIN 4296/31, sample 897/1; D_1, overall view of the broken specimen; D_2, view on the basal part of sclerite with a rounded attachment structure. Scale bar: A_1, B_1, C, D, 300 µm; A_2, B_4, B_5, 120 µm, A_3, 60 µm, B_2, B_3, 30 µm.

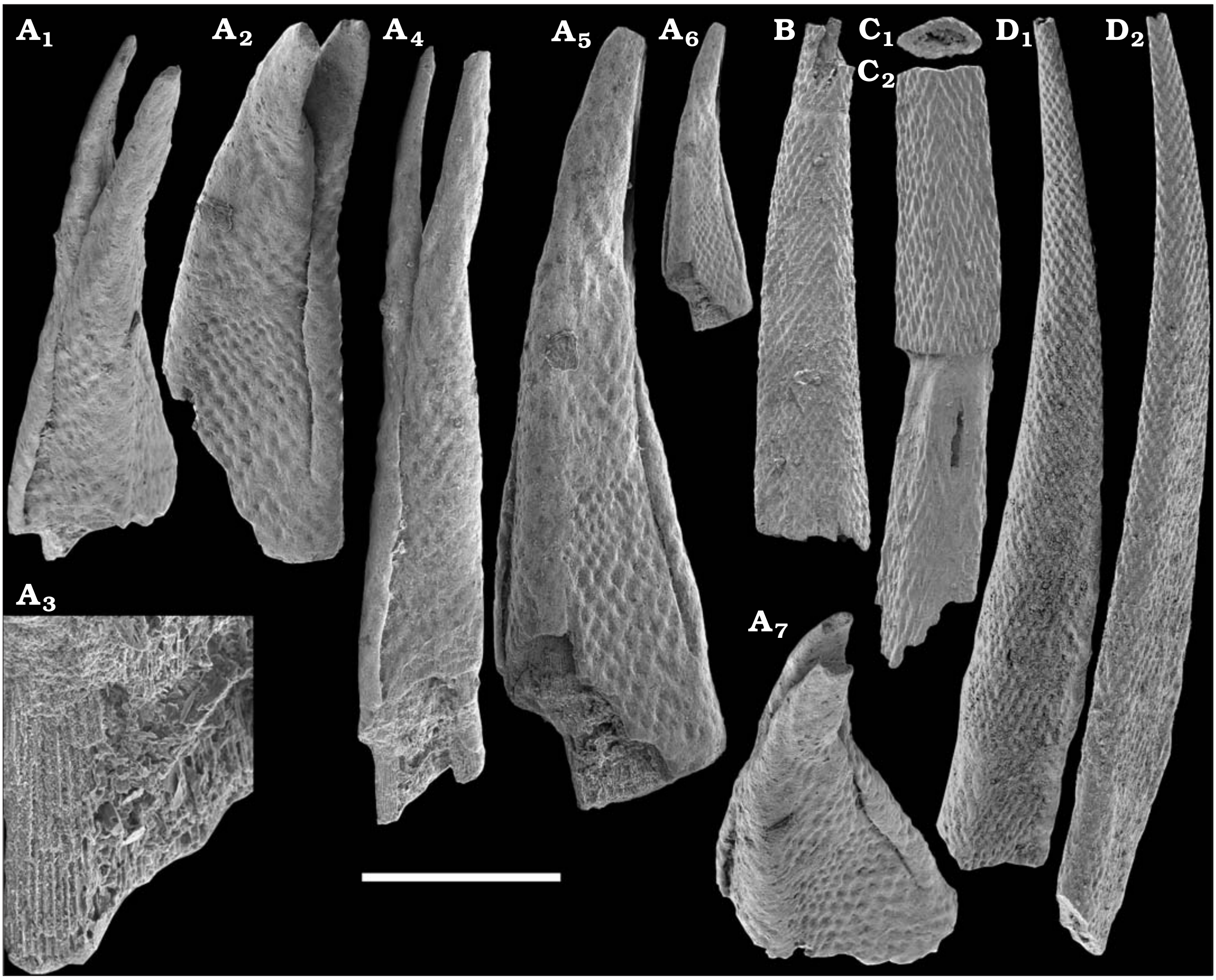
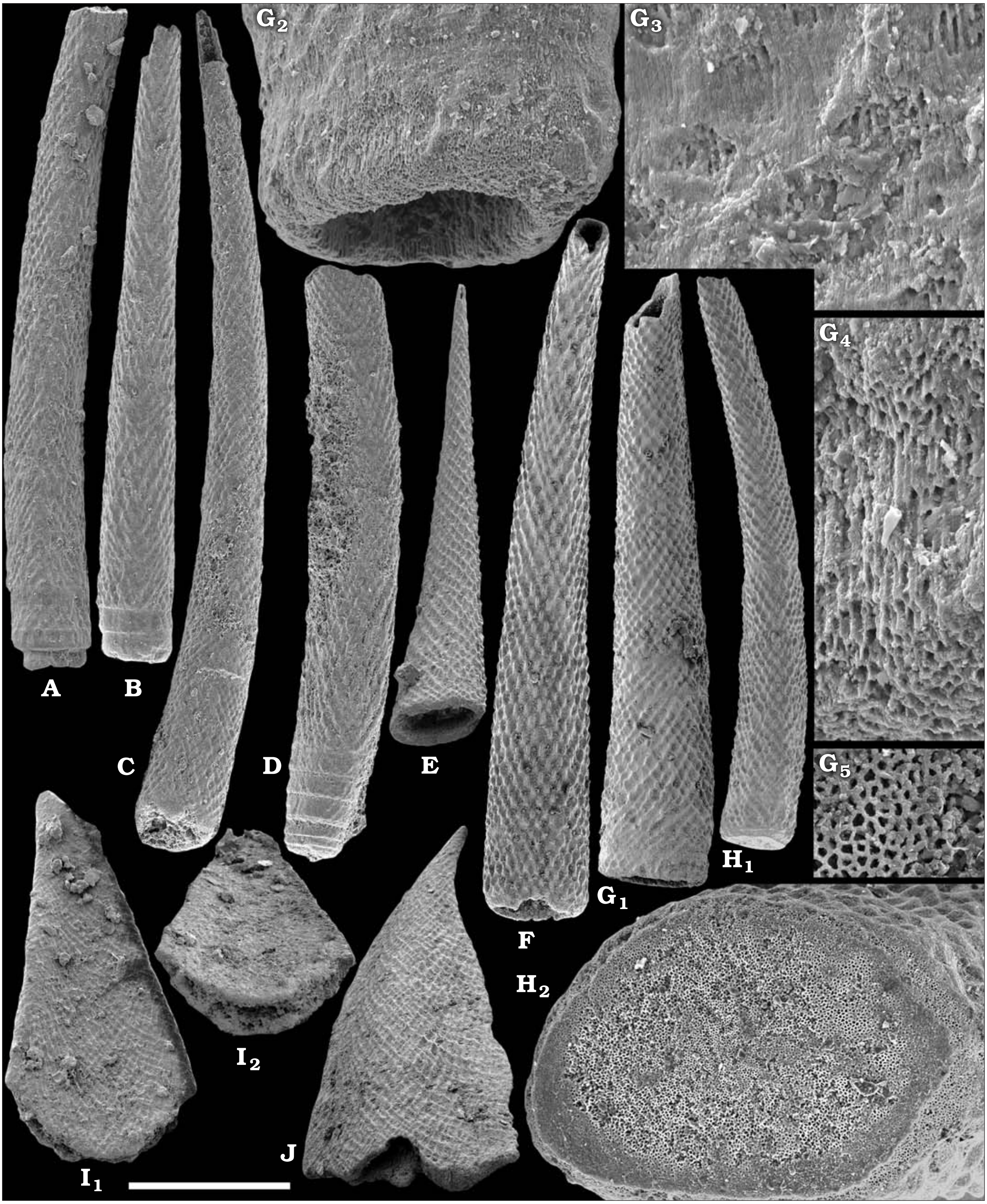


Fig. 50. Problematicum *Rhombocorniculum insolutum* Missarzhevsky in Missarzhevsky and Mambetov, 1981 from lower Cambrian Emyaksin Formation, Bol'shaya Kuonamka River, Anabar Uplift, Siberia; sample 7/19. **A**. Sclerite with twinned apical parts, SMNH X 4727; A_1, oblique lateral view; A_2, close-up of A_1; A_3, close-up of basal end showing microstructure; A_4–A_6, lateral views; A_7, oblique apical view. **B**. SMNH X 4728; lateral view. **C**. SMNH X 4729; C_1, general view; C_2, view on the transversally compressed sclerite. **D**. SMNH X 4730; D_1 and D_2, lateral views. Scale bar: A_1, A_2, A_4, A_5, A_7, 120 μm; A_3, 30 μm; A_6, B–D, 300 μm.

of *R. cancellatum* are also twisted longitudinally and clearly asymmetrical transversally, with one of their lateral sides being blade-like, more flat than the other one. The central lumen is also different in general, being relatively smaller in diameter and more isodiametrically rounded in cross-section.

It has already been reported that *Rhombocorniculum* sclerites grew continuously by basal-internal accretion (Landing et al. 1980; Landing 1995) and contain canals oriented oblique to the wall surface (Li et al. 2003). Co-occurrence of dextral and sinistral sclerites of *R. cancellatum* suggests a bilaterally symmetrical animal, whereas the slender and broad elements probably represented distinct sclerite types within a scleritome. Although superficially similar to some bradoriid spines, microstructural data suggest that *Rhombocorniculum* is difficult to associate with arthropods (Skovsted et al. 2006). Judging from the similar diameter of the tubules in the wall and the fine longitudinal stria on its outer surface, it seems that they are formed by the same organic threads, interpreted herein as microvilli. These microvilli likely extended from chaetoblast-like secreting cells at the base of the sclerites. Such an interpretation of the microstructure in combination with the bristle-like appearance of *Rombocornicu-*

Fig. 51. Problematicum *Rhombocorniculum insolutum* Missarzhevsky in Missarzhevsky and Mambetov, 1981 from lower Cambrian Emyaksin Formation, Bol'shaya Kuonamka River, Anabar Uplift, Siberia. **A**–**D**. Slender sclerites, sample 7/25.6. **A**. SMNHX 4731; lateral view. **B**. SMNHX 4732; lateral view. **C**. SMNHX 4733; lateral view. **D**. SMNHX 4734; lateral view. **E**. Sclerite of transitional morphology, SMNH X 4739, sample 7/27.5; lateral view. **F**–**H**. Slender sclerites, sample 7/27.5. **F**. SMNH X 4735. **G**. SMNH X 4736; G_2, proximal end of sclerite in G_1; G_3 and G_4, close-up of G_2, tubules and longitudinal striation; G_5, transversal view on →



the tubules of the proximal end of sclerite. **H**. SMNH X 4737; H_2, close-up of the proximal end of sclerite in H_1. **I**. Broad sclerite, SMNH X 4740, sample 7/25.6; I_1, concave (ventral?) surface of sclerite; I_2, proximal end of sclerite with lumen. **J**. Broad sclerite, view on the convex (dorsal?) side, SMNH X 4738; sample 7/27.5. Scale bar: 300 µm, except G_2, H_2, 60 µm, G_3–G_5, 15 µm.

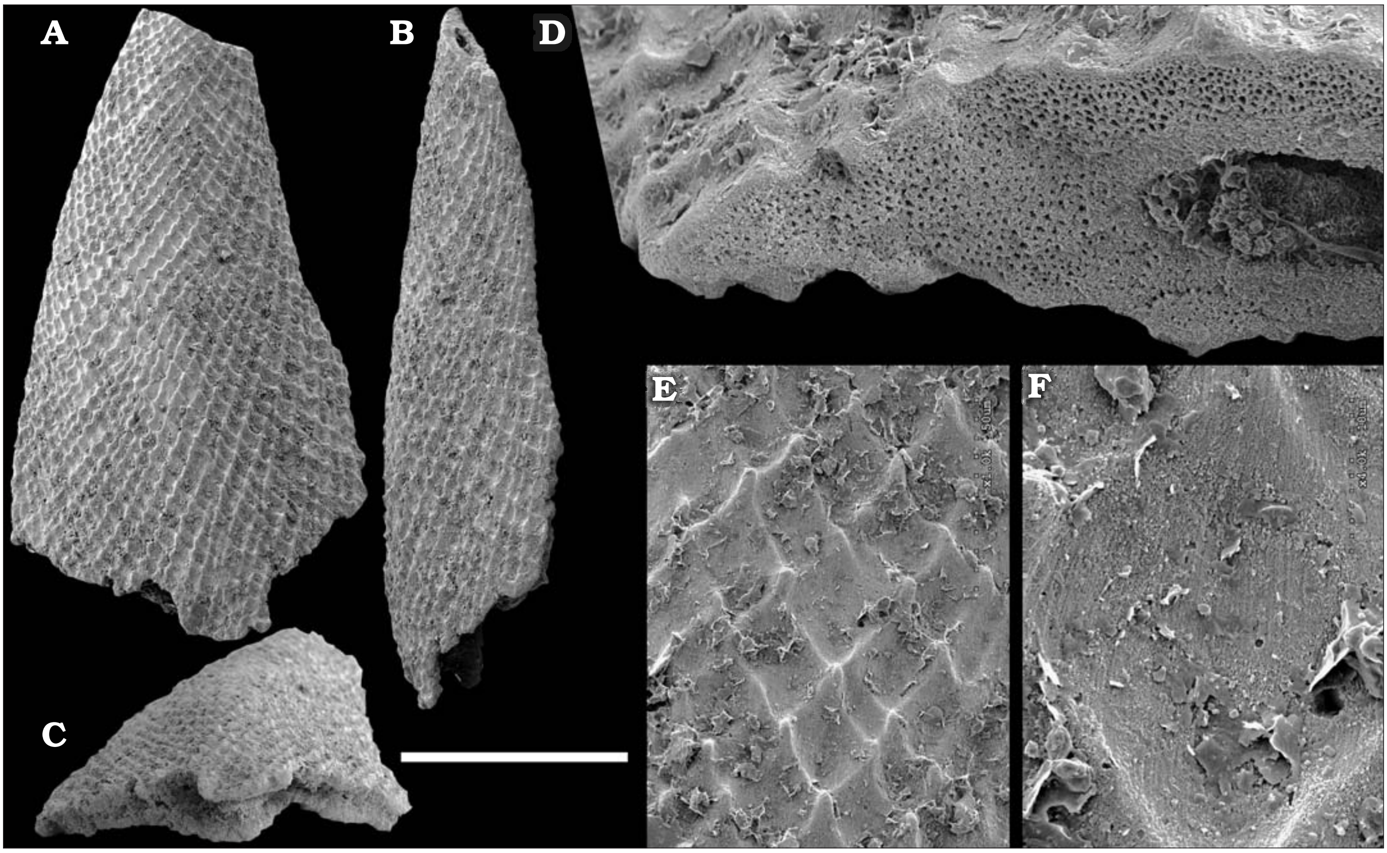


Fig. 52. Problematicum *Rhombocorniculum insolutum* Missarzhevsky in Missarzhevsky and Mambetov, 1981 from lower Cambrian Emyaksin Formation, Malaya Kuonamka River, Anabar Uplift, Siberia; SMNH X 4741; sample 3/42. **A**. View on the convex (dorsal?) side. **B**. Lateral view. **C**. View on the proximal end with broad lumen. **D**. Apical end with tubular microstructure and central lumen. **E**. External ornamentation. **F**. Close-up of E, longitudinal fibres. Scale bar: A–C, 300 μm; D, 30 μm; E, 60 μm; F, 15 μm.

lum sclerites suggests that they may represent chaetae of the type occurring in annelids. In modern polychaetes, microvilli produce longitudinally oriented tubules of a similar diameter by means of deposition by a chaetoblast of sclerotised chitin at their bases and their subsequent retraction (Hausam and Bartolomaeus 2001). Peripheral microvilli may be responsible for the formation of the surface sculpture of the sclerite. The earliest known annelids are non-mineralised fossils from the early Cambrian Sirius Passet fauna of North Greenland (Conway Morris and Peel 2008), but their first hard (diagenetically mineralised) remains are scolecodonts from the upper Cambrian (Eriksson et al. 2004). Scolecodonts have a similar network of pores produced by systems of tubules 0.1–0.25 μm in diameter and exposed on the eroded surfaces of denticles (Szaniawski and Gaździcki 1978).

Stratigraphic and geographic range.—*Rhombocorniculum insolutum* was first described from the lower Atdabanian of the Siberian Platform (Missarzhevsky and Mambetov 1981). It was also reported from the upper portion of Bed 14 of the Pestrotsvet Formation, Isit section, middle Lena River, from the middle *Dokidocyathus lenaicus* Zone of the Tommotian Stage (Sokolov and Zhuravleva 1983; Rozanov and Sokolov 1984; Brasier 1989a; Rozanov and Zhuravlev 1992; Shabanov et al. 2008). The latter occurrence is coeval with the lowermost ones reported herein from the eastern Anabar Uplift (see section Material above). *R. insolutum* has not been recovered herein from beds containing *R. cancellatum* above the δ^{13}C trough between peaks IV and V (Fig. 2; Brasier et al. 1994; Kouchinsky et al. 2001). The stratigraphical distribution of *R. insolutum* in the Malaya and Bol'shaya Kuonamka sections covers the entire area of excursion IV, ranging from the upper *Dokidocyathus lenaicus* Zone of the Tommotian through the lower *Delgadella anabara* Zone of the Atdabanian Stage (Fig. 2). *R. insolutum* is also reported from the *Camenella baltica* Zone of Avalonia (SE Newfoundland, Brasier 1984, 1986, 1989a; Landing 1988; Landing et al. 1998; and Britain, Brasier 1986) and *Schmidtiellus mickwitzi* Zone of Baltica (Bornholm, Poulsen 1967; Brasier 1989a).

Phylum ?Chaetognatha Leuckart, 1854

Class, order, and family uncertain

Genus *Amphigeisina* Bengtson, 1976

Type species: Hertzina? *danica* Poulsen, 1966; lower middle Cambrian; Bornholm.

Remarks.— By contrast with other species of "protoconodonts" herein (see also Kouchinsky et al. 2011), *Amphigeisina danica* does not exhibit longitudinal fibrous microstructure of the type available in grasping spines of chaetognaths (e.g., Vannier et al. 2007).

Amphigeisina danica (Poulsen, 1966)

Fig. 53E.

Material.—One figured sclerite SMNH X 4763 and two additional specimens from sample 1/9; carbonate concretions of the basal Kuonamka Formation, Malaya Kuonamka River; *Bergeroniellus expansus* Zone, upper Botoman Stage.

Description.—Slender, gently curved, simple bilaterally symmetrical calcium phosphatic sclerites. A relatively narrow concave side extends from the tip towards the base. The opposite, broader, strongly convex side of the sclerite is open in the slightly flared basal part. The internal cavity extends to the tip. The wall is composed of two layers with amorphous microstructure. The surface of the convex side is smooth, whereas faint transverse folds are present on the concave side. The two sides meet to produce two longitudinal carinae flanked by two thin flanges formed by the outer layer. The flanges reduce gradually towards the tip, where they merge with the carinae.

Stratigraphic and geographic range.—The occurrence of *Amphigeisina danica* reported herein from the lower part of Cambrian Stage 4 (upper Botoman Stage) is the earliest known from the Siberian Platform, where it also occurs in the Toyonian Stage representing the upper portion of Stage 4 (as *Protohertzina yudomica*, after Demidenko 2006) and in the middle Cambrian Stage 5, in the Kuonamka Formation of the Malaya Kuonamka and Bol'shaya Kuonamka rivers (Kouchinsky et al. 2011). The species is also known from the upper part of Series 2 of Kazakhstan (Gridina 1991), Avalonia, Britain (Hinz 1987), and Laurentia (Landing 1974; John S. Peel, personal communication 2010) and from Series 3 of Baltica (Poulsen 1966; Bengtson 1976) and South and North China (Qian et al. 2004; Steiner et al. 2007).

Genus *Gapparodus* Abaimova, 1978

Type species: Hertzina? *bisulcata* Müller, 1959; upper Cambrian, Sweden.

Gapparodus bisulcatus (Müller, 1959)

Fig. 53A–D.

Material.—Four illustrated sclerites, SMNH X 4764–4767, and 12 additional specimens from sample 1/9; carbonate concretions of the basal Kuonamka Formation, Malaya Kuonamka River; *Bergeroniellus expansus* Zone, upper Botoman Stage.

Description.—Slender, gently curved, simple bilaterally slightly asymmetrical, and laterally flattened calcium phosphatic sclerites. The longitudinally convex side of the sclerite has a strongly convex surface, whereas the opposite, longitudinally concave side is transversely gently convex or flattened. The two sides have almost the same width. Two longitudinal lateral furrows extend from the basal opening towards the tip. The internal cavity extends to the tip of sclerite. The wall has a lamellar fibrous structure (Fig. 53D$_2$).

Stratigraphic and geographic range.—The occurrence of *Gapparodus bisulcatus* reported herein from the lower part of Cambrian Stage 4 is the earliest known from the Siberian Platform, where it also occurs in Stage 5 (Kuonamka Formation, Malaya Kuonamka and Bol'shaya Kuonamka rivers; Müller et al. 1995; Kouchinsky et al. 2011). The species ranges from Series 2 through the Furongian Series in South and North China (Dong and Bergström 2001; Babcock et al. 2007; Steiner et al. 2007). It is also known from the middle–upper Cambrian of Baltica (Bengtson 1976; Müller and Hinz 1991), upper Series 2–Series 3 of Laurentia (Clark and Miller 1969; Clark and Robison 1969; Landing 1974; John S. Peel, personal communication 2010), Cambrian of Western Gondwana (Turkey, Özgül and Gedik 1973), upper Cambrian of Eastern Gondwana (South Korea, Lee 1975), and middle–upper Cambrian of Kazakhstan (Abaimova and Ergaliev 1975).

Genus *Hagionella* Xie, 1990

Type species: Protohertzina cultrata Missarzhevsky, 1977; upper Atdabanian Stage; lower reaches of the Sinyaya River, middle Lena River basin, Siberian Platform.

Hagionella cultrata (Missarzhevsky, 1977)

Fig. 53G, I, J.

Material.—Single fragment SMNH X 4768 from sample 7/39.5; two specimens, including SMNH X 4769, from sample 7/47.5; Emyaksin Formation, Bol'shaya Kuonamka river; correlated with the *Delgadella anabara* Zone, Atdabanian Stage. Three sclerites, including SMNH X 4770, from sample 1/9; carbonate concretions of the basal Kuonamka Formation, Malaya Kuonamka River; *Bergeroniellus expansus* Zone, upper Botoman Stage.

Description.—Gently curved, simple, laterally narrowed and bilaterally symmetrical calcium phosphatic sclerites. The convex side forms a longitudinal median flange. The internal cavity extends to the apex.

Stratigraphic and geographic range.—*Hagionella cultrata* is known from the Atdabanian Stage (Stage 3; Missarzhevsky 1977 and herein) and Cambrian Stage 5 of Siberia (Kouchinsky et al. 2011), Series 2 of Kazakhstan (Bengtson 1983), lower–middle Cambrian of South and North China (see Qian et al. 2004; Li et al. 2004a; Steiner et al. 2007), middle Cambrian of Baltica (Bengtson 1976), upper Series 2 of Laurentia (John S. Peel, personal communication 2010), and probably Avalonia, Britain (Hinz 1987).

Undetermined form 1

Fig. 53F.

Material.—Single apical fragment, SMNH X 4771 from sample 1/9; carbonate concretions of the basal Kuonamka Formation, Malaya Kuonamka River; *Bergeroniellus expansus* Zone, upper Botoman Stage.

