Estudios Geológicos
julio-diciembre 2019, 75(2), e113
ISSN-L: 0367-0449
https://doi.org/10.3989/egeol.43595.568

Big guns of the Cambrian Explosion: macroskeletal benthic assemblage in the lower Cambrian Stage 2 of the Olenek Uplift, Arctic Siberia

Grandes hitos de la Explosión Cámbrica: asociación bentónica macrobioclástica en el Piso cámbrico inferior 2 del Olenek Uplift, Siberia ártica

Z.A. Sarsembaev[1,2], V.V. Marusin[1,2]

[1]Department of Stratigraphy and Sedimentology, Trofimuk Institute of Petroleum Geology and Geophysics of SB RAS, prospect Akademika Kortyuga 3, Novosibirsk 630090, Russia. Email: zhigser@gmail.com, marussin.vas@gmail.com; ORCID ID: https://orcid.org/0000-0003-4198-9276, https://orcid.org/0000-0002-0526-0392
[2]Department of Geology and Geophysics, Novosibirsk State University, ulitsa Pirogova 1, Novosibirsk 630090, Russia.

ABSTRACT

The basal Cambrian Stage 2 strata of the Olenek Uplift host diverse assemblages of macroscopic fossils, which closely resemble certain small skeletal taxa early reported from this section and typical for the Terreneuvian Epoch. Herein studied macroscopic assemblage includes helcionellid, stenothecid and kharkhaniid molluscs, and anabaritids and circothecid hyoliths. Among the assemblage, only anabaritids and some citrcothecid hyoliths exhibit relics of calcite shell, whereas most of the fossils reveal no evidence of rigid biomineralized exoskeleton. Hence, at least these problematic Cambrian organisms had reached macroscopic sizes (up to 35 mm long) and were covered with calcite shells at the very beginning of the Cambrian Age 2.

Keywords: Cambrian explosion; Biomineralization; Cambrian; Siberian Platform

RESUMEN

Los estratos basales del Piso cámbrico 2 del Olenek Uplift albergan diversos conjuntos de fósiles macroscópicos, que se asemejan mucho a ciertos pequeños taxones esqueléticos documentados en esta sección y típicos del Terranoviense. En este caso, la asociación macroscópica estudiada incluye moluscos helcionélidos, estenotécidos y kharkhánidos, así como hiolitos de tipo anabarítido y circotécidos. Entre ellos, sólo los anabarítidos y algunos hiolitos circotécidos muestran restos de concha calcítica, mientras que la mayoría de los fósiles carecen de exoesqueleto rígido biomineralizado. Por tanto, al menos estos organismos cámbricos problemáticos habrían alcanzado tamaños macroscópicos (de hasta 35 mm de largo) y estaban cubiertos con conchas calcíticas al principio del Pisp cámbrico 2.

Palabras clave: Explosión cámbrica; Biomineralización; Cámbrico; Plataforma siberiana.

Recibido el 10 de mayo de 2019; Aceptado el 1 de julio de 2019; Publicado online el 27 de noviembre de 2019

Citation / Cómo citar este artículo: Sarsembaev, Z.A. & Marusin, V.V. (2019). Big guns of the Cambrian Explosion: macroskeletal benthic assemblage in the lower Cambrian Stage 2 of the Olenek Uplift, Arctic Siberia. Estudios Geológicos 75(2): e113. https://doi.org/10.3989/egeol.43595.568.

Introduction

The Ediacaran-Cambrian transitional strata record one of the most important evolutionary turnovers in marine ecosystems, associated with the origin and diversification of modern phyla (the Cambrian Explosion; e.g. Erwin *et al*., 2011; Zhuravlev & Wood, 2018; Wood *et al*., 2019). One of the major innovations that first appeared in the terminal Ediacaran benthic communities was mineralized exoskeleton. Small skeletal fossils (SSF; a diverse polyphyletic group of mm-sized biomineralized fossils) first appeared in the terminal Ediacaran and flourished in the Terreneuvian. They commonly reveal considerable morphological similarity with typical Cambrian macroscopic mineralized eumetazoans (molluscs, brachiopods, hyoliths etc.), but their phylogenetic affinity as well as the exact time of emergence of macroscopic mineralized benthos in the Terreneuvian remain debatable. Herein we report morphologically-diverse complex of macroscopic fossils from the basal Cambrian Stage 2 strata of the Olenek Uplift (northeastern Siberian Platform), which closely resemble certain small skeletal taxa, typical for the Terreneuvian.

