Trace Fossils from the Vendian-Cambrian Transitional Strata of the Igarka Uplift (Northwestern Siberian Platform)

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Abstract—The Vendian—Cambrian transitional strata of the Igarka Uplift (northwestern Siberian Platform), originally erected as the Sukharikha Formation, are one of the key objects revealing evolution of marine ecosystems in the late Vendian. Herein we describe dwelling burrows *Skolithos* and *Arenicolites* from dolostones in the middle Sukharikha Formation (Nemakit-Daldynian Regional Stage). High density and local distribution of these burrows in the Sukharikha Formation demonstrate that the terminal Vendian shallow-marine sediments became occupied by vertical-burrowing benthic organisms, mirrored in the geological record as an archetypical Phanerozoic ichnoassemblage (*Skolithos* ichnofacies).

Keywords: Vendian, Nemakit-Daldynian Regional Stage, trace fossils, Siberian Platform **DOI:** 10.1134/S0031030119060030

INTRODUCTION

The Cambrian deposits of the Igarka Uplift (northwestern Siberian Platform) are characterized by a very representative paleontological record (Rosanov et al., 1992; Repina, 1972; Luchinina et al., 1997; Rowland et al., 1998; Kouchinsky et al., 2010; etc.) and hence they comprise one of the key objects for both regional and global reconstruction of the Early Phanerozoic ecosystems. However, the Vendian-Cambrian transitional deposits, erected as the Sukharikha Formation (excluding its uppermost 2 m) within the Igarka Uplift, are quite poorly characterized paleontologically. The absence of (a) the typical associations of small skeletal fossils (Anabarites trisulcatus and Purella antiqua Assemblage Zones) and (b) trace fossils in the Vendian part of the section makes both intraregional and interregional correlation highly controversial (Rozanov et al., 1992; Kouchinsky et al., 2007; Maloof et al., 2010); as therefore reconstruction of benthicassemblages evolution evolution in the Late Vendian-Early Cambrian in the northwestern Siberian Platform (modern coordinates) becomes complicated.

The fossils described in the present work have been reported earlier from the Sukharikha Formation in the eastern limb of an anticline, located 15 km upstream the Sukharikha River mouth. However, the earlier researchers provided no detailed description and images of the material (Luchinina et al., 1997). Herein we report a representative fossil assemblage from the middle Sukharikha Fromation in the western limb of this anticline, collected during the fieldworks in 2015. The detailed study of morphology and taphonomy demonstrate, that these forms are trace fossils, and also reveal ethology (behavior) and ecological conditions of the producers.

GEOGRAPHIC AND STRATIGRAPHIC SETTING

The described fossils were discovered in the outcrops on the left bank of Sukharikha River, 45 km upstream its mouth (67°12'39.5" N, 87°19'47.3" E) (Figs. 1a, 1b). Structurally, the findings are located in the western limb of the anticline (Figs. 1c; 2b). The fold is composed of the Vendian-Cambrian transitional rocks: the uppermost Izluchin, Sukharikha, Krasny Porog, and Shumny formations (Fig. 2b). The Izluchin and Sukharikha formations (excluding the uppermost 2 m of the latter) refer to the Vendian (Rozanov et al., 1992). Microphytolites (Nubecularites antis and N. varius), calcareous cyanobacteria (Renalcis sp. and Girvanella sp.) (Rozanov et al., 1992), and scarce small tubular fossils Anabarites sp. (Rowland et al., 1998) from the upper Sukharikha Formation refer it to the Nemakit-Daldynian Regional Stage of the Upper Vendian. Based on the representative assemblages of small skeletal fauna, archaeocyaths, and trilobites, the uppermost 2 m of the Sukharikha Formation and overlying strata (Krasny Porog Formation and lower Shumny Formation) correspond to the



Fig. 1. (a) The location of sampling sites for the studied material in the Siberian Platform (triangle denotes the area shown in Fig. 1b in detail); (b) geographic position of the section, from which the described ichnofossil assemblage originates (gray triangle marks the area shown in detail in Fig. 1c); (c) the fragment of a geological map of the Igarka Uplift with localities of the studied specimens. Legend: (1) outcrop, from which the described ichnoassemblage originates; (2) fault; (3) Izluchin Formation; (4) Sukharikha Formation; (5) Krasny Porog Formation The stratigraphic relationships between the formations are shown in Fig. 2.