Description.—Gently curved bilaterally symmetrical apical fragment of a calcium phosphatic sclerite, 0.8 mm long. Cross-section rhomboidal (or star-shaped), with concave

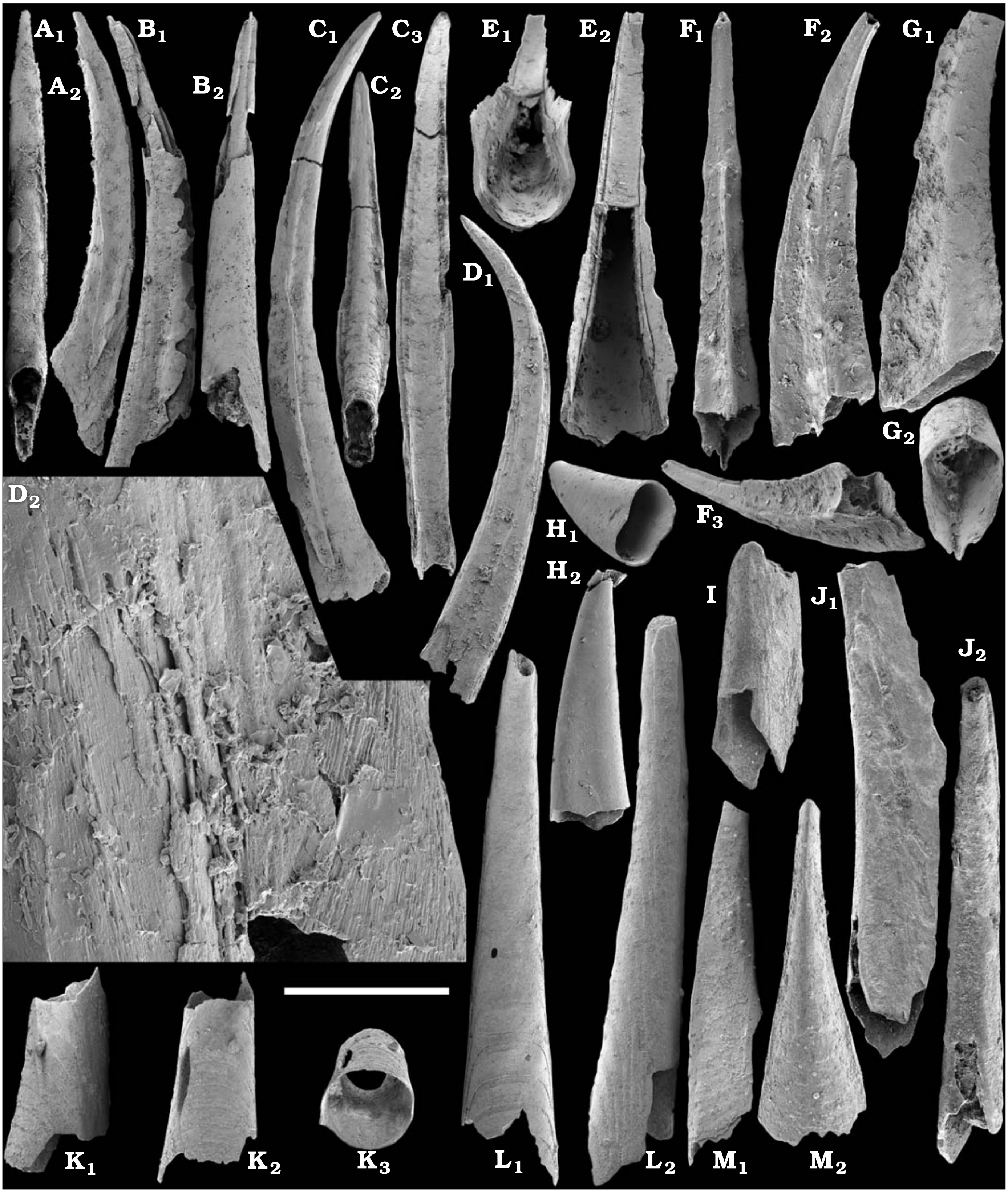


Fig. 53. Protoconodonts from lower Cambrian basal Kuonamka Formation, Malaya Kuonamka River and Emyaksin Formation, Bol'shaya Kuonamka River, Anabar Uplift, Siberia. **A**–**D**. *Gapparodus bisulcatus* (Müller, 1959), sample 1/9. **A**. SMNH X 4764; A_1, view on the longitudinally concave side and basal opening of sclerite; A_2, lateral view. **B**. SMNH X 4765; B_1, lateral view; B_2, view on the longitudinally concave side. **C**. SMNH X 4766; C_1, lateral view; C_2, oblique view on the longitudinally concave side and basal opening of sclerite; C_3, view on the longitudinally concave side. **D**. SMNH X 4767; D_1, lateral view; D_2, close-up of basal part of D_1. **E**. *Amphigeisina danica* (V. Poulsen, 1966), SMNH X 4763; sample 1/9; E_1, view on the basal →

sides. Two distinct keels are situated in the middle of the longitudinally convex (more prominent keel) and concave sides of sclerite. Two other keels run along the middle of the lateral sides of sclerite, but reach the concave side near the apex.

Undetermined form 2

Fig. 53H.

Material.—Single apical fragment, SMNH X 4772 from sample 1/9; carbonate concretions of the basal Kuonamka Formation, Malaya Kuonamka River; *Bergeroniellus expansus* Zone, upper Botoman Stage.

Description.—Gently curved smooth bilaterally symmetrical apical fragment of a calcium phoshatic sclerite, ca. 1 mm long. Cross-section oval, laterally compressed, with lateral sides shallowly invaginated in the middle. The depression disappears towards the apex.

Undetermined form 3

Fig. 53K, L.

Material.—Two incompletely preserved calcium phosphatic sclerites, SMNH X 4773 and 4774, from samples 6/3.9 and 6/6.8 (respectively); Emyaksin Formation, Bol'shaya Kuonamka River; correlated with the *Dokidocyathus regularis* Zone, Tommotian Stage.

Description.—Gently curved sclerites with nearly circular cross-section. The surface of the longitudinally concave side of the sclerite shows distinct growth lines sharply bent towards the base of the sclerite laterally, where they run further nearly parallel along the lateral sides.

Undetermined form 4

Fig. 53M.

Material.—Single incompletely preserved calcium phosphatic sclerite, SMNH X 4775 from sample 7/33; Emyaksin Formation, Bol'shaya Kuonamka River; correlated with the *Delgadella anabara* Zone, Atdabanian Stage.

Description.—Sclerite gently curved, with a broad base and laterally compressed apical part. The longitudinally convex side is smooth at the base, with a semi-circular cross-section. A ridge emerges in the apical part, where the sclerite becomes laterally compressed. The longitudinally concave side of the sclerite is significantly shorter, with its broad basal part open, but becoming close and smooth towards the apex. The outer surface is covered with growth lines.

opening; E_2, view on the concave side of sclerite. **G**, **I**, **J**. *Hagionella cultrata* (Missarzhevsky, 1977), **G**. SMNH X 4770, sample 1/9; G_1, lateral view; G_2, view on the basal opening of sclerite. **I**. SMNH X 4768, sample 7/39.5; oblique lateral view. **J**. SMNH X 4769, sample 7/47.5; J_1, lateral view; J_2, view on the longitudinally concave side. **F**. Undetermined form 1, SMNH X 4771; sample 1/9; F_1, view on the longitudinally concave side; lateral (F_2) and oblique basal (F_3) views. **H**. Undetermined form 2, SMNH X 4772; sample 1/9; oblique basal (H_1) and lateral (H_2) views. **K**, **L**. Undetermined form 3. **K**. SMNH X 4773, sample 6/6.8; lateral (K_1) and basal (K_3) views; K_2, view on the longitudinally concave side. **L**. SMNH X 4774, sample 6/3.9; L_1, view on the longitudinally concave side; L_2, lateral view. **M**. Undetermined form 4, SMNH X 4775; sample 7/33; M_1, lateral view; M_2, view on the convex side of sclerite. Scale bar: 600 μm, except F, I, J, M, 300 μm; D_2, 60 μm.

Phylum, class, order, and family uncertain

Genus *Fengzuella* He and Yu, 1992

Type species: Fengzuella zhejiangensis He and Yu, 1992; Qiongzhusian Stage?, lower Cambrian; Hetang Formation, Wujialing, Jiangshan County, Zhejiang Province, South China.

Fengzuella zhejiangensis He and Yu, 1992

Fig. 54.

Material.—Single laterally flattened bilaterally symmetrical sclerite, SMNH X 4776, from sample 7/45 (Fig. 54A) and two curved bilaterally symmetrical sclerites, SMNH X 4777 and 4778, from samples 7/55.8, and 7/64 (respectively). Emyaksin Formation, Bol'shaya Kuonamka; correlated with the *Delgadella anabara* and *Judomia* zones, Atdabanian Stage. An additional specimen, SMNH X 4779, derives from sample 2001-11b, collected along the Sinyaya River, tributary of the Lena River in the middle reaches (Rozanov and Missarzhevsky 1966), Atdabanian Stage, but the exact stratigraphic position of the sample is not known.

Description.—Calcium phosphatic sclerites of planispiral and curved types. The planispiral sclerite is ca. 0.3 mm in diameter and consists of 1¼ whorls. The curved sclerites are 0.5–0.8 mm long. Along each side of the sclerites, the wall has two longitudinal depressions separated from each other by a ridge. The central cavity extends from the aperture to the apex, and has an oval or rhomboidal, star-shaped cross-section with convex sides. The wall is multi-layered and consists of basally secreted and adapically overlapping thin growth lamellae (Fig. 54A_4, B_2, D_4).

Remarks.—Steiner et al. (2003) noted that curved sclerites predominate (85%) and the planispiral type is rare. It has been also suggested that the scleritome consisted of densely packed growing sclerites with their proximal parts attached to a soft tissue. Presumably, the sclerites had originally a sclerotised organic (non-mineralised?) composition. The outer parts of the growth lamellae were deposited externally, probably within an invaginated tissue.

Stratigraphic and geographic range.—Problematic sclerites of *Fengzuella zhejiangensis* He and Yu, 1992 were originally described from South and North China, from beds that possibly correlate with the *Anabarites trisulcatus–Protohertzina anabarica* Assemblage Zone of the lower Meishucunian Stage (Steiner et al. 2003). That correlation is not certain, however, and the beds might alternatively be correlated with the Qiongzhusian Stage of China and Atdabanian Stage of Siberia (Steiner et al. 2003, 2007). A single planispiral sclerite similar to *Fengzuella* is reported, as a coiled and flat discoidal problematicum, from lower middle Cambrian strata of the Kuonamka Formation, Khorbusuonka River, Olenyok Uplift, Siberian Platform (Müller et al. 1995: 114, fig. 5E, F). Planispiral and transitional sclerites of, probably, a new

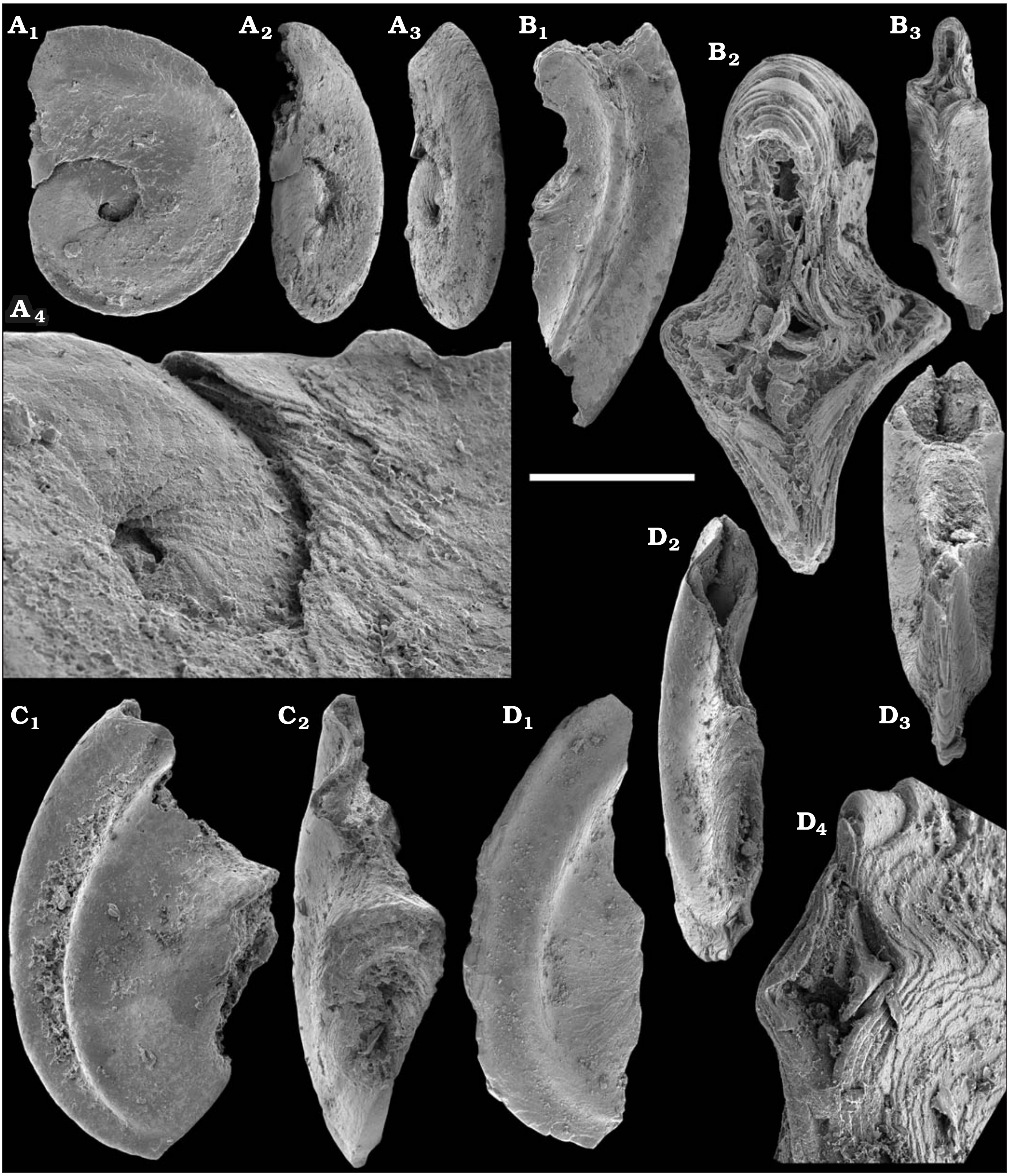


Fig. 54. Problematicum *Fengzuella zhejiangensis* He and Yu, 1992 from lower Cambrian Emyaksin Formation, Bol'shaya Kuonamka River, Anabar Uplift and middle Lena River, Siberia. **A**. Planispiral sclerite, SMNH X 4776, sample 7/45; A_1, lateral view on the sclerite; A_2 and A_3, oblique views; A_4, close-up of overlapping growth increments. **B**. Curved sclerite, SMNH X 4778, sample 7/64; B_1, lateral view of the fragment; B_2, close-up of B_3; B_3, view on the cross-section of sclerite, in the upper part of B_1. **C**. Curved sclerite, SMNH X 4777, sample 7/55.8; C_1, lateral view on the sclerite; C_2, transversal view. **D**. Curved sclerite, SMNH X 4779, sample 2001-11b; lateral (D_1), oblique transversal (D_2), and oblique apical (D_3) views; D4, close-up of the apical end of sclerite. Scale bar: 200 μm, except D_1–D_3, 300 μm; A_4, B_2, D_4, 60 μm.

species of *Fengzuella* are also available from the upper Series 2 of Laurentia (North Greenland; AK and John S. Peel, unpublished observation).

Phylum Tardipolypoda Chen and Zhou, 1997
Class Xenusia Dzik and Krumbiegel, 1989
Order Scleronychophora Hou and Bergström, 1995
Family Eoconchariidae Hao and Shu, 1987
Genus *Microdictyon* Bengtson, Matthews, and Missarzhevsky, 1986

Type species: Microdictyon effusum Bengtson, Matthew, and Missarzhevsky, 1986; *Rhombocorniculum cancellatum* Zone, lower Cambrian; Geres Member of the Shabakty Group, Ushbas River, Lesser Karatau, Kazakhstan.

Remarks.—For discussion of the validity of the genus and species see Demidenko (2006: 237).

Microdictyon cf. *M. rhomboidale* Bengtson, Matthews, and Missarzhevsky, 1986

Fig. 55.

Material.—One complete sclerite, SMNH X 4780 and two fragments from sample 7/54. Emyaksin Formation, Bol'shaya Kuonamla River; correlated with the middle *Judomia* Zone, Atdabanian Stage.

Description.—The sclerite is weakly convex, with a subcentrally situated apex; thin and rhombic in plan view, with a maximum dimension of ca. 1 mm. The sclerite (as illustrated in Fig. 55A_2) has semicircular upper and lower margins and protrudes into distinct angulations laterally. The upper (as illustrated in Fig. 55A_2) margin of the sclerite forms a flattened limb covered with ca. 5 μm tubercles oriented to the right in Fig. 55A_5. The opposite margin has a weakly expressed reentrant (Fig. 55A_2). The sclerite has distinct, almost circular holes surrounded by 5–7 nodes. The holes range from ca. 10 μm in diameter at the margin of the sclerite to 80 μm in its central part. The nodes have an initial diameter of ca. 10 μm at the margin of the sclerite, increasing up to at least 80 μm centrally. These nodes start at the margin as low flattened tubercles and progress into larger cones, >25 μm tall, with flared bases and tips shifted towards the centre of the sclerite (Fig. 55A_3). The holes are not closed from below.

Remarks.—In articulated lobopodians from Chengjiang and their reconstructions (e.g., Hou and Bergström 1995), the sclerites are approximately bilaterally symmetrical across a vertical plane representing their anatomical orientation along the worm-like body of the animal, and with their eventual spines pointed in dorsal direction. Therefore, the upper ends of the nodes would rather also point towards the dorsal margin of the sclerite. For that reason and in accordance with Kouchinsky et al. (2011: 159), orientation of sclerites in Fig. 55 is presumed to be anatomically dorso-ventral. It is not clear, however, which of the margins herein (lower or upper, as illustrated in Fig. 55) is dorsal or ventral, for the nodes tend to point towards the centre of sclerite.

The holotype of *Microdictyon rhomboidale* Bengtson, Matthews and Missarzhevsky, 1986 (SMNH X 2111), derives from the Bateny Hills, Tamdytau, Altai-Sayan Folded Area; upper Atdabanian Stage (Bengtson et al. 1986). The sclerite of *Microdictyon* cf. *M. rhomboidale* herein has a strong similarity to the holotype and paratypes of *M. rhomboidale* (Bengtson et al. 1986: fig. 4A–D; Fig. 55B herein), but has somewhat larger nodes and holes, and an almost indistinct reentrant (compare lower parts of Fig. 55A_2, B_3). Both are distinguished from sclerites of other lobopodian species by their rhombic outline and a flattened tuberculated limb. The latter has not been previously described from any of the species.

Remarks.—*Microdictyon rhomboidale* was described from the upper Atdabanian (Stage 3) of the Altai-Sayan Folded Area in Siberia (Tamdytau Mountains, Kyzyl-Kum). *Microdictyon* cf. *M. rhomboidale* is reported from the Sekwi Formation, Mackenzie Mountains, Canada and the upper Campito Formation, White Mountains, California, both from the lower *Nevadella* Zone, correlated with the middle Atdabanian Stage of Siberia (Bengtson et al. 1986: 98). *Microdictyon* aff. *rhomboidale* also is described from Shaanxi Province in China, from the upper *Eoredlichia*-*Wutingaspis* Zone, correlated with the upper Atdabanian Stage of Siberia (Zhang and Aldridge 2007). The new occurrence in Siberia is roughly equivalent in age to those above. Chemostratigraphy (Fig. 2 and Kouchinsky et al. 2001) indicates that it belongs to the middle *Judomia* Zone, or middle *Nochoroicyathus kokoulini* Zone of the upper Atdabanian Stage.

Microdictyon sp.

Fig. 56.

Material.—Single fragments from samples 3/60 and 6/66.2; two, SMNH X 4782 and 4783, from sample 7/34.7 and six fragments from sample 7/39.5; Emyaksin Formation, Malaya Kuonamka and Bol'shaya Kuonamka rivers; correlated with the upper *Delgadella anabara* Zone (samples 7/34.7 and 7/39.5) and *Judomia* Zone, Atdabanian Stage.

Description.—Fragments of *Microdictyon* sclerites with partly preserved margin (margin in the lower part of the Fig. 56A_2, A_3, B_4). The fragments have distinct rounded, almost circular holes surrounded by 5–8 cap-like nodes. Additionally, smaller nodes are present along the margin of sclerite (Fig. 56A_2, A_3). The diameter of the holes increases from ca. 15 μm at the very margin of the sclerite to at least 70 μm centrally. The nodes have an initial diameter of ca. 10 μm at the margin of the sclerite, increasing up to at least 50 μm proximally. These nodes start at the margin as tubercles and progress into larger cones, >30 μm tall, with flared bases and tips shifted towards the centre of the sclerite. The holes are not closed from below.

Remarks.—*Microdictyon* sp. described herein is similar to *Microdictyon rhomboidale,* described above, but determination of its affinity is hampered by incomplete preservation. Chemostratigraphy (Fig. 2 and Kouchinsky et al. 2001, 2012) indicates that *Microdictyon* sp., from the upper *Delgadella anabara* Zone, Atdabanian Stage, is the earliest lobopodian

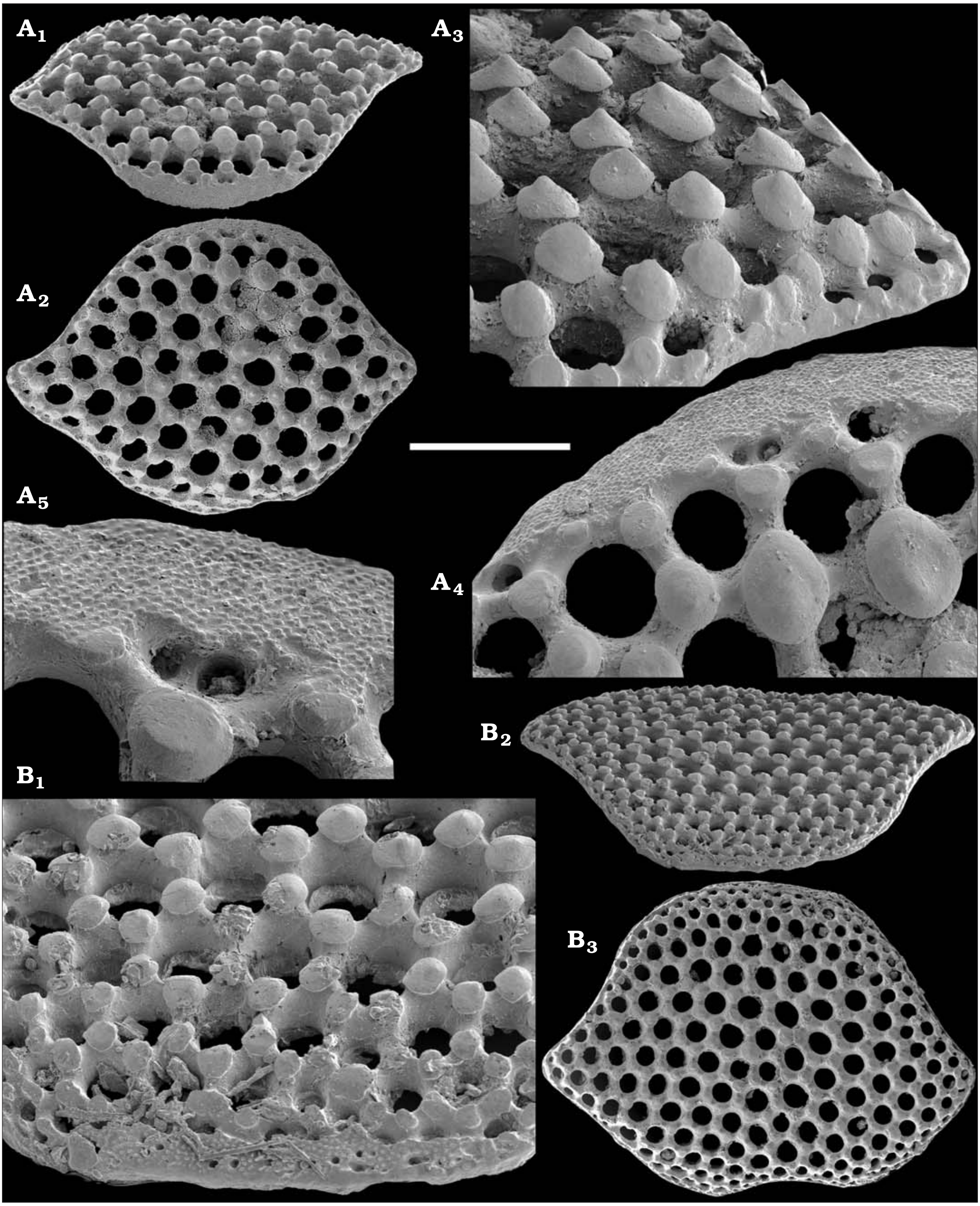


Fig. 55. Lobopodian *Microdictyon* cf. *M. rhomboidale* Bengtson, Matthews, and Missarzhevsky, 1986 from lower Cambrian Emyaksin Formation, Bol'shaya Kuonamka River, Anabar Uplift, Siberia compared to the paratype of *M. rhomboidale* from lower Cambrian of the Altai-Sayan Folded Area. **A**. *Microdictyon* cf. *M. rhomboidale* Bengtson, Matthews, and Missarzhevsky, 1986; SMNH X 4780, sample 7/54; A_1, A_2, general views of sclerite; →