Stratigraphic context

Within the Olenek Uplift, the Ediacaran-Cambrian transitional strata comprise a mixed carbonate-siliciclastic succession that is defined as the Kessyusa Group, including three formations (in stratigraphical order): Syhargalakh, Mattaia and Chuskuna (Nagovitsin *et al*., 2015). The studied material originates from the upper part of the Mattaia Formation, representing a coarsening-upward succession (92 m thick) from offshore siltstones and mudstones to the lower shoreface cross- and wave-bedded coarse-grained sandstones, oolitic grainstones and calcimicrobe framestones (Marusin, 2016).

The studied fossils are localized in the package of the lower shoreface calcimicrobe framestones and intraclastic limestones that have been early referred to as the Suordakh Member and interpreted as a microbial-dominated, isolated carbonate platform (16.6 m thick) (Nagovitsin *et al*., 2015; Marusin, 2016). This informal unit also hosts diverse small skeletal assemblages (association of *Nochoroicyathus sunnaginicus* Siberian Assemblage Zone), including proposed index-taxa of the Cambrian Stage 2 *Watsonella crosbyi* and *Aldanella attleborensis* (Khomentovsky & Karlova, 1993; Nagovitsin *et al*., 2015). Strongly positive $\delta^{13}C_{carb}$ values (up to +4.4‰) in carbonates of the Suordakh Member and U-Pb zircon age 529.7 ± 0.3 Ma of tuffs in the middle of the interval (Kaufman *et al*., 2012; Marusin, 2016) further confirm the Cambrian Age 2 of the fossil-bearing upper Mattaia Formation (Fig. 1). Similar facies in the overlying Chuskuna Formation also bear macroscopic forms, herein studied.

Results

The fossils comprise macroscopic (3.5-92 mm) steinkerns (internal moulds of shells), exposed on the bedding planes and weathered and shear surfaces of the limestones of the Suordakh Member. The fossils are filled with intraclastic and micritic limestones, similar to the host rock (Fig. 2) and generally lack any relics of mineralized walls. It considerably limits standard preparation technique, applied for extraction of small skeletal fossils (slow rock-dissolution in 2% or 5-10% acetic acid), because of high risk of the fossil being dissolved.

Far exceeding typical size of the small skeletal fossils, the studied material reveals striking morphological similarity with specific Fortunian and Cambrian Age 2 small skeletal taxa, which were early documented in the upper Mattaia Formation (Khomentovsky & Karlova, 1993; Nagovitsin *et al*., 2015). The macroscopic assemblage of the upper Mattaia Formation includes helcionellid, stenothecid and kharkhaniid molluscs, anabaritids and circothecid hyoliths (Fig. 1).

In the study section, hecionellid molluscs include flat cap-shaped forms with circular cross-section and sub-central or slightly posteriorly-displaced apex *Asiapatella sinuata* (up to 7 mm in diameter; Fig. 2A) and *Asiapatella undulata* (up to 9 mm; Fig. 2B); laterally-compressed flat cap-shaped moulds with rounded apex inclined posteriorly, convex anterior field and short concave posterior *Bemella parula* (4-7 mm; Fig. 2D) and *Bemella simplex* (3.5-7 mm; Fig. 2C); moderately-high cap-shaped, laterally-compressed specimens with the apex, going far off the posterior margin *Igorella emeiensis* (10–21 mm;

