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A new tannuolinid problematic from the lower Cambrian of the Sukharikha River in northern Siberia

ARTEM KOUCHINSKY, STEFAN BENGTSON, and DUNCAN J.E. MURDOCK



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A new species of tannuolinid, *Tannuolina pavlovi*, is reported from the basal Krasnoporog Formation cropping out along the Sukharikha River at the northwestern margin of the Siberian Platform. The new material expands the geographic range of tannuolinids onto the Siberian Platform and extends their stratigraphic range into the basal Tommotian Stage of the traditional Lower Cambrian. The oldest appearance of tannuolinids in the fossil record is shown herein to have occurred as early as the oldest appearance of the linguliformean brachiopods, of which tannuolinids have been suggested to be a stem group. The sellate sclerites of *T. pavlovi* sp. nov. are different from those of the other known species of *Tannuolina* in the consistent absence of a pronounced sella and duplicature on the respective sides of sclerites, as well as in having regularly distributed large setal pores on the lateral edges. The mitral sclerites of *T. pavlovi* sp. nov. do not clearly show asymmetry of left and right forms, manifested in other species by the presence of the carina on the interior surface. Large pores aligned along the lateral margins of sellate sclerites regularly coalesce below the wall surface from an apically and an aperturally directed basal branch, forming a nearly right angle.

Key words: Tommotiida, Brachiopoda, *Tannuolina*, Cambrian, Tommotian, Siberia.

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Introduction

Tannuolinids are Early Cambrian fossils represented by two types of phosphatic sclerites—mitral and sellate ones. In most cases the sclerites are asymmetrical, with dextral and sinistral forms present. The sclerites show basal-internal accretionary growth and an extensive system of pores. Tannuolinids are preserved as disarticulated sclerites—no complete body fossils have been found, although there are occasional examples of adjacent sclerites that have merged during growth (Qian and Bengtson 1989; Li and Xiao 2004). Traditional reconstructions generally favour a bilaterally symmetrical body with paired rows of serially repeated sclerites (Li and Xiao 2004), but a recent reconstruction suggests that they were sessile animals with mitral and sellate sclerites homologous to ventral and dorsal valves, respectively, of the linguliformean brachiopods (Holmer et al. 2008). Tannuolinids have been suggested to be a stem group leading to the linguliformean brachiopods in general (Williams and Holmer 2002; Li and Xiao 2004; Holmer et al. 2008) or to the linguloids (Skovsted et al. 2009c), on the basis of morphology, ultrastructure, and an interpretation of the pores in the sclerite walls as housing setae of lophotrochozoan type. The present paper describes *Tannuolina pavlovi* sp. nov., the first tannuolinid described from the Siberian Platform and the oldest known representative of the group.

Institutional abbreviation.—SMNH, Museum of Natural History, Stockholm, Sweden. Collection deposited under the numbers X4102–X4116.

Geological setting

The material described herein was collected in August 2004 along the Sukharikha River (right tributary of the Enisej River) in northern Siberia (Fig. 1) by Vladimir Pavlov and Vladimir Vodovozov (both from the Institute of Physics of the Earth, Moscow, Russian Federation). The fossils are derived from lime mudstones of the basal Krasnoporog Formation exposed at 67°12.472'N; 87°22.753'E on the left bank of the river. The sedimentary sequence and biostratigraphy of the area have been described in detail (e.g., Luchinina et al. 1997; Rowland et al. 1998) and complemented by $\delta^{13}C$ chemostratigraphy (Kouchinsky et al. 2007). The fossiliferous sample is equivalent to sample A301 (see Kouchinsky et al. 2007: fig. 5). The age of the fossils is attributed to the *Nochoroicyathus sunnaginicus* Biozone of the basal Tommotian Stage of Siberia.

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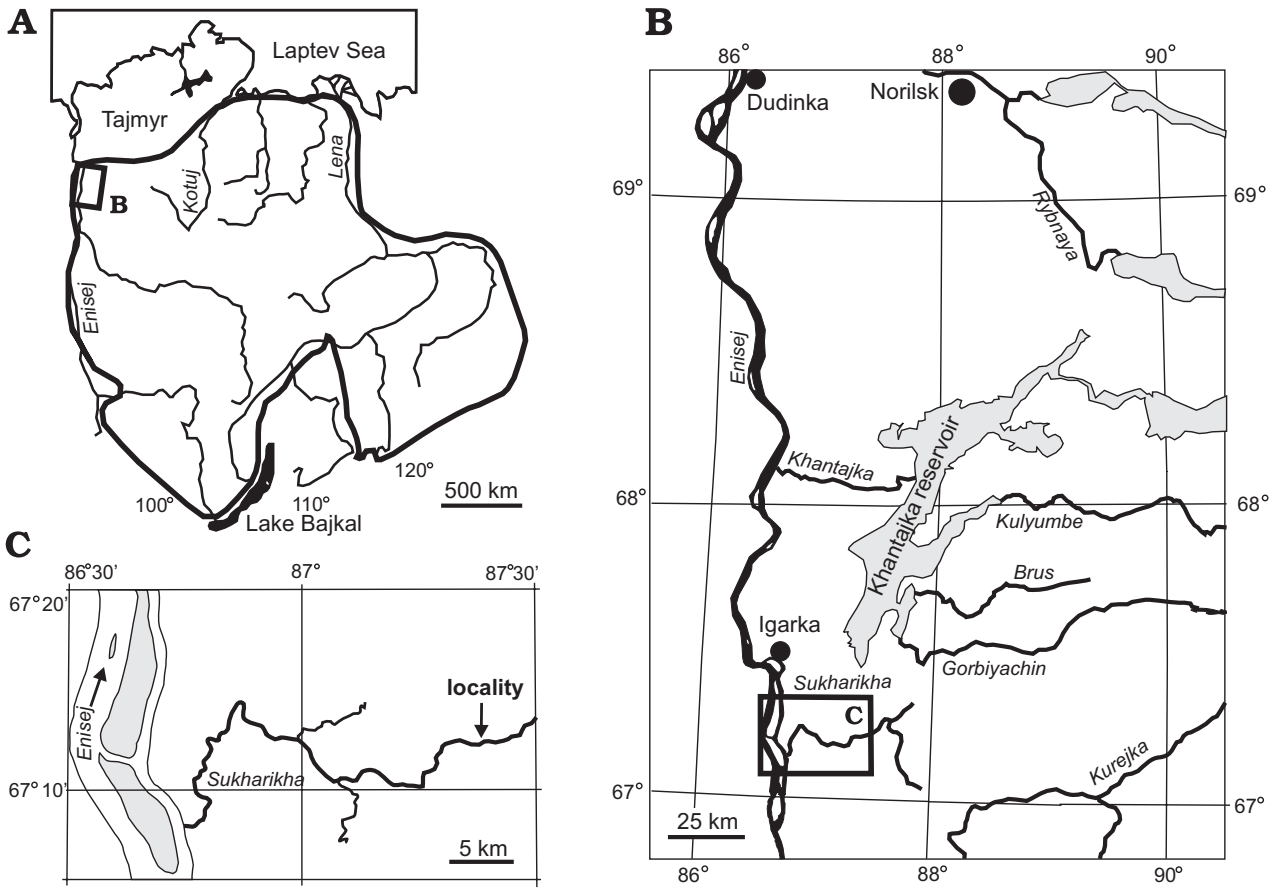