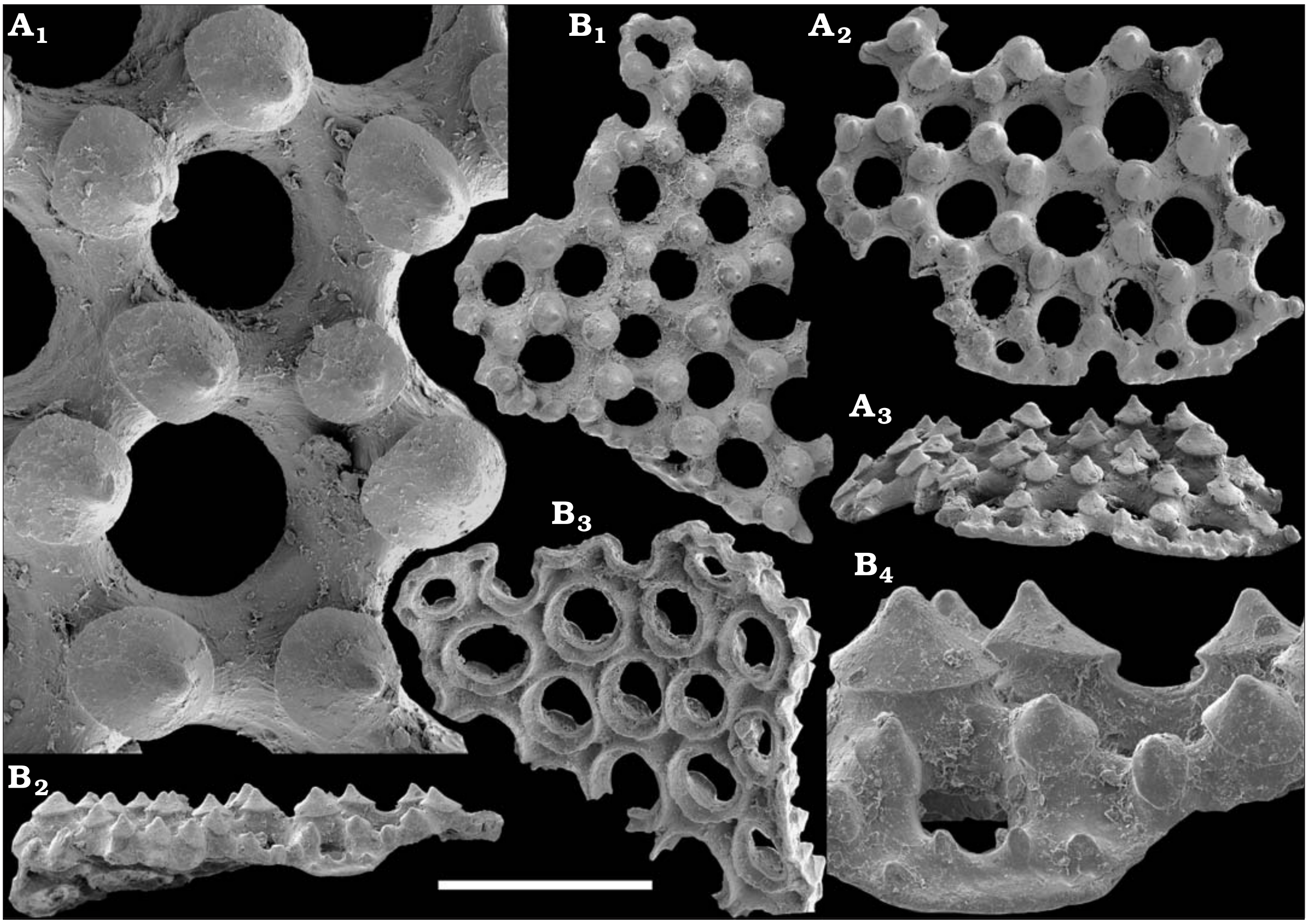


Fig. 56. Lobopodian *Microdictyon* sp. from lower Cambrian Emyaksin Formation, Bol'shaya Kuonamka River, Anabar Uplift, Siberia; sample 7/34.7. **A**. Outer surface of the fragment, SMNH X 4782; A_1, close-up of A_2; A_2, view on the outer surface of sclerite; A_3, oblique view on the lower margin of sclerite. **B**. SMNH X 4783; B_1, B_2, general views of the fragment; B_3, inner surface; B_4, close-up of the edge of sclerite. Scale bar: 200 µm, except A_1, B_4, 60 µm.

fossil known from Siberia. This occurrence is correlated chemostratigraphically (Dilliard et al. 2007) with the regional first appearance of *Microdictyon* sp. and *Microdictyon* cf. *M. rhomboidale* in the lower *Nevadella* Zone of Laurentia (see above, Bengtson et al. 1986; Voronova et al. 1987) and, probably, with the first occurrence of *M. sphaeroides* Hinz, 1987 in the *Camenella baltica* Zone of Avalonia (Hinz, 1987) and *Microdictyon depressum* Bengtson in Bengtson et al., 1990 in the *Abadiella huoi* Zone of Australia (Topper et al. 2011; Kouchinsky et al. 2012).

Phylum ?Priapulida Delage and Hérouard, 1897

Class Palaeoscolecida Conway Morris and Robison, 1986

Order Palaeoscolecida Conway Morris and Robison, 1986

Family Palaeoscolecidae Whittard, 1953

Genus *Hadimopanella* Gedik, 1977

Type species: *Hadimopanella oezgueli* Gedik, 1977; middle Cambrian, Taurus Mountains, Turkey.

Hadimopanella knappologica (Bengtson, 1977)

Fig. 57.

Material.—Hundreds to thousands of individual sclerites, including SMNH X 4784–4797, from samples K1-2B, 1/5, 3/60, 3/61.5, 3/62.5, 3/63.5, 3/65, 6/66.2, 7/55, 7/55.8, 7/60, 7/62, and 7/64. Emyaksin Formation, Malaya Kuonamka and Bol'shaya Kuonamka rivers; correlated with the lower *Judomia* Zone, Atdabanian Stage–*Calodiscus*-*Erbiella* Zone, Botoman Stage.

Description.—Disk-like circular to oval phosphatic sclerites with one side convex and smooth, and the opposite side consisting of a conical surface capped with one or several tubercles. Smaller sclerites with a single or a few tubercles

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A_3, close-up of the right part of sclerite in A_2; A_4, close-up of the tuberculated limb in the upper part of A_2; A_5, detail of A_4 enlarged. **B**. *Microdictyon rhomboidale* Bengtson, Matthews, and Missarzhevsky, 1986, paratype, SMNH X 4781; B_2, B_3, general views of sclerite; B_1, close-up of the tuberculated limb in the lower part of B_2. Scale bar: 400 µm, except A_3, A_4, B_1, 120 µm; A_5, 60 µm.

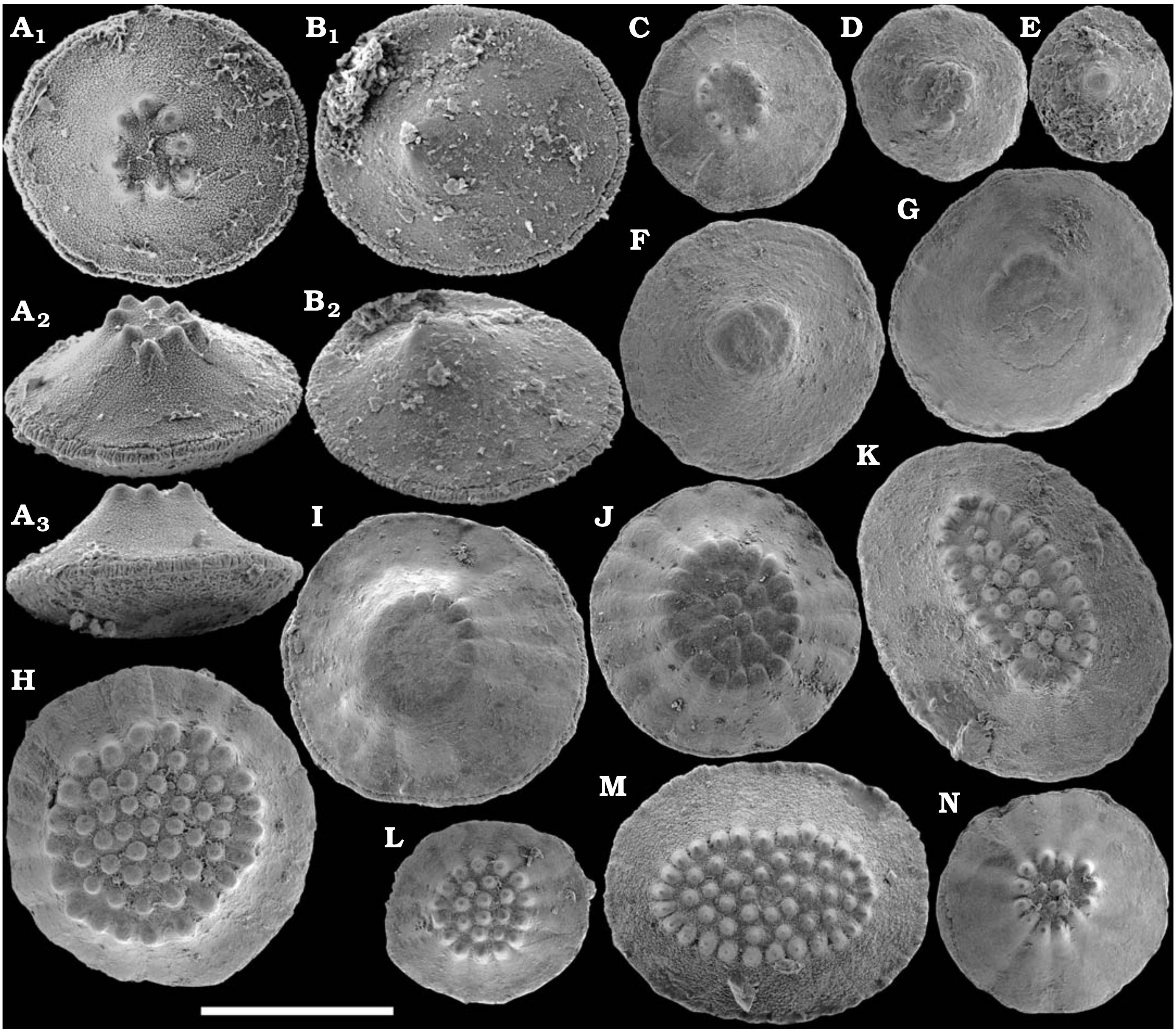

Fig. 57. Paleoscolecids *Hadimopanella knappologica* (Bengtson, 1977) from lower Cambrian Emyaksin Formation, Malaya Kuonamka River and Bol'shaya Kuonamka River, Anabar Uplift, Siberia; disarticulated sclerites. **A**. SMNH X 4784, sample 3/61.5; A_1, view on the outer surface; A_2, oblique lateral view; A_3, oblique basal views on the sclerite. **B**. SMNH X 4785, sample 3/61.5; B_1, view on the outer surface; B_2, oblique lateral view. **C**. SMNH X 4786, sample 3/60; view on the outer surface. **D**. SMNH X 4787, sample 3/60; view on the outer surface. **E**. SMNH X 4788, sample 3/60; view on the outer surface. **L**. SMNH X 4795, sample 7/62; view on the outer surface. **M**. SMNH X 4796, sample 7/62; view on the outer surface. **N**. SMNH X 4797, sample 7/62; view on the outer surface. **F**. SMNH X 4789, sample 7/60; view on the outer surface. **G**. SMNH X 4790, sample 7/60; view on the outer surface. **H**. SMNH X 4791, sample 7/60; view on the outer surface. **I**. SMNH X 4792, sample 7/60; view on the outer surface. **J**. SMNH X 4793, sample 7/60; view on the outer surface. **K**. SMNH X 4794, sample 7/60; view on the outer surface. Scale bar: 120 µm, except A, B, 60 µm.

are circular or slightly oval, 80–100 µm in diameter. The tubercles form a circle, sometimes around a central group of 3–5 others. In larger sclerites, a group of up to tens of closely situated tubercles form a flat surface with a rounded or oval outline parallel to the margin of sclerite, with the latter up to 200 µm in larger diameter. The conical surface is either smooth or covered with a fine granulation and straight and fine radial striae. The two surfaces pass into each other with a distinct angulation, marked in some specimens by numerous short subradial rugae.

Remarks.—Disarticulated button-shaped palaeoscolecidan sclerites without affinity to known palaeoscolecidan scleritomes are usually attributed to the form genus *Hadimopanella* Gedik, 1977 (Ponomarenko 2005; Topper et al. 2010; García-Bellido et al. 2013; Barragán et al. 2014a, b). The sclerites described herein fall within the size variation of *H. knappologica* and are most similar to specimens described by Bengtson (1977). Sclerites from scleritomes of paleoscolecids known from the Botoman Stage of the southeastern Siberian Platform show a different sculpture (Ivantsov and Wrona

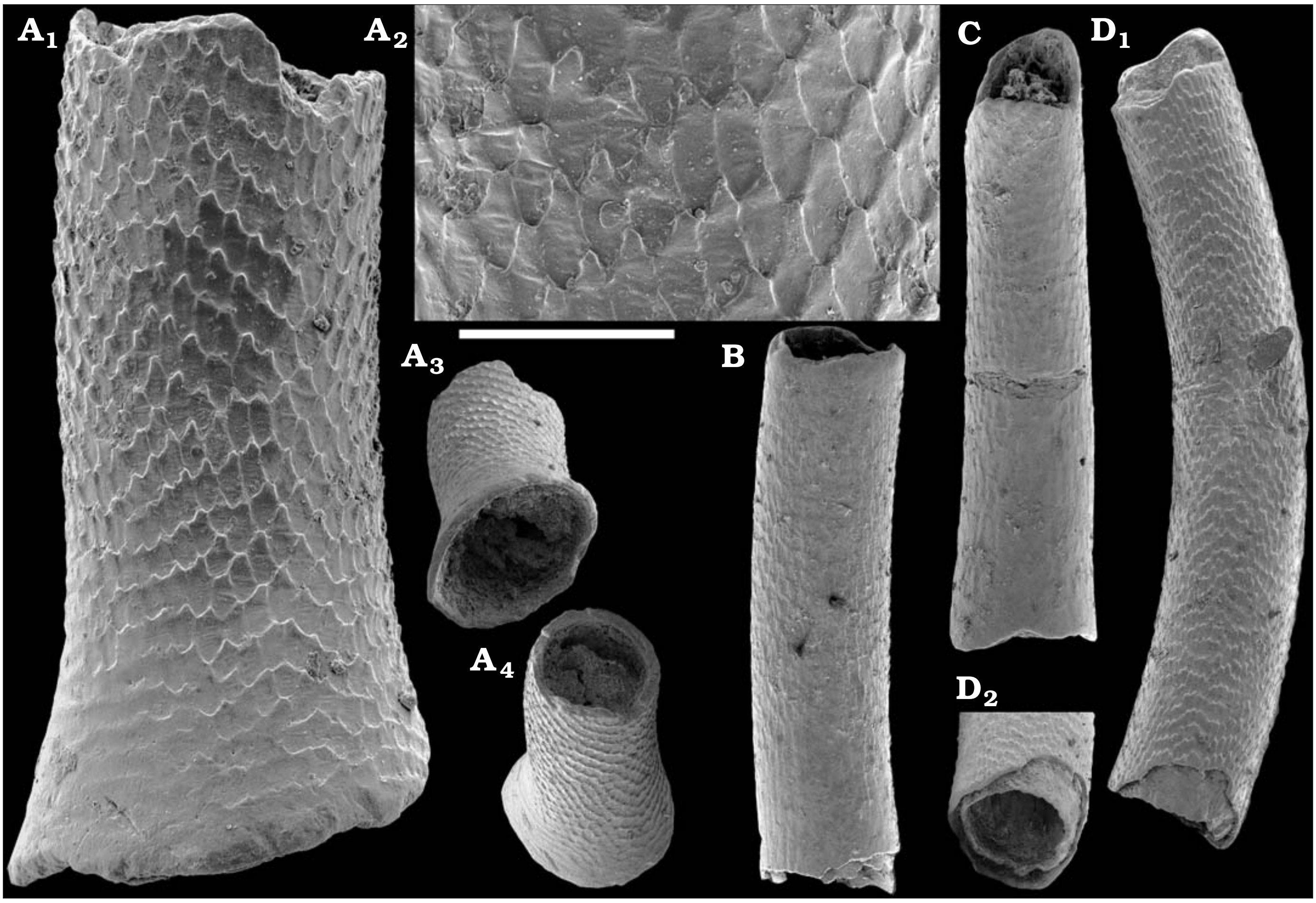

Fig. 58. Bradoriids *Mongolitubulus spinosus* (Hinz, 1987) from lower Cambrian Emyaksin Formation, Bol'shaya Kuonamka River and basal Kuonamka Formation, Malaya Kuonamka River, Anabar Uplift, Siberia, fragments of spines. **A**. SMNH Ar 63450, sample 7/55; A_1, lateral view; A_2, close-up of A_1 showing ornamentation; A_3, oblique basal view; A_4, oblique transversal view on the apical end of the fragment. **B**. SMNH Ar 63452, sample 1/9; lateral view. **C**. SMNH Ar 63453, sample 1/9; lateral view. **D**. SMNH Ar 63451, sample 7/70; D_1, lateral view; D_2, oblique transversal view on the basal end of the fragment. Scale bar: 300 µm, except A_1, 120 µm; A_2, 60 µm.

2004). *H. apicata* Wrona, 1982 from the upper Stage 3–Stage 4 of Gondwana and Laurentia is, however, similar in size and morphology to smaller single-tubercle individuals available in the collection, but attributed herein to *H. knappologica.* The number of tubercles in *H. apicata* varies from one to four in larger specimens, with the diameter of larger sclerites reaching ca. 150 µm. In addition, sclerites of *H. antarctica* Wrona, 1987 co-occur with those of *H. apicata* and would have formed part of the same scleritome (Topper et al. 2010), although Australian sclerites are significantly smaller (11–26 µm) than those from the type material of *H. apicata*. For that reason, a preliminary definition of the earliest palaeoscolecid sclerites from the Emyaksin Formation as *H. apicata* (see Kouchinsky et al. 2012) is here considered untenable. The sclerites are therefore redefined herein as *H. knappologica.* Similar sclerites are also described from the middle Cambrian Kuonamka Formation, Anabar Uplift by Kouchinsky et al. (2011) and as *Hadimopanella* aff. *H. oezgueli* Gedik, 1977 by Müller et al. (1995). Morphologically similar sclerites of the type species, *Hadimopanella oezgueli* described from the middle–upper Cambrian of Gonwana and Kazakhstan are probably also available from Siberia (see Geyer et al. 2014). Ranges of morphological variability in both form species are, however, broad and overlap, so that it is not possible to associate them with a single or several natural species (Barragán et al. 2014a, b).

Stratigraphic and geographic range.—Lower and probably middle Cambrian, Siberian Platform.

Phylum Arthropoda von Siebold and Stannius, 1845

Class uncertain

Order Bradoriida Raymond, 1935

Family Mongolitubulidae Topper, Skovsted, Harper, and Ahlberg, 2013

Genus *Mongolitubulus* Missarzhevsky, 1977

Type species: *Mongolitubulus squamifer* Missarzhevsky, 1977; Botoman Stage, lower Cambrian; Salany-Gol River, Mongolia.

Remarks.—It has been suggested that *Mongolitubulus*-like hollow ornamented spines may represent detached fragments of different panarthropod origin, such as bradoriids or phosphatocopids (Melnikova 2000; Skovsted and Peel 2001;

Topper et al. 2007), lobopodians (Dzik 2003; Caron et al. 2013), or trilobites (Li et al. 2012). Employment of the name *Mongolitubulus* Missarzhevsky, 1977 for such fossils should therefore be verified by investigation of the type or topotype material of *Mongolitubulus squamifer* Missarzhevsky, 1977 from western Mongolia.

Mongolitubulus spinosus (Hinz, 1987)

Fig. 58.

Material.—Ten specimens from samples 6/59.3, 6/66.2, 7/54, and 7/55, including SMNH Ar 63450 from sample 7/55; correlated with the *Judomia* Zone, upper Atdabanian Stage; ten specimens, including SMNH Ar 63451, from sample 7/70; *Calodiscus*-*Erbiella* Zone, lower Botoman Stage; Emyaksin Formation, Bol'shaya Kuonamka River. Seven specimens, including SMNH Ar 63452 and 63453, from sample 1/9; carbonate concretions in the basal Kuonamka Formation, Malaya Kuonamka River; *Bergeroniellus expansus* Zone, upper Botoman Stage.

Description.—Gently curved hollow calcium phosphatic spines nearly circular in cross-section. The wall consists of two layers. The outer layer has a cancellate ornamentation consisting of irregular transversal rows of polygons with serrated edges. The polygons are extended longitudinally, with their apical part somewhat raised and pointed towards the apex of the spine. Inner layer without sculpture, smooth and folded at the base of spine (Fig. 58D$_2$). The basal part is flaring (Fig. 58A). The specimens reach 3 mm long and are up to 0.2 mm in diameter.

Remarks.—In addition to the type species, *M. squamifer* Missarzhevsky, 1977, such other specias as *M. aspermachaera* Topper, Skovsted, Harper, and Ahlberg, 2013, *M. henrikseni* Skovsted and Peel, 2001, *M. reticulatus* Kouchinsky, Bengtson, Clausen, Gubanov, Malinky, and Peel, 2011, *M. spinosus* (Hinz, 1987), *M. unialata* (Zhang, 2007), and *M. unispinosa* Topper, Skovsted, Brock, and Paterson, 2007 are included within *Mongolitubulus* Missarzhevsky, 1977, shown to represent the spines of a bradoriid (Skovsted and Peel 2001; Topper et al. 2007, 2013).

Ornamentation of *M. spinosus* herein is very similar to that of *M. spinosus* from Britain, described as *Rushtonites spinosus* by Hinz (1987: 11) and Brasier (1989a: pl. 7.2), as well as to the spines attributed to *Tubuterium ivantsovi* Melnikova, 2000 from Siberia (lower Kutorgina Formation, middle Lena River, Botoman Stage; Melnikova 2000: pl. 8; Ponomarenko 2005: pls. 29, 30). The apically raised edges of polygons in *Rushtonites spinosus* (Hinz 1987: pl. 11: 2, 4, 7, 9) appear to be more rounded, however, than in *M. spinosus* herein and in *Tubuterium ivantsovi*, but this can be a preservational effect. *Tommotitubulus grausmanae* (Vasil'eva 1994: pl. 1: 1 therein and Vasil'eva 1998: pl. 46: 2, 5, 6) from the lower Botoman Stage of Siberia is considered herein to be a junior synonym of *M. spinosus*.

M. spinosus differs from the other, younger, species from the Kuonamka Formation, *M. reticulatus*, in ornamentation and in having a straight, not bent apical part. The outer layer in *M. reticulatus* has a reticulate ornamentation consisting of longitudinally extended polygons forming a regular pattern of straight or gently spiralling rows directed towards the apex (Kouchinsky et al. 2011: figs. 33–35). The wrinkled outer surface of *M. aspermachaera* from the Furongian of Baltica bears tubercles (Topper et al. 2013). The ornamentation of *M. henrikseni* Skovsted and Peel, 2001 from the beds equivalent to the Botoman Stage in Greenland and Australia (Skovsted and Peel 2001; Skovsted et al. 2006) and *M. squamifer* Missarzhevsky, 1977 from beds in Mongolia, Kazakhstan, and Greenland correlated with the upper Atdabanian–Botoman Stages (Missarzhevsky 1977; Missarzhevsky and Mambetov 1981; Skovsted and Peel 2001) represents well-defined scale-like protuberances. The outer surface of *M. unispinosa* spines bears short second-order spines and rhombic scales inclined adapically, but subdued in the apical area (Topper et al. 2007). A flaring basal part is known from all species attributed herein to *Mongolitubulus*, except for *M. squamifer* (Skovsted and Peel 2001).