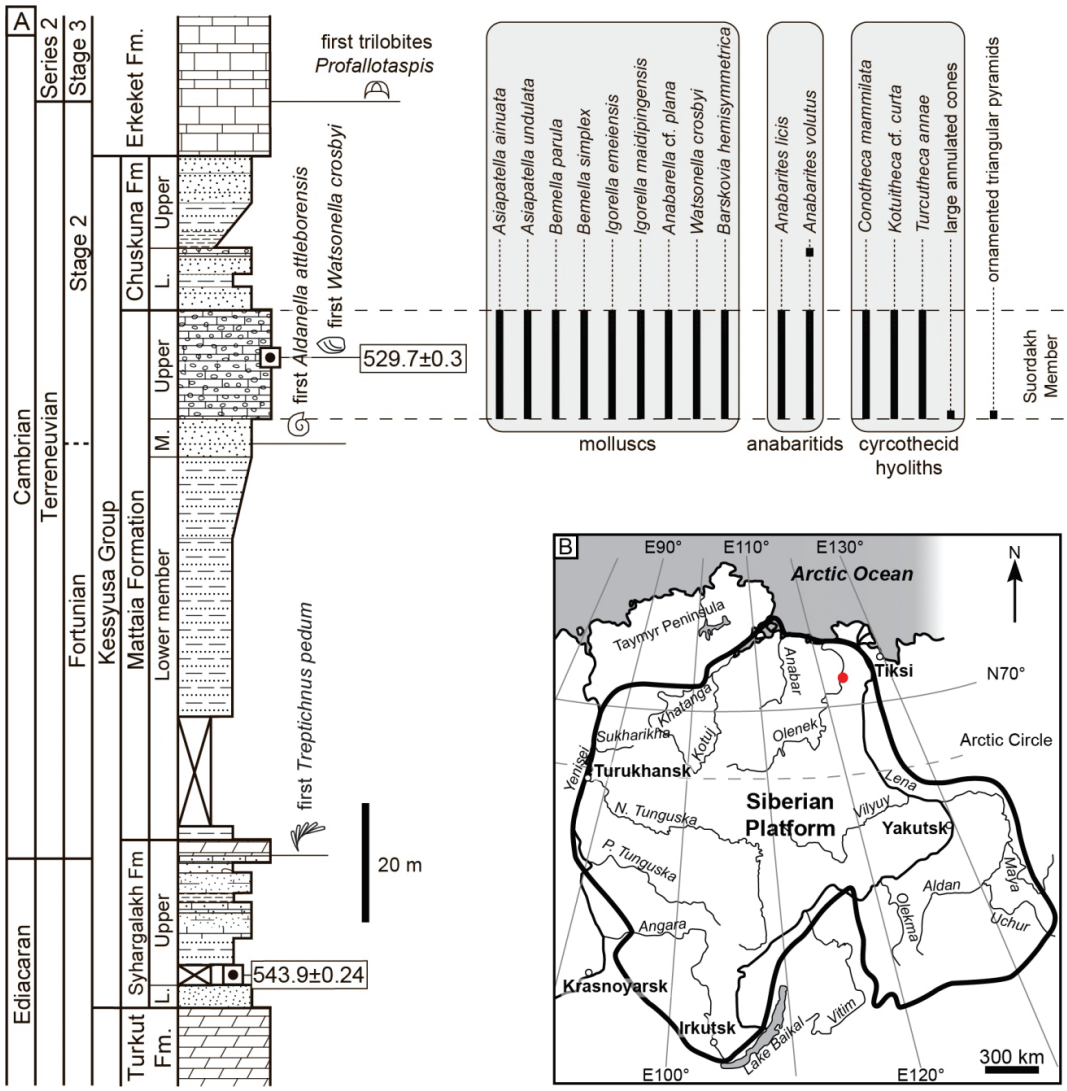

Figure 1.—A. Stratigraphic distribution of macroscopic skeletal fossils in the Kessyusa Group. B. Sketch map of the Siberian Platform with the area of study (Olenek Uplift) marked with red dot.

Fig. 2E) and *I. maidipingensis* (5.5-10 mm long; Fig. 2F).

Stenothecid molluscs are herein preserved as laterally-compressed bilateral cap-shaped steinkerns, semicircular in lateral view and ornamented with thin concentrical ribs and folds, with distinct (*Anabarella* cf. *plana*; up to 4.5 mm; Fig. 2G) or small rounded apex (*Watsonella crosbyi*; up to 8 mm; Fig. 2H), reaching or even overhanging the short concave posterior margin. The only species *Barskovia hemisymmetrica* of kharkhaniid molluscs is identified in the Suordakh Member. It comprises internal mould (5 mm in diameter) of low turbospiral sinistral shell with no evidence of internal sculpture (Fig. 2I).

The identified anabaritids are preserved as straight triradial tubular steinkerns (up to 35 mm long and up to 5 mm in diameter), with smooth surface and rounded triangular cross-section (*Anabarites licis*; Fig. 2J, L) and with helicoidal bands (*Anabarites volutus*; Fig. 2K).

