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A new Early Permian “lithistid” sponge (Porifera: Demospongiae: Anthaspidellidae) from the Polar Urals

K.A. Kolesnikov[1,2*], N.S. Inkina[3], J.V. Shuvalova[2], A.Yu. Zhuravlev[1,2]

[1] Department of Biological Evolution, Lomonosov Moscow State University, Leninskie Gory 1-12, Moscow 119234 Russia.
[2] Borissiak Palaeontological Institute, Russian Academy of Sciences, Profsoyuznaya St. 123, Moscow 117647 Russia.
[3] Yushkin Institute of Geology, FRC, Komi Scientific Centre, Uralian Branch, Russian Academy of Sciences, Pervomayskaya St. 54, Syktyvkar, Komi Republic 167982 Russia.
** Corresponding author*
Kirill Kolesnikov: kolkir@mail.ru ORCID https://orcid.org/0000-0002-7609-335X
Natalia Inkina: nsinkina@geo.komisc.ru
Andrey Zhuravlev: ayzhur@mail.ru ORCID https://orcid.org/0000-0003-1611-6916
Julia Shuvalova: pinmuse@gmail.com ORCID https://orcid.org/0000-0002-5075-6952

ABSTRACT: A new genus and species of an anthaspidellid (“lithistid”) demosponge is described from the Lower Permian strata of the Polar Urals. This small branching modular anthaspidellid with a highly regularly organized choanosomal ladder-like skeleton built of equally spaced straight dendroclones without accessory spicules. This relatively simple anthaspidellid with a highly regularly organized skeleton became a forerunner of the last diversification bloom of this family in the Permian.
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KEY WORDS: sponges, Anthaspidellidae, Demospongiae, Early Permian, Polar Urals.

Новая раннепермская «литистидная» губка (Porifera: Demospongiae: Anthaspidellidae) с Полярного Урала

К.А. Колесников[1,2*], Н.С. Инкина[3], Ю.В. Шувалова[2], А.Ю. Журавлев[1,2]

[1] Кафедра биологической эволюции, Московский государственный университет им. М.В. Ломоносова, Ленинские горы 1-12, Москва 119234 Россия.
[2] Палеонтологический институт им. А.А. Борисяка РАН, ул. Профсоюзная 123, Москва 117647 Россия.
[3] Институт геологии им. Н.П. Юшкина ФИЦ Коми НЦ УрО РАН, ул. Первомайская 54, Сыктывкар, Республика Коми 167982 Россия.
** Ответственный за переписку: kolkir@mail.ru*

РЕЗЮМЕ: Новый род и вид «литистидных» обыкновенных губок из семейства Anthaspidellidae описан из нижнепермских отложений Полярного Урала. Небольшая ветвящаяся губка выделяется среди других антаспиделлид хоаносомальным скелетом с равномерным расположением прямых дендроклонов без второстепенных спикул. Дендроклоны образуют своего рода перекладины на очень правильных радиально расходящихся «лестничных маршах». Эта достаточно простая губка с очень регулярно организованным скелетом стала предтечей последней вспышки разнообразия антаспиделлид в пермском периоде.

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КЛЮЧЕВЫЕ СЛОВА: губки, Anthaspidellidae, Demospongiae, раннепермская эпоха, Полярный Урал.

Introduction

Lithistids represent one of the most diverse groups of fossil demosponges, comprising about 34 families (Pisera, 2002). Extant lithistids comprise less than 15 families, which is a relatively insignificant figure by comparison with the overall demosponge number (Schuster *et al*., 2015). Lithistids are now recognized by both molecular and morphological data as an artificial polyphyletic group of sponges, which independently have acquired a rigid choanosomal skeleton of various articulated desmas (Dendy, 1921; Reid, 1968; Kelly Borges, Pomponi, 1994; Pisera, Lévi, 2002). The most recent revision of extant lithistid families, based on both morphological (mostly microsclere appearance) and molecular data, led to the abandon of the order Lithistida. The accepted families are placed within several different orders (Morrow, Cárdenas, 2015; Schuster *et al*., 2015).

Anthaspidellid demosponges were the first sponges that develop a rigid massive siliceous skeleton of the lithistid type originated by an articulation of individual spicules. They appeared at the very end of the early Cambrian and actually substituted of hypercalcified aspiculate archaeocyath sponges after their extinction as major poriferan reef builders around the world (Okulitch, Bell, 1955; Kruse, 1983, 1996; Shapiro, Rigby, 2004; Johns *et al.*, 2007; Kruse, Zhuravlev, 2008; Kruse, Reitner, 2014; Lee *et al.*, 2016, 2019). Commonly, anthaspidellid skeletons consisting of dendroclones in a very regular ladder-like arrangement, which were secondarily replaced by calcite, had been ascribed to archaeocyaths (Grabau, 1922; Wilson, 1950; Öpik, 1956; Debrenne *et al.*, 1984; Lee, 2024). Their acme was in the Early and Middle Ordovician when various and abundant anthaspidellids flourished in reefs and other level-bottom palaeocommunities (van Kempen, 1978; Rigby, Webby, 1988; Liu *et al.*, 1997; Pisera, 2002; Carrera, Rigby, 2004; Muir *et al*., 2013; Rhebergen, 2014; Hong *et al*., 2015; Church, 2017). Since the Silurian onwards, these sponges became less ubiquitous elements of diversified sponge assemblages and totally disappeared during the Permian-Triassic mass extinction event (Finks, 1960; Finks, Rigby, 2004).