Stratigraphic and geographic range.—*Mongolitubulus spinosus* (Hinz, 1987) occurs in the Lower Comley Limestones (Beds Ac2–Ac3, after Brasier 1989b), *Callavia* Zone, Britain, correlated with the upper Atdabanian–lower Botoman Stages. On the Siberian Platform, it is known from the *Judomia* Zone of the upper Atdabanian Stage and from the Botoman Stage.

Carapace fragments of ?bradoriids

Figs. 59–61.

Material.—Tuberculated cuticular fragments, including spines and low cones: single spine from sample 3/65; two spines from sample 6/59.3; two spines, including SMNH Ar 63454, seven cones, including SMNH Ar 63455, and one fragment with a short smooth spine SMNH Ar 63456 from sample 6/66.2; two spines and one cone from sample 7/47.5; one cone from sample 7/48.5; over thirty cuticular fragments from sample 7/54, including sixteen cones and five spines, including SMNH Ar 63457 and 63458; two cuticular fragments with paired cones, SMNH Ar 63459 and 63461, thirty two cones and eighteen spines from sample 7/55; basal part of a large tuberculated spine SMNH Ar 63460, one additional spine and one cone from sample 7/55.8; uppermost *Delgadella anabara* and *Judomia* zones. Carapace? fragments from samples K3-24B and 7/27.5, including SMNH Ar 63462; correlated with the *Repinaella* Zone. All from the Emyaksin Formation, Malaya Kuonamka and Bol'shaya Kuonamka rivers; Atdabanian Stage.

Remarks.—Phosphatised cuticular fragments, including prominent spines and low cones, that are ornamented with tubercles and polygonal network. Evidence of elastic deformation (Figs. 59A$_3$, 60) suggests an originally non-mineralised or weakly mineralised wall. The wall is subdivided into a thin outer layer and a much thicker inner layer. The outer layer produces folds and reticulation covering the outer surface (Fig. 59A, C). The outer layer is partly exfoliated, and

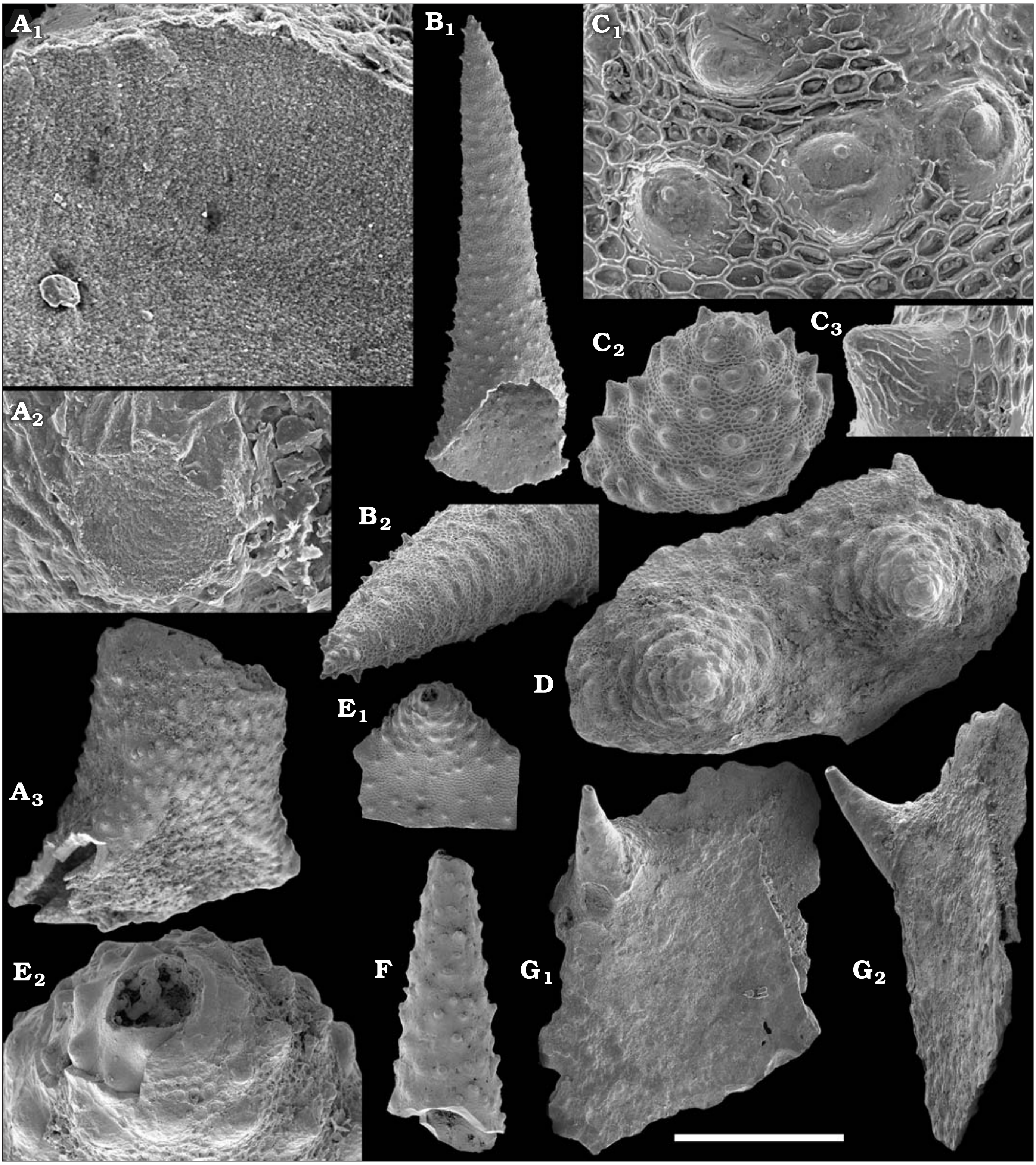

Fig. 59. Carapace fragments of ?bradoriids from lower Cambrian Emyaksin Formation, Bol’shaya Kuonamka River, Anabar Uplift, Siberia. **A**. SMNH Ar 63460, sample 7/55.8; A_1, lamellar microstructure of the wall; A_2, concentric lamellae in a broken off tuberculum; A_3, general view of a spine with deformed base. **B**. SMNH Ar 63454, sample 6/66.2; B_1, lateral view of a prominent spine; B_2, view on the apical part of the spine covered with reticulation and tubercles. **C**. SMNH Ar 63455, sample 6/66.2; C_1, close-up of C_2, tubercles and surface reticulation; C_2, overall view of a tuberculate cone; C_3, tuberculum enlarged. **D**. Paired tuberculate cones, SMNH Ar 63459, sample 7/55; plan view. **E**. Tuberculate cone, SMNH Ar 63457, sample 7/54; E_1, general view; E_2, close-up of E_1, tubercules and surface reticulation. **F**. Prominent spine with weathered tubercles, SMNH Ar 63458, sample 7/54; lateral view. **G**. SMNH Ar 63456, sample 6/66.2; G_1, G_2, cuticular fragment with conical spine and residual reticulation. Scale bar: A_1, A_2, 15 μm; C_1, C_3, 60 μm; E_2, 120 μm; B_2, C_2, D, G, 300 μm; A_3, B_1, E_1, F, 600 μm.

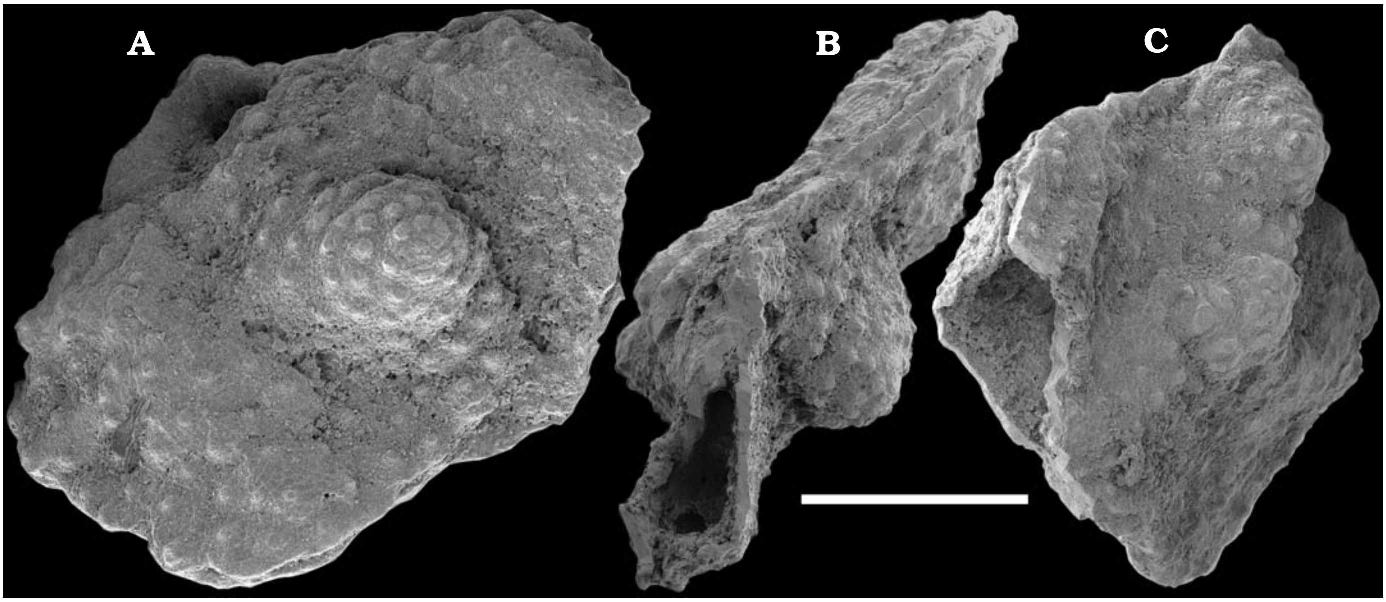

Fig. 60. Carapace fragment of a ?bradoriid from lower Cambrian Emyaksin Formation, Bol'shaya Kuonamka River, Anabar Uplift, Siberia; SMNH Ar 63461, sample 7/55. **A**. Plan view. **B**, **C**. Oblique views on the fragment. Scale bar 300 µm.

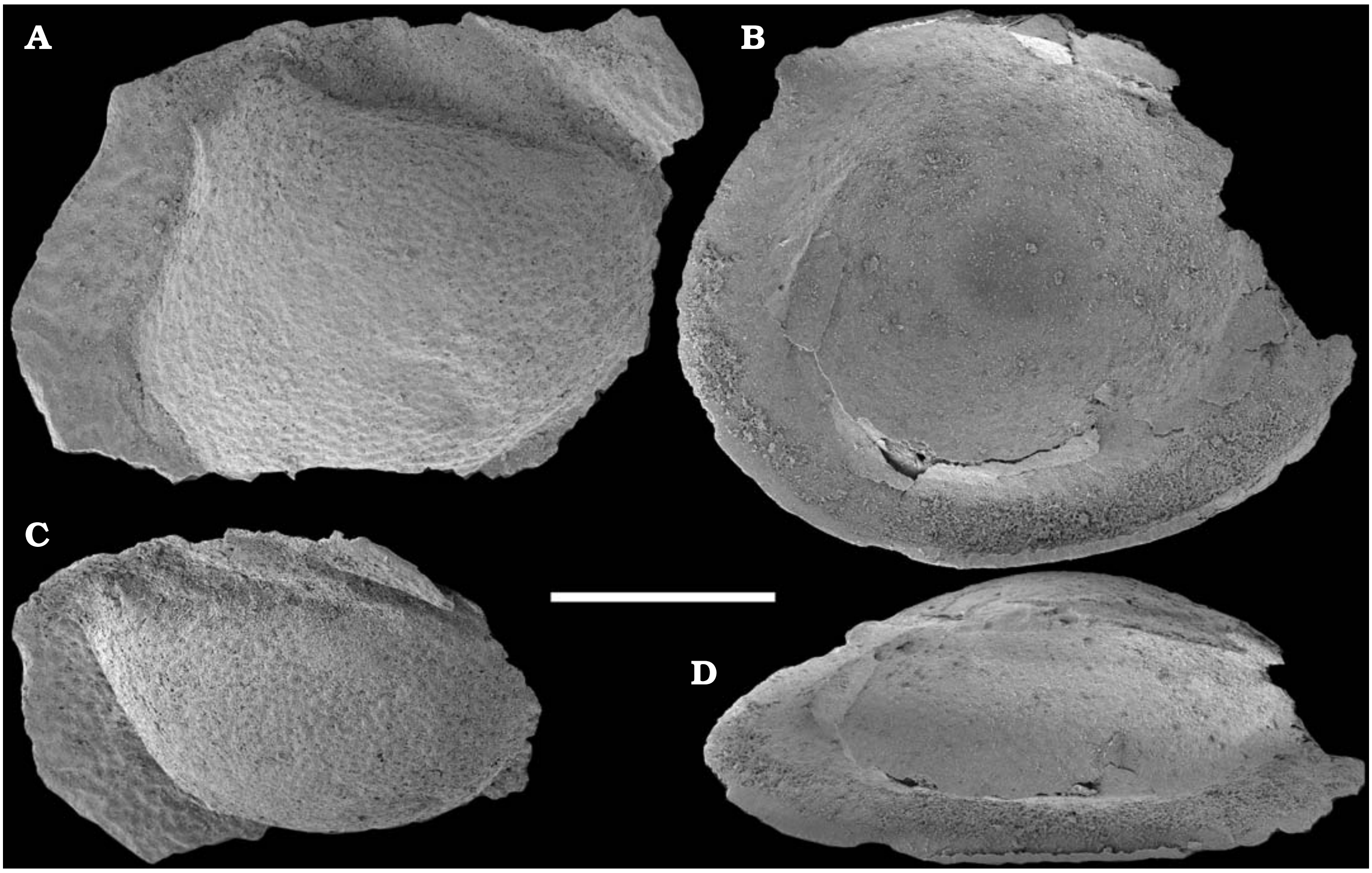

Fig. 61. Carapace fragment of a ?bradoriid from lower Cambrian Emyaksin Formation, Bol'shaya Kuonamka River, Anabar Uplift, Siberia; SMNH Ar 63462, sample 7/27.5. A. View on the outer surface. **B**. View on the inner surface. **C**. Oblique view on the outer surface. **D**. Oblique view on the inner surface. Scale bar 600 µm.

the sculpture is fragmentarily and indistinctly preserved. The inner layer is composed of thin laminae. Lamination is present in fracture sections of the spines (Fig. 59A). Individual laminae are ca. 0.5 µm thick and run parallel to the surface of the wall (Fig. 59A$_1$). Concentric lamination is also observed in broken-off tubercles (Fig. 59A$_2$).

Similar cap-like tuberculated cones of calcium phosphatic composition were described as *Cambrocassis verrucatus* Missarzhevsky, 1977, from the Atdabanian Stage of Siberia and Mongolia (Missarzhevsky 1977; see also *Cambrocassis* sp. in Missarzhevsky 1989: pl. 30: 3). The specimens described herein are also very similar to *Nikolarites spasskyi* Vasil'eva, 1994 from the upper Atdabanian Stage of the Lena-Aldan region in Siberia (Vasil'eva 1994, 1998). These fossils probably represent parts of arthropod, probably bradoriid carapaces (Dzik 2003; Skovsted et al. 2006). Low tuberculate cones are twice as abundant as tuberculate spines in the collection (62 cones and 32 spines can be recognised). This may suggest that there were at least two low cones per tuberculate spine on each side of carapace. This is also consistent with the presence of cuticular fragments with paired cones (Figs. 59D, 60A$_3$).

Two fragments representing almost isodiametric valves presumably formed an originally bivalved carapace (Fig. 61). The outer surface of the valves is convex and covered with a subdued reticulation. A duplicature is present along the inner side of one of the valves (Fig. 61A$_4$).

Phylum Echinodermata Klein, 1734

Class Eocrinoidea Jaekel, 1918

Order and family uncertain

Brachiolar plates A

Fig. 62.

Material.—Several hundred brachiolar (and thecal) plates from sample 7/42.3, including figured SMNH Ec 31488–31495, and several tens of plates from sample 7/45. Emyaksin Formation, Bol'shaya Kuonamka River; correlated with the *Delgadella anabara* Zone, Atdabanian Stage. The plates occur as accumulations within a ~2.5 m thick interval of the Emyaksin Formation. Their abundance sharply declines in a silty, sandy limestone sample 7/45, in comparison to an older clayey limestone sample 7/42.3. Echinoderm plates from samples 7/42.3 and 7/45 are mainly replacements of the original calcite by dolomite.

Description.—The brachiolar plates are preserved as articulated pairs (Fig. 62A–C, G, H) or isolated elements (Fig. 62E, F) that are crescent- or hoof-shaped in section. The plates may reach 1 mm in length, but commonly are ca. 0.5 mm long. Most of the plates are elongated, with a length-to-width ratio of 1–2 (Fig. 62), taper distally and are slightly to strongly twisted longitudinally (Fig. 62A$_2$). Two opposed plates abut along two narrow longitudinal ridges (Fig. 62A$_1$, A$_4$, B$_2$, H), which delimit a large, oval aboral canal, up to ½ of the articulated pair in width (Fig. 62G, H). The articulation between the two opposite plates is median and symmetric. The aboral surface is convex. The oral surface of the articulated pairs is highly concave, with variable oral opening and high lateral walls (about ½ of ossicle in height). The oral surface is composed of a median furrow bordered by fine, slightly developed ridges and flanked by two variably developed lateral depressions (Fig. 62A$_1$, B$_1$, C). The distal and proximal articulation surfaces range from almost flat (Fig. 62A, G, H) to irregularly undulose (Fig. 62B, C) and have a depression surrounding the aboral canal (Fig. 62G, H).

Remarks.—At least one species with blastozoan feeding appendages is present in the studied assemblage. The absence of brachioliferous thecal, "basal" and columnal plates from the assemblage precludes, however, any reconstruction of the theca, whereas the associated thecal plates (see below; Fig. 62G–L) may derive from non-eocrinoid species. The elongated conical shape of most of the brachiolar plates suggests that each brachiole, unbranched and helically twisted, consisted of a relatively few stacked biserial plates. Helically twisted brachioles are known from different gogiids, including the middle Cambrian *Gogia spiralis* (Robison, 1965). The oral groove of the brachiolar plates represents a complex tripartite food groove, probably originally lined with the radial water vessel in the middle and two lateral neural strings (Clausen et al. 2009). The large longitudinal canal penetrating the brachioles and underlying the food groove presumably housed a neural branch (Clausen et al. 2009; Sprinkle 1973). Sprinkle (1973) described such a canal from middle Cambrian gogiids, such as *Gogia spiralis* and a younger derived eocrinoid (Sprinkle 1973: fig. 5c), but noted that the canal is usually absent from blastozoan appendages.

The described plates from the middle Atdabanian Stage of Siberia are among the earliest record of echinoderm skeletal elements (Clausen and Peel 2012; Kouchinsky et al. 2012; Zamora et al. 2013). Together with an elongated fragment of a brachiolar plate from the upper Atdabanian Stage of Siberia (Rozhnov et al. 1992: pl. 6: 12), they are probably the oldest brachiolar remains reported so far. Most authors agree that blastozoans ("brachiole bearing echinoderms") are probably derived (e.g., David et al. 2000; Paul and Smith 1984) from edrioasteroids (without feeding appendages). The oldest known edrioasteroids are also reported from the upper part of Cambrian Stage 3–lower Stage 4 (see below; Zamora et al. 2013). Therefore, the earliest brachioliferous echinoderms from Siberia demonstrate a very fast but still poorly illustrated initial diversification of echinoderms during Stage 3.

Brachiolar plates B

Fig. 63A–D.

Material.—Several tens of disarticulated plates from sample 7/70, including figured SMNH Ec 31500–31503, samples 7/64 and K1-3B. Emyaksin Formation, Bol'shaya Kuonamka and Malaya Kuonamka rivers; *Judomia* Zone (sample 7/64), Atdabanian Stage and *Calodiscus*-*Erbiella* Zone, lower Botoman Stage. The plates discussed here and below preserve the original stereom microstructure coated and/or replaced by phosphate.

Description.—The brachiolar plates are preserved as disarticulated elements, crescent- or hoof-shaped in cross-section (Fig. 63A, B$_1$, C$_2$, D$_2$) and slightly tapering distally (<5°). The plates reach 0.5 mm in length, but are commonly 0.3–0.4 mm

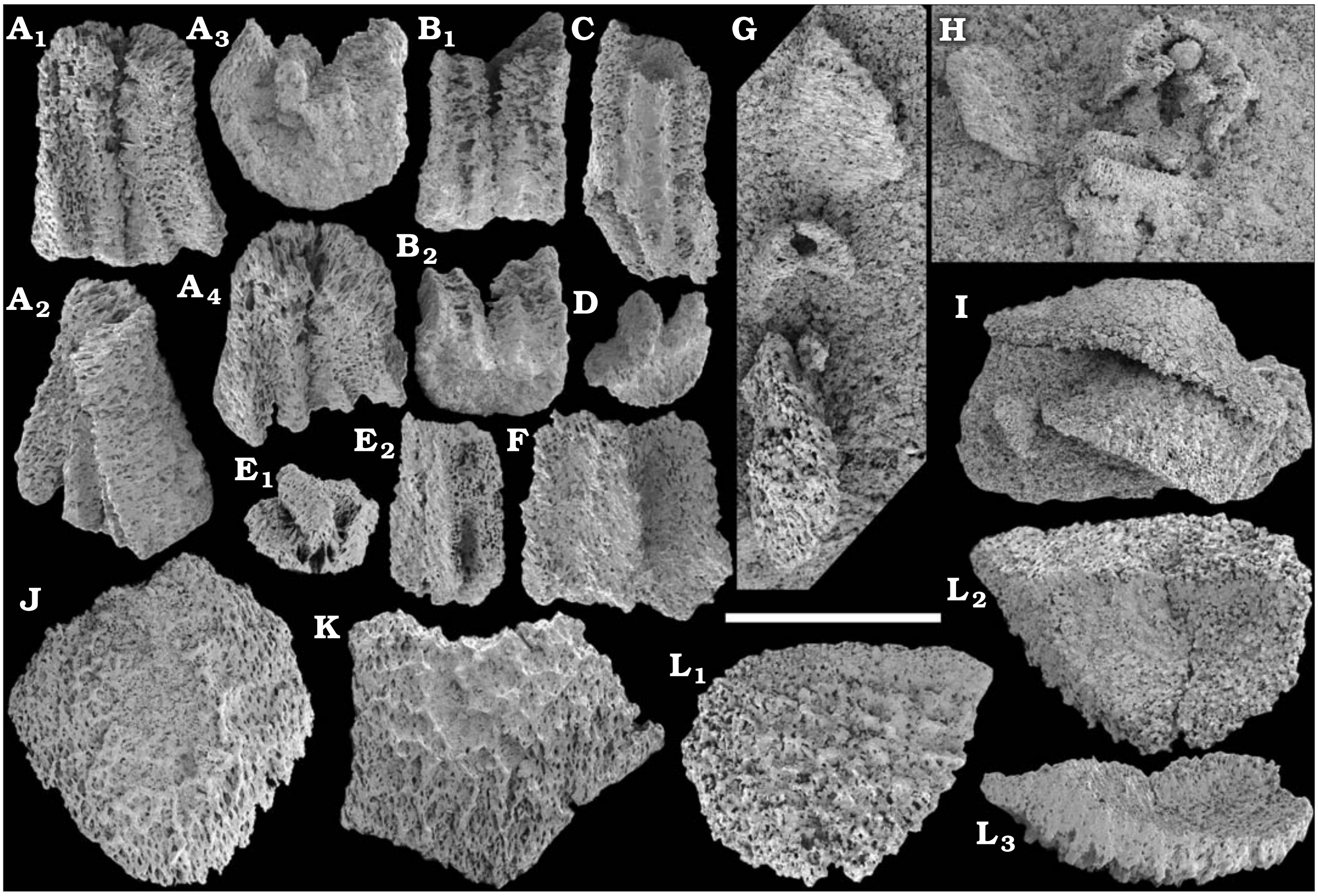

Fig. 62. Eocrinoid brachiolar plates A (A–H) and associated thecal-plates (I–L) from lower Cambrian Emyaksin Formation, Bol'shaya Kuonamka River, Anabar Uplift, Siberia; sample 7/42.3. **A**. Twisted, elongated, brachiolar-plate, SMNH Ec 31488, A_1, view of longitudinal articulation (proximal articulation to the base); A_2, lateral, oral view (proximal articulation to the base); A_3, close-up of proximal articulations with depression surrounding the aboral canal (to the left) and oral groove on the left (composed of half median-furrow and lateral depression to the right); A_4, oblique view of distal (upward) and longitudinal articulations. **B**. Plates articulated longitudinally with irregularly undulose proximal and distal articulation facets, SMNH Ec 314899; B_1, oral view with aboral canal visible upward due to the slightly eroded floor of oral, median furrow (proximal articulation to the base); B_2, oblique view of proximal articulation with crescentic concavity (aboral canal most probably secondary filled) and distinct tripartite food-groove. **C**. Oral view of 2 plates articulated longitudinally with undulose, offset proximal (to the base) and distal articulations, SMNH Ec 31490. **D**. Distal view of isolated brachiolar plates with concave articulation, wide oral-groove (upper-left) and large, oval aboral-groove (upper-right), SMNH Ec 31491. **E**. Flat and elongated brachiolar plate, SMNH Ec 31492; E_1, oblique view of proximal articulation (aboral canal to the right); E_2, oblique aboral view of the longitudinal articulation (made of two longitudinal ridges delimiting aboral canal; to the right), the flat distal (to the top) and the angular proximal articulation (to the base). **F**. Flat brachiolar-plate in lateral (median) view with flat longitudinal articulation-ridge (aboral canal to the right), SMNH Ec 31493. **G**. Two articulated brachiolar plates (to the middle) delimiting a large, oval aboral-canal partly preserved in diagenetized matrix with thecal plates of unknown affinity (to the top and base), SMNH Ec 31494. **H**. Articulated (in the middle, aboral canal filled by exogenous grain) and isolated brachiolar plates partly preserved in diagenetized matrix, SMNH Ec 31495. **I–L**. Rounded to polygonal, concavo-convex thecal plates of unknown affinity. **I**. Outer view of plates partly preserved in matrix, SMNH Ec 31496. **J**, **K**. Outer views of plates ornamented with meshwork, SMNH Ec 31497 and SMNH Ec 31498, respectively. **L**. SMNH Ec 31499, slightly broken, rounded thecal-plates; L_1, outer-surface ornamented with tubercles; L_2, inner and L_3, lateral view showing the smouth concave inner surface. Scale bar: 600 μm, except I, 1200 μm.

long. The elongation of the brachiolars varies, from a length-to-width ratio >1 (Fig. 63D_1) to 1/3 (Fig. 63B_2). Two opposed plates abutted along two flattened articulation surfaces (Fig. 63A–D, arrowed) which delimited an aboral canal. The posterior articulation surface can be significantly larger than the anterior one and forms up to half the ossicle in height. The concave oral surface of the articulated pair of brachiolars was delimited by lateral walls and consisted of a median furrow flanked by two furrows located in the lateral walls. In lateral view, the lateral walls are generally straight along the oral aperture, but the lateral articulation (between the two opposite rows of plates) varies from almost flat (Fig. 63D_1, left side) to triangular (Fig. 63C_1, right side). Proximal and distal facets carry a depression surrounding the aboral canal and are delimited by a peripheral rim.