Fig. 1. Map showing position of the locality with *Tannuolina pavlovi* on the Siberian Platform. **A**. Siberian Platform outlined. **B**. Igarka-Norilsk region enlarged from A. **C**. Locality in the Sukharikha River basin enlarged from B.

Material and methods

Fossils were extracted from the limestone using a buffered solution of 7–10% acetic acid. Mud was removed from the resultant acid-insoluble residue by heating to boiling point in water and decanting the suspension. The fossils were recovered subsequently by manually sorting through the residue under a binocular microscope. Fossils were then coated with gold for examination using a scanning electron microscope Hitachi S4300 at the SMNH. Two specimens were further investigated by means of synchrotron radiation X-ray tomographic microscopy (SRXTM) at the TOMCAT beamline of the Swiss Light Source, Paul Scherrer Institute, Villigen, Switzerland (see Supplementary Online Material at http://app.pan.pl/SOM/app55-Kouchinsky_etal_SOM.pdf).

Systematic palaeontology

Phylum and class Uncertain (?stem-group Brachiopoda)

Order Tommotiida Missarzhevsky, 1970

Family Tannuolinidae Fonin and Smirnova, 1967

Genus *Tannuolina* Fonin and Smirnova, 1967

Tannuolina pavlovi sp. nov.

Figs. 2–6.

Etymology: In honour of geophysicist Dr. Vladimir Pavlov (Institute of Physics of the Earth, Moscow, Russian Federation) for his contributions to the geology of Siberia.

Type material: Holotype: SMNH X4102, a complete sellate sclerite (Figs. 2A, 3). Paratypes: SMNH X4103–X4106, nearly complete sellate sclerites (Fig. 2B–E) and SMNH X4107–X4115, partial mitral sclerites (Figs. 4, 5A–C).

Type locality: 67°12’31’’N; 87°22’58’’E, Sukharikha River (right tributary of the Enisej River), Igarka region, northern Siberia (Fig. 1).

Type horizon: Base of the Krasnoporog Formation (same as sample A301 in Kouchinsky et al. 2007: fig. 5), *Nochoroicyathus sunnaginicus* Biozone, Tommotian Stage, Lower Cambrian.

Material.—The material investigated consists of 10 nearly complete sellate sclerites, 15 partial mitral sclerites (usually fragments with apex), and more than 50 other fragments from the same sample. All fossils are preserved as calcium phosphate.

Diagnosis.—Species of *Tannuolina* with bilaterally symmetrical sellate and slightly asymmetrical mitral sclerites. Sellates with gently coiled apex and transversely convex sides without pronounced sella and duplicature; the lateral

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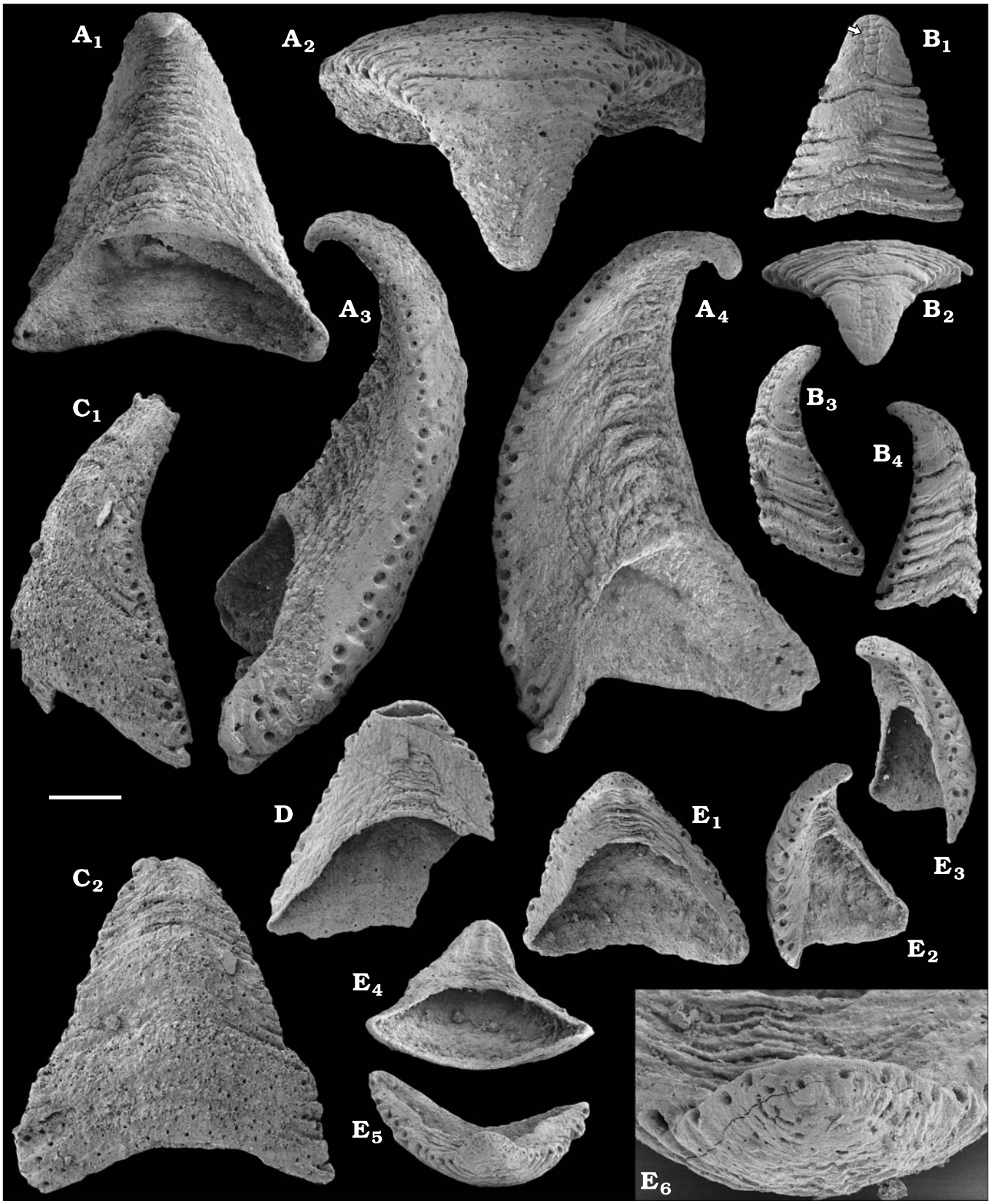