Circothecids comprise a diverse morphological group of extinct Cambrian organisms, putatively assigned to orthothecid hyoliths, with conical mineralized shell, simple morphology and no dorso-ventral

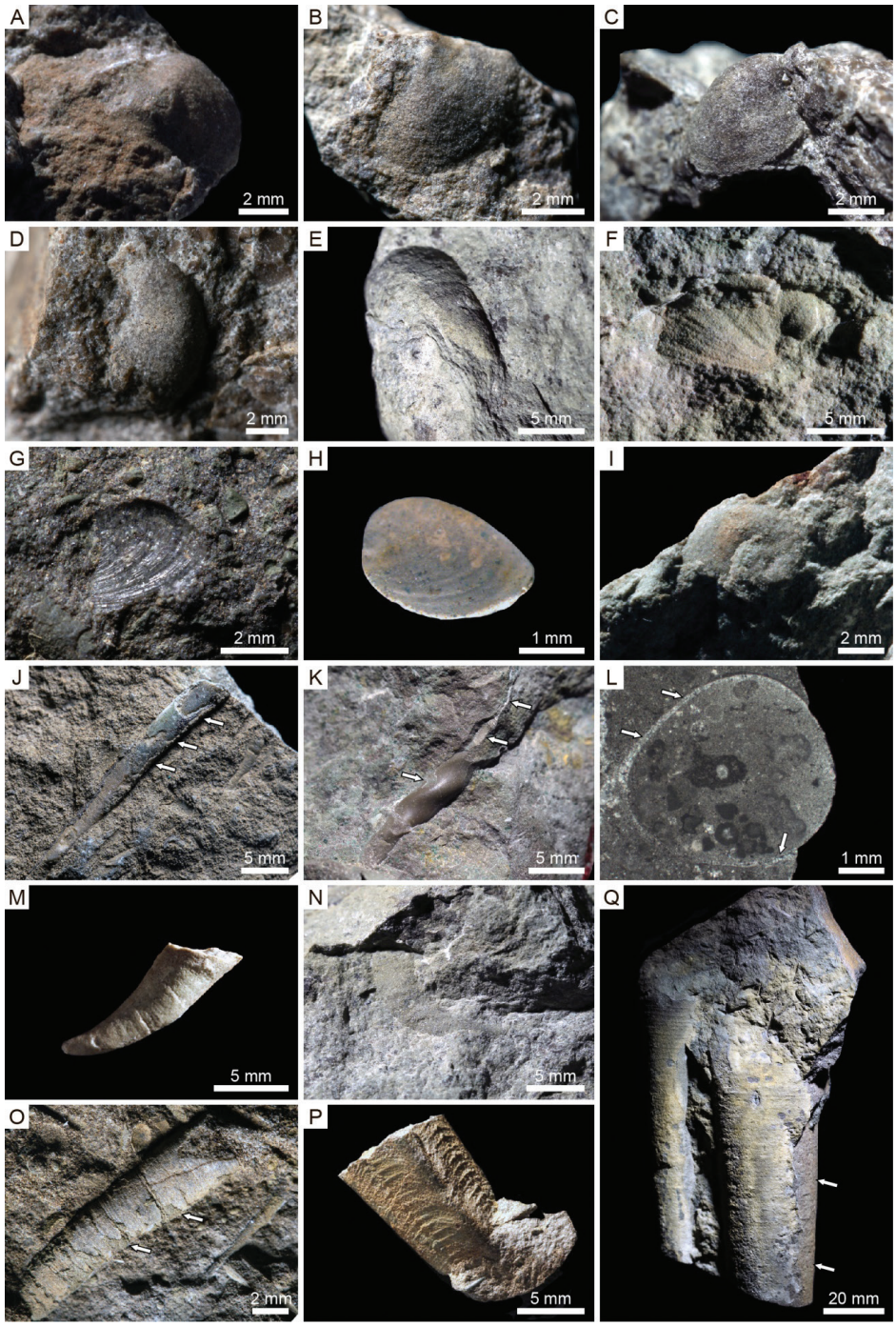

Figure 2.—Macroscopic skeletal fossils from the Kessyusa Group. Helcionellid molluscs: A. *Asiapatella sinuata* (CSGM 2028-126). B. *Asiapatella undulata* (CSGM 2028-132). C. *Bemella simplex* (CSGM 2028-110). D. *Bemella parula* (CSGM 2028-119). E. *Igorella emeiensis* (CSGM 2028-117). F. *Igorella maidipingensis* (CSGM 2028-118). Stenothecid molluscs: G. *Anabarella* cf. *plana* (CSGM 2028-217). H. *Watsonella crosbyi* (CSGM 2028-244). Kharkhaniid molluscs: I. *Barskovia hemisymmetrica* (CSGM 2028-135). Anabaritids (white arrows point relics of calcite wall): J. *Anabarites licis* (CSGM 2028-197); K. *Anabarites volutus* (CSGM 2028-133); L. transverse thin section of *Anabarites licis* (CSGM 2028-162) with well-preserved calcite wall. Circothecid hyolits: M. *Conotheca mammilata* (CSGM 2028-157); N. *Kotuitheca* cf. *curta* (CSGM 2028-163); O. *Turcutheca annae* (CSGM 2028-226) with poorly-preserved relics of calcite shell; Q. Two large-sized pyritized tubular fossils (CSGM 2028-190) with thin transverse annulations, putatively assigned to circothecid hyoliths (Marusin & Grazhdankin, 2018). White arrows point thin pyritized crust, covering the steinkerns. P. Problematic triangle-pyramidal fossils with series of chevron-like ridges on the outer surface (CSGM 2028-50).

differentiation (Missarzhevsky, 1989). These fossils are abundant in the Suordakh Member and represent gently-curved conical steinkerns with circular cross-section and thin transverse ornamentation (*Conotheca mammilata*; 4-15 mm long; Fig. 2M), horn-shaped smooth conical moulds (*Kotuitheca* cf. *curta*; 12 mm long; Fig. 2N) and straight or gently-curved forms with oval to egg-shaped cross-section and thin transverse ornamentation (*Turcutheca annae*; up to 30 mm long; Fig. 2O). The basal interval of the Suordakh Member also embeds large-sized fragments (up to 92 mm long; up to 24.5 mm in diameter) of conical steinkerns, circular to ovoidal in the cross-section (Fig. 2Q). The fossils exhibit no relics of calcite wall, but covered with thin transverse-annulated crust. Although fragmental preservation limits precise phylogenetic affinity, the primitive morphology of these forms putatively assigns them to circothecids (Marusin & Grazhdankin, 2018).