Remarks.—The ossicles constituted a biserial, probably unbranched appendage, rounded in cross-section, slowly tapered distally, but not twisted, like most eocrinoid and blastozoan appendages. Within the biserial brachioles the plates were opposite (with a straight suture and flat lateral articulation) to offset (undulose suture and triangular lateral articulation). Similar to the brachiolar plates A (see above), there was a complex tripartite food groove, probably lined with a radial water vessel in the middle and two lateral neural strings; a large longitudinal canal underlying the food groove presumably housed a neural branch. This described anatomy of the brachiolar plates might have been common in the earliest blastozoans (but see Sprinkle 1973). The brachiolar plates B may belong to an unknown eocrinoid species. However, based on the difference in articulation and associated brachioliferous plates without aboral canal as well as brachial plates (see below), several brachioliferous taxa may have been present in the assemblage.

Brachioliferous thecal plates

Fig. 63J, K.

Material.—Two disarticulated plates SMNH Ec 31504 and 31505 from sample 7/70. Uppermost Emyaksin Formation, Bol'shaya Kuonamka River; *Calodiscus-Erbiella* Zone, lower Botoman Stage. The plates are secondarily phosphatised.

Description.—Brachioliferous plates, rounded to polygonal, with a concave interior and convex exterior surface. The exterior convexity leads to a single (Fig. 63J, arrowed) or double (Fig. 63K_1, K_2, arrowed) lateral insertion facet for brachioles. The insertion facets are circular to triangular, with an oblique food groove opening to the plate margin. There is no definitive evidence for an aboral canal. Epispires either absent or more or less developed rounded, without peripheral rim (Fig. 63K_3).

Class, order, and family uncertain

Brachial plates

Fig. 63E–I.

Remarks.—On account of overall similarities, the nomenclature adopted below is based on the terminology generally dedicated to crinoid arm description. It should not be interpreted as a tentative assignation to this taxon, and the plates are described under open nomenclature. Uniserial unbranched ossicles and bifurcating elements can be recognised in the studied material, but their external features differ significantly, so that they may represent different taxa. For this reason, they are described separately in the following section. These plates also exhibit characters known from both blastozoan and crinozoan appendages (Clausen et al. 2009, 2012; Guensburg et al. 2010). The diagnostic features or apomorphies of both groups are debatable, since the plasticity of appendage structure of Cambrian pelmatozoans has been convincingly illustrated (Zamora and Smith 2011).

Brachial, unbranched ossicles (brachitaxial)

Fig. 63E–H.

Material.—Five plates, including SMNH Ec 31506–31509, from sample 7/70. Uppermost Emyaksin Formation, Bol'shaya Kuonamka River; *Calodiscus-Erbiella* Zone, lower Botoman Stage.

Description.—Arm ossicles (brachials), cylindrical with a circular to slightly oval cross-section, slightly convex latus and a concave oral furrow. They are 0.4–0.6 mm in length and 0.3–0.5 mm in width/height, with a length-to-width ratio of 0.7–1.3. A longitudinal food groove runs along the entire length of the oral surface between relatively high (ca. ⅓ of the ossicle height) lateral walls. It is composed of a central furrow bounded by two relatively low ridges and flanked by a pair of lateral shallow furrows. Proximal and distal articulation surfaces are hoof-shaped and bounded by a distinct and raised peripheral rim, which extends to the edges of the food groove. The rim delimits a central concavity that leads to an oval to crescent-shaped canal 0.05–0.15 mm wide, up to ⅓ of the the articulation surface in width and height, slightly shifted towards the median furrow of the food groove. The canal is more or less filled (with a secondary claustrum-like stereom?) at a distance from the articulation surface. The distal and proximal articulation surfaces range from flat to highly irregularly undulose. Up to four "culminae" and "crenella" are observed on the undulose articulum (Fig. 63F_3). The stereom of the latus is generally obliterated and secondarily filled. The stereom underlying the oral food groove represents a coarse and open, labyrinthine meshwork. The articulation concavity of well-preserved specimens apparently carries aligned structures (Fig. 63H_2), probably representing the galleried stereom (for insertion of ligament bundles).

Brachial, bifurcating ossicle (axillary)

Fig. 63I.

Material.—Single specimen, SMNH Ec 31510, from sample 7/70. Uppermost Emyaksin Formation, Bol'shaya Kuonamka River; *Calodiscus-Erbiella* Zone, lower Botoman Stage.

Description.—The ossicle is cylindrical and tapers slightly distally, ca. 0.8 mm high, ca. 1 mm long and wide, almost quadrangular in oral view, with a slightly ovate cross section. A thin, shallow, longitudinal food groove runs between low-relief oblique lateral walls along the entire length of the oral surface. The groove branches heterotomously at ca. ⅔ length from the proximal facet, producing distal bifurcation of the ossicle. Proximal and distal branches of the furrow are similar in organization. They are composed of two parallel, thin and shallow furrows (~50 μm in width and depth) separated by a median, relatively large ridge (~100 μm wide) with flat to convex upper surface, without transverse channels. The furrows are bounded laterally by oblique, slightly convex walls, which bear rounded notches prolonged to the food groove (Fig. 63I, arrowed). The notches alternate on the two sides of the ossicles. There are four or five notches on the non-bifurcating side, whereas there are two notches below and one above the bifurcation on the opposite side. The two distal facets are confluent adaxially. The larger distal facet is aligned with the proximal facet, whereas the smaller

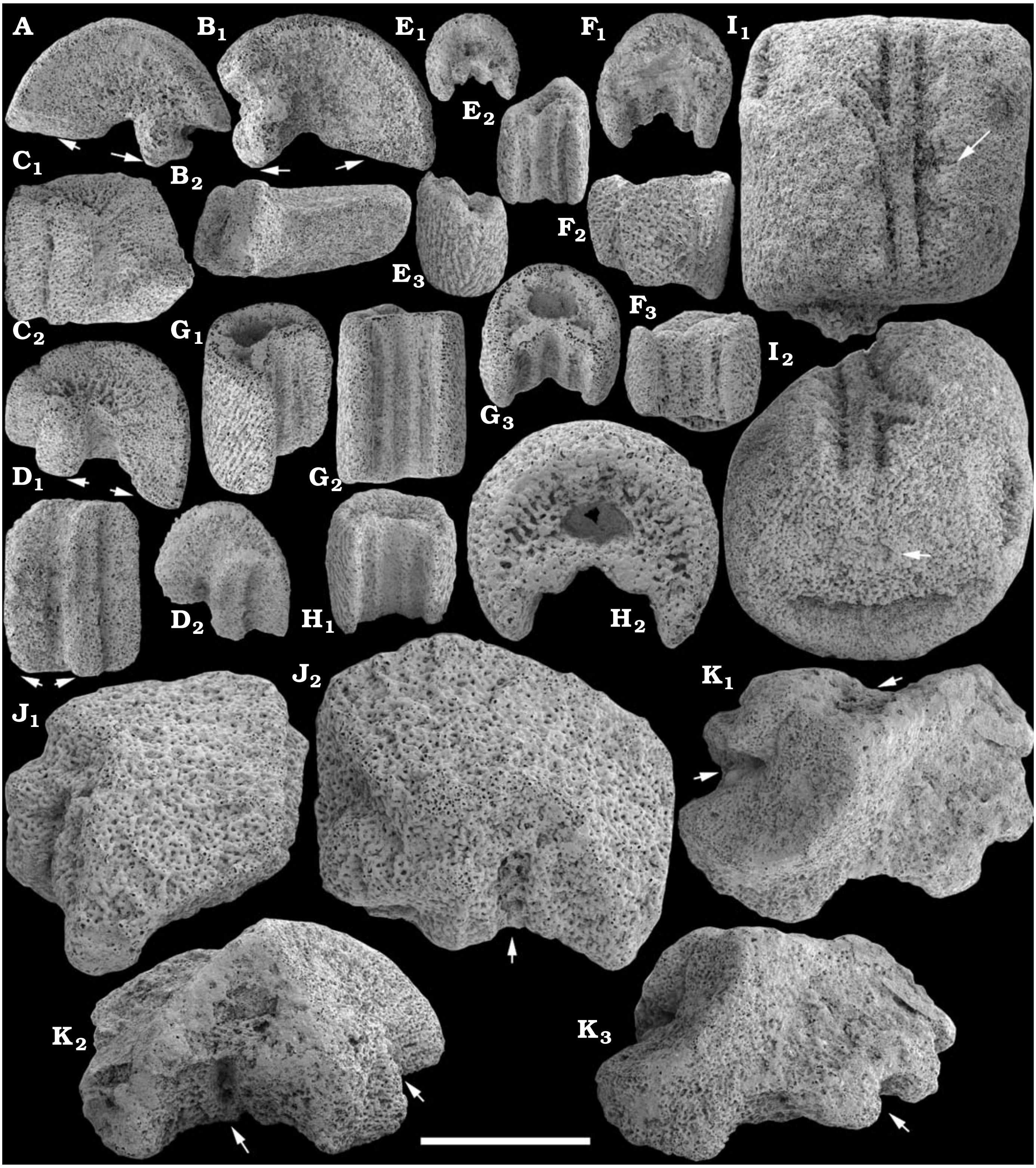

Fig. 63. Eocrinoid brachiolar B (A–D) and brachioliferous (J, K) plates, with associated uniserial brachitaxial (E–H) and axillary (I) plates of unknown affinity from lower Cambrian Emyaksin Formation, Bol'shaya Kuonamka River, Anabar Uplift, Siberia; sample 7/70. **A**. Axial view of brachiolar plate (oral groove to the right) with longitudinal articulation surfaces arrowed, SMNH Ec 31500. **B**. Brachiolar plate with a low length-to-width ratio and concave distal and proximal articulation surfaces, SMNH Ec 31501; B_1, axial view (longitudinal articulation surfaces arrowed); B_2, lateral view (oral groove to the left in B_1 and B_2). **C**. Brachiolar plate with almost triangular lateral articulation, SMNH Ec 31502; C_1, lateral view of longitudinal articulation and oral groove (to the left); C_2, oblique view of concave axial-facets and longitudinal articulation surfaces (arrowed). **D**. Elongated brachiolar plate with almost straight, posterior longitudinal articulation, SMNH Ec 31503; D_1, lateral view of longitudinal articulations (arrowed) and oral groove (to the right); D_2, oblique view of slightly depressed axial-articulation (oral groove to the right). **E**. Brachial unbranched ossicle (brachitaxis) with oval aboral canal, →

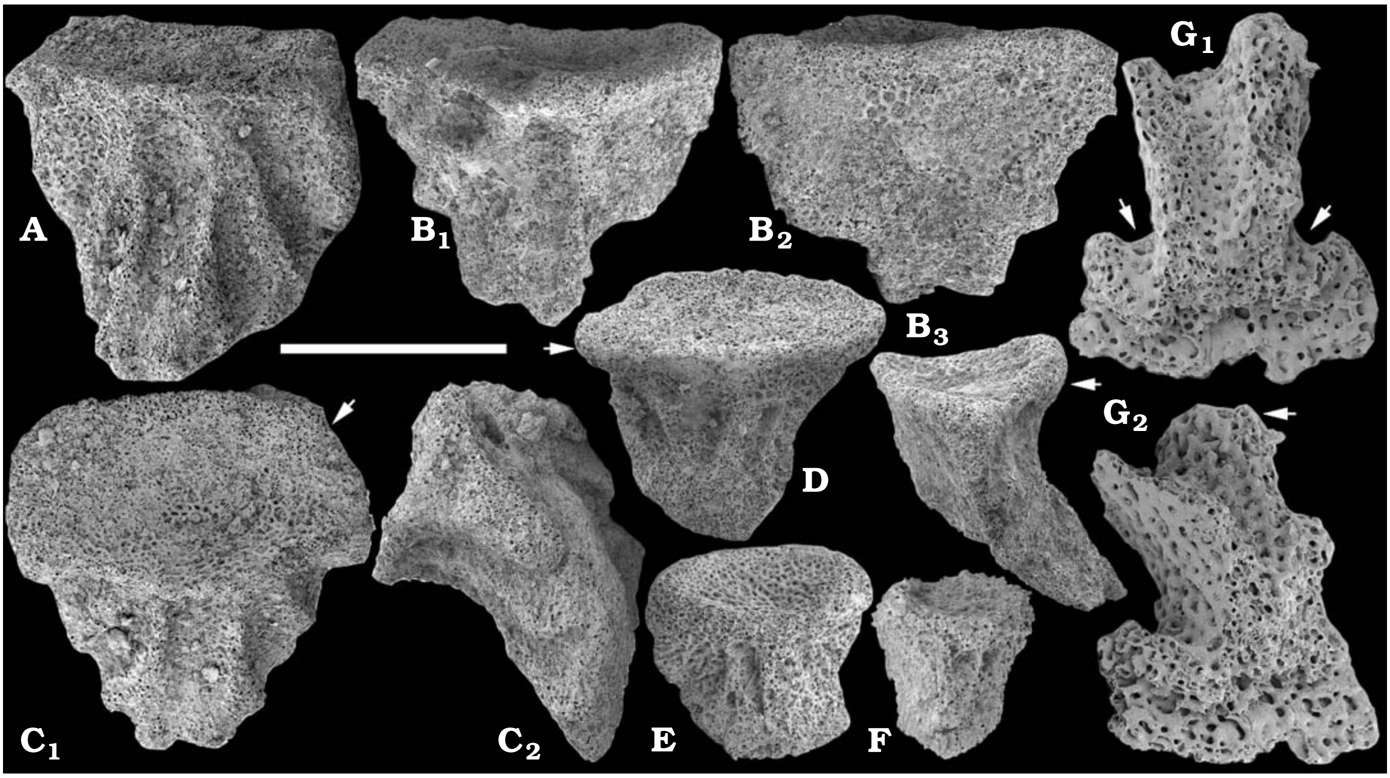

Fig. 64. Edrioasteroid thecal-plates from lower Cambrian Emyaksin Formation, Bol'shaya Kuonamka River, Anabar Uplift, Siberia. **A**. SMNH Ec 31511, sample 7/70; view of triangular-surface of a thecal-plate with 6 ridges radiating from concave base (at the top). **B**. SMNH Ec 31512, sample 7/70; B_1, view of triangular surface with 4 ridges radiating from the concave base (at the top); B_2, view of the opposite, smooth triangular surface; B_3, lateral view (peripheral rim of concave base arrowed) of the claw-like plate. **C**. SMNH Ec 31513, sample 7/70; C_1, oblique view of concave base (peripheral rim arrowed) and triangular surface bearing radiating ridges; C_2, lateral view. **D**. SMNH Ec 31514, sample 7/70; view of triangular, ridged surface and perpendicular concave base (rim arrowed). **E**. SMNH Ec 31515, sample 7/70; view of trapezoidal surface with faint ridges and perpendicular, rimmed concave-base (to the top). **F**. SMNH Ec 31516, sample 7/64; view of faintly ridged surface and concave base (at the top). **G**. Edrioasteroid ambulacral plate, SMNH Ec 31517, sample 7/70; G_1, upper view (lateral sutural pore/gap arrowed); G_2, oblique view (lateral, abradial? prong arrowed). Scale bar: 600 µm, except G, 300 µm.

one (~0.4 mm wide) is inclined at about 45°. Articulation facets are flat and oval, with a large crescent-shaped pit on the aboral part. A faint median depression (median canal?) is visible on a best-preserved, larger distal-facet (Fig. 63I_2, arrowed), but seems to be filled by secondary, labyrinthine dense and coarse stereom.

Remarks.—The uniserial ossicles described herein are the earliest known so far. They differ from each other by the presence or absence of the aboral canal and by the structure of their oral food groove. They may come from different taxa or from different portions (proximal/distal) of the same appendage. A possible interpretation is that these uniserial plates would represent distal/proximal portions of a biserial appendage represented by the brachiolars described above. However, the uniserial and brachiolar plates clearly differ in terms of the organization of the oral food groove and lateral walls. Uniserial brachials are also described from the middle Cambrian of Australia (Clausen et al. 2009) and Laurentia (Clausen and Peel 2012), but their affinity is still debated (see Guensburg et al. 2010). Uniserial plates are also known from Ordovician blastozoans (e.g., *Rhipidocystites*; Guensburg et al. 2010) and paracrinoids (Parsley and Mintz 1975). However, as in *Rhipidocystites*, blastozoan uniserial brachioles have the morphology of two fused brachiolar plates, most probably representing biserial arrangement with a "suppressed" biserial suture (still visible in some cases; Sprinkle 1973: fig.

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tripartite oral-groove and one undulose articulation-facet, SMNH Ec 31506; E_1, axial view of articulation facet; E_2, oral view showing the flat (to the base) and undulose (to the top) articulation surfaces; E_3, aboral view. **F**. Brachitaxis with (secondarily?) filled aboral canal and undulose articulum, SMNH Ec 31507; F_1, axial view; F_2, lateral view showing the taller aboral-culminae; F_3, oral view illustrating the offset proximal and distal culminae. **G**. Elongated brachitaxis with almost flat articulation surfaces and large elliptical aboral canal surrounding by crescentic, concave area, SMNH Ec 31508; oblique lateral (G_1), oral (G_2), and oblique oral (G_3) views. **H**. Well-preserved brachitaxis with relatively large, oval aboral-canal, almost close half-way by a claustrum like structure, surrounded at articulation surface by a concavity made by aligned structures, SMNH Ec 31509; H_1, oral view, H_2, axial view of articulation surface and aboral canal. **I**. Brachial, bifurcating ossicle (axillary), SMNH Ec 31510; I_1, oral view with lateral notches of the food groove arrowed; I_2, distal view with (secondarilly) filled aboral canal arrowed. **J**. Brachioliferous plate lacking epispires, SMNH Ec 31504; J_1, lateral view; J_2, upper view (median canal of insertion facet arrowed). **K**. Brachioliferous plate with two insertion-facets for free-appendage and rounded epispires, SMNH Ec 31505; K_1, upper view (insertion facets arrowed); K_2, lateral view of insertion facets (arrowed); K_3, lateral view showing one articulation facet (to the left) and rounded epispire (arrowed). Scale bar: 600 µm, except H_2, 300 µm.

5C). In *Rhipidocystites*, the uniserial plating is not constant. In *Haimacystis* (Sumrall et al. 2001), this apparent uniseriality is present only distally on the appendage. Rare solute blastozoans also exhibit uniseriality, probably owing to cryptic aboral suture (*Minervaecystis* Caster, 1968). In paracrinoids, the primary uniserial arms have a large aboral cavity, which connects with the thecal cavity (e.g., *Comarocystites*; Parsley and Mintz 1975). The cavity disappears distally and in the "pinnules" (lateral branches of the arms). However, the structure of the feeding groove in paracrinoids is still poorly illustrated, and comparison with the peculiar feeding groove of the axillary plate described herein is not possible.

Recent data based on disarticulated remains (including the newly described Siberian assemblage) demonstrate that the feeding appendages of the earliest echinoderms are actually more diverse in structure than previously assumed and that the uniserial feeding appendage is present since the Cambrian Stage 3–Stage 4 transition. Brachiolar plates described herein also demonstrate that the aboral canal was present in the earliest blastozoans and indicates that the absence of such a structure in some early Ordovician crinoids and numerous blastozoans may be a derived state.

Class Edrioasteroidea Billings, 1858

Order and family uncertain

Edrioasteroid thecal plates

Fig. 64A–F.

Material.—Five disarticulated plates, SMNH Ec 31511–31515, from sample 7/70, two plates from sample K1-3B, and one, SMNH Ec 31516, from sample 7/64. Emyaksin Formation, Bol'shaya Kuonamka and Malaya Kuonamka rivers; uppermost *Judomia* Zone, upper Atdabanian Stage (sample 7/64) and *Calodiscus-Erbiella* Zone, lower Botoman Stage.

Description.—Plates triangular or trapezoidal, nearly symmetrical in plan view and curved claw-like in the lateral view. They consist of a concave and an opposite convex triangular or trapezoidal surface, perpendicular to a slightly concave and smooth face surrounded by a rounded rim (Fig. 64B_3, C_1, D, arrowed). The two sides converge towards an embayed rounded edge. The embayments are produced by four to six more or less distinct ridges radiating from the face on the concave surface of the plate. These ridges are divided into two sets and are situated almost bilaterally symmetrically on the plate. The median pair of ridges runs almost parallel, whereas the lateral ones diverge. The opposite surface lacks ridges (Fig. 64B_2).

Remarks.—Similar plates were illustrated by Hinz (1987: pl. 15; 11), from the Lower Comley Limestone *Callavia* Zone of Avalonian Britain (correlated with the upper Atdabanian–lower Botoman Stages (Brasier 1989b; Brasier et al. 1992), by Landing and Bartowski (1996: 755, fig. 8) and Skovsted (2006: figs. 7.7, 7.8), from the *Bonnia-Olenellus* Zone of Laurentia correlated with Cambrian Stage 4. Two apparently similar plates were also described by Rozhnov et al. (1992: pl. 6: 8, 9) from the uppermost Atdabanian Stage of southeastern Siberian Platform. The plates were tentatively regarded by Landing and Bartowski (1996) as edrioasteroid ambulacral plates, based on comparision with the middle Cambrian *Totiglobus* Bell and Sprinkle, 1978 and with the late early Cambrian echinoderm plates illustrated by Sprinkle (1973: pl. 25) that were later identified as edrioasteroid plates by Sprinkle (see Landing and Bartowski 1996: 755). Plates described by Hinz (1987), Landing and Bartowski (1996), and herein are different, however, from the plates of the mouth frame of *Totiglobus*, which carry sets of more regular deeper vertical parallel ridges and notches oriented along the plate peristomal margin. They are more similar to the plates from the basal attachment disc of *Totiglobus*, which bear parallel to radiating ridges along their inner and outer surfaces (Bell and Sprinkle 1978; Clausen and Peel 2012). Together with the ambulacral plate (see below), the edrioasteroid plates described herein are among the oldest occurrences of edrioasteroids, demonstrating that the latter were already widespread in Cambrian Stage 4 (Clausen and Peel 2012; Zamora et al. 2013).