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Fig. 2. (a) The integrated section of the Vendian–Cambrian transitional strata of the Igarka Uplift, and the carbon isotope curve $(\delta^{13}C)$ with indices of isotope excursions after (Kouchinsky et al., 2007). The boundaries of stratigraphic units of the General Stratigraphic Scale of Russia (GSSR) are after (Luchinina et al., 1997) and those of the ICC are after (Kouchinsky et al., 2007; Maloof et al., 2010), with the correlations between them provided after (Zhamoida, 2008). (b) The geological profile along the Sukharikha River with the locations of sites where the ichnofossils were collected; the formation colors correspond to those in Figs. 1b and 1c. (c) The sketch of ichnofossil relationships with the host hummocky cross-bedded dolostones. Lithology and fossils: (1) thin-bedded siltstones and mudstones; (2) plane- and cross-bedded sandstones; (3) alternatingdolostones and limestones, and their transitional varieties; (4) thin-bedded limestones; (5) first appearance in the Sukharikha Formation of (a) small skeletal fossils *Anabarites* (240 m above the base) and (b) small skeletal fossils and arvhaeocyaths of the Tommotian *Nochoroicy-athus sunnaginicus* Assemblage Zone GSSR (2 m below the top) are reported after (Luchinina et al., 1997; Rowland et al., 1998). Abbreviations: (izl) Izluchin Formation; (kp) Krasny Porog Formation; (tom) Tommotian Stage; (atd) Atdabanian Stage.

Tommotian, Atabanian, and the lowermost Botoman stages of the Lower Cambrian (Rozanov et al., 1969; Rowland et al., 1998) (Fig. 2a).

Nowadays an international geological community conducts the research aimed at detalization of the geological record in the Precambrian—Phanerozoic boundary interval (Peng et al., 2012; Babcock et al., 2014; etc.). Due to the ongoing development of the criteria for determining global boundaries between stages and series of the Cambrian in the International Chronostratigraphic Chart (ICC), the comparison of ICC with the Lower Cambrian units of the General Stratigraphic Scale of Russia is, in many aspects, disputable (Rozanov et al., 1997; Parkhaev et al., 2011). Based on the comparison between the carbon-isotope variations in carbonates of the Sukharikha Formation and the composite curve of $\delta^{13}C_{carb}$ values (Peng et al., 2012), the earlier researchers (Kouchinsky et al., 2007) supposed the Fortunian Age (in terms of the ICC) for at least lowermost 370 m of this unit due to the similar shift of $\delta^{13}C_{carb}$ from highly negative to positive values up the section (Maloof et al., 2010). Since the materialherein studied does not specify the correlation between the International and Russian stratigraphic charts, we use the correlation scheme ratified in 2008 by the Interdepartmental Stratigraphic Committee of Russia (Zhamoida, 2008).

The fossils studied in the framework of the present work were found in the middle part of the Sukharikha Formation, 284 m above its base, and hosted in dark gray granulous-bedding dolostones (Fig. 2a). The Sukharikha Formation (570 m thick) is majorly composed of light and dark gray dolostones, limestones, and dolomitized limestones, characterized by different clay contents, with locally distributed small domal bioherms. The lower part of the formation includes interbeds and packages of middle-grained cross-bedded sandstones, while desiccation cracks occur on the bed tops in the upper ones. The Sukharikha Formation deposited in shallow shelf environments, within the subtidal proximal carbonate ramp (Rowland et al., 1998).

FOSSIL MORPHOLOGY

Earlier, individual similar findings were reported from the middle the Sukharikha Formation in natural outcrops alongside the Sukharikha River, in the eastern limb of the anticline (Luchinina et al., 1997). They were illustrated only with schematic drawings and interpreted as trace fossils of soft-bodied organisms. Our findings originate from the western limb of the anticline and demonstrate both considerably higher density and morphological diversity. All the fossils are from an isolated outcrop of hummocky cross-bedded dolostones (several meters thick) in the middle part of the unit (Fig. 2c).