Here we describe a new anthaspidellid sponge collected from the Lower Permian strata of the Polar Urals, the interval, from which a few such sponges have been detected until now.

Material and methods

The twelve nearly complete fossil sponges were collected in the Lower Permian (Cisuralian) Sezym Formation exposed in the upper Usa River basin on the western slope of the Polar Urals in the Republic of Komi (Russia) during field works of 2010, 2015 and 2021 (Fig. 1A–C). These strata were ascribed to the Asselian and Sakmarian stages of the Cisuralian Series based on foraminifers, ammonoids and conodonts (Inkina, 2019).

The Sezym Formation consists either of an alternation of carbonates and mixtites (fine-grained sedimentary rocks of mixed silty-argillaceous-calcareous composition) [Usa-1 and Kech-Shor Creek (KS) sections; Fig. 1B]. In the Usa-1 section, occurring in the vicinity of the town of Vorkuta on the left bank of the Usa River, the formation is underlain and overlain by the Tsementozavod and Gusin formations, respectively. In these sections, the thickness of the Sezym Formation varies from 12.8 to 13.8 m. Abundant sponges were discovered in an incomplete auxiliary section Usa-1b on the opposite right bank of the river. These strata were probably filled shallow depressions on the shelf. On the right bank of Lek-Elets River, about 9 km of its mouth on the Usa River (LE section; Fig. 1C), the Sezym Formation consists entirely of limestone of 10 m in thickness. Along the strike, thin-bedded bioclastic (mostly crinoid) limestone encloses a large massive block interpreted as a mud mound about 20–25 m in thickness (Saldin, 2005).

The sponge skeletons are visible on a naturally weathered rock surface and restricted to shelly bryozoan-crinoid wackestones and packstones as well as to massive reef rocks of the mud mound. Also, these lithologies contain unsorted fragments and some