Edrioasteroid ambulacral plate

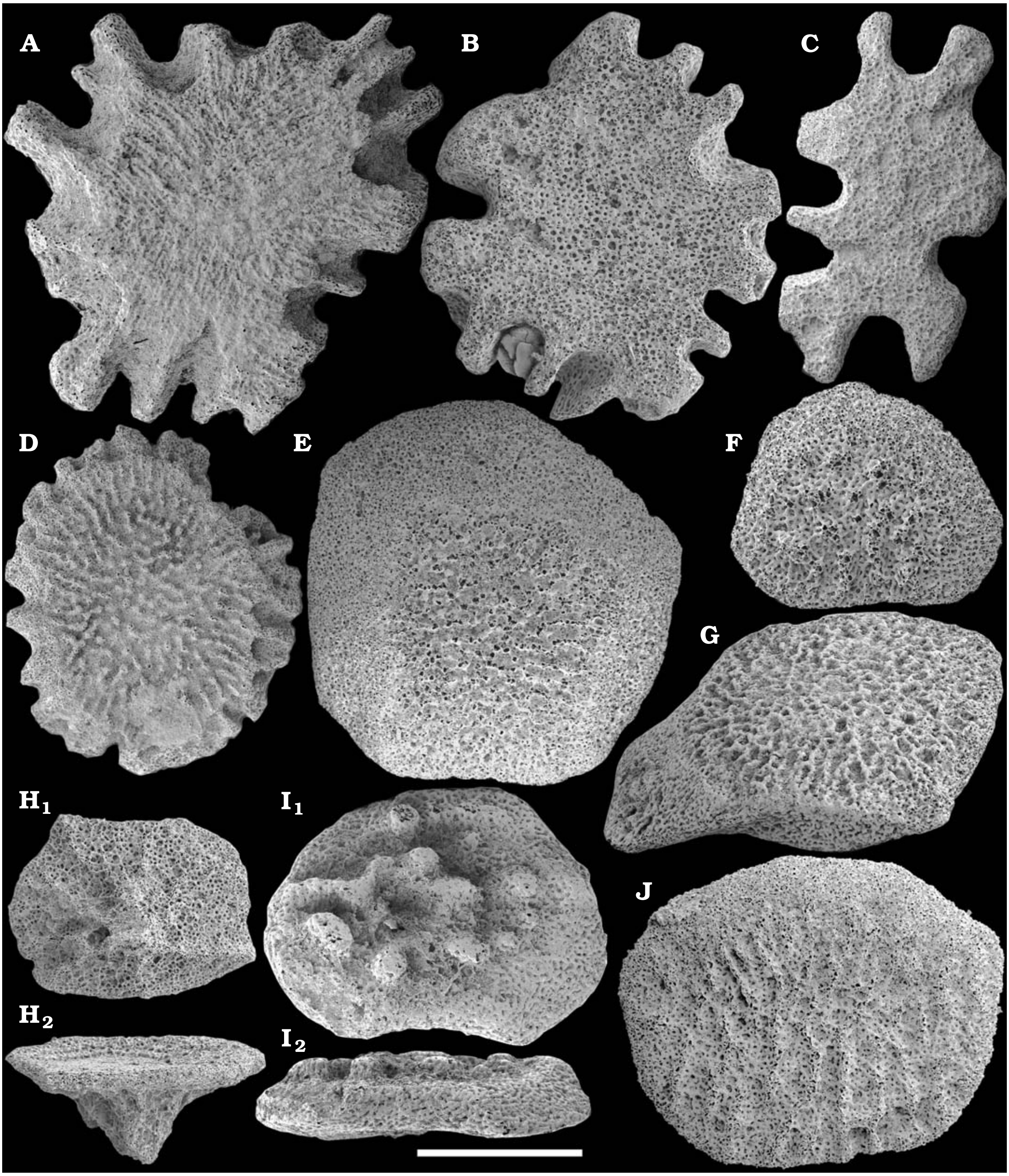
Fig. 64G.

Material.—Single plate, SMNH Ec 31517, from sample 7/70. Uppermost Emyaksin Formation, Bol'shaya Kuonamka River; *Calodiscus-Erbiella* Zone, lower Botoman Stage.

Description.—Ambulacral flooring plate, hourglass-shaped in plan view, ~0.5 mm long. The external (upper) side can be divided into a wider and relatively flat face (adradial?; ~0.4 mm wide) and an elongated, narrower portion (abradial?; ~0.25 mm wide) carrying two poorly delimited elongated lateral sutural pores/gaps (shared with adjacent ambulacral plates when articulated; Fig. 64G_1, arrowed). The abradial(?) portion bears on its upper surface a wide groove that opens abradially(?), bordered by high lateral rims. The rims form short prongs at the extremity of the abradial(?) portion (Fig. 64G_2, arrowed). The adradial(?) facet appears to consist of two flattened portions: the lower one built of an open coarse labyrinthine to reticulated stereom and the upper one of a denser labyrinthine stereom (Fig. 64G_1, G_2, lower part).

Remarks.—An hourglass-shaped plate was also described and illustrated by Hinz (1987: pl. 15: 18) from the Lower Comley Limestone of Avalonian Britain, *Callavia* Zone, but preservation precludes undoubted assignment of the plate. Although the fossil described herein is poorly preserved, it is possible to recognise it as one of the oldest occurrences of ambulacral flooring plates in the fossil record (see also discussion in

Fig. 65. Echinoderm thecal-plates of unknown affinity from lower Cambrian Emyaksin Formation, Bol'shaya Kuonamka River and Malaya Kuonamka River, Anabar Uplift, Siberia; sample 7/70, except J, sample K1-3B. **A**. SMNH Ec 31518; outer view of a plate with large and numerous epispires and external surface ornamented with ridges. **B**, **C**. Smooth, slightly concave inner surface of epispire-bearing plates with various shape and size. **B**. SMNH Ec 31519. **C**. SMNH Ec 31520. **D**. SMNH Ec 31521; outer surface of epispire-bearing plate ornamented with ridges and tubercles. **E**. SMNH Ec 31533; →



outer view of a thick, polygonal-plate lacking epispire and faintly ornamented externally with meshwork sculpture. **F**. SMNH Ec 31522; convex outer surface of rounded to trapezoidal plate, lacking epispire and ornamented with meshwork sculpture. **G**. SMNH Ec 31535; oblique view of slightly convex outer surface of irregular plate ornamented with meshwork sculpture and lateral elliptical, flat abutment surface (to the base). **H**. SMNH Ec 31523, polygonal plate lackning epispires, with almost pyramidal outer surface ornamented with stellate sculpture, and smooth and slighlty concave inner surface; outer (H_1) and lateral (H_2) views. **I**. SMNH Ec 31524, rounded plate with outer surface ornamented with tubercles and lateral, flat abutment-surface; outer (I_1) and lateral (I_2) views. **J**. SMNH Ec 31527, rounded to polygonal plate lacking epispire, with external meshwork ornamentation. Scale bar 600 µm.

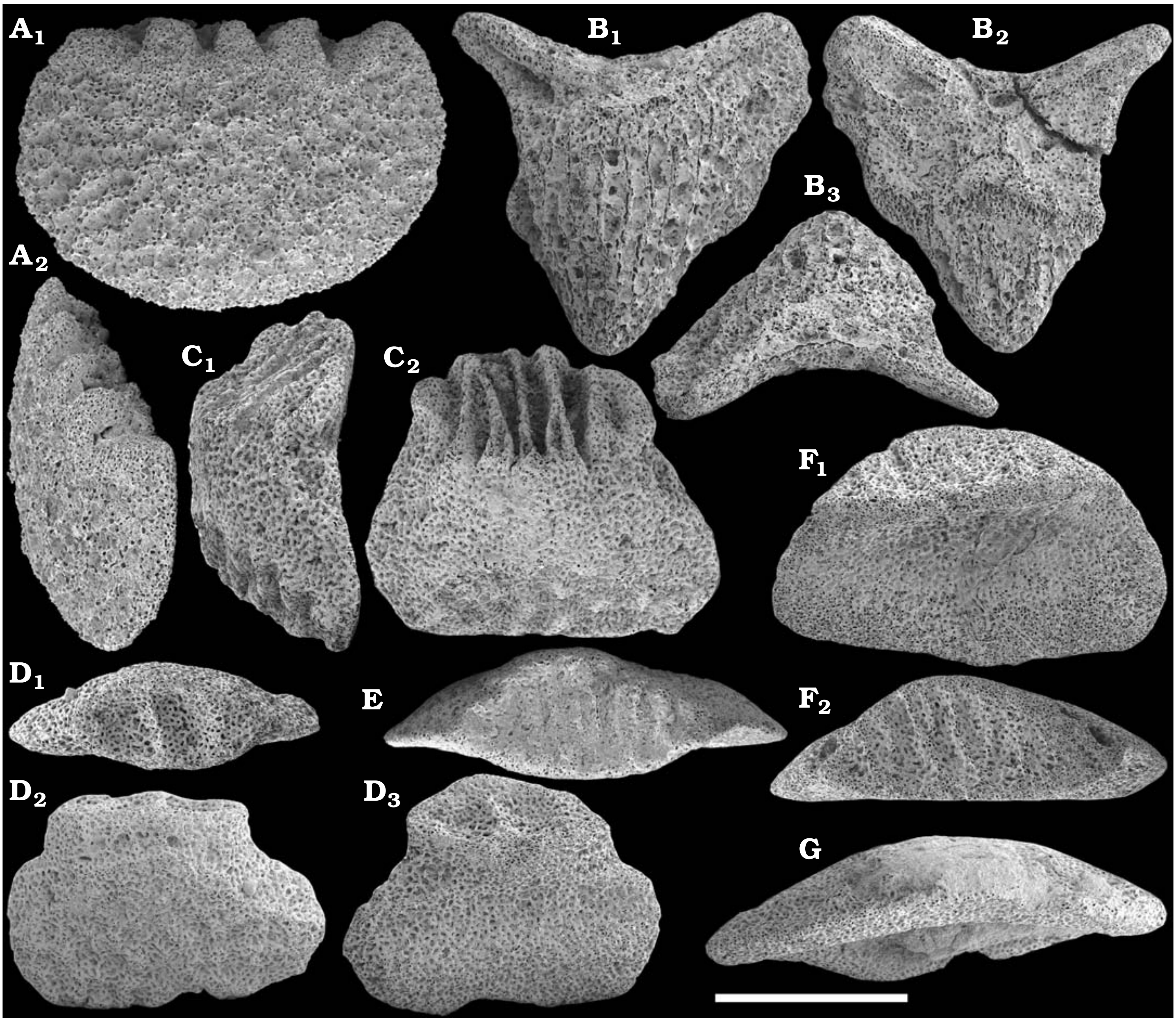


Fig. 66. Echinoderm thecal-plates of unknown affinity from lower Cambrian Emyaksin Formation, Bol'shaya Kuonamka River, Anabar Uplift, Siberia; sample 7/70, except A, sample K1-3B. **A**. SMNH Ec 31528, outer view of elliptical plate with straight truncated-margin bearing 4 notches; external (A_1) and oblique lateral (A_2) views. **B**. SMNH Ec 31529, triangular, thick plate with one curved (abutment?) surface; B_1, outer?, convex surface; B_2, inner?, concave surface; B_3, view of curved abutment? surface (to the top in B_1 and B_2). **C**–**F**. Rounded to trapezoidal-plate with truncated margin bearing comb-like structure (sutural-gaps?). **C**. SMNH Ec 31530, trapezoidal plate with comb-like structure (to the top) and opposite, tuberculated, facet (to the base); lateral (C_1) and outer? (C_2) views. **D**. SMNH Ec 31531, plate with reduced comb-like structure on truncated margin; D_1, view of truncated margin; D_2, convex, outer? surface (truncated-margin to the top); D_3, concave, inner? surface (truncated-margin to the top). **E**. View of ellipsoidal truncated margin bearing shallow comb-like structure; SMNH Ec 31532. **F**. SMNH Ec 31530, rounded plate; F_1, oblique, inner? view; F_2, comb-like structure. **G.** SMNH Ec 31534, smooth, concavo-convex thecal-plate bearing small rounded epispires (to the back-right); oblique lateral-view. Scale bar 600 µm.

Kouchinsky et al. 2011, Clausen and Peel 2012, and Zamora et al. 2013). Edrioasteroidea Billings, 1858 and Helicoplacoidea Durham and Caster, 1963, both possess ambulacral plates similar to the above described. The oldest representatives of both classes are known from the Cambrian Stage 4 of Laurentia, where helicoplacoids are endemic. Erosion of both extremities of the plates precludes any definite recogniton of the adradial face, but abradial prongs, described from some edrioasteroids, are unknown from helicoplacoids.

Class, order, and family uncertain

Thecal plates

Figs. 62I–L, 65, 66.

Material.—Several hundred thecal plates from sample 7/42.3, including figured SMNH Ec 31496–31499, and several tens of plates from sample 7/45. Emyaksin Formation, Bol'shaya Kuonamka River; correlated with the *Delgadella anabara* Zone, Atdabanian Stage. Occurrence and preservation same as described above for the Atdabanian brachiolar plates.

Tens of secondarily phosphatised disarticulated plates from sample 7/70, including figured SMNH Ec 31518–31526 and 31529–31535; several plates from samples K1-3B (including SMNH Ec 31527) and 7/64; one fragmentary plate from sample 7/55. Emyaksin Formation, Bol'shaya Kuonamka and Malaya Kuonamka rivers; *Judomia* Zone, Atdabanian Stage (samples 7/55 and 7/64) and *Calodiscus-Erbiella* Zone, lower Botoman Stage.

Remarks.—It is generally difficult to determine the systematic affinity of disarticulated thecal plates. For example, epispire-bearing thecal plates are described from crinoids, eocrinoids, stylophorans, edrioasteroids, and cinctans. The described assemblage obviously embraces different, but unidentifiable taxa, as demonstrated by the diversity of plate ornamentation and epispire morphology. They are illustrated without detailed description in order to complete the fossil assemblages and facilitate future studies.

The thecal plates are rounded or polygonal in outline, have a plane to concave (presumably internal) and plane to convex (external) surfaces. The plates thin out at the margins, but in some specimens a flattened abutment(?) face occurs. The internal surface is relatively smooth (Fig. 65B, C), whereas the external surface can be ornamented with ridges (Fig. 65A), meshwork (Figs. 62J, K; 65E–G, J; 66A$_1$), tubercles (Figs. 62L$_1$, 65D, I$_1$, 66C$_2$), or pyramidal and stellate sculpture (Fig. 65H). Epispires are indistinct in the Atdabanian thecal plates (Fig. 62G–L), but can be well developed in the Botoman plates (Fig. 65A–D). Some plates are trapezoidal in outline and have a truncated margin, which bears comb-like structures of the sutural gap, whereas the rest of the margin is smooth (Fig. 66A, C–F). Rounded thecal plates with a similar truncated margin carrying comb-like structures were described by Rozhnov et al. (1992: pls. 5, 6) from the upper Stage 3 of Siberia and attributed to eocrinoids. One plate of an oval outline has a straight truncated margin with four notches (Fig. 66A). Another single plate has a triangular outline and one side convexly curved (Fig. 66B).

Phylum and class uncertain

Order Hyolithelminthida Fisher, 1962

Family Hyolithellidae Walcott, 1886

Genus *Hyolithellus* Billings, 1871

Type species: Hyolithes micans Billings, 1871; *Bonnia-Olenellus* Zone, Dyeran Stage; Troy, New York State, USA.

Hyolithellus cf. *H. insolitus* Grigor'eva in Voronin et al., 1982

Fig. 67A, C, D, F.

Material.—Several calcium phosphatic tubes, including SMNH X 4798–4801, from samples 7/19, 7/36.7, and 7/39.5. Emyaksin Formation, Bol'shaya Kuonamka River; correlated with the *Dokidocyathus lenaicus* Zone, Tommotian Stage (sample 7/19) and *Delgadella anabara* Zone, Atdabanian Stage.

Description.—Straight, slightly diverging, a few mm long, fragments of tubes with circular cross-section, 0.2–0.6 mm in diameter (Fig. 67A, C, D, F). The external ornamentation consists of weak concentric ribs and faint longitudinal ridges and furrows undulating between the ribs.

Remarks.—The forms herein are similar to *Hyolithellus insolitus* Grigor'eva in Voronin et al., 1982 described from the lower Cambrian of Mongolia (see also Esakova and Zhegallo 1996) and southeastern Siberian Platform (Sokolov and Zhuravleva 1983). Other forms illustrated herein under *Hyolithellus* sp. (Fig. 67B, E, G) lack longitudinal striation. *H. insolitus* or similar tubes with transversal annulation and longitudinal stiation are also reported from the lower Cambrian of India (Brasier and Singh 1987), South China (Esakova and Zhegallo 1996), Australia (Skovsted and Peel 2011), lower–middle Cambrian of Laurentia (Skovsted and Holmer 2006), and middle–upper Cambrian of Kazakhstan (Esakova and Zhegallo 1996).

The tubes from samples 7/36.7, 7/39.5, and an eroded specimen of *Hyolithellus* sp. from sample 7/25.6 (Fig. 67E), have numerous circular or oval to rounded sub-rectangular holes, 20–60 μm in diameter, in their wall. These are interpreted to result from bioerosion which occured before deposition into the sediment (see Discussion in *Torellella* below). According to Skovsted and Holmer (2006), the species may be a junior synonym of *H. grandis* Missarzhevsky in Rozanov et al., 1969, but the holotype of the latter is much larger and preserved on the rock slab.

Family Torellellidae Holm, 1893

Genus *Torellella* Holm, 1893

Type species: Hyolithes laevigatus Linnarson, 1971; lower Cambrian, Sweden.

Torellella cf. *T. laevigata* (Linnarson, 1871)

Fig. 67H–M.

Material.—Several calcium phosphatic tubes, including SMNH X 4805–4810, from samples 3/25, 6/6.6, 6/14, 7/25.5, 7/27.5, 7/33, and 7/36.7. Emyaksin Formation, Malaya Kuonamka and Bol'shaya Kuonamka rivers; correlated with the *Dokidocyathus regularis* Zone, Tommotian Stage–*Delgadella anabara* Zone, Atdabanian Stage.

Description.—Undulating and/or curved tubes, diverging at 10–15°, with transversal outline rounded at the initial part (Fig. 67H$_2$, L) but lenticular at the aperture. The external ornamentation consists of frequent concentric growth lines. A longitudinal continuous narrow furrow (Fig. 67L, M) marks each narrow keel-like side of the tubes.

Remarks.—The fossils are also similar to *T. lentiformis* (Sysoev, 1960), and the latter may be a junior synonym of *T. laevigata* (Linnarson, 1871). Longitudinal ornamentation of the narrow sides is not, however, described from the latter two forms. Commonly attributed to *Torellella* Holm, 1893,

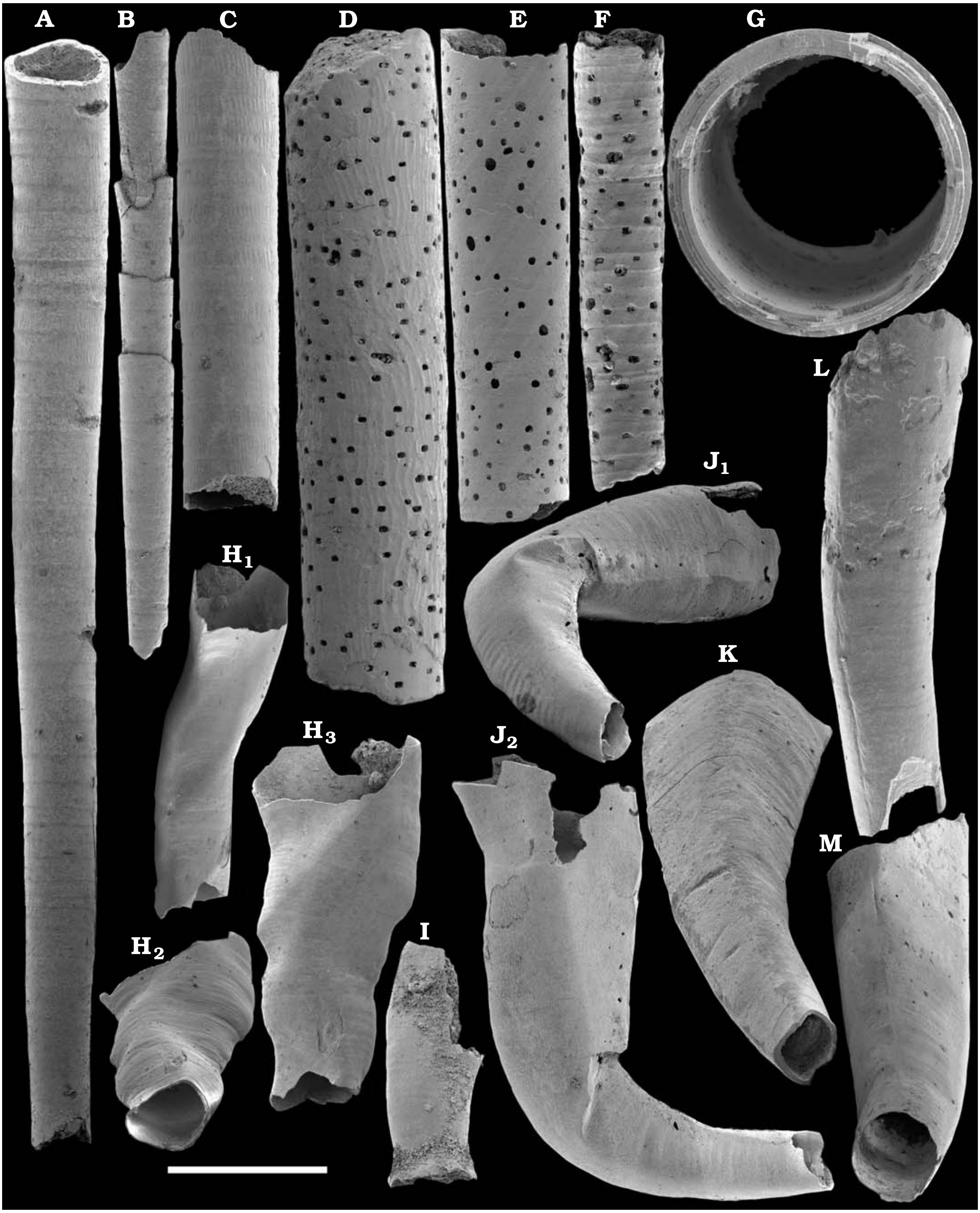


Fig. 67. Hyolithelminths from lower Cambrian Emyaksin Formation, Bol'shaya Kuonamka River and Malaya Kuonamka River, Anabar Uplift, Siberia. **A**, **C**, **D**, **F**. *Hyolithellus* cf. *H. insolitus* Grigor'eva in Voronin et al. 1982. **A**. SMNH X 4798, sample 7/19; longitudinal view. **C**. SMNH X 4799, sample →

the fossils are also very similar to those described from the Qiongzhusian–lower Canglangpuan Stages of China as Sphenothallus Hall, 1847 (Li et al. 2004b). The middle Qiongzhusian *Torellella bisulcata* Li, 2004 and lower Cambrian *T. lentiformis* have a narrow sulcus along each of the narrow sides, similar to longitudinal furrows in *Torellella* cf. *T. laevigata* herein. A single apical fragment with a flared open attachment structure is also present in the material described (Fig. 67I).