The fossils comprise majorly straight, weakly bent, and, rarely, U-shaped tubular forms, subvertical and slightly inclined. Cross-sections of the fossils clearly reveal two zones: the inner one (1-3 mm in diameter), filled with large-crystalline calcite, and the outer one (up to 8 mm wide), represented by fine-crystalline dolostone, more light-colored compared to the host rock (Pl. 3, figs. 1, 3, 6). The inner tubes of some specimens are only partially filled, so that cylindrical inner cavity can be seen (Pl. 3, fig. 4). The maximum documented diameter of the outer zone reaches 20 mm. The outer zone can either have an indistinct gradual outer contact with the host rock (Pl. 3, figs. 3–6), or be separated from it with a thin patina of dark-colored grains (Pl. 3, fig. 7). The visible length of fossils range from few to 15-20 cm, however, due to a thick-bedding of the host rocks, it is impossible to establish their real lengths in most cases. In the longitudinal section, the central tube sometimes can be distorted or have local transverse constrictions. Fossils are unbranched. Within the bed they occur densely, however, arranged separately, with no intersects, overlaps, and merges of central cylindrical tubes being observed. In some specimens, the outer zones of two closely located parallel tubes are documented.

The morphological simplicity, high density, spatial arrangement, and the morphological features reveal that these objects comprise vertical burrows produced by benthic organisms in the sediment. The presence of lithologic differentiation of the substance within and outside the fossils, as well as the general morphology, suggest that the central cylindrical parts are the open burrows in substrate where organisms lived. This is supported by recrystallization of the central part of a burrow, which is quite common taphonomic feature for open burrows in carbonate sediments (Kemp, 1995; Myrow, 1995). In contrast, the outer zone, which often has a indistinct outer boundary, is ahalo produced by diagenetic alteration of sediment around the burrow walls, cemented with a slime of a tracemaker (Myrow, 1995; Pemberton and Gingras, 2005; Buatois and Maágano, 2011). There are two main morphological categories of the burrows in the studied collection: straight (or weakly bent) subvertical and vertical U-shaped ones. The former are referred to the ichnogenus Skolithos Haldeman, 1840; the latter, Arenicolites Salter, 1857.

DESCRIPTION OF FOSSIL MATERIAL

The described material is stored at the Central Siberian Geological Museum (CSGM, Novosibirsk), collection no. 2091.

Burrows Arenicolites are comparatively rare in the Sukharikha Formation: the only poorly-preserved specimen (CSGM no. 2091/1) is found. Unfortunately, the absence of a representative collection and bad preservation limit precise identification of the specimen within the Arenicolites ichnogenus. The described specimen is a U-shaped vertical burrow in the negative endorelief, preserved as a groove outlining the outer zone (diagenetic halo) around the burrow, in dark gray dolostones (Pl. 3, fig. 8). The halo is up to 1 cm in diameter and transit gradually in the host rock. The visible depth of the burrow is 3 cm; the distance between axes is 2.5 cm. Due to a specific weathering and preservation, central cylindrical burrow is almost not represented in the specimen- only a short (7 mm) fragment of 3 mm in diameter is seen. It is filled with well recrystallized calcite, with no indications of constrictions or structured filling (Pl. 3, figs. 5-7). The space between vertical segments of the burrow has no traces of sediment rework: the sediment is structurally and lithologically identical to the host rock.

The absence of intense sediment-reworkof the space between the vertical segments of the burrow (spreite-structures) and the unstructured burrow infill robustly distinguish the material from *Diplocraterion* Torell, 1870 and refer them to the *Arenicolites* ichnogenus. The *Arenicolites* trace fossils are subvertical U-shaped burrows in substrate (domichnia), produced by suspension feeding benthic organisms (e.g., see (Fürsich, 1975; Pickerill et al., 1984; Bromley, 1996; MacEachern et al., 2012)). They are widespread in siliciclastic and carbonate shallow-marine shelf deposits with active hydrodynamics and comprise one of indicator taxa of the *Skolithos* ichnofacies (Sei-



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lacher, 1964; Howard and Frey, 1984; MacEachern et al., 2012; Knaust et al., 2012). Suspension-feeding annelids or crustaceans are supposed as the *Arenicolites* tracemakers (Pickerill et al., 1984). In the geological record, these trace fossils became the most widespread since the Cambrian Stage 2 (yet undefined second stage of the Cambrian System in the ICC) (Mángano and Buatois, 2014). However, the oldest rare findings are reported from the Upper Vendian deposits (Oji et al., 2018).