Fig. 2. Tannuolinid problematic *Tannuolina pavlovi* sp. nov. from the Lower Cambrian Krasnoporog Formation, Sukharikha River, northern Siberia, sellate sclerites. **A**. SMNH X4102, holotype; A_1, duplicatural side; A_2, apical; A_3, lateral; A_4, oblique lateral views. **B**. SMNH X4103; B_1, sellate side (a narrow median zone at the apex is arrowed); B_2, apical; B_3, lateral; B_4, lateral views. **C**. SMNH X4104; C_1, lateral view; C_2, sellate side. **D**. SMNH X4105; duplicatural side. **E**. SMNH X4106; E_1, duplicatural side; E_2, E_3, oblique lateral; E_4, apertural; E_5, apical views; E_6, close-up of apex in E_5. Scale bars 200 μm, except A_1 (300 μm) and E_6 (50 μm).

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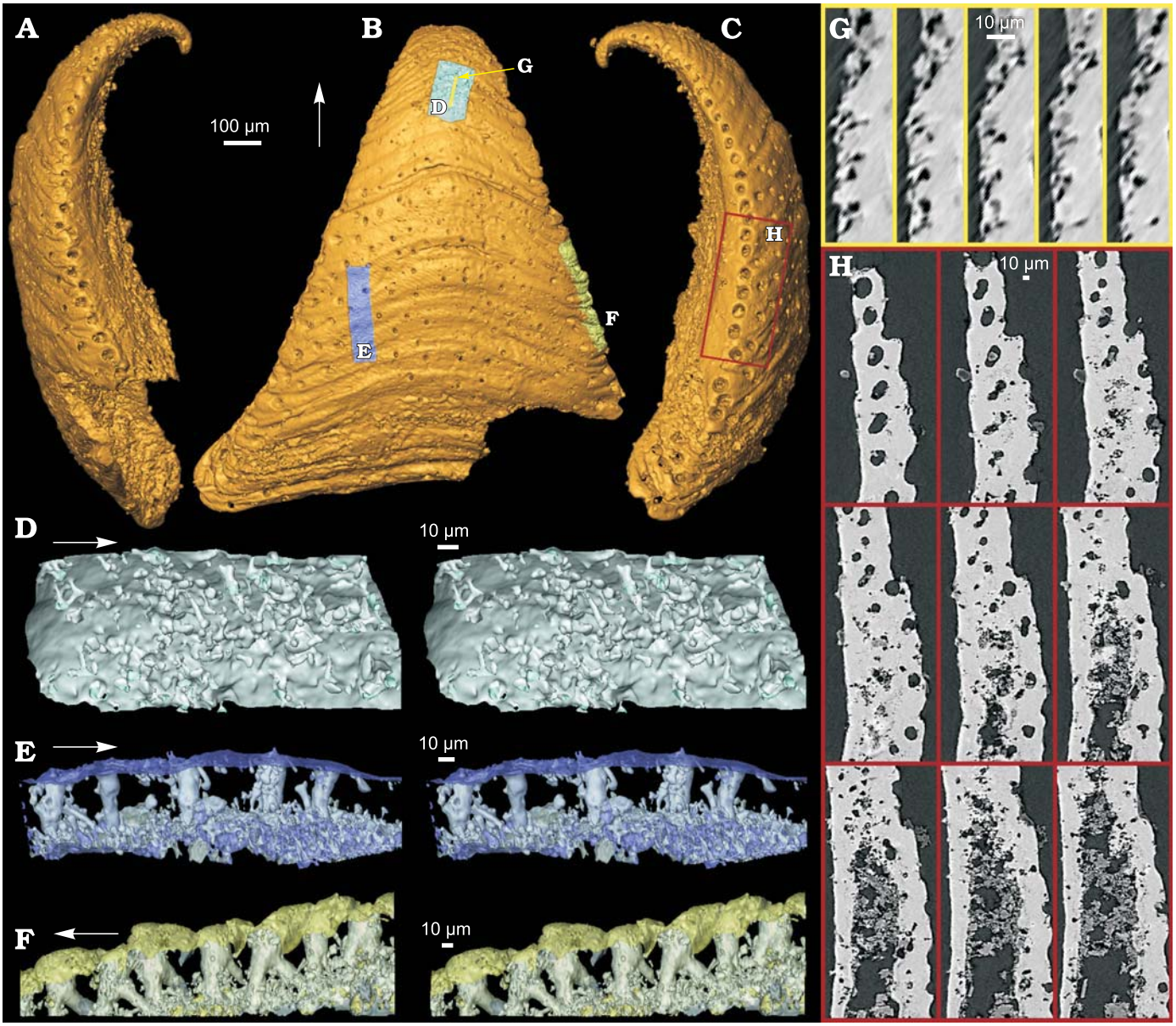


Fig. 3. Tannuolinid problematic *Tannuolina pavlovi* sp. nov. from the Lower Cambrian Krasnoporog Formation. Sellate sclerite, SMNH X4102, holotype (also figured in Fig. 2A), SRXTM renderings (see Materials and Methods section) to show the nature of the pores. **A**–**C**. Isosurface renderings. **D**–**F**. Surface renderings (stereo pairs) of volumes defined by thresholding. **G**–**H**. Virtual slices at 1.5 µm (**G**) and 5 µm (**H**) intervals. Arrows in D–F show the direction of the apex. The surface rendering in D shows the outer surface from the inside, with the fine pores (about 1 µm in diameter; represented as negative "molds") penetrating the sclerite wall. The same region is shown in orthoslices in G. The surface rendering in E shows both outer (top) and inner (bottom) wall surfaces, as well as coarse and fines pores penetrating the wall from both sides. The surface rendering of the lateral edge in F also shows outer and inner wall surfaces as well as fine and coarse pores, the latter resulting from coalescence of two finer pores. The opposite lateral edge is shown in H as oblique slices, where the coalescence can be followed in sequential slices.

edges carry prominent rows of macropores that bifurcate toward the inner wall surface. Mitrals with apex slightly overhanging a flattened decrescent side and without carina on the inner surface.