Fragments of *Torellella* sp. (Fig. 68) demonstrate that the wall, originally phosphatic in composition, consists of multiple layers arranged in a plywood stucture, where adjacent layers have orthogonal orientation of the constituent fibers (Fig. 68D_1; see also Bengtson et al. 1990, Skovsted and Peel 2011). Tube fragments of *Torellella* from samples 6/66.2, 7/25.6, 7/30, 7/39.5, and 7/60 are eroded and perforated by numerous rounded-squared or rounded-rectangular holes, 20–60 µm in diameter (Fig. 68). In some fragments, the holes incompletely penetrate the wall from the inside of tube (Fig. 68A) and, therefore, are unlikely the result of attacks by a predator from outside. In other specimens, the perforations are combined with eroded outer and inner surfaces (Fig. 68D–G). Some of the holes have rounded broken-off edges (Fig. 68B_2), demonstrating that erosion had taken place after the holes were formed and before deposition into the sediment. These holes expand moderately inwards into the tube wall, and their margins are oriented parallel to the orthogonal direction of fibers in the wall (Fig. 68C). Similar holes in the wall are found in *Hyolithellus*, but other fossils described herein. They are also observed in hyolithelminths from Series 2 of Laurentia (Christian Skovsted and AK, unpublished observation 2012). Thus, it appears that the perforations have a biological origin (e.g., sponge galleries or holdfasts attachment sites), made before deposition of abandoned tubes into the sediment.

Phylum, class, and order uncertain

Family Anabaritidae Missarzhevsky, 1974

Genus *Anabarites* Missarzhevsky in Voronova and Missarzhevsky, 1969

Type species: Anabarites trisulcatus Missarzhevsky in Voronova and Missarzhevsky, 1969; *Anabarites trisulcatus* Zone, Nemakit-Daldynian Stage, lower Cambrian; mouth of the Kotujkan River, Anabar Uplift, Siberian Platform.

Anabarites trisulcatus Missarzhevsky in Voronova and Missarzhevsky, 1969

Fig. 69A, E.

Material.—Two calcium phosphatic internal moulds, SMNH X 4818 and 4819, from sample 7/25.6. Emyaksin Formation, Bol'shaya Kuonamka River; correlated with the *Profallotaspis jakutensis* Zone, lower Atdabanian Stage.

Description.—Irregularly curved, slowly expanding internal moulds with tri-fold transverse profiles. Three rounded lobes are separated by narrow and shallow but distinct, grooves. The smaller mould (presumably a younger growth stage) carries transverse growth lines (Fig. 69E).

Remarks.—*Anabarites* spp. described herein are the first occurrences of anabaritids from Stage 3 in Siberia. These forms often occur within the Terreneuvian Medvezhya and lower Emyaksin Formations of the Anabar Uplift (see Kouchinsky et al. 2009). *Anabarites trisulcatus* is indicated from the lower part of the section by Val'kov (1975: 12; see also Val'kov 1987: fig. 3). Outside the Siberian Platform anabaritids are reported to range into the Cambrian Series 2, Atdabanian–Botoman equivalent strata, in Mongolia (Esakova and Zhegallo 1996), South and North China (Feng 2005; Li et al. 2007; Steiner et al. 2007), Australia (Bengtson et al. 1990), Baltica (Kouchinsky et al. 2009), and possibly in the Mediterranean region (Elicki 1994).

Stratigraphic and geographic range.—Lower Cambrian worldwide (see Kouchinsky et al. 2009).

Anabarites cf. *A. kelleri* Missarzhevsky, 1989

Fig. 69B, C.

Material.—One calcium phosphatic internal mould, SMNH X 4820 (Fig. 69B), from sample 3/53.5; one from sample 6/6.8; one, SMNH X 4821 (Fig. 69C), from sample 6/59.3. Emyaksin Formation, Malaya Kuonamka and Bol'shaya Kuonamka rivers; correlated with the *Dokidocyathus regularis* Zone, Tommotian Stage, *Delgadella anabara* and *Judomia* zones, Atdabanian Stage.

Description.—Small straight internal moulds with rounded triangular cross-section, shallow faint longitudinal grooves, and thin straight growth lines.

Anabarites cf. *A. biplicatus* (Missarzhevsky, 1989)

Fig. 69D.

Material.— One specimen, SMNH X 4822, from sample 3/59. Emyaksin Formation, Malaya Kuonamka River; correlated with the *Delgadella anabara* Zone, Atdabanian Stage.

Description.—Internal mould flattened laterally, with two shallow and wide longitudinal depressions and one of the lobes more extended than the other two sides, and curved in one plane. The mould is oval in cross-section, but rounded and more isodiametrical in the initial growth stage.

7/39.5; longitudinal view. **D**. SMNH X 4800, sample 7/36.7; longitudinal view. **F**. SMNH X 4801, sample 7/36.7; longitudinal view. **B**, **E**, **G**. *Hyolithellus* sp. **B**. SMNH X 4802, sample 7/16; longitudinal view. **E**. SMNH X 4804, sample 7/25.6; longitudinal view. **G**. SMNH X 4803, sample 7/16 ; transversal view. **H**–**M**. *Torellella* cf. *T. laevigata* (Linnarson, 1871). **H**. SMNH X 4805, sample 7/27.5; H_1, longitudinal view on the narrower side; H_2, oblique transversal view on the apical end; H3, longitudinal view on the broader side of the tube. **I**. Apical fragment SMNH X 4806, sample 7/25.5; longitudinal view. **J**. SMNH X 4807, sample 3/25; oblique apical (J_1) and longitudinal (J_2) views. **K**. SMNH X 4808, sample 6/6.6; oblique apical view. **L**. SMNH X 4809, specimen with a furrow on narrower sides, sample K7-6.3B; longitudinal view. **M**. SMNH X 4810, sample 6/14; oblique apical view. Scale bar: 600 µm, except G, 150 µm.

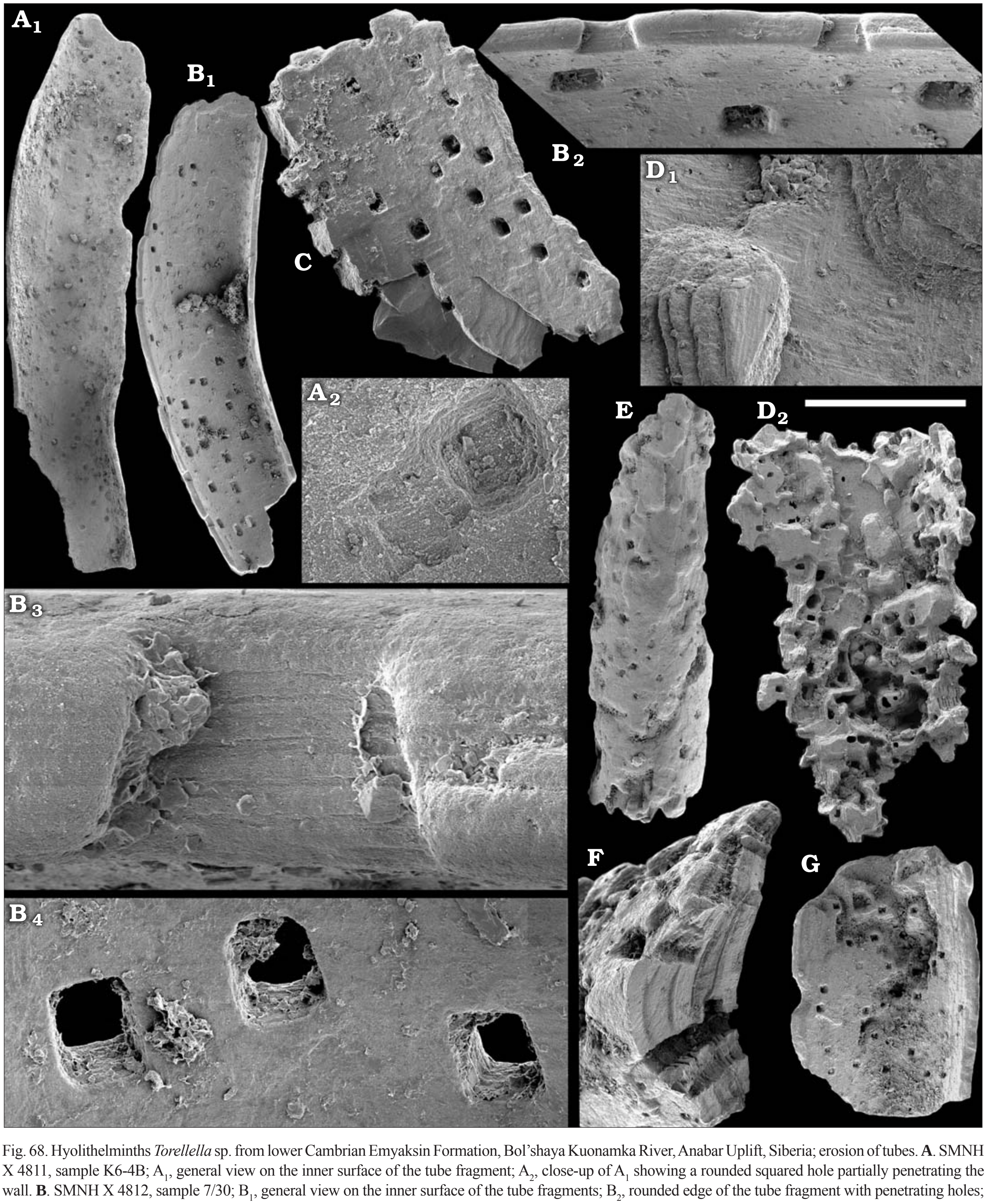


Fig. 68. Hyolithelminths *Torellella* sp. from lower Cambrian Emyaksin Formation, Bol'shaya Kuonamka River, Anabar Uplift, Siberia; erosion of tubes. **A**. SMNH X 4811, sample K6-4B; A_1, general view on the inner surface of the tube fragment; A_2, close-up of A_1 showing a rounded squared hole partially penetrating the wall. **B**. SMNH X 4812, sample 7/30; B_1, general view on the inner surface of the tube fragments; B_2, rounded edge of the tube fragment with penetrating holes; B_3, close-up of B_2; B_4, close-up of B_1. **C**. SMNH X 4813, sample 7/30; general view on the inner surface of the tube fragments. **D**. SMNH X 4814, sample 6/66.2; D_1, close-up of D_2, orthogonal orientation of fibres in adjacent layers of the wall; D_2, general view of an eroded fragment of tube. **E**. SMNH X 4815, sample 7/25.6; view on the outer surface. **F**. SMNH X 4816, sample 7/60; broken edge of a tube fragment with layers in the wall penetrated by holes. **G**. SMNH X 4817, sample 7/39.5; view on the inner surface. Scale bar: A_1, B_1, D_2, E, G, 600 µm; C, F, 300 µm; B_2, 120 µm; B_4, D_1, 60 µm; A_2, 30 µm; B_3, 20 µm.

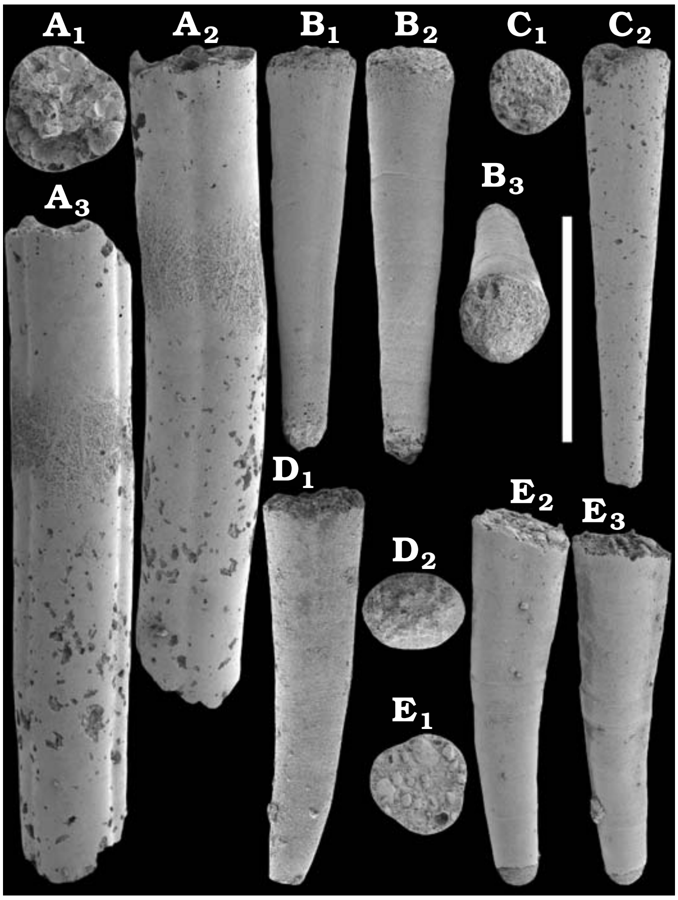


Fig. 69. Anabaritids from lower Cambrian Emyaksin Formation, Bol'shaya Kuonamka River and Malaya Kuonamka River, Anabar Uplift, Siberia. **A**, **E**. *Anabarites trisulcatus* Missarzhevsky in Voronova and Missarzhevsky, 1969; sample 7/25.6. **A**. SMNH X 4818; transversal (A_1) and longitudinal (A_2, A_3) views. **E**. SMNH X 4819; transversal (E_1) and longitudinal (E_2, E_3) views. **B**, **C**. *Anabarites* cf. *A. kelleri* Missarzhevsky, 1989. **B**. SMNH X 4820, sample 3/53.5; longitudinal (B_1, B_2) and oblique transversal (B_3) views. **C**. SMNH X 4821, sample 6/59.3; transversal (C_1) and longitudinal (C_2) views. **D**. *Anabarites* cf. *Kotuithes biplicatus* Missarzhevsky, 1989; SMNH X 4822, sample 3/59; longitudinal (D_1) and transversal (D_2) views. Scale bar 600 µm.

Phylum Porifera Grant, 1836

Class Hexactinellida Schmidt, 1870

Order and family uncertain

Pentactines with a long acanthose ray

Fig. 70M, N, Q.

Material.—Several tens of spicules total, from samples 3/44, 3/49, 3/49.5, 3/50, 6/39.1, 6/41.7, 7/33, 7/34, 7/34.7, 7/34.8, and hundreds, including SMNH Sp 10301–10303 from sample 7/36.7. Emyaksin Formation, Malaya Kuonamka and Bol'shaya Kuonamka rivers; correlated with the *Delgadella anabara* Zone, Atdabanian Stage. One, from sample 6/0.3; Emyaksin Formation, Bol'shaya Kuonamka; correlated with the lower *Dokidocyathus regularis* Zone, Tommotian Stage.

Description.—Siliceous spicules composed of five rays containing axial canals. One of the rays is much longer, sometimes curves distally (Fig. 70M), and is covered with low, irregularly situated, and longitudinally extended tubercles. The ray can be somewhat swollen at the base (Fig. 70N), but commonly only slightly reduced in diameter distally from its base. Four other rays taper gently at 60–120° to each other in plan view and are inclined at 20–30° away from that plane, perpendicular to the base of the longer ray. The rays are covered with less distinct and smaller tubercles.

Remarks.—The specimens described herein are most similar to those illustrated by Fedorov in Shabanov et al. (1987: pl. 35: 6) and by Vasil'eva (1998: pl. 24: 2) from the Atdabanian Stage, upper Emyaksin Formation, southeastern flanks of the Anabar Uplift and to those reported by Kouchinsky et al. (2011: fig. 40N–Q) from Stage 5 beds of the Malaya Kuonamka River. The tubercles probably represent weathered distally directed barbs similar to those described from some pentacts and hexacts of Cambrian hexactinellids (Rigby 1975; Bengtson 1986b: fig. 8; Bengtson et al. 1990: fig. 15A–F). Similar spicules, but preserved in carbonate surrounded by organic sheaths are reported from the lower Cambrian Forteau Formation of Newfoundland (Harvey 2010).

Hexactines with a long acanthose ray

Fig. 70O, P.

Material.—Over ten spicules, including SMNH Sp 10304 and 10305, from samples 7/33, 7/34.7, 7/34.8, and 7/36.7. Emyaksin Formation, Bol'shaya Kuonamka River; correlated with the *Delgadella anabara* Zone, Atdabanian Stage.

Description.—Siliceous spicules composed of six rays containing axial canals. Four gently tapering rays meet at ca. 90° to each other in one plane, perpendicular to the base of the long ray and to an opposite shorter ray. The longer perpendicular ray tapers slightly from its base and may curve distally. It is covered with longitudinally extended tubercles. The other rays are relatively smooth and straight, but the four of them situated in one plane are covered with less distinct and smaller tubercles.

Pentactines with smooth tapering rays

Fig. 70U.

Material.—Several spicules from samples 3/46.5, 7/33, 7/34.7, and several tens from samples 7/34.8 and 7/36.7, including SMNH Sp 10306. Malaya Kuonamka and Bol'shaya Kuonamka rivers, Emyaksin Formation; *Delgadella anabara* Zone, Atdabanian Stage.

Description.—Siliceous spicules, 0.8–1 mm in size, composed of five tapering rays with a smooth surface and axial canals. Four of the rays are situated in nearly the same plane at 80–100° between their proximal parts. The fifth ray is almost perpendicular to the other four. Some of the rays curve distally.

Regular hexactines with smooth tapering rays

Fig. 70S.

Material.—Seven spicules, including SMNH Sp 10307, from samples 7/33 and 7/70. Emyaksin Formation, Bol'shaya Kuonamka River; correlated with the *Delgadella anabara* Zone, Atdabanian Stage (sample 7/33) and *Calodiscus-Erbiella* Zone, lower Botoman Stage.

Description.—Siliceous spicules, ca. 0.5 mm in size, composed of six morphologically similar tapering rays with smooth surface and axial canals. The opposite rays are situated respectively along three axes crossed at nearly right angles with each other.

Remarks.—Similar spicules were reported from the middle Cambrian of Siberia (Kouchinsky et al. 2011: fig. 40E–G), lower Cambrian of Laurentia (Skovsted and Holmer 2006: fig. 5G, H), middle–upper Cambrian of Australia (Bengtson 1986b: fig. 9E; Mehl 1998: pl. 1: 1) and South China (Dong and Knoll 1996: fig. 7.1), and upper Cambrian of Argentina (Heredia et al. 1987).

Pentactines with smooth inflated rays

Fig. 70G–L.

Material.—Thirty spicules, including SMNH Sp 10308–10313, from samples 3/49 and 3/49.5. Emyaksin Formation, Malaya Kuonamka River; correlated with the *Delgadella anabara* Zone, Atdabanian Stage.

Description.—Siliceous spicules, 0.3–0.5 mm in size, consisting of five rays with smooth surface and axial canals. Four of the rays diverge at nearly right angles to each other in one plane, and the fifth ray is relatively perpendicular or somewhat inclined. The surface opposite to the perpendicular ray is convex. The rays commonly have an inflated appearance.

Remarks.—Similar spicules were described by Fedorov (in Shabanov et al. 1987: pl. 34: 14 and pl. 35: 1–4, 7) from the Atdabanian Stage, upper Emyaksin Formation, southeastern flanks of the Anabar Uplift and as *Cjulanciella asimmetrica* Fedorov in Fedorov and Pereladov, 1987, from the Cambrian Stage 4, Kuonamka Formation, northeastern Siberian Platform (see also Rozanov and Zhuravlev 1992: 228; Vasil'eva 1998: 96; Buslov et al. 2002: 787; Ponomarenko 2005: 54). Another similar spicule attributed to *Thoracospongia follispiculata* Mehl, 1996 is illustrated by Mehl (1998: pl. 1: 3) from the middle Cambrian of Australia. In some of the spicules, however, the angles of divergence between adjacent rays situated in one plane may vary between 45° and 160° (Fedorov in Shabanov et al. 1987: 131).

Hexactines with four acanthose rays

Fig. 70W–Z.

Material.—Several spicules, including SMNH Sp 10314–10317, from sample 3/46.5. Emyaksin Formation, Malaya Kuonamka River; correlated with the *Delgadella anabara* Zone, Atdabanian Stage.

Description.—Siliceous spicules composed of six rays. Four of the rays are covered with irregularly scattered tubercles, can be a little inflated at a short distance from the base, taper distally, cross at ca. 90° to each other in the plan view, but inclined at ca. 20° away from that plane. The other two straight smooth tapering rays are situated along one axis perpendicular to the latter plane. One of those rays is usually reduced and the four acanthose rays are inclined away from it. A single aberrant spicule has the fifth acanthose ray intercalated among the other four (Fig. 70W).

Hexactines with bulbous acanthose rays

Fig. 70E, F.

Material.—Three spicules, including SMNH Sp 10318 and 10319, from sample 6/0.3. Emyaksin Formation, Bol'shaya Kuonamka River; lower *Dokidocyathus regularis* Zone, Tommotian Stage.

Description.—Rare siliceous spicules composed of six rays situated at right angles to each other. One or two of the rays are reduced, bulbous and covered with acute tubercles. The other rays are smooth, longer and gradually taper distally.

Pentactines and hexactines with slim rays

Fig. 70A–D, R, T, V.

Material.—Several hundred pentactines of the first type, including SMNH Sp 10320 and 10321 (see below) and several tens of pentactines of the second type, including SMNH Sp 10322 and 10323, are available from sample 6/0.3; correlated with the lower *Dokidocyathus regularis* Zone, Tommotian Stage. Pentactines similar to the second type derive from samples 3/46.5, 3/49.5, 7/33, 7/34.7, and 7/36.7, where-

Fig. 70. Spicules of hexactinellids from lower Cambrian Emyaksin Formation, Bol'shaya Kuonamka River and Malaya Kuonamka River, Anabar Uplift, Siberia. **A**. Pentactine of type 1, SMNH Sp 10320, sample 6/0.3; lateral view. **B**. Pentactine of type 1 modified with the sixth ray, SMNH Sp 10321, sample 6/0.3; lateral view. **C**. Pentactine of type 2, modified with three intercalated rays, SMNH Sp 10322, sample 6/0.3; general view. **D**. Pentactine of type 2, SMNH Sp 10323, sample 6/0.3; lateral view. **E**, **F**. Hexactines with bulbous acanthose rays; sample 6/0.3. **E**. SMNH Sp 10318; general view. **F**. SMNH Sp 10319; general view. **G**–**L**. Pentactines with inflated rays. **G**. SMNH Sp 10308, sample 3/49; plan view. **H**. SMNH Sp 10309, sample 3/49; plan view. **I**. SMNH Sp 10310, sample 3/49; general view. **J**. SMNH Sp 10311, sample 3/49.5; J_1, oblique lateral view; J_2, plan views on the radiating rays. **K**. SMNH Sp 10312, sample 3/49; lateral view. **L**. SMNH Sp 10313, sample 3/49.5; plan view. **M**, **N**, **Q**. Pentactines with a long acanthose ray, sample 7/36.7. **M**. SMNH Sp 10301; general view. **N**. SMNH Sp 10302; lateral view. **Q**. SMNH Sp 10303; oblique view on presumadby distal end of the spicule. **O**, **P**. Hexactines with a long acanthose ray. **O**. SMNH Sp 10304, sample 7/36.7; lateral view. **P**. SMNH Sp 10305, sample 7/33; general view. **R**. Hexactine with slim rays, SMNH Sp 10324, sample 7/33; general view. **S**. Hexactines with smooth tapering rays, SMNH Sp 10307, sample 7/33; oblique view on presumably distal end of the spicule. **T**. Hexactine with slim rays, SMNH Sp 10325, sample 7/34.7; lateral view. **U**. Pentactines with smooth tapering rays, SMNH Sp 10306, sample 7/36.7; U_1, plan view on the radiating rays; U_2, lateral view. **V**. Pentactine with slim rays, SMNH Sp 10326, sample 7/36.7; V_1, plan view on the radiating rays; V_2, lateral view. **W**–**Z**. Hexactines with four acanthose rays, sample 3/46.5. **W**. SMNH Sp 10314; lateral view. **X**. SMNH Sp 10315; X_1, plan view on presumably distal end of the spicule; X_2, lateral view. **Y**. SMNH Sp 10316; general view. **Z**. SMNH Sp 10317; plan view. Scale bar: 600 μm, except E–I, J_1, K, L, 300 μm.