Multiple vertical and slightly inclined cylindrical burrows of 1-3 mm in diameter and having visible lengths from few to 15 cm (particular specimens are up to 20 cm long), occurring in the same beds in the middle Sukharikha Formation, are referred to the Skolithos verticalis (Hall, 1843) ichnospecies (Pl. 3, figs. 1-7). The burrows are mainly straight, sometimes gently bending or with flexural bends (Pl. 3. fig. 5). The burrows are filled with large-crystalline structureless calcite. The central part of the burrow sometimes can be hollow (Pl. 3, fig. 4). The cylindrical burrows always have a surrounding giagenetic halo (up to 2 cm in diameter) around them, composed of lightcolored fine-crystalline dolostone. The boundary between the halo and the host dark gray dolostone is predominantly indistinct and gradual; however, in some specimens, it is highlighted with thin patina of dark-colored grains (Pl. 3, fig. 7). Diagenetic halos of closely located burrows can merge forming a single eliptical one (Pl. 3, figs. 1, 3, 4). The burrows within the bed are arranged quite densely, but separately, not intersecting or overlapping each other. On the bedding planes, the diagenetic halos are weathered more intensely than the host rock and represented by rounded cup-shaped hollows, with a cylindrical burrow slightly raising in thecenter (Pl. 3, fig. 1).

S. verticalis differ from the type ichnospecies Skolithos linearis Haldeman, 1840, which is the most similar in morphology, in relatively less diameter of burrows (1–4 mm for S. verticalis versus 3–12 mm for S. linearis) and less depths of the burrows. Also, the diagnostic feature of S. verticalis is the predominantly subvertical orientation and minimal bending of burrows.

The Skolithos burrows are morphologically most similar to simple vertical burrows Monocraterion Torell, 1870, with the only difference in the absence of funnel-shaped terminal openings of a burrow. The problem about validity of the Monocraterion ichnotaxon has been repeatedly raised by various researchers (Alpert, 1974; Bromley, 1996; Jensen, 1997), since the presence of the main diagnostic feature of this ichnogenus (funnel-shaped openings) in many cases depends on the preservation conditions of a material under study. Preservation of the studied material from the Sukharikha Formation does not shows no evidence considering this nomenclatural problem. However, the absence of funnel-like broadened parts in the samples containing projections of the vertical burrows on the bedding planes (Pl. 3, figs. 1, 2) give us a solid ground to refer them to the Skolithos ichnogenus. The trace fossils of similar preservation were described by V.A. Astashkin (1985) from the Lower Cambrian (Nokhoroi member, Kutorgina and Keteme forma-

Explanation of Plate 3

All specimens are collected from the same locality: northwestern Siberian Platform, Igarka Uplift, Sukharikha River; Sukharikha Formation, 284 m from the base, Nemakit-Daldynian Regional Stage of the Upper Vendian.

Fig. 1. Projections of subvertical *Skolithos verticalis* burrows (arrows) on the weathered bedding plane of hummocky cross-bedded dolostones in a negative epirelief. Dashed lines denote the outer contours of diagenetic halo around the burrows. Specimen CSGM no. 2091/2.

Fig. 2. Longitudinal section of vertical and inclined burrows *Skolithos verticalis* on the weathered cleavage surface of hummocky cross-beddeddolostones. Arrows indicate burrows filled with large-crystalline calcite; dashed lined, outer contours of diagenetic halo around the burrows. Specimen CSGM no. 2091/3.

Fig. 3. Cross-cut (subparallel to the bedding plane) of *Skolithos verticalis* burrows, isolated and with merged diagenetic halos (light-colored rounded zones). Rectangle marks the fragment enlarged in fig. 4. Specimen CSGM no. 2091/4.

Fig. 4. Enlarged fragment of fig. 3 with cross-cuts of *Skolithos verticalis* burrows. An arrow indicates the burrow cross-sections with the central cavity partially not filled with calcite. White rectangles mark the zones where diagenetic halo gradually transit to the host rock. Specimen CSGM no. 2091/4.

Fig. 5. Longitudinal section of parallel, straight, and weakly bending subvertical burrows *Skolithos verticalis* (arrows) and surrounding light-colored diagenetic halos with an indistinct outer boundary (dashed lines) with the host rock. Specimen CSGM no. 2091/5.

Fig. 6. Thin section with a cross-cut of a subvertical *Skolithos verticalis* burrow . A rectangle shows the zone of a gradual transition from fine-crystalline dolomite filling the diagenetic halo around the cylindrical burrow filled with well crystallized calcite (black arrow) to the host sparitic dolostone. Specimen CSGM no. 2091/6.