Description.—The sellate sclerites are bilaterally symmetrical and triangular in outline, ranging in size (length of the available specimens in the plane of symmetry) between 0.5 and 2.0 mm, with an apical divergence angle of 45–60° (Fig. 2). The apex overhanging the duplicatural side is coiled, up to 3/4 whorls in the largest specimen (holotype; Figs. 2A, 3). The aperture is lens-like in apertural view (corresponding to the cross-section perpendicular to the wall) (Fig. 2E$_4$), but is crescent-like with the opposite growing edges arched towards the apex in duplicatural view (corresponding to a section oblique to the wall; Fig. 2A$_1$, D, E$_1$). The sellate and duplicatural surfaces of the sclerites are transversally convex, because of the absence of a pronounced sella and duplicature as developed in other species of *Tannuolina*. A narrow median depressed zone may be situated at the apex, on the sellate side (arrowed in Fig. 2B$_1$). This zone, which may

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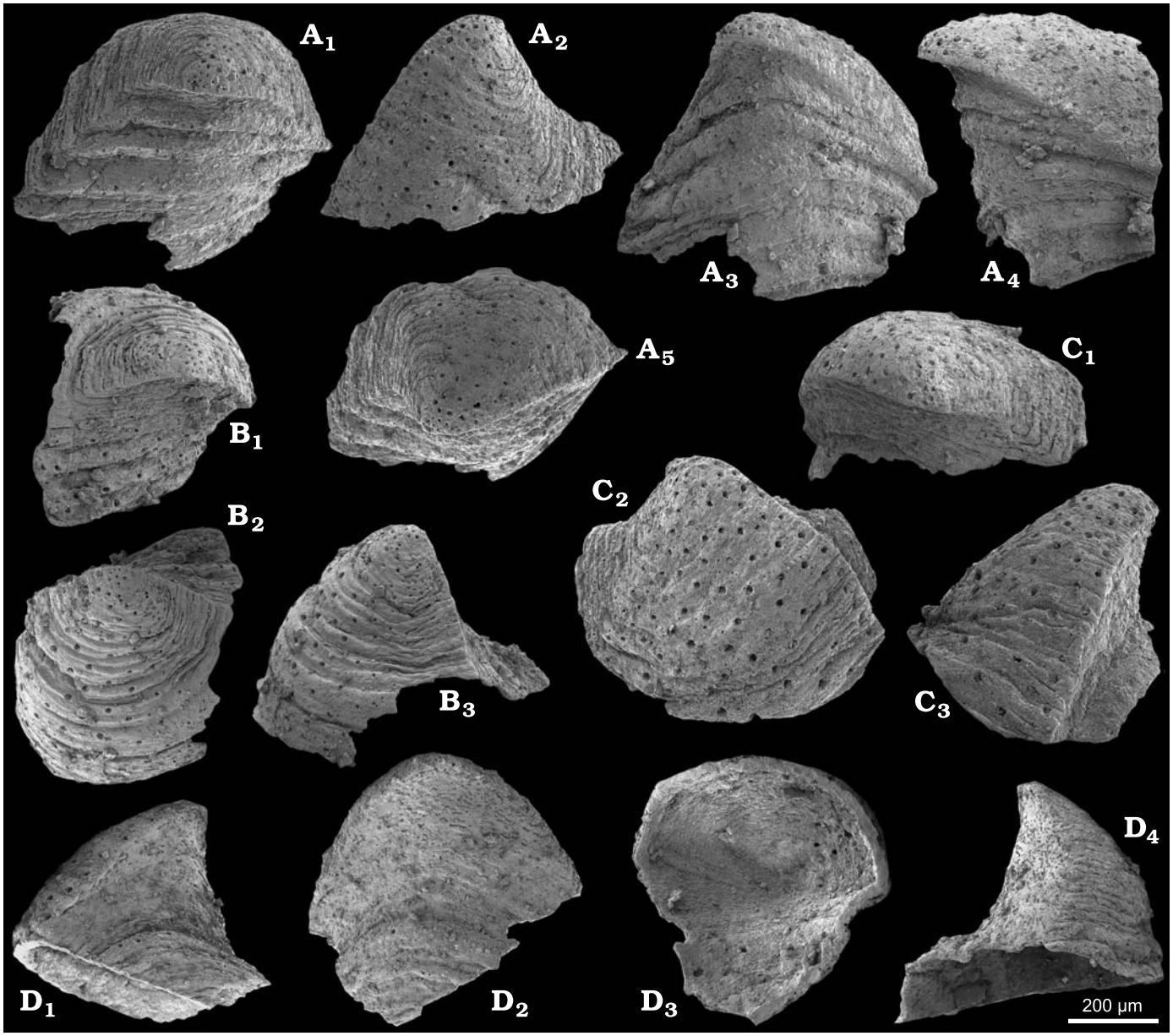


Fig. 4. Tannuolinid problematic *Tannuolina pavlovi* sp. nov. from the Lower Cambrian Krasnoporog Formation, Sukharikha River, northern Siberia, mitral sclerites. **A**. SMNH X4107; A_1, oblique apical view on the decrescent side; A_2, lateral view; A_3, view on the decrescent side; A_4, oblique lateral view on the decrescent side; A_5, view on the apex. **B**. SMNH X4108; B_1, oblique apical view on the decrescent side; B_2, view on the apex; B_3, lateral view. **C**. SMNH X4109; C_1, oblique apical view on the decrescent side; C_2, view on the accrescent side; C_3, lateral view. **D**. SMNH X4110; D_1, oblique lateral view on the decrescent side; D_2, view on the decrescent side; D_3, apertural view on the inner surface; D_4, lateral view.

be homologous to the sella, can be traced through a deflection of the co-marginal folds toward the apex at later growth stages (Fig. $2B_1$). The co-marginal folds cover the sellate and lateral sides of the sclerites (Fig. $2A_2$, B, C_2). The duplicatural side has narrower co-marginal folds with irregular boundaries and a lateral curvature toward the aperture (Fig. $2A_1$, A_3, A_4, D, E_1). Fine pores, 1–2 µm in diameter, are situated on the sellate side (Figs. $2A_2$, C, 3B). These penetrate to about 3–15 µm depth and usually end in a bulb-like swelling, 3–4 µm in diameter (Fig. 3D, G). Coarser pores are aligned along the lateral margins, increasing in diameter towards the aperture from 5 µm at the tip of the apex (Fig. $2E_6$) to 40 µm in larger specimens (Figs. $2A_3$, A_4, B_3, B_4, C_1, E_2, E_3, E_5, 3). They regularly coalesce about 30–40 µm below the wall surface from an apically and an aperturally directed basal branch, forming an angle of nearly 90° (Fig. 3F, H). Pores of intermediate size concentrated to the sellate side do not show such a coalescence (Fig. 3E).