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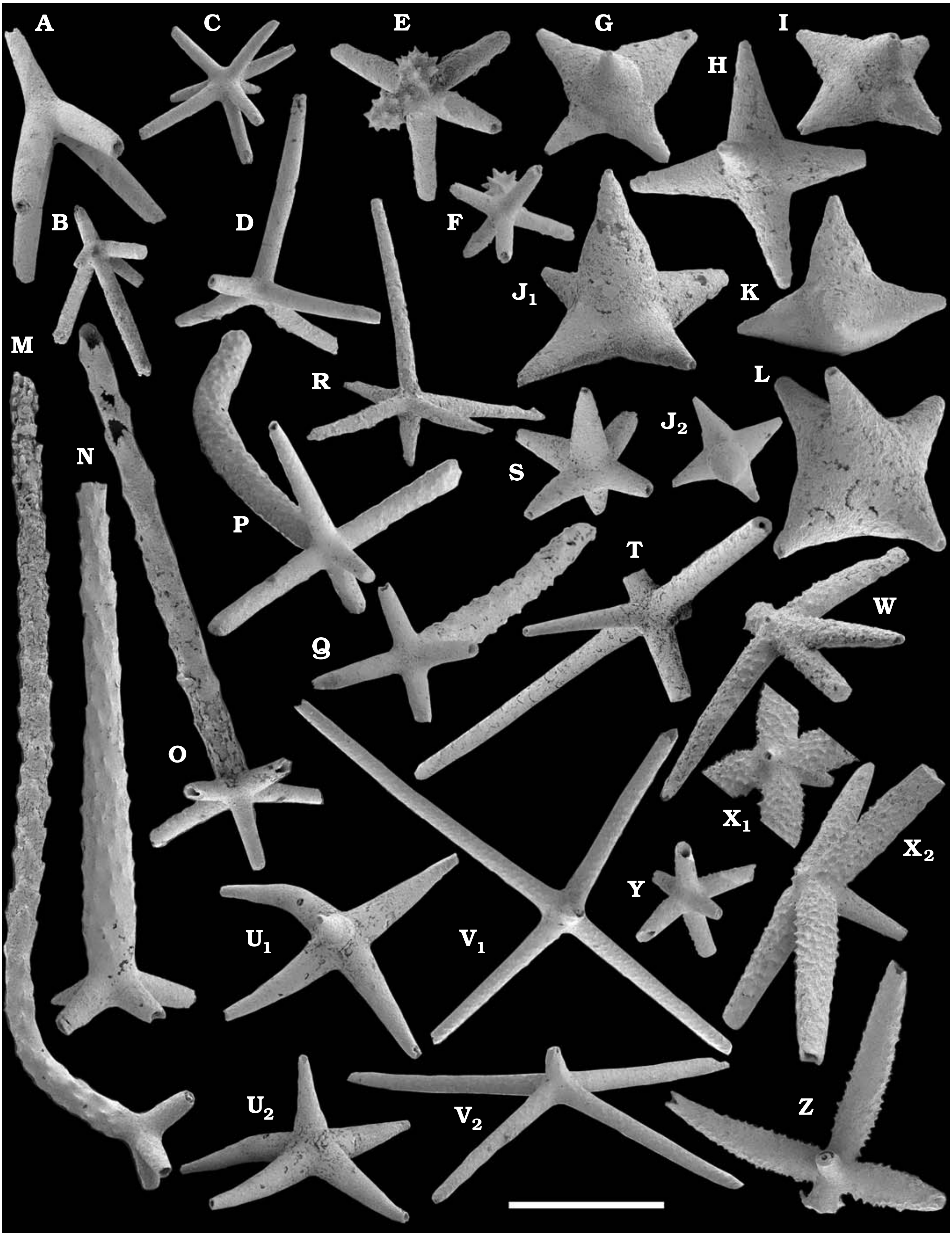
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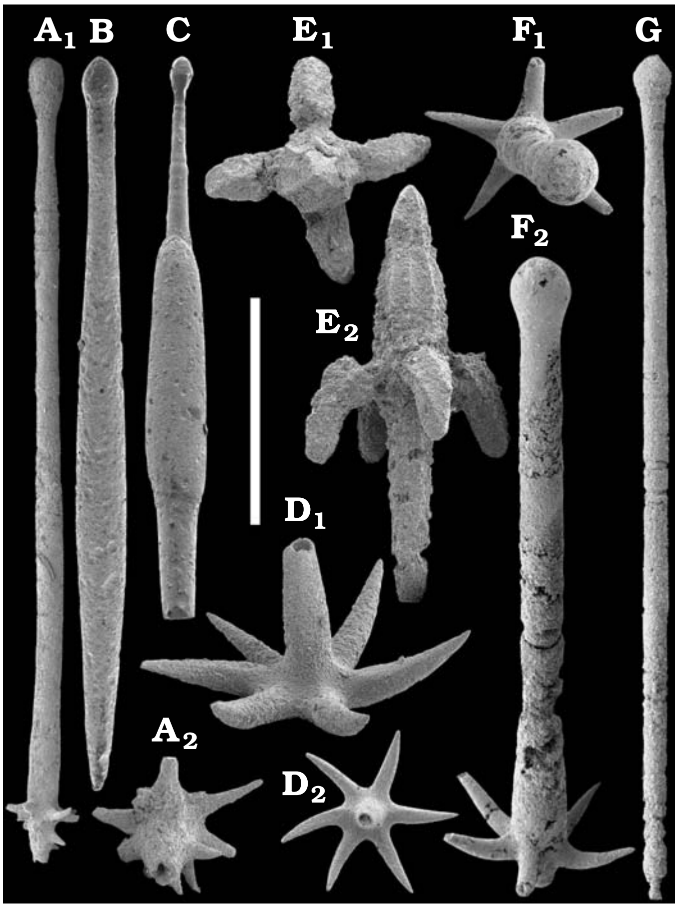

Fig. 71. Hexactinellid? spicules from lower Cambrian Emyaksin Formation, Bol'shaya Kuonamka River, Anabar Uplift, Siberia. **A**. Monaxon with bulbous and barbed ends, SMNH Sp 10328, sample 6/0.3; A_1, lateral view; A_2, close-up of the barbed end. **B**, **C**, **G**. Monaxons with a bulbous end. **B**. SMNH Sp 10329, sample 7/34.7; lateral view. **C**. SMNH Sp 10330, sample 7/34.7; lateral view. **G**. SMNH Sp 10331, sample 7/36.7; lateral view. **D**, **F**. *Nabaviella*-like spicules. **D**. SMNH Sp 10332, sample 7/34.7; D_1, oblique lateral view; D_2, plan view on the radiating rays and broken termination of presumably proximal ray. **F**. SMNH Sp 10333, sample 7/36.7; F_1, plan view on the radiating rays and rounded tip of presumably proximal ray; F_2, lateral view. **E**. Hexactine with ribbed and bent rays, SMNH Sp 10327, sample 7/37.8; E_1, plan view on the radiating rays and tip of the ribbed presumably distal ray; E_2, lateral view. Scale bar: 600 µm, except A_2, D_1, E, 300 µm.

as several hexactines with slim rays, including SMNH Sp 10324–10326, are found in samples 3/46.5, 3/49, 7/33, 7/34.7, and 7/36.7; correlated with the *Delgadella anabara* Zone, Atdabanian Stage. Emyaksin Formation, Malaya Kuonamka and Bol'shaya Kuonamka rivers.

Description.—Pentactines of the first type (Fig. 70A) have slim rays, four of which are directed away from the fifth ray, at ca. 60° to the plane perpendicular to that ray. Pentactines of the second type (Fig. 70D) have slim rays, with four of the rays directed away from the fifth ray, at ca. 10–15° to the plane perpendicular to that ray.

Remarks.—One spicule, otherwise a pentactine of the first type, shows the sixth ray situated on the same axis as the fifth ray and opposite to the latter (Fig. 70B). A single polyactine from sample 6/0.3 (Fig. 70C), probably represents an aberrant pentactine with three additional rays. Hexactines with slim long rays usually co-occur with pentactines of the second type.

Class, order, and family uncertain

Hexactine with ribbed and bent rays

Fig. 71E.

Material.—A single spicule, SMNH Sp 10327, from sample 7/37.8. Emyaksin Formation, Bol'shaya Kuonamka River; correlated with the *Delgadella anabara* Zone, Atdabanian Stage.

Description.—Siliceous spicule composed of six rays. Four of them radiate from the base at ca. 90º to each other and strongly curve in the same direction. Two straight rays opposite to each other are situated perpendicular to the base. One is wider than the other, conical and bears eight longitudinal ridges. The ridges are also present on the lateral rays and make them angular in cross-section.

Monaxonous spicules

Fig. 71A–D, F, G.

Material.—Several spicules, including SMNH Sp 10328–10333, from samples 7/34.7, 7/34.8, and 7/36.7. Emyaksin Formation, Bol'shaya Kuonamka River; correlated with the *Delgadella anabara* Zone, Atdabanian Stage.

Remarks.—Simple spindle-like, monaxonous siliceous spicules with a bulbous termination at one end and the opposite end pointed (Fig. 71B, C?, and G). In some specimens, the pointed end carries barbs (Fig. 71A) or is blunt, with five slightly curved pointed rays (Fig. 71F). The spicules are most similar to *Tanchaiella* sp. illustarted by Vasiljeva (1998: pl. 25: 1, 4, 5) from the Emyaksin Formation of the Malaya Kuonamka River, Atdabanian Stage and tylostyles from Cambrian Stage 3 *Eoredlichia-Wutingaspis* Zone of South China (Zhang and Pratt 1994: fig. 3C, D). Ponomarenko (2005: 48) noted similarity between *Tanchaiella* and "barbed pentactines" (pl. 14: 5, 6 therein) from the Botoman Stage of middle Lena River and reported that *Tanchaiella* is nomen nudum being provided by Vasiljeva (1998) without diagnosis and type species. Simple monaxonous spicules are also similar to those of uncertain affinity from the Silurian of Wisconsin (Watkins and Coorough 1997: fig. 4). One of the specimens (Fig. 71D) represents a broken off termination with six recurved rays similar to that in Zhang and Pratt (1994: fig. 3B, C) or in *Nabaviella*-like spicules known from the Cambrian strata worldwide (Mostler and Mosleh-Yazdi 1976; Bengtson 1986b; Bengtson et al. 1990; Zhang and Pratt 1994; Dong and Knoll 1996; Ponomarenko 2005 and references therein).

?Class Calcarea Bowerbank, 1864

Order Heteractinida Hinde, 1887

?Family Eiffeliidae Rigby, 1986

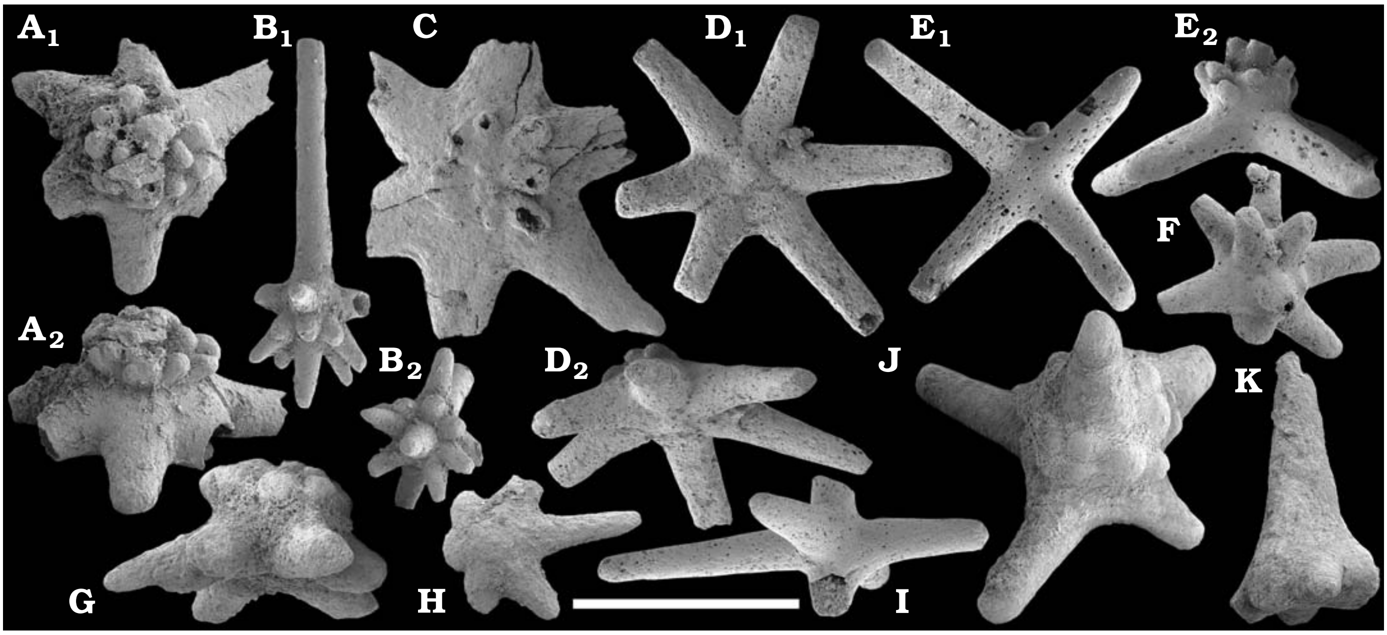

Fig. 72. Spicules of heteractinid sponges from lower Cambrian Emyaksin Formation, Bol'shaya Kuonamka River and Malaya Kuonamka River, Anabar Uplift, Siberia; sample 7/70 (A–D, H), sample K1-3B (E–G, I–K). **A**. SMNH Sp 10334; plan (A_1) and lateral (A_2) views. **B**. SMNH Sp 10335; B_1, lateral view; B_2, plan view on the distal end. **C**. SMNH Sp 10336; plan view. **D**. SMNH Sp 10337; plan (D_1) and oblique lateral (D_2) views. **E**. SMNH Sp 10338; plan (E_1) and lateral (E_2) views. **F**. SMNH Sp 10339; general view. **G**. SMNH Sp 10340; lateral view. **H**. SMNH Sp 10341; plan view. **I**. SMNH Sp 10342; lateral view. **J**. SMNH Sp 10343; oblique view. **K**. SMNH Sp 10344; lateral view. Scale bar 600 µm.

Heteractinida indet.

Fig. 72.

Material.—Hexaradiate spicules with a bunch of partial rays on one side (seven, from sample 7/70, including SMNH Sp 10334, 10336, and 10337, and eleven, from sample K1-3B, including SMNH Sp 10340) and one hexaradiate with a massive perpendicular ray, SMNH Sp 10344, from sample K1-3B; tetraradiate spicules with a bunch of partial rays on one side (one, from sample 7/70; eight, from sample K1-3B, including five ones with a single massive perpendicular ray on the same side, SMNH Sp 10338 and 10343), and polyactinous spicules with short rays with or without one elongated ray (SMNH Sp 10335 and 10339, from samples 7/70 and K1-3B). Several tetraradiate hexactines, including SMNH Sp 10342, from samples 7/70 and K1-3B are also considered here as probably related. Uppermost Emyaksin Formation, Bol'shaya Kuonamka and Malaya Kuonamka rivers; *Calodiscus-Erbiella* Zone, lower Botoman Stage.

Remarks.—Secondarily phosphatised spicules, presumably of original calcareous composition, with four, six, or more rays. The four-rayed spicules consist of four slender smooth rays with rounded ends diverging at ca. 90° from the base and at 20–30° to the basal plane (Fig. 72E, J). The central part of the convex side of the spicules carries several short rays or nodes and, in some, a single longer ray (Fig. 72J). The six-rayed spicules occur more often and consist of six slender smooth rays diverging at ca. 60° from the base and at 10–20° from the basal plane (Fig. 72A, C, D, G, H). The central part of the convex side of the spicule carries several nodes. The latter type is similar to the spicules of *Eiffelia* Walcott, 1920 (see e.g., Bengtson et al. 1990) known to appear globally in the Cambrian Stage 3 (Kozur et al. 2008). In the latter spicules nodes scatteded on the convex side are not as prominent as in the form reported herein, although tetractines are also described from *Eiffelia* (Botting and Butterfield 2005). Polyactinous (Fig. 72B, F) and hexactinous (Fig. 72I) spicules co-occur in the assemblage discussed herein. Polyactines consist of several short rays diverging from the same center, but one of the rays can be a long rhabd (Fig. 72B1). *Eiffelia* has been attributed to stem-group sponges in which the body wall is formed of a single layer of spicules with internal canals and includes smaller tetraradiate spicules (some of them hexactines) in spaces among larger hexaradiate spicules without perpendicular rays (Botting and Butterfield 2005).

The spicules also resemble those of *Conwaymorrisispongia* spp. from the *Abadiella huoi* Zone of Stage 3 of South Australia (Kozur et al. 2008), but the latter are characterised by eight massive rays instead of the six in our material. In accordance with the morphological terminology used by Kozur et al. (2008), four or six main rays radiating from the base are paratangential, and nodes in the central part represent branching of the distal ray into partial rays, whereas a proximal ray is not developed. In another spicule, the proximal ray is very massive and six massive paratangential rays radiate from its base (Fig. 72K). In polyactine spicules, all types of rays can be reduced, but some of the spicules carry a longer proximal ray and four short paratangential rays in a perpendicular plane. Rare phosphatised regular hexacts (Fig. 72I) similar in the morphology of individual rays co-occur with the spicules

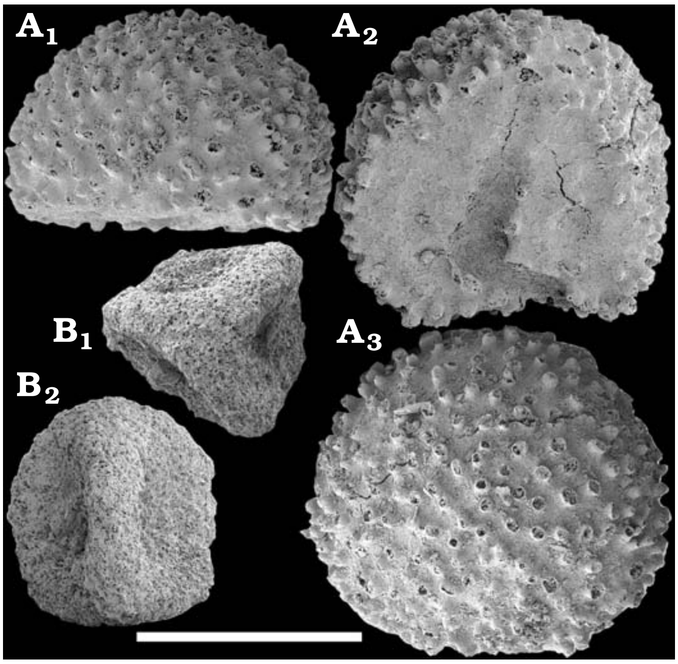

Fig. 73. Globules from lower Cambrian Emyaksin Formation, Bol'shaya Kuonamka River and Malaya Kuonamka River, Anabar Uplift, Siberia. **A**. *Aetholicopalla adnata* Conway Morris in Bengtson et al., 1990, SMNH X 4823, sample 7/70; lateral (A_1) and upper (A_3) views; A_2, view on the flattened side presumably representing attachment surface. **B**. Globule showing symmetrical tri-lobate deformation, SMNH X 4824, sample 3/50; plan (B_1) and lateral (B_2) views. Scale bar: A, 600 µm, B, 300 µm.

discussed above and may derive from the same sponges, although their hexactinellid affinity cannot be excluded.

Kingdom, phylum, class, order, and family uncertain

Genus *Aetholicopalla* Conway Morris in Bengtson et al., 1990

Type species: Aetholicopalla adnata Conway Morris in Bengtson et al., 1990; *Abadiella huoi* Zone, lower Cambrian; Curramulka, Yorke Peninsula, Australia.

Aetholicopalla adnata Conway Morris in Bengtson et al., 1990

Fig. 73A

Material.—One specimen, SMNH X 4823, from sample 7/70; uppermost Emyaksin Formation, Bol'shaya Kuonamka River; *Calodiscus-Erbiella* Zone, lower Botoman Stage.

Description.—Phosphatised globule, ca. 1 mm in diameter. The surface is semi-spherical, densely covered with bumps, 20–40 µm wide, having open or broken-off tips. The other side is smooth and slightly concave, with rare bumps and a curved channel-like cast in the middle (Fig. 73A_2).

Remarks.—While otherwise similar to *Aetholicopalla adnata*, the fossil does not display a double-wall or tubular pillars. The fossil also resembles single-walled *Archaeooides* in having a regular pustulose surface, but has a flattened portion typical of *Aetholicopalla adnata* and presumably related to an encrusting habit. Globules frequently occur in the samples, but their preservation prevents identification. Globules, 0.5–1 mm in size, with sphaerical or distorted wall often bearing tubercles occur in samples K7-6.3B, 6/16, 3/8, 3/11, 3/16.5, 3/23, 3/34, 3/40, 3/53.5, from the Emyaksin Formation of the Malaya Kuonamka and Bol'shaya Kuonamka rivers, ranging from the *Dokidocyathus regularis* Zone, Tommotian Stage to the *Delgadella anabara* Zone, Atdabanian Stage. Smaller globules of unknown affinity, 0.15–0.3 mm in size, of which deformation often produces a tri-lobate shape (Fig. 73B), occur in samples 3/29, 3/49, 3/50, 3/62.5, 6/59.3, K7-6.3B, 7/27.5, and 7/34.7 from the Tommotian and Atdabanian strata of the same localities.

Stratigraphic and geographic range.—*Aetholicopalla adnata* is also described from Cambrian Series 2 of the Montagne Noire, France (Kerber 1988) and the Görlitz Syncline, eastern Germany (Elicki and Schneider 1992; Elicki 1998), Australia (Bengtson et al. 1990; Gravestock et al. 2001), Antarctica (Wrona 2004), and from the Series 2–3 boundary interval of Sardinia (Elicki and Pillola 2004).

Conclusions

The described fossil assemblages from the Tommotian–lower Botoman Stages of Siberia record the evolutionary process of the early Cambrian bilaterian radiation. On the Siberian Platform, the Atdabanian Stage is marked with the first appearance and rapid evolutionary radiation of skeletonised ecdysozoans and echinoderms, as well as further diversification of sponges and lophotrochozoan groups (Kouchinsky et al. 2012). The normal marine fauna of the Emyaksin Formation contains the earliest Siberian and global first appearances of lobopodians, paleoscolecids and echinoderms. Their disarticulated skeletal elements have a significant potential to elucidate the earliest diversification of ecdysozoan and deuterostomian groups (Kouchinsky et al. 2012 : fig. 2).

The first lobopodian sclerites known from Siberia can thus be correlated with the regional first occurrences of *Microdictyon* in the lower *Nevadella* Zone of Laurentia, *Camenella baltica* Zone of Avalonia and *Abadiella huoi* Zone of Australia (Kouchinsky et al. 2012). Sclerites of paleoscolecids from the lower *Judomia* Zone of Siberia are probably the earliest known so far (Kouchinsky et al. 2012). The first appearance of echinoderms in the Emyaksin Formation can be correlated with time-equivalent deposits containing thecal plates in the lower part of the *Nevadella* Zone of Laurentia, lower Ovetian Stage of West Gondwana (Spain), Qiongzhusian Stage of South China and lower *Abadiella huoi* Zone of Australia (Kouchinsky et al. 2012; Zamora et al. 2013). In addition to the earliest record of biserial (brachiolar, blastozoan-type) and uniserial ("brachial") organisation of echinoderm feeding appendages, the material also reveals presence of edrioasteroid-grade echinoderms in the upper Atdabanian–lower Botoman Stages of Siberian Platform. Such a palaeontological evidence questions the hypothesis on that blastozoans would have diverged from edrioasteroid-grade echinoderms and provides major information on the fact that initial echinoderm disparity and diversity increased more rapidly than was previously known.

A number of fossils described herein demonstrate excellent preservation of fine details of skeletal ultrastructures replicated by calcium phosphate, notably among hyoliths and molluscs. Based on new microstructural data, problematic organophosphatic sclerites of *Rhombocorniculum* are reinterpreted as chaetae of the type occurring in annelids.

The fauna of the Emyaksin Formation comprises species in common or morphologically very close to coeval faunas known from Gondwana (molluscs, protoconodonts, *Rhombocorniculum*, *Fengzuella*, *Aetholicopalla*), Laurentia (molluscs, hyoliths, protoconodonts, *Fengzuella*), and Baltica (protoconodonts and *Rhombocorniculum*; SOM 4). Problematic sclerites of *Fengzuella* have not been previously reported from outside China. The latest occurrence of anabaritids in Stage 3 is documented herein the first time from Siberia, where such fossils commonly occur in older beds of the Terreneuvian Series (e.g., Kouchinsky et al. 2009).

Carbon isotope chemostratigraphy is applied for correlation of the Emyaksin Formation with archaeocyath- and trilobite-based zones of the Tommotian–Botoman Stages of stratotype sections in southeastern part of the Siberian Platform. Combined with biostratigraphical constraints, chemostratigraphy enables further correlation of the studied sections with IUGS chronostratigraphical scheme for the Cambrian. The exceptional continuity of fossil record along with their disparity and diversity observed makes outcrops of the lower–middle Cambrian carbonates along the Bol'shaya Kuonamka River very important for improvement of the Cambrian stratigraphy and for unravelling the finer-scale pattern of the Cambrian explosion.

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