Fig. 7. Thin section with cutting subparallel to the beddingof an inclined *Skolithos verticalis* burrow. Black arrow marks the cylindrical burrow filled with well crystallized calcite; white rectangle, the contact between the diagenetic aureole (light-colored fine-crystalline dolomite) surrounding the burrow and the host crystalline dolostone (the contact is highlighted with a patina of fine dark-colored grains). Specimen CSGM no. 2091/7.

Fig. 8. Cross-cut of the U-shaped vertical burrow *Arenicolites* isp. on the weathered cleavage surface of hummocky cross-bedded dolostone. An arrow indicates the short fragment of calcite-filled cylindrical burrow; dashed line outlines the boundary of diagenetic halo. Specimen CSGM no. 2091/1.

tions) of the Anabar-Sinsk facies region (middle stream of Lena and Botoma rivers) as burrows Aulophycus repens Fenton et Fenton, 1939. However, in contrast to the material from the Sukharikha Formation, theforms described by V.A. Astashkin are characterized by significantly broader morphological variations: in addition to straight and bending subvertical and inclined segments, tubular trace fossils are also widespread subhorizontally on the bedding planes (Astashkin, 1985, pl. LIII, figs. 2, 3), where they form polychotomically branching systems of cylindrical tubes. Based on their morphology, the described trace fossils from Lower Cambrian of the southeastern Siberian Platform putatively comprise three-dimensional systems of open burrows Thalassinoides Ehrenberg, 1944. A.Yu. Zhuravlev et al. (2014) supposed that these trace fossils may refer to Ophiomorpha Lundgren, 1891. But, first, the figures provided in this work do not indicate reliably that the burrow walls are encrusted with spherical pellets (diagnostic feature for this ichnogenus), and, second, the oldest Ophiomorpha ichnogenus appear in the fossil record as late as the Permian (Droser and Bottjer, 1993; Buatois and Mángano, 2011).

The *Skolithos* burrows are interpreted as passively filled dwelling burrows (domichnia), made in the substrate by suspension feeders (Alpert, 1974; Häntzschel, 1975; Bromley, 1996). Due to the morphological simplicity of the burrows, they can be formed by a wide range of marine benthic organisms. In the Paleozoic strata, vertical burrows *Skolithos* mostly characterize shallow-water marine depositional environments with active hydrodynamics and constant influx of sediment and nutrients. These burrows are the key taxon for the shallow-marine ichnofacies of the same name (Seilacher, 1964; Buatois and Mángano, 2011).

The burrows *Skolithos* are extremely widespread in the fossil record of benthic ichnocommunities since the base of the Cambrian (mostly, from the Cambrian Stage 2) (Buatois and Mángano, 2014). However, the oldet *Skolithos* are known from the Redkino Regional Stage, Upper Vendian of the East European Platform (Fedonkin, 1985), and from the Upper Vendian Nemakit-Daldynian Regional Stage of Siberia (Fortunian Stage of the Cambrian in the ICC) (McIlroy and Brasier, 2017).

DISCUSSION AND CONCLUSIONS

The only local discovery of the numerous vertical dwelling burrows in the Sukharikha Formation within the monofacies interval is caused by, most likely, the following factors. First, the fragmentary outcrop of this interval in the western limb of the anticline, in contrast to the character of formation layers outcropped in the eastern limb (relatively continuous exposure of steeply and subvertically dipping layers, often amalgamated to form thick members and packages), coupled with the limited access to the bedding planes; that extremely complicates the search for and identification of trace fossils. Second, the local distribution of *Skolithos* and *Arenicolites* in the Sukharikha Formation can be related to the increasing degree of recrystallization of carbonate deposits up the section, which drastically limits preservation potential of the burrows. Most probably, this ichnoassemblage ubiquitously characterize all overlying strata of the Sukharikha Formation, which is supported by previous individual findings of similar burrows published with no description and images (Luchinina et al., 1997).

The findings of *Skolithos* and *Arenicolites* in the Sukharikha Formation agree with the earlier formulated facial interpretation of this interval (Rowland et al., 1998). In the Phanerozoic, deposits accumulated within the proximal carbonate ramp is characterized by the *Skolithos* ichnofacies, which is composed of various but morphologically simple domichnia of suspension feeders (*Skolithos, Arenicolites, Ophiomorpha, Psilonichnus, Rhizocorallium*, and others), produced in the environments with a high hydrodynamic activity (Knaust et al., 2012).