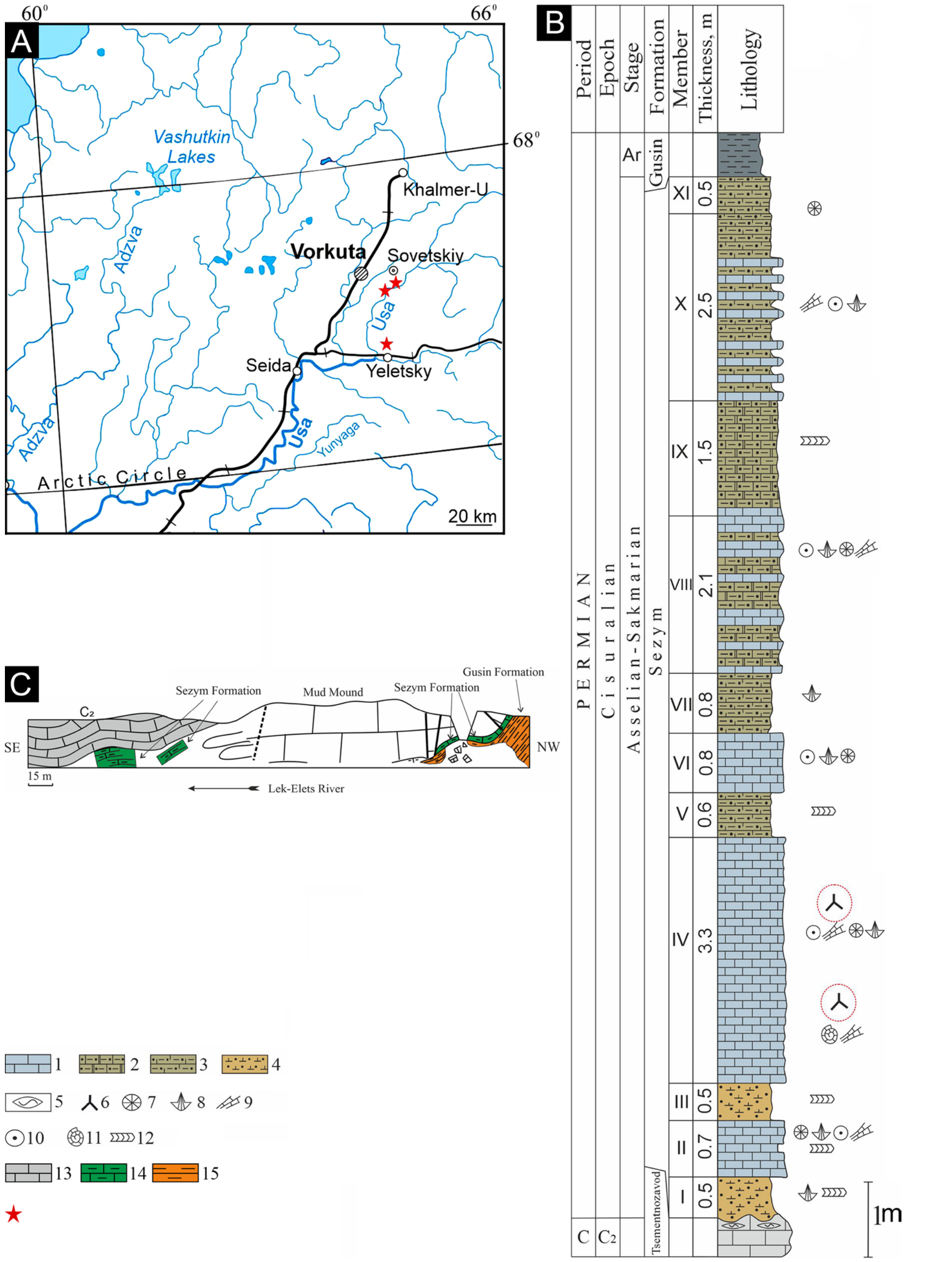

Fig. 1. Sections of the Sezym Formation, where the *Usaspongia tchernyshevi* gen. et sp.n. specimens were collected and their location, Asselian-Sakmarian stages, Cisuralian Series, Permian System, Polar Urals (Republic of Komi, Russia). A — map indicating the location of the sections; B — Usa-1 section, litho- and chronostratigraphic column; C — Lek-Elets River, right bank (LE) section, geological profile. Legend: 1 — limestone; 2 — siliciclastic-carbonate rock (calcite and dolomite together account for over 50% of the rock volume); 3 — mixtit; 4 — siltstone; 5 — silica concretions; 6–11 — fossils (6 — anthaspidellid sponges; 7 — rugose corals; 8 — brachiopods; 9 — bryozoans; 10 — crinoids; 11 — ammonoids); 12 — trace fossils; 13 — limestone of the Tsementnozavod Formation; 14 — crinoid-bryozoan clastic bedded limestone of the Sezym Formation; 15 — argillite of the Gusin Formation.

unbroken shells of brachiopods, gastropods and bivalves, foraminifer tests, problematic *Tubiphytes* thick irregular calcareous tubes and oncolites. All the fragments are from <0.1 mm to >1 mm in size.

The skeletal fine morphology was examined in thin sections under polarizing microscope Nikon Eclipse LV 100 ND. Macrophotographs were taken by Nikon D90. Final images were prepared with Adobe Photoshop. Measurements of the spicules' length and diameter were carried out using ImageJ2 from macrophotographs.

Ancient collections of possible anthaspidellids from the Cisuralian/Lower Permian of the South Urals (Stuckenberg, 1895; Tchernychev, 1898; collections nos. 305 and 317 respectively) were examined in the Central Scientific-Research Geological-Exploring Museum named after Th.N. Tchernyshev (CNIGR, All-Russian Geological Research Institute of A.P. Karpinsky, St. Petersburg) in order to check their possible similarity with the new sponge.

The terminology is followed Reid (1968), de Freitas (1991), Pisera, Lévi (2002), Finks and Rigby (2004).

The specimens are housed in the Chernov Geological Museum, Yushkin Institute of Geology, FRC, Komi Scientific Centre, Uralian Branch, Russian Academy of Sciences (CGM), collection no.14.

Systematics

Demospongiae Sollas, 1885
Orchocladina Rauff, 1895
Anthaspidellidae Ulrich in Miller, 1889
Usaspongia **gen.n.**

DIAGNOSIS. Low obconical to branching sponge with multiple narrow branching canals, whose skeleton is built of uniformly arranged and spaced I-shaped amphiarborescent dendroclones with straight central shafts and terminal digitate zygomes interlocking to form a highly regular ladder-like rigid choanosomal network of prominent radial, upwardly and outwardly divergent, porous trabs (column-like structures) and cross-connected runglike dendroclones. Any other auxiliary endosomal and ectosomal spicules and microscleres are absent.

DEFINITION. Anthaspidellid demosponge with multiple branching canals and highly regular choanosomal ladder-like skeleton built of equally spaced straight dendroclones.

REMARKS. Several Carboniferous and Permian localities yield anthaspidellids. These are in ascending order Lower Pennsylvanian strata of Texas (Finks, 1960), Oklahoma (Rigby *et al*., 1970), Arkansas (Rigby, Manger, 1994) and León, Spain (García-Bellido, Rigby, 2004); Cisuralian/Lower Permian basin facies of the South Urals (Stuckenberg, 1895; Tchernychev, 1898) and Texas (Finks, 1960); Guadalupian/Middle Permian epicontinental reefs of Texas (Gerth, 1927; Finks, 1960) and Wyoming (Rigby, Boyd, 2004); Cisuralian and Guadalupian deeper-water facies of the Timor Island (Gerth, 1927, 1929, 1931); and Lopingian/Upper Permian reefs of Guangxi, China (Deng, 1981).