The basal beds of the Suordakh Member also contain numerous macroscopic fossils, comprising triangular pyramids (4-20.5 mm long), filled with the sediment identical to the host. The surface of the pyramids is covered with various symmetrical sculptural elements (isolated bumps on the median line of the faces, series of chevron-like ridges tapering towards the aperture) (Fig. 2P). The lateral faces of the pyramids commonly display plastic deformations. Phylogenetic affinity of the fossils remains debatable, since their general morphology meets analogues among conulariids, orthothecid hyoliths or anabaritids.

Among all the macroscopic forms documented in the Kessyusa Group, only anabaritids and circothecids *Turcutheca* occasionally reveal relics of calcite wall, which can be noted both macroscopically on the specimens (Fig. 2K, O) and in thin sections (Fig. 2L).

Discussion and conclusions

There are two major hypotheses that alternatively explain the morphological similarity and stratigraphic discrepancy of the earliest skeletal macro- and microfossils: (i) the late Ediacaran and earliest Cambrian small skeletal fauna is a phylogenetic ancestor of the Cambrian macroscopic organisms, exhibiting similar morphology (e.g. Rozanov *et al*., 1969; Runnegar & Jell, 1976); and (ii) small skeletal fossils comprise taphonomical artifacts. The second hypothesis assumes that all SSF represent larval or juvenile ontogenetic stages of macroscopic skeletal organisms. In contrast, preservation potential of thin calcareous shells of adult forms was crucially limited by preservation conditions (sediment reworking and compaction) and techniques applied for extraction of the mineralized forms from the rock (Dzik, 1991; Martí Mus *et al*., 2008). Our study reveals that typical Terreneuvian small skeletal fossils (anabaritids, molluscs, circothecid hyoliths) co-occur with their macroscopic analogues, and hence challenges the first hypothesis.

The relics of calcite wall, fragmentally preserved and exclusively associated with anabarithids and certain circothecid hyoliths (Fig. 2K, L, O) on the studied material, demonstrate that at least these Cambrian problematic conical and tubular benthic organisms had already reached macroscopic sizes (up to 35 mm long) and were covered with calcite shells at the very beginning of the Cambrian Age 2. In contrast, abundant plastic deformations documented on the largest fossils (Fig. 2P, Q) implicates that ~530 Ma these benthic organisms were most likely covered by semi-rigid, possibly non-mineralized exoskeleton.