The evolution of endobenthic communities and organism-substrate interactions in the late Precambrian-Cambrian transition is known as "the First Agronomic Revolution" (Seilacher and Pflüger, 1994; Seilacher, 1999). In the sequence of evolving types of sediment rework by burrowers, the Late Vendian stage (Nemakit-Daldynian Regional Stage), roughly corresponding to the Fortunian Age of the Cambrian in the ICC, is characterized by widespread and diverse horizontal burrows. In contrast, vertical dwelling domichnia are relatively rare, gradually becoming more abundant closer to the beginning of the Cambrian Age 2 (~530 Ma ago) (Mángano and Buatois, 2017), which loosely corresponds to the beginning of the Tommotian Age in the General Stratigraphic Scale of Russia (Parkhaev et al., 2011; Zhuravlev and Wood, 2018). Further colonization by sedentary suspension feeders of shallow-water marine environments in the Cambrian has led to the formation of specific sedimentary rocks, so called "the pipe-rocks" (Desjardins et al., 2010). The abundant findings of vertical dwelling burrows (Skolithos and Arenicoliltes) in the Sukharikha Formation of the Igarka Uplift indicate that the formation of typical Phanerozoic recurrent shallowwater shelf ichnoassociations (Skolithos ichnofacies) began in the shallow-water marine environments with carbonate sedimentation as early as the Nemakit-Daldynian time, although less extensively than in theyounger analogs.

FUNDING

The study was carried out in the framework of Research Program no. IX.126.1 and was supported by the Russian Foundation for Basic Research (project no. 17-05-00852).

REFERENCES

Alpert, S.P., Systematic review of the genus *Skolithos*, *J. Paleontol.*, 1974, vol. 48, pp. 661–669.

Astashkin, V.A., Problematic rock-forming organisms in the Lower Cambrian deposits of the Siberian Platform, in *Problematiki pozdnego dokembriya i paleozoya* (Problematic Organisms of the Late Precambrian and Paleozoic), Tr. Inst. Geol. Geofiz. Sib. Otd. Akad. Nauk SSSR, vol. 632, Moscow: Nauka, 1985, pp. 144–149.

Babcock, L.E., Peng Sanchi, Zhu Maoyan, Xiao Shuhai, and Ahlberg, P., Proposed reassessment of the Cambrian GSSP, *J. Afr. Earth Sci.*, 2014, vol. 98, pp. 3–10.

Bromley, R.G., *Trace Fossils: Biology, Taphonomy and Applications*, London: Chapman & Hall, 1996, 2nd ed.

Buatois, L.A. and Mángano, M.G., *Ichnology. Organism– Substrate Interactions in Space and Time*, Cambridge: Cambridge Univ. Press, 2011.

Desjardins, P.R., Mángano, M.G., Buatois, L.A., and Pratt, B.R., Skolithos pipe rocks and associated ichnofabrics from the southern Rocky Mountains, Canada: Colonization trends and environmental controls in an early Cambrian sand-sheet complex, *Lethaia*, 2010, vol. 43, pp. 507– 528.

Droser, M.L. and Bottjer D.J., Trends and patterns of Phanerozoic ichnofabrics, *Annu. Rev. Earth Planet. Sci.*, 1993, vol. 21, pp. 205–225.

Fedonkin, M.A., Paleoichnology of the Vendian Metazoa, in *Vendskaya sistema. Istoriko-geologicheskoe i paleontologicheskoe obosnovanie* (Vendian System: Historical-Geological and Paleontological Evidence), vol. 1: *Paleontologiya* (Paleontology), Moscow: Nauka, 1985, pp. 112–117.

Fürsich, F.T., Trace fossils as environmental indicators in the Corallian of England and Normandy, *Lethaia*, 1975, vol. 8, pp. 151–172.

Häntzschel, W., Miscellanea, in *Treatise on Invertebrate Paleontology*. Part W. Suppl. 1: *Trace Fossils and Problematica*, Teichert, C., Ed., Lawrence: Geol. Soc. Am., 1975, 2nd ed.