The genera of the Anthaspidellidae are distinguished mostly on the basis of an overall body shape, an arrangement of various pores and canals, dendroclone modifications and a presence of accessory spicules. Thus, the new genus differs from *Aulacospongia* Gerth, 1927 by the absence of surface grooves; from *Mastophyma* Gerth, 1927 and *Timidella* de Laubenfels, 1955 (nom.n. pro *Timorella* Gerth, 1927) by the absence of conical protuberances at the surface and radial canals; from *Palaeojerea* Gerth, 1927 and *Pseudomultistella* Deng, 1981 by the absence of a regular canal system; from *Palaeophyma* Gerth, 1927 by the absence of surface grooves and canals opening at their bottoms; from *Phacellopegma* Gerth, 1927 by the absence of surface anastomosing grooves and apochetes (upward sweeping canals); from *Pycnospongia* Gerth, 1927 by the absence of modified dendroclones; from *Multistella* Finks, 1960 by the absence of radiating astrorhizae at the surface formed by stellate clusters of apopores; from *Jereina* Finks, 1960 by the absence of surficial grooves and axial apochetes; from *Virgaspongia* Rigby and Manger, 1994 by the presence of branching canals; from *Virgaspongiella* Rigby and Boyd, 2004 by the absence of coring oxeas and styles; from *Incrustatospongia* Rigby and Boyd, 2004 by the absence of monoaxial spicules forming spinose armoring skeletal elements.

South Uralian sponges deserve special interest because they are geographically and stratigraphically the closest sponges to the new fossil and similar forms can be expected among them. Stuckenberg (1895, p. 20–22, pl. IV, figs 2, 3, pl. XVIII, fig. 2) originally ascribed his fossils to corals under the names *Kazania elegantissima, K. grunewaldti* and *K. ufimiana*. They were subsequently redescribed as sponges and the later one was designated as the type species of a new genus *Stuckenbergia*; also, *K. uralica* was added to this list (Tchernychev, 1898). In turn, later on, this generic name was replaced due to its preoccupation by *Tschernyschevostuckenbergia* (Zhuravleva in Rezvoi *et al*., 1962). Subsequently, *Kazania* (type species, *K. elegantissima* Stuckenberg, 1895, CNIGR 305/в91a) was placed among the Haplistiidae de Laubenfels, 1955 due to a presence of oxeas and "spiculofibers" in its thin sections CNIGR 317/в47 and 317/в47 (Finks, Rigby, 2004). In fact, these spicules and fibers form thick rod-like elements diverging from the skeletal center and lintels between them, which compose the skeleton itself. In addition, tiny trabs are also present within these rods, while "spiculofibers" can be attributed to secondary silicified spongine fibers. *K.*

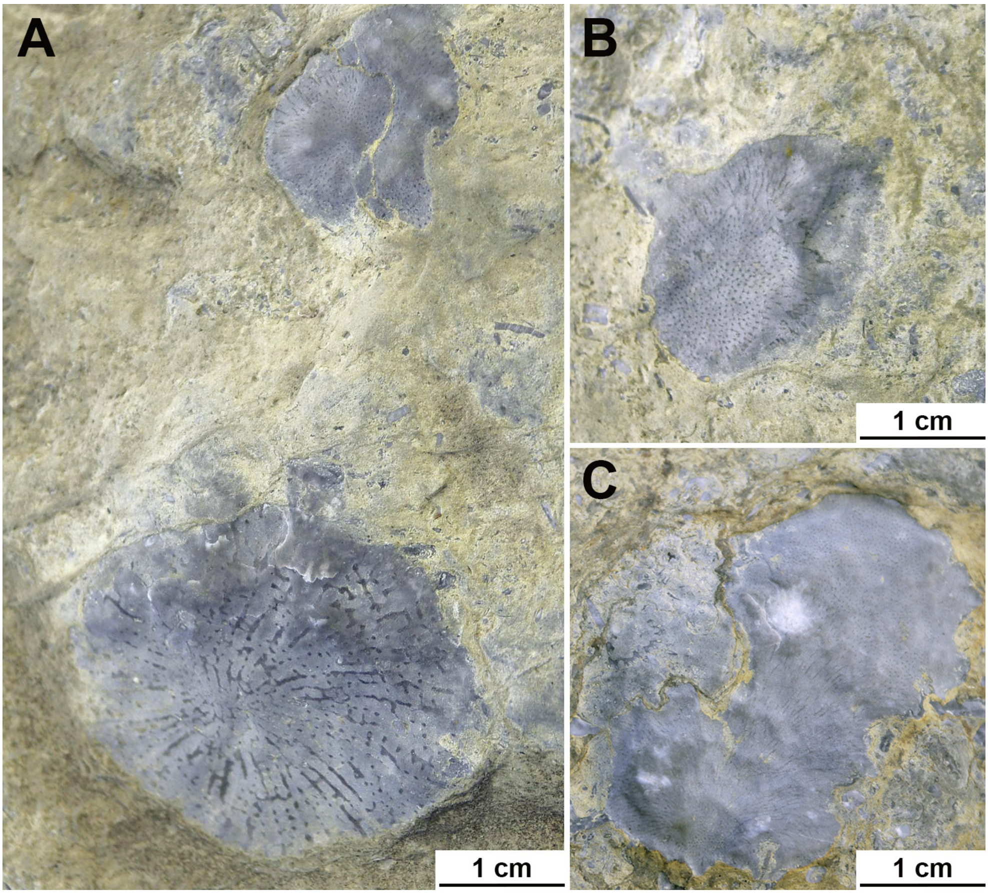

Fig. 2. *Usaspongia tchernyshevi* gen. et sp.n., holotype CGM-14/1, Sezym Formation, Asselian-Sakmarian stages, Cisuralian Series, Permian. Usa-1 section, left bank, a slab of bioclastic limestone (0.5 × 0.5 × 0.2 m) from a dump at the foot of the bedrock. A — a general view of a group of sponge branches preserved *is situ* on a bedding surface; B — another part of a branching sponge with a slightly thickened outer wall; C — lateral view of another part of the same branching sponge.