The mitral sclerites are slightly asymmetrical, rapidly expanding cones covered with co-marginal folds (Figs. 4, 5). The asymmetry is expressed by deflection of the apical part clockwise (Fig. $4A_5$) or counter-clockwise (Fig. $4C_2$) when the sclerites are seen in apical view. These forms may be homologous to the D- and L-forms of *Tannuolina* mitrals, respec-

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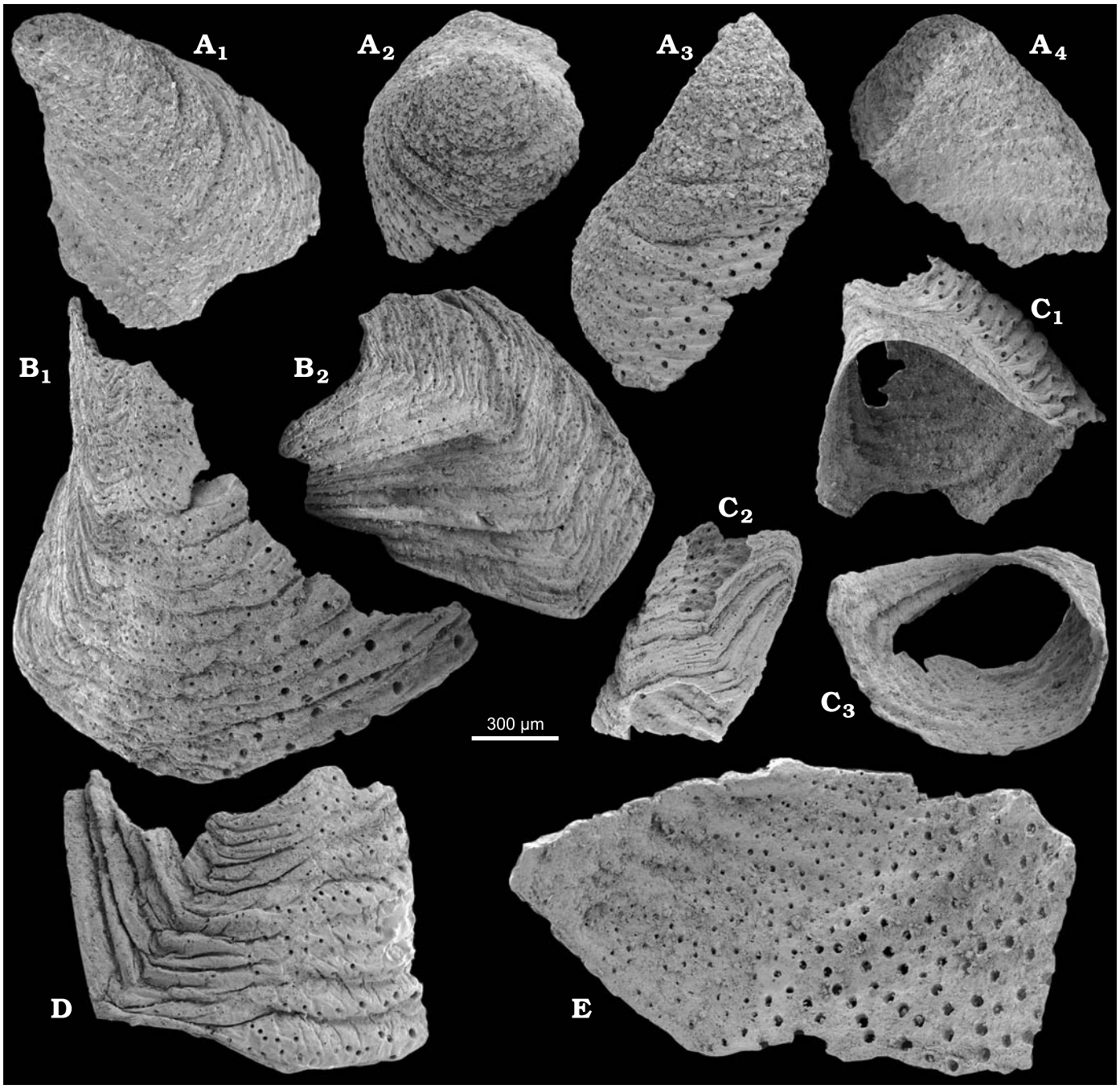


Fig. 5. Tannuolinid problematic *Tannuolina pavlovi* sp. nov. from the Lower Cambrian Krasnoporog Formation, Sukharikha River, northern Siberia, mitral sclerites. **A**. SMNH X4111; A_1, oblique lateral view of the apex; A_2, apical view; A_3, view on the accrescent side; A_4, view on the decrescent side. **B**. SMNH X4112; B_1, view on the accrescent side; B_2, lateral view. **C**. SMNH X4113; C_1, oblique lateral view on the decrescent side; C_2, lateral view; C_3, apertural view. **D**. SMNH X4114; fragment with the outer surface showing growth folds changing direction (lateral side of sclerite). **E**. SMNH X4115; fragment with the inner surface showing pores decreasing in size towards the lateral side of sclerite.

tively (Qian and Bengtson 1989). Judging from larger fragments available in the material, the apertural width reached 2 mm (Fig. 5B, D, E). The decrescent side is flattened and triangular in shape (Figs. $4A_3$, D_2, $5A_4$). It is delimited by sharp edges, where the growth lines change direction (Figs. $4A_1$, C_1, $5A_1$, B, C_2, D). The opposite (accrescent) side of the sclerite is convex (Fig. $4A_2$, B_3, C_3) and passes into flattened lateral sides (Fig. $4A_1$, A_5, B_1, D_3). The apex is tapered and overhangs the decrescent side (Figs. $4A_4$, C_3, D_4, $5A_1$). The aperture is not completely preserved in any of the specimens, but it appears to be broadly oval and more or less isometric, with the growing edge at the decrescent side arched towards the apex (Fig. $5C_1$). Pores are present on the entire surface, including the initial part. They are, however, scarce on the decrescent side (Fig. $4B_1$) and numerous on the accrescent side (Figs. 4A–C, $5A_3$, B_1, C_1). The pores increase in size towards the aperture and