Howard, J.D. and Frey, R.W., Characteristic trace fossils in nearshore to offshore sequences, Upper Cretaceous of east-central Utah, *Can. J. Earth Sci.*, 1984, vol. 21, pp. 200–219.

Jensen, S., *Trace Fossils from the Lower Mickwitzia Sandstone, South-Central Sweden*, Fossils and Strata, no. 42, Oslo: Scandinavian Univ. Press, 1997.

Kemp, A.E.S., Variation of trace fossils and ichnofacies in Neogene and Quaternary pelagic sediments from the eastern equatorial Pacific Ocean (Leg 138), *Proc. Ocean Drilling Program, Sci. Results*, Pisias, N.G., Mayer, L.A., Janecek, T.R., Palmer-Julson, A., and van Andel, T.H.. Eds., Texas: College Station, 1995, vol. 138, pp. 177–190.

Knaust, D., Curran, H.A., and Dronov, A.V., *Shallow-marine carbonates, Trace Fossils as Indicators of Sedimentary Environments, Developments in Sedimentology*, vol. 64, Amsterdam: Elsevier, 2012, pp. 705–750.

Kouchinsky, A., Bengtson, S., and Murdock, D.J.E., A new tannuolinid problematic from the lower Cambrian of the Sukharikha River in northern Siberia, *Acta Palaeontol. Pol.*, 2010, vol. 55, no. 2, pp. 321–331.

Kouchinsky, A., Bengtson, S., Pavlov, V., Runnegar, B., Torssander, P., Young, E., and Ziegler, K., Carbon isotope stratigraphy of the Precambrian–Cambrian Sukharikha River section, northwestern Siberian platform, *Geol. Mag.*, 2007, vol. 144, pp. 609–618.

Luchinina, V.A., Korovnikov, I.V., Sipin, D.P., and Fedoseev, A.V., Upper Vendian–Lower Cambrian biostratigraphy of the Sukharikha River section, *Russ. Geol. Geophys.*, 1997, vol. 38, no. 8, pp. 1385–1397.

MacEachern, J.A., Bann, K.L., Gingras, M.K., Zonneveld, J-P., Dashtgard, S.E., and Pemberton, S.G., The ichnofacies paradigm, in *Trace Fossils as Indicators of Sedimentary Environments*, Knaust, D. and Bromley, R., Eds., Developments in Sedimentology, vol. 64, Amsterdam: Elsevier, 2012, pp. 103–138.

Maloof, A.C., Porter, S.M., Moore, J.L., Dudás; F.Ö., Bowring, S.A., Higgins; J.A., Fike; D.A., and Eddy, M.P., The earliest Cambrian record of animals and ocean geochemical change, *GSA Bull.*, 2010, vol. 122, nos. 11–12, pp. 1731–1774.

Mángano, M.G. and Buatois, L.A., Decoupling of bodyplan diversification and ecological structuring during the Ediacaran–Cambrian transition: evolutionary and geobiological feedbacks, *Proc. R. Soc. London, Ser. B*, 2014, vol. 281, art. no. 20140038.

Mángano, M.G. and Buatois, L.A., The Cambrian revolutions: Trace-fossil record, timing, links and geobiological impact, *Earth-Sci. Rev.*, 2017, vol. 173, pp. 96–108.

McIlroy, D. and Brasier, M.D., Ichnological evidence for the Cambrian Explosion in the Ediacaran to Cambrian of Tanafjord, Finnmark, northern Norway, in *Earth System Evolution and Early Life: a Celebration of the Work of Martin Brasier*, Brasier, A.T., McIlroy, D., and McLoughlin, N.L., Eds., Geol. Soc. London, Spec. Publ., vol. 448, London: Geol. Soc., 2017, pp. 351–368.

Myrow, P.M., Thalassinoides and the enigma of Early Paleozoic open-framework burrow systems, *Palaios*, 1995, vol. 10, pp. 58–74.

Oji, T., Dornbos, S.Q., Yada, K., Hasegawa, H., Gonchigdorj, S., Mochizuki, T., Takayanagi, H., and Iryu, Y., Penetrative trace fossils from the late Ediacaran of Mongolia: early onset of the agronomic revolution, *R. Soc. Open Sci.*, 2018, vol. 5, art. no. 172250.