uralica Tchernychev, 1898 (p. 18–19, pl. II, figs. 14, 15, 22, pl. III, fig. 1, pl. IV, fig. 5, text-figs 10, 11; CNIGR 317/58) is very similar to *K. elegantissima* and differs from it by thinner skeletal elements only. It can be the same sponge at a younger stage of the development. His new species *Pemmatites artiensis* Tchernychev, 1898 (p. 11–13, pl. II, figs. 13, 16, pl. IV, fig. 1, 2, text-fig. 2) can be a junior synonym of the same sponge due to an identical skeletal structure.

K. ufimiana (CNIGR 305/416) was selected as the type species of a new genus (nowadays, *Tschernyschevostuckenbergia*) by Tchernychev (1898, p. 14) due to its essentially different skeletal structure in comparison with the type species of *Kazania,* but the researcher incorrectly cited it as *K. ufensis*. This sponge is characterized by a very fine anthaspidellid-type skeletal fabric and cylindrical overall shape. By these features it differs from the new sponge. The only skeleton of *K. grunewaldti* Stuckenberg, 1895 (CNIGR 305/в93) is dissolved completely and it is difficult to compare it with other sponges. Certainly, it did not belong to the genus *Kazania* as noted by Tchernychev (1898) who tentatively placed it in the *Haplistion* Young ye Young, 1877. However, its affinities with anthaspidellids seem to be more plausible because neither rhizoclones nor oxeas typical of the Haplistiidae can be responsible for its skeletal pattern preserved as voids in the rock. Finally, a different species *Stuckenbergia artiensis* Tchernychev, 1898 (p. 28–29, pl. III, fig. 4, 5, pl. V, fig. 4–6, text-fig. 17, 18), again has an anthaspidellid-type skeleton with branching canals. This species is attributed here to the new genus *Usaspongia* as a different species.

TYPE SPECIES. *Usaspongia tchernyshevi*, sp.n.

ETYMOLOGY. The genus name is after the Usa River on the Polar Urals.