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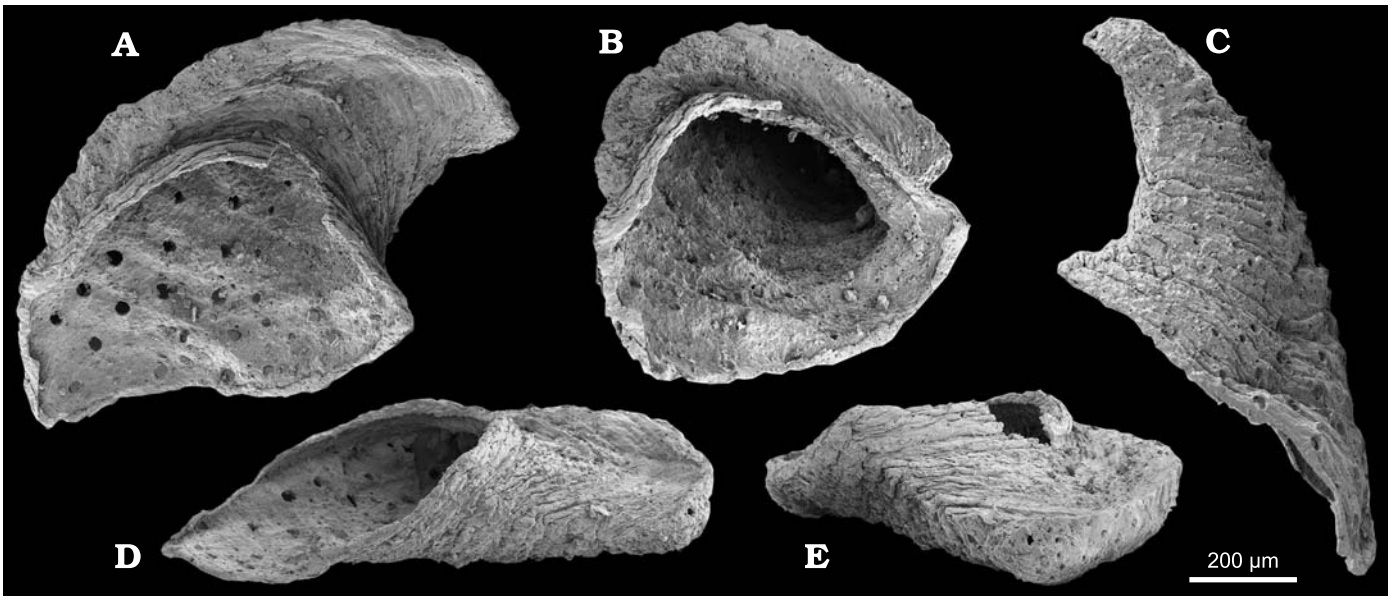


Fig. 6. Tannuolinid problematic *Tannuolina pavlovi* sp. nov. from the Lower Cambrian Krasnoporog Formation, Sukharikha River, northern Siberia, aberrant mitral sclerite, SMNH X4116. **A**. View on the decrescent side with pores and aperture. **B**. Apertural view. C. Lateral view on the convex lateral side. **D**. Lateral view on the concave lateral side. **E**. Olique apical view.

medially, from 5–10 µm (Fig. 5B, D, E) to 40 µm (in bigger specimens). There is no evidence of coalescence of pores such as in the lateral areas of the sellate sclerites. No internal lamination has been observed in the specimens investigated with SRXTM (Fig. 3 and Supplementary Online Material at http://app.pan.pl/SOM/app55-Kouchinsky_etal_SOM.pdf).

Comparison.—*Tannuolina* Fonin and Smirnova, 1967 includes three other species, *T. multifora* Fonin and Smirnova, 1967, *T. zhangwentangi* Qian and Bengtson, 1989, and *T. fonini* Esakova in Esakova and Zhegallo, 1996. The sellate sclerites of *T. pavlovi* sp. nov. are different from those of the other three species in the consistent absence of a pronounced sella and duplicature on the respective sides of sclerites, as well as in having regularly distributed large pores on the lateral edges. Qian and Bengtson (1989), however, noted that in some "sellate" sclerites of *T. zhangwentangi* the sella is less developed or absent, and that in those cases the duplicature is tightly adpressed to the apex. One of the "non-sellate sellates" they figured (Qian and Bengtson: fig. 54B) also has a recurved apex, similar to those of *T. pavlovi* and *T. fonini*, although it lacks the distinct row of lateral pores seen in *T. pavlovi*. In contrast to the other three species, the asymmetry of the mitral sclerites of *T. pavlovi* sp. nov. is not expressed by a radial furrow on the outer surface and a corresponding internal carina. Thus, there is no clear distinction between the carinate and obcarinate (lateral) sides. The mitral sclerites of *T. pavlovi* are also different from those of the other species in their having a tapered and slightly overhanging apex, and from *T. multifora* and *T. fonini* in having a more flattened decrescent side. Sclerites of *Tannuolina* from other localities typically have an internal wall structure consisting of loose, curving lamellae (cf. Fonin and Smirnova 1967). Such structures in the tomography scans of *T. pavlovi* sclerites are absent.

Remarks.—A single sclerite, flattened in the direction facing the decrescent side and curved laterally (Fig. 6), is interpreted as an aberrant mitral sclerite of the same species. The sclerite carries pores on the accrescent side (Fig. 6A).