Parkhaev, P.Yu., Karlova, G.A., and Rozanov, A.Yu., Taxonomy, stratigraphy and biogeography of *Aldanella attleborensis*—a possible candidate for defining the base of Cambrian Stage 2, *Bull.–Mus. North. Ariz.*, 2011, no. 76, pp. 298–300.

Pemberton, S.G. and Gingras, M.K., Classification and characterizations of biogenically enhanced permeability, *AAPG Bull.*, 2005, vol. 89, pp. 1493–1517.

Peng, S.C., Babcock, L.E., and Cooper, R.A., The Cambrian Period, in *The Geological Time Scale*, Gradstein, F.M., Ogg, J.G., Schmitz, M., and Ogg, G., Eds., Amsterdam: Elsevier, 2012, pp. 437–488.

Pickerill, R.K., Fillion, D., and Harland, T.L., Middle Ordovician trace fossils in carbonates of the Trenton Group between Montreal and Quebec City, St. Lawrence Lowland, eastern Canada, *J. Paleontol.*, 1984, vol. 58, pp. 416– 439.

Repina, L.N., On the problem of the evolution of the trilobite family Protolenidae (Siberia), in *Problemy biostratigrafii i paleontologii nizhnego kembriya Sibiri* (Problems of Biostratigraphy and Paleontology of the Lower Cambrian of Siberia), Moscow: Nauka, 1972, pp. 15–30. Rowland, S.M., Luchinina, V.A., Korovnikov, I.V., Sipin, D.P., Tarletskov, A.I., and Fedoseev, A.V., Biostratigraphy of the Vendian–Cambrian Sukharikha River section, northwestern Siberian Platform, *Can. J. Earth Sci.*, 1998, vol. 35, pp. 339–352.

Rozanov, A.Yu., Missarzhevskii, V.V., Volkova, N.A., et al., *Tommotskii yarus i problema nizhnei granitsy kembriya* (Tommotian Stage and the Problem of the Cambrian Lower Boundary), Tr. Geol. Inst. Akad. Nauk SSSR, vol. 206, Moscow: Nauka, 1969.

Rozanov, A.Yu., Repina, L.N., Apollonov, M.K., et al., *Kembrii Sibiri* (The Cambrian of Siberia), Repina, L.N. and Rozanov, A.Yu., Eds., Tr. Inst. Geol. Geofiz. Ross. Akad. Nauk, vol. 788, Novosibirsk: Nauka, 1992.

Rozanov, A.Yu., Semikhatov, M.A., Sokolov, B.S., Fedonkin, M.A., and Khomentovskii, V.V., The decision on the Precambrian–Cambrian boundary stratotype: A breakthrough or misleading action?, *Stratigr. Geol. Correl.*, 1997, vol. 5, no. 1, pp. 19–28.

Seilacher, A., Biogenic sedimentary structures, in *Approaches to Paleoecology*, New York: Wiley, 1964, pp. 296–316.

Seilacher, A., Biomat-related lifestyles in the Precambrian, *Palaios*, 1999, vol. 14, pp. 86–93.

Seilacher, A. and Pflüger, F., From biomats to benthic agriculture: A biohistoric revolution, in *Biostabilization of Sediments*, Odenburg: Bibliotheks und Informationssystem der Carl von Ossietzky Universität, 1994, pp. 97–105.

Zhamoida, A.I., Sostoyanie izuchennosti stratigrafii dokembriya i fanerozoya Rossii. Zadachi dal'neishikh issledovanii (State-of-the-Art of the Stratigraphic Knowledge for the Precambrian and Phanerozoic of Russia: Aims of Further Research), Postanovleniya Mezhved. Stratigr. Kom. ego Postoyan. Kom., vol. 38, St. Petersburg: Vseross. Nauchno-Issled. Geol. Inst. (VSEGEI), 2008.

Zhuravlev, A.Yu. and Wood, R.A., The two phases of the Cambrian Explosion, *Nature Sci. Rep.*, 2018, vol. 8, art. no. 16656.

Zhuravlev, A.Yu., Gámez Vintaned, J.A., and Tabachnick, K.R., Comment on "An enigmatic, possibly chemosymbiotic, hexactenellid sponge from the early Cambrian of South China" by Joseph P. Botting, Lucy A. Muir, Xiang-Feng Li, and Jin-Pai Lin, *Acta Palaeontol. Pol.*, 2014, vol. 59, pp. 475–476.

Translated by N. Astafiev