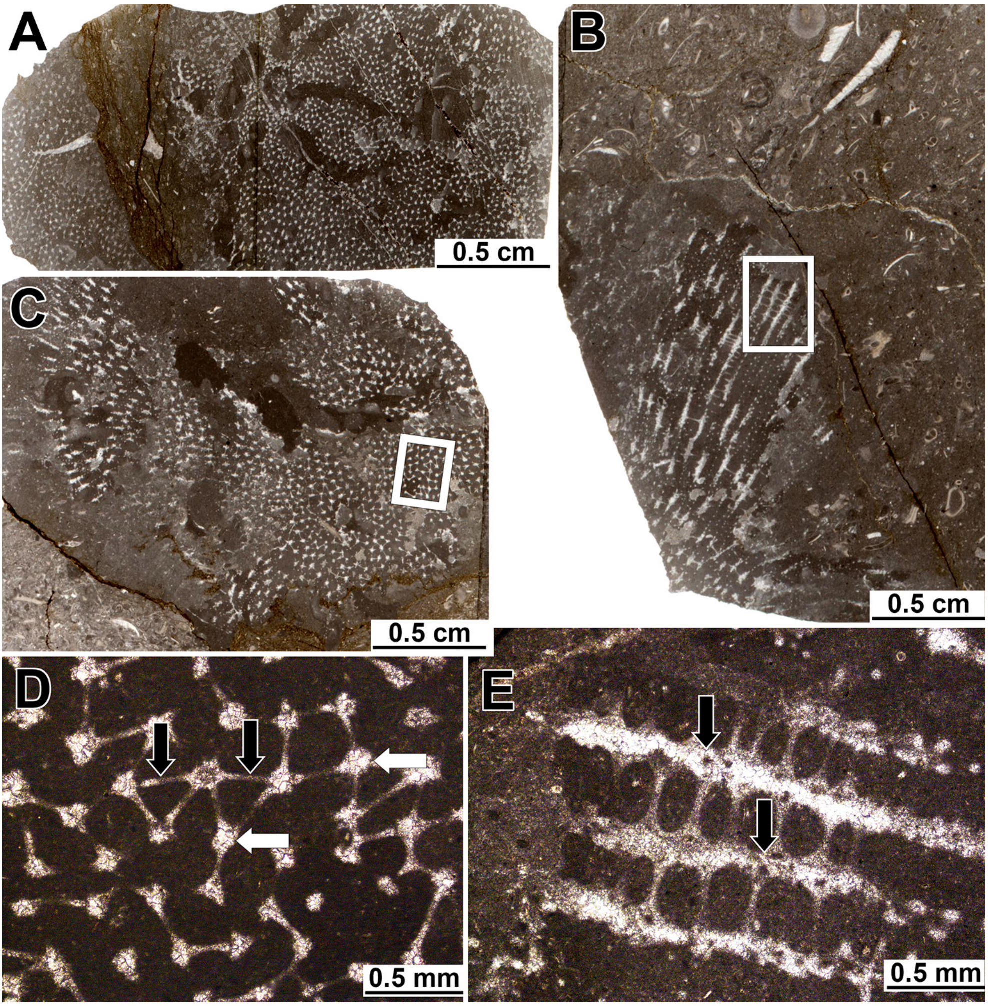

Fig. 3. *Usaspongia tchernyshevi* gen. et sp.n., photomicrographs of thin sections, Sezym Formation, Asselian-Sakmarian stages, Cisuralian Series, Permian. A — paratype CGM-14/4, tangential section of a choanosomal skeleton with branching canals and trabs; B–E — holotype CGM-14/1: B — fragment of a cross-section showing radially diverging trabs formed by zygomes of cross-connected dendroclones; C — oblique-cross section of a choanosomal skeleton with branching canals; D — enlarged area of a tangential section (framed on C) showing trabs (arrowed white) and dendroclone shafts (arrowed black); E — enlarged area of a cross section (framed on B) showing porous trabs (pores are arrowed) and cross-connected dendroclones.

COMPOSITION. The type species and *U. artiensis* (Tchernychev, 1898).

Usaspongia tchernyshevi **sp.n.**
Figs 2–3.

MATERIAL. Holotype: CGM-14/1, Usa-1b section (67°23′58″ N, 64°27′53″ E). Paratypes: CGM-14/2 to 14/12, sections Usa-1, Usa-1b and LE (67°06′20″ N, 64°15′46″ E). Usa River basin, Polar Urals, Republic of Komi, Sezym Formation, Asselian and Sakmarian stages, Cisuralian Series, Permian.

DIAGNOSIS. As in genus.

DESCRIPTION. Low obconical to branching modular sponges from 20 to 90 mm in diameter, basally attached to the substrate, without a spongocoel, but with multiple narrow branching canals extending axially and laterally (Figs 2A–C, 3A, C). The diameter of canals varies from 0.3 mm to 0.6 mm. The rigid skeleton is composed of I-shaped amphiarborescent dendroclones representing the only choanosomal spicules. Each dendroclone consists of a long, generally 0.1–0.2 mm in length (mean = 0.17; SD = 0.036; N = 19), smooth straight central shaft branching at both terminations to produce digitate articulatory zygomes of subequal sizes (Fig. 3D, E). Shafts are 0.02–0.04 mm in diameter (mean = 0.037; SD < 0.01; N = 19). Each zygome consists of about four to six thin and short slightly diverging branches, 0.02–0.04 mm in diameter (mean = 0.03; SD < 0.01; N = 11) and 0.06–0.1 mm in length (mean = 0.08; SD = 0.01; N = 11). Zygomes of adjacent dendroclones are interlocked to each other to form prominent radial, upwardly and outwardly divergent, porous trabs of 0.1–0.2 mm in thickness (mean = 0.14; SD = 0.02; N = 41), which are spaced 0.16–0.37 mm apart (mean = 0.24; SD = 0.05; N = 50) (Fig. 3D, E). (Small pores are appeared due to an incomplete fusion of zygomes.) A highly regular spacing of trabs themselves and cross-connected dendroclones with runglike shafts, arranged with their long axes paratangential to the sponge upper and outer growing surface, resulted in an equidimensional ladder-like choanosomal network. Dendroclones are spaced at intervals of about 0.1-0.4 mm in a single radial ladder-like row, arranged in horizontal layers (Fig. 3B, E). The trab heads are slightly project outside as hemispherical bumps, 0.1–0.3 mm in diameter. The entire network of dendroclone shafts and zygomes imparts the sponge surface a delicate triangular pattern (Fig. 3D). The surficial outmost trab heads and dendroclones are slightly thickened (Fig. 2B).

ETYMOLOGY. The species is named in honor of the first investigator of poriferan faunas of the Urals and Timan Th. N. Tchernyshev.

DISTRIBUTION. Usa River basin, Polar Urals, Republic of Komi, Sezym Formation, Asselian and Sakmarian stages, Cisuralian Series, Permian.

REMARKS. Spicules, although are opaque in thin sections, lack primary silica, which is replaced by blocky calcite (Fig. 3D, E). The replication, which is typical for silica in a carbonate host rock, follows in details the exact structure of dendroclones with zygomes but does not preserve their axial canals.

The new species differs from *U. artiensis* (Tchernychev, 1898) by finer skeletal elements, both dendroclones and trabs and by a more regular skeletal structure.

Conclusions

The new sponge confirms the suggestion of Finks (1960) that primitive anthaspidellids with very regular choanosomal skeleton revived again in the Permian to form abundant and diverse sponge faunas in terms of species and individuals. During this period, they successfully re-established in reef, shallow water level bottom and deeper water palaeocommunities. The appearance of the new sponge together with anthaspidellids, which were identified from the latest Carboniferous-earliest Permian of the Urals in the late 19th century by Stuckenberg (1895) and Tchernychev (1898), forerun proliferation of the Anthaspidellidae during the later Permian.

Compliance with ethical standards

CONFLICTS OF INTEREST: The authors declare that they have no conflicts of interest.

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References

Carrera M.G., Rigby J.K. 2004. Sponges // B.D. Webby, M.L. Droser (eds). The Great Ordovician Biodiversification Event. New York: Columbia University Press. P.102–111.