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

Discussion

The material presented herein contains the first description of a tannuolinid from the Siberian Platform. Although *Tannuolina* sp. was reported from the uppermost 1 m of the Sukharikha Formation, Sukharikha River section (Luchinina et al. 1997; Rowland et al. 1998), neither description nor illustration was provided therein. We have not found *Tannuolina* in the uppermost Sukharikha Formation, only in the basal Krasnoporog Formation. Tannuolinids (*Tannuolina multifora*) were first described from the Atdabanian-equivalent beds of the Altai-Sayan fold belt (Fonin and Smirnova 1967). Other occurrences of *Tannuolina* are: *T. fonini* Esakova, 1996, from the Botomian-equivalent beds of western Mongolia (Esakova and Zhegallo 1996), *Tannuolina* sp., from the Lower Ovetian Stage of southern Spain correlated with the Atdabanian Stage of Siberia (Fernández-Remolar 2002), and *T. zhangwentangi* Qian and Bengtson, 1989, from the *Sinosachites flabelliformis–Tannuolina zhangwentangi* Assemblage Zone of the Yangtze Platform (Qian and Bengtson 1989; Conway Morris and Chen 1990; Li and Xiao 2004). The last occurrence was broadly correlated with the Tommotian–Atdabanian Stages (Li and Xiao 2004), and is now more precisely attributed to the lower Atdabanian (Steiner et al. 2007). In addition to *Tannu-*

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olina, the family Tannuolinidae also includes *Micrina* Laurie, 1986, a bimembrate brachiopod-like tommotiid reported from the Atdabanian–Botomian equivalent deposits of Australia (Laurie 1986; Ushatinskaya 2001, 2002; Williams and Holmer 2002; Holmer et al. 2008) and China (Li and Xiao 2004). Therefore, *Tannuolina pavlovi* sp. nov. recovered from the *Nochoroicyathus sunnaginicus* Biozone of the Tommotian Stage in Siberia, is the oldest tannuolinid described.

The sellate and mitral sclerites from the Sukharikha River are considered conspecific based on their identical surface ornament with comarginal folds and pores, similar size range, and on the co-occurrence of both types of sclerites in other localities containing tannuolinids. The mitral sclerites of *Tannuolina pavlovi* sp. nov. do not clearly show asymmetry of left and right forms, manifested in other species by the presence of the carina on the interior surface. In contrast with the other species, the bilaterally symmetrical sellate sclerites of *T. pavlovi* are characterised by the absence of a conspicuous sella and duplicature on their respective convex sides. Hence, the mitral and sellate sclerites of the new species are more similar to each other and have a simpler morphology than those of younger species of *Tannuolina*.

The family Tannuolinidae is included in the tommotiids (sensu lato), or the Order Tommotiida, a widely distributed group of fossil animals with external organophosphatic sclerites (Bengtson 1970; Bengtson 2004). The biological affinities of tommotiids, traditionally regarded as "problematica", have long remained completely obscure. A possible relationship to machaeridians, recently interpreted as annelids (Vinther et al. 2008), was initially suggested by Bengtson (1970, but see 1977: 37) and followed by Dzik (1986). Bengtson (1977: 57–58) also briefly discussed the possibility that the tannuolinids represent stem-group brachiopods, on account of the morphological similarities between the mitral sclerites of *Tannuolina etheridgei* (now *Micrina etheridgei*) and the ventral valve of some inarticulate brachiopods.

The concept of tannuolinids as a stem-group of linguliform brachiopods was elaborated by Williams and Holmer (Holmer et al. 2002; Williams and Holmer 2002), based on similarities in shell microstructure between *Micrina* and linguliform brachiopods (Williams and Holmer 2002; Holmer et al. 2002, 2008). This concept was expanded to halkieriids (Holmer et al. 2002, following Conway Morris and Peel 1995) and to other tommotiids and the problematic *Mickwitzia*, proposed as stem-groups of the brachiopods (Holmer et al. 2002, 2008; Skovsted et al. 2009a, b, c) and phoronids (Skovsted et al. 2008). Presently, the tommotiids (sensu lato) are regarded as a paraphyletic brachiopod stem-group (Skovsted et al. 2009a; Balthasar et al. 2009). Based on the differences in sclerite morphology, microstructure and scleritome construction, a "camenellan" clade has been interpreted to form a sister group of a clade that includes *Eccentrotheca*, *Paterimitra*, tannuolinids, and brachiopods (Skovsted et al. 2009a, c). Microstructures of paterinid brachiopods are more similar to those of *Eccentrotheca* and *Paterimitra* than to those of other lingulids (Balthasar et al. 2009), while tannuolinids were originally compared to the linguloid brachiopods (Williams and Holmer 2002). Whilst the detailed topology of stem-group brachiopods remains fluid, tannuolinids are interpreted as being likely stem group linguloids, whereas other tommotiids (e.g., *Kulparina* and *Paterimitra*) probably lie in the stem of the paterinids (see discussion in Skovsted et al. 2009c). Articulated scleritomes of the tommotiids *Eccentrotheca* (Skovsted et al. 2008) and *Paterimitra* (Skovsted et al. 2009c) suggest that the bivalved brachiopod skeleton and body plan evolved through transition from vagrant to sessile mode of life, shortening and specialisation of an attached tubular scleritome, and numerical reduction of sclerites (Skovsted et al. 2008, 2009a, b, c).

The tommotiids are usually preserved as disarticulated sclerites and were traditionally reconstructed as slug-like bilaterians with dorsally situated anterior-posterior rows of imbricating sclerites (Bengtson 1970, 1977; Landing 1984; Qian and Bengtson 1989; Conway Morris and Chen 1990; Li and Xiao 2004). Ushatinskaya (2001, 2002), Holmer et al. (2002), and Williams and Holmer (2002) and interpreted the sellate and mitral sclerites of *Micrina* as the anterior and posterior shells, respectively, of a *Halkieria*-like bilaterian with or without intermediate sclerites; the shells would be homologous with the dorsal and ventral valves, respectively, of an ancestral brachiopod. Articulated tubular scleritomes of the tommotiids *Eccentrotheca* (Skovsted et al. 2008) and *Paterimitra* (Skovsted et al. 2009c) imply that these had an attached sessile mode of life. Tannuolinids are currently reconstructed as probably sessile animals too, with *Micrina* having only two valves (sclerites) and the closely related *Tannuolina* having a tripartite scleritome consisting of one sellate opposed to two mitrals (Holmer et al. 2008).

The order Tommotiida usually incorporates five families (Tommotiidae, Lapworthellidae, Kennardiidae, Sunnaginidae, and Tannuolinidae), but there is no consensus on their composition (Landing 1984, 1995; Dzik 1986; Laurie 1986; Missarzhevsky 1989; Bengtson et al. 1990; Conway Morris and Chen 1990; Esakova and Zhegallo 1996). Similarities in morphology and microstructure of sclerites of Tommotiidae, Lapworthellidae, and Kennardiidae suggest that they likely form a monophyletic group, termed the "camenellan clade" within the Tommotiida by Skovsted et al. (2009a). They are reconstructed as vagrant animals covered with bilaterally arranged dorsal sclerites (Skovsted et al. 2009a). The family Sunnaginidae includes forms with irregular mode of secretion of sclerites, but the question of whether they form a natural group needs further investigation following the discovery of articulated tubular scleritomes of *Eccentrotheca* and *Paterimitra* indicating an attached mode of life (Skovsted et al. 2008, 2009c). The family Tannuolinidae is believed to comprise the most derived forms of tommotiids and can be defined as a natural group sharing similarities in shell microstructure and presence of shell-penetrating setae (Williams and Holmer 2002; Li and Xiao 2004; Holmer et al. 2008; Skovsted et al. 2009c). The presence of non-mineralised setae in other tommotiids cannot be excluded, however, because setae are considered plesiomorphic for the Spiralia

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(cf. Peterson and Eernisse 2001). Moreover, lateral macropores in the sellate sclerites of *Tannuolina pavlovi* sp. nov. show that large and presumably relatively long setae were present at the margins of the sclerites, thus setae may well also have been intercalated between the sclerites of other tommotiids.