ACKNOWLEDGEMENTS

The core of the study was funded by the Russian Foundation for Basic Research grant no. 17-05-00852 and the Russian Science Foundation grant no. 17-17-01241. We thank Georgiy E. Markov (IPGG SB RAS, NSU, Novosibirsk) for specimens of *Watsonella crosbyi*, kindly provided for study. All the studied material is reposited in the Paleontological Section of the Central Siberian Geological Museum (Trofimuk Institute of Petroleum Geology and Geophysics SB RAS, Novosibirsk, Russia), collection no. 2028.

References

Dzik, J. (1991). Is fossil evidence consistent with traditional views of the early metazoan phylogeny? In: The early evolution of Metazoa and the significance of problematic taxa (Simonetta, A.M. & Conway Morris, S., Eds.). Cambridge University Press, Cambridge, 47–56.

Erwin, D.H.; Laflamme, M.; Tweedt, S.M.; Sperling, E.A.; Pisani, D. & Peterson, K.J. (2011). The Cambrian conundrum: Early divergence and later ecological success in the early history of animals. Science, 334: 1091–1097. https://doi.org/10.1126/science.1206375

Kaufman, A.J.; Peek, S.; Martin, A.J.; Cui, H.; Grazhdankin, D.; Rogov, V.; Xiao, S.; Buchwaldt, R. & Bowring, S. (2012). A shorter fuse for the Cambrian Explosion? Geological Society of America Abstracts with Programs, 44: 326.

Khomentovsky, V.V. & Karlova, G.A. (1993). Biostratigraphy of the Vendian-Cambrian beds and the lower Cambrian boundary in Siberia. Geological Magazine, 130: 29–45. https://doi.org/10.1017/S0016756800023700

Martí Mus, M.; Palacios, T. & Jensen, S. (2008). Size of the earliest mollusks: did small helcionellids grow to become large adults? Geology, 36: 175-178. https://doi.org/10.1130/G24218A.1

Marusin, V.V. (2016). Trace fossils from the Vendian-Cambrian transitional strata of the Olenek Uplift of Siberian Platform. PhD Thesis, IPGG, Novosibirsk, 275 pp. [in Russian]

Marusin, V.V. & Grazhdankin, D.V. (2018). Enigmatic large-sized tubular fossils from the Terreneuvian of Arctic Siberia. Paläontologische Zeitschrift, 92: 557–560. https://doi.org/10.1007/s12542-018-0420-x

Missarzhevsky, V.V. (1989). Oldest skeletal fossils and stratigraphy of Precambrian-Cambrian boundary strata. Transactions GIN, 443: 1-237 (Raaben, M., Ed.). Nauka, Moscow. [in Russian]

Nagovitsin, K.E.; Rogov, V.I.; Marusin, V.V.; Karlova, G.A.; Kolesnikov, A.V.; Bykova, N.V. & Grazhdankin, D.V. (2015). Revised Neoproterozoic and Terreneuvian stratigraphy of the Lena-Anabar Basin and north-western slope of the Olenek Uplift, Siberian Platform. Precambrian Research, 270: 226–245. https://doi.org/10.1016/j.precamres.2015.09.012

Rozanov, A.Yu.; Missarzhevsky, V.V.; Volkova, N.A.; Voronova, L.G.; Krylov, I.N.; Keller, B.M.; Korolyuk, I.K.; Lendzion, K.; Michniak, R.; Pyhova, N.G. & Sidorov, A.D. (1969). The Tommotian Stage and the Cambrian Lower Boundary Problem. Transactions GIN, 206: 1–380 (Raaben, M., Ed.). Nauka, Moscow. [in Russian]

Runnegar, B. & Jell, P.A. (1976). Australian Middle Cambrian molluscs and their bearing on early molluscan evolution. Alcheringa, 1: 109–138. https://doi.org/10.1080/03115517608619064

Wood, R.; Liu, A.G.; Bowyer, F.; Wilby, P.R.; Dunn, F.S.; Kenchington, C.G.; Cuthill, J.F.H.; Mitchell, E.G. & Penny, A. (2019). Integrated records of environmental change and evolution challenge the Cambrian Explosion. Nature, Ecology and Evolution, 3: 528–538. https://doi.org/10.1038/s41559-019-0821-6

Zhuravlev, A.Yu. & Wood, R. (2018). The two phases of the Cambrian Explosion. Scientific Reports, 8: 16656. https://doi.org/10.1038/s41598-018-34962-y