Church S.B. 2017. Efficient ornamentation in Ordovician anthaspidellid sponges // Paleontol. Contributions. No.18. P.1–8.

Debrenne F., Rozanov A.Yu., Webers G.F. 1984. Upper Cambrian Archaeocyatha from Antarctica // Geol. Mag. Vol.121. P.291–299.

de Freitas T.A. 1991. Ludlow (Silurian) lithistid and hexactinellid sponges, Cape Phillips Formation, Canadian Arctic // Can. J. Earth. Sci. Vol.28. P.2042–2061.

de Laubenfels M.W. 1955. Porifera // R.C. Moore (ed.). Treatise on Invertebrate Paleontology, Part E Archaeocyatha and Porifera. Boulder: Geological Society of America; Lawrence: University of Kansas. P. E21–E112.

Dendy A. 1921. The tetraxonid sponge spicule: a study in evolution // Acta Zool. Vol.2. P.95–152.

Deng Z.Q. 1981. Upper Permian sponges from Laibin of Quangxi // Acta Palaeontol. Sin. Vol.20. P.418–425.

Finks R.M. 1960. Late Paleozoic sponge faunas of the Texas region: the siliceous sponges // Bull. Am. Mus. Natl. Hist. Vol.120. P.1–160.

Finks R.M., Rigby J.K. 2004. Paleozoic demosponges // R.L. Kaesler (ed.). Treatise on Invertebrate Paleontology, Part E (Revised), Porifera. Vol.3: Porifera (Demospongiae, Hexactinellida, Heteractinida, Calcarea). Lawrence, Kansas: The Geological Society of America; The University of Kansas Press. P.9–174.

García-Bellido D.C., Rigby J.K. 2004. Devonian and Carboniferous sponges from Spain // J. Paleontol. Vol.78. P.431–455.

Gerth H. 1927. Die Spongien aus dem Perm von Timor // Jaar. Mijn. Nederland.-Indië Verhandel. Bd.25. S.91–132.

Gerth H. 1929. Die Spongien aus dem Perm von Timor // J. Wanner (ed.). Paläontologie von Timor, nebst kleineren Beiträgen zur Paläontologie einiger anderen Inseln des ostindischen Archipels, Ergebnisse der Expeditionen G. A. F. Molengraaff, J. Wanner und F. Weber. Vol.16. Stuttgart: E. Schweizerbart'sche Verlagsbuchhandlung (Erwin Nägele) GmbH. S.1–36.