Finely striated tubes in the tannuolinid *Micrina* and the proposed stem-group brachiopod *Mickwitzia* have been interpreted as setal tubes homologous to those in brachiopods (Holmer et al. 2002, 2008; Williams and Holmer 2002). Recent discoveries of bundles of phosphatised setae within blindly ending striated epipunctae of Ordovician brachiopods (Jin et al. 2007) seem to provide support for this interpretation of the tubes as well as an explanation of the fine striation of the tube walls as being the impressions of setal canals. The 1–2 μm pores in *Tannuolina pavlovi* that end in a bulb-like swelling (Fig. 3D, G) may be interpreted as abandoned fine setae that were sealed from the inside when new growth lamellae were deposited. The basal swelling may then reflect the presence of a setal follicle. The coarser pores on the lateral sides of the sellate sclerites resulting from merging of two adjacent smaller pores (Fig. 3F) might be explained as produced by converging pairs of setae. The two setae originate, however, in different positions, and such a model would need to explain how they could so consistently find each other to join in a common pore. We are not aware of any direct analogue to the coalescing double type seen in *T. pavlovi*.

Tommotiid sclerites are composed of alternating laminae, presumably different in original phosphatic versus organic-rich composition (Balthasar et al. 2009). Among them, tannuolinids are characterised by alternation of thin compact and thicker spacious layers penetrated by open setal tubes (Conway Morris and Chen 1990; Williams and Holmer 2002; Li and Xiao 2004), whereas sclerites of the "camenellan clade" as well as *Eccentrotheca* and *Paterimitra* differ in their denser lamination and the lack of setal tubes. Denser microstructures are suggested to be more primitive among tommotiids (Balthasar et al. 2009). Sclerites of *Tannuolina* typically have an internal wall structure consisting of loose laminae (cf. Fonin and Smirnova 1967). Sclerites of *T. pavlovi* show co-marginal folds on the surface, interpreted herein as growth increments that presumably continued into the wall as growth laminae. The apparent absence of lamination in the tomography scans and fractured sections of *T. pavlovi* sclerites may be due to an originally compact arrangement of growth laminae with boundaries diagenetically obscured by calcium phosphate.

Classical tommotiids, such as *Camenella* Missarzhevsky, 1966 in Rozanov and Missarzhevsky (1966), are known from the lower Tommotian deposits of the Siberian Platform. They have also been reported, without description or illustration (Rozanov et al. 1969; Meshkova et al. 1976; Fedorov and Shishkin 1984; Khomentovsky and Karlova 1993; Luchinina et al. 1997), from apparently older beds (Kouchinsky et al. 2001, 2007) of the northern Siberian Platform. The first appearances of tommotiids in Western Mongolia (Brasier et al. 1996), South China (Qian and Bengtson 1989; Li et al. 2007), and Avalonia (Landing et al. 1989) are older than the base of the Tommotian Stage in its stratotype in the southwestern part of the Siberian Platform. Hence, the initial diversification of tommotiids, including tannuolinids, occurred no later than the appearance of brachiopods in the fossil record, supporting interpretation of tommotiids as stem group brachiopods.

Based on molecular data showing brachiopod monophyly and interpretation of tommotiids as part of the brachiopod stem-group, Balthasar (2008) and Balthasar et al. (2009) suggested that the organophosphatic skeletal composition of brachiopods is plesiomorphic, while calcareous shells are derived. Molecular data suggest, however, that phosphatic biomineralisation is a derived condition within the brachiopods and that calcareous biomineralisation arose separately in articulates and inarticulates (craniiforms) (Cohen and Weydmann 2005).

The earliest brachiopod with an organophosphatic shell, the paterinid *Aldanotreta sunnaginensis* Pelman, 1977, is reported to have appeared first on the Siberian Platform in the *N. sunnaginicus* Biozone of the Tommotian Stage (Bengtson et al. 1987; Ushatinskaya and Malakhovskaya 2001). The reportedly earliest brachiopods with calcareous shell are *Nochoroiella isitica* Pelman, 1983 and *Obolella* sp. from the *Dokidocyathus lenaicus* Biozone of the Tommotian Stage of Siberia. They are assigned to obolellids, although the affinity of *Nochoroiella isitica* with brachiopods was questioned by Popov and Holmer (2000: 206–207), who mentioned that it is poorly known and may be an operculum. Chemostratigraphic correlation with Siberia suggests, however, that these occurrences are likely predated by *Khasagtina primaria* Ushatinskaya, 1987 from Western Mongolia, assigned to kutorginids. This form occurs in beds containing high $\delta^{13}C$ peaks known just below the lower Tommotian boundary in Siberia (Brasier et al. 1996; Kouchinsky et al. 2001, 2005, 2007; Maloof et al. 2005).

Tianzhushanellids seem to be the best candidates for calcitic-shelled stem-group brachiopods, but their preservation does not provide as many features as tommotiids for evaluation of their affinity with brachiopods (Balthasar 2008). The Family Tianzhushanellidae Conway Morris in Bengtson et al. 1990 includes calcareous shelly fossils reconstructed as bivalved and morphologically resembling brachiopods. *Tianzhushanella* Liu, 1979 was proposed as a senior synonym of *Lathamella* Liu, 1979 (Parkhaev 2001, but Li 2009), and these earliest representatives of tianzhushanellids, like the first tommotiids, are reported from beds of the Middle Meishucunian Stage, containing the *Paragloborilus subglobosus–Purella squamulosa* Assemblage Zone 2 fossils (Li and Chen 1992; Steiner et al. 2007). Hence, the order of appearance of calcareous and phosphatic brachiopods in the Cambrian Stage 2, as well as the first appearances of their putative stem groups in the fossil record of the Fortunian Stage need further investigation.

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