Gerth H. 1931. Onz paleontologische kennis van Nederlansche Oost-Indië in 1930. 4. Porifera // Leidse. Geol. Meded. Bd.5. S.115–119.
Grabau A.W. 1922. Ordovician fossils from North China // Palaeontol. Sin. Ser. Vol.13. P.12–15.
Hong J., Choh S.-J., Lee D.-J. 2015. Untangling intricate microbial-sponge frameworks: The contribution of sponges to Early Ordovician reefs // Sediment. Geol. Vol.318. P.75–84.
Inkina N.S. 2019. New data on the Sezym Formation (Lower Permian, Polar Urals) // Dokl. Earth Sci. Vol.489. P.1269–1272.
Johns R.A., Dattilo B.F., Spincer B. 2007. Neotype and redescription of the Upper Cambrian anthaspidellid sponge, *Wilbernicyathus donegani* Wilson, 1950 // J. Paleontol. Vol.81. P.435–444.
Kelly Borges M., Pomponi S.A. 1994. Phylogeny and classification of lithistid sponges (Porifera: Demospongiae): a preliminary assessment using ribosomal DNA sequence comparisons // Mol. Mar. Biol. Biotechnol. Vol.3. P.87–103.
Kruse P.D. 1983. Middle Cambrian *'Archaeocyathus'* from the Georgina Basin is an anthaspidellid sponge // Alcheringa. Vol.7. P.49–58.
Kruse P.D. 1996. Update on the northern Australian Cambrian sponges *Rankenella, Jawonya, Wagima* // Alcheringa. Vol.20. P.161–178.
Kruse P.D., Reitner J.R. 2014. Northern Australian microbial-metazoan reefs after the mid-Cambrian mass extinction // Mem. Assoc. Australas. Palaeontols. Vol.45. P.31–53.
Kruse P.D., Zhuravlev A.Yu. 2008. Middle-Late Cambrian *Rankenella-Girvanella* reefs of the Mila Formation, northern Iran // Can. J. Earth Sci. Vol.45. P.619–639.
Lee J.-H. 2024. Limiting the known range of archaeocyath to the middle Cambrian: *Antarcticocyathus webersi* Debrenne et al. 1984 is a lithistid sponge // Hist. Biol. Vol.36. P.209–213.
Lee J.-H., Woo J., Lee D.-J. 2016. The earliest reef-building anthaspidellid sponge *Rankenella zhangxianensis* n. sp. from the Zhangxia Formation (Cambrian series 3), Shandong Province, China // J. Paleontol. Vol.90. P.1–9.
Lee J.-H., Dattilo B.F., Mrozek S., Miller J.F., Riding R. 2019. Lithistid sponge-microbial reefs, Nevada, USA: Filling the late Cambrian 'reef gap' // Palaeogeogr. Palaeoclimatol. Palaeoecol. Vol.520. P.251–262.
Liu B., Rigby J.K., Jiang Y., Zhu Z. 1997. Lower Ordovician lithistid sponges from the eastern Yangtze Gorge area, Hubei, China // J. Paleontol. Vol.71. P.194–207.
Miller S.A. 1889. Class Porifera // North American geology and palaeontology for the use of amateurs, students, and scientists. Cincinnati, Ohio: Western Methodist. P.152–167.
Morrow C., Cárdenas P. 2015. Proposal for a revised classification of the Demospongiae (Porifera) // Front. Zool. Vol.12. Art.7.
Muir L.A., Botting J.P., Carrera M.G., Beresi M. 2013. Cambrian, Ordovician and Silurian non-stromatoporoid Porifera // D.A.T. Harper, T. Servais (eds). Early Palaeozoic Biogeography and Palaeogeography. Mem. Geol. Soc. L. Vol.38. P.81–95.
Okulitch V.J., Bell W.G. 1955. *Gallatinospongia*, a new siliceous sponge from the Upper Cambrian of Wyoming // J. Paleontol. Vol.29. P.460–461.
Öpik A.A. 1956. Cambrian geology of the Northern Territory // XX International Geological Congress, Mexico. Vol.2. P.25–54.
Pisera A. 2002. Fossil 'lithistids': An overview // J.N.A. Hooper, R.W.M. Van Soest (eds.). Systema Porifera: A Guide to the Classification of Sponges. Vol.2. New York: Kluwer Academic/Plenum Publishers. P.388–402.
Pisera A., Lévi C. 2002. 'Lithistid' Demospongiae // J.N.A. Hooper, R.W.M. Van Soest (eds.). Systema Porifera: A Guide to the Classification of Sponges. Vol.2. New York: Kluwer Academic/Plenum Publishers. P.299–301.
Rauff H. 1895. Paleospongiologie. Zweiter Theil. Fortsetzung. Spongien des Silurs // Palaeontogr. Bd.43. S.223–272. Pl.20–26.
Reid R.E.H. 1968. Microscleres in demosponge classification // Univ. Kansas Paleontol. Contributions. No.35. P.1–37.
Rezvoi P.D., Zhuravleva I.T., Koltun V.M. 1962. [Phylum Porifera. Sponges] // Yu.A. Orlov (ed.). Osnovy paleontologii. Vol.2. Gubki, arkheotsiaty, kishechnopolostnye, chervi. Moscow: AN SSSR. P.17–74 [in Russian].
Rhebergen F. 2014. A new Late Ordovician erratic anthaspidellid sponge (Porifera) originating from Baltica // Scripta Geol. Vol.146. P.1–15.
Rigby J.K., Boyd D.W. 2004. Sponges from the Park City Formation (Permian) of Wyoming // J. Paleontol. Vol.78. P.71–76.
Rigby J.K., Manger W.L. 1994. Morrowan lithistid demosponges and hexactinellids from the Ozark Mountains of northwestern Arkansas // J. Paleontol. Vol.68. P.734–746.
Rigby J.K., Webby B.D. 1988. Late Ordovician sponges from the Malongulli Formation of central New South Wales, Australia // Palaeontogr. Am. No.56. P.1–147.
Rigby J.K., Chamberlain C.K., Black B.A. 1970. Mississippian and Pennsylvanian sponges from the Ouachita Mountains of Oklahoma // J. Paleontol. Vol.44. P.816–832.
Saldin V.A. 2005. Organogenic structure in the Sezym Formation of the Upper Paleozoic of the Polar Urals // Geology of Reefs: Proceedings of the International Symposium. Syktyvkar: Geoprint. P.139–142.
Schuster A., Erpenbeck D., Pisera A., Hooper J., Bryce M., Fromont J., Wörheide G. 2015. Deceptive desmas: Molecular phylogenetics suggests a new classification and uncovers convergent evolution of lithistid demosponges // PLOS ONE. Vol.10. Art.e116038.
Shapiro R.S., Rigby J.K. 2004. First occurrence of an in situ anthaspidellid sponge in a dendrolite mound (Upper Cambrian; Great Basin, USA) // J. Paleontol. Vol.78. P.645–650.
Sollas W.J. 1885. A classification of the sponges // Ann. Nat. Hist. Ser. 5. Vol.16. P.395.
Stuckenberg A. 1895. [Korallen und Bryozoen der Steinkohlenablagerungen des Ural und des Timan] // Mém. Comité Géol. Vol.10. P.1–244 [in Russian and German].
Tchernychev Th. 1898. [Notes on Artinskian and Carboniferous sponges of the Urals and Timan] // Bull. Acad. Impér. Sci. St.-Pétersbourg. Ser.V. Vol.9. P.1–36 [in Russian].
van Kempen T.M.G. 1978. Anthaspidellid sponges from the Early Paleozoic of Europe and Australia // N. Jb. Geol. Paläontol., Abh. Vol.156. P.305–337.
Wilson J.L. 1950. An Upper Cambrian pleospongid (?) // J. Paleontol. Vol.24. P.591–593.
Young J., Young J. 1877. On a Carboniferous *Hyalonema* and other sponges from Ayrshire // Ann. Mag. Nat. Hist. Ser.4. Vol.20. P.425–432.

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