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An elusive middle Cambrian protospongiid (Porifera: Hexactinellida) from the Siberian Platform

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ABSTRACT: Sponges played a crucial role in the shaping of Cambrian marine ecosystems, commonly being principal filter feeders among the benthos. While calcified archaeocyaths were main Cambrian reef builders, spiculate and soft sponges were ubiquitous elements of other level-bottom palaeocommunities. Of them, representatives of the family Protospongiidae possessing a peculiar regular skeleton of cross-like spicules (stauractines) occurred in the majority of the Cambrian Lagerstätten worldwide. A find of a *Protospongia* skeleton in the middle Cambrian (c. 504–502 million years ago) of the south-eastern Siberian Platform further expands data on the global distribution of this genus and the family as a whole and provides a new information on their specific skeletal morphology.
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KEY WORDS: sponges, Protospongiidae, Reticulosa, middle Cambrian, Siberia.

Призрачная среднекембрийская протоспонгиида (Porifera: Hexactinellida) Сибирской платформы

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РЕЗЮМЕ: Губки сыграли ключевую роль в формировании экосистем кембрийских морей, будучи важнейшей группой бентосных фильтраторов. Если при этом обызвествлённые археоциаты были главными кембрийскими рифостроителями, спикульные и мягкие губки стали обычными элементами других донных палеосообществ. Среди последних представители семейства Protospongiidae, выделявшиеся необычным скелетом из крестовидных спикул (ставрактин), встречались в большинстве кембрийских лагерштеттов по всему миру. Находка хорошо сохранившегося фрагмента скелета *Protospongia* sp. в среднекембрийских отложениях, сформировавшихся около 504–502 млн лет назад на юго-востоке Сибирской платформы, ещё больше расширяет наши представления о распространённости представителей данного рода и всего семейства и позволяет лучше понять морфологические особенности данной группы.

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КЛЮЧЕВЫЕ СЛОВА: губки, Protospongiidae, Reticulosa, средний кембрий, Сибирь.

Introduction

The Cambrian Explosion appears to be an evolutional event when adaptational responses of living beings on external challenges were expressed in the diversification of numerous short-lived taxa. This pattern greatly complicates the search evolutionary pathways of the principal invertebrate phyla due to a rapid appearance of their apparent crown groups in the fossil record accompanied by a number of extinct high-rank taxa often independently attaining similar morphological traits (Erwin, Valentine, 2013).

An appearance of hexactinellids is not an exemption. The majority of possible Cambrian hexactinellids had only superficial morphological similarity with modern representatives of the class Hexactinellida Schmidt, 1870 *sensu stricto* and did not reveal clearly class origin. Fossils are mostly restricted to macroscleres while other visible features are either absent or meaningless for proper systematics due to incomplete preservation and post-mortem transformation of skeletal remains. Even being intact, early Palaeozoic sponges commonly lack microscleres, which would allow researches a direct comparison with crown hexactinellids (Reiswig, 2002a).

The extinct order Reticulosa is an example of such a discrepancy. This order was established by Reid (1958) to include sponges with a thin-walled skeleton formed by tangential hexactines. It was ascribed to the subclass Amphidiscophora Reid, 1958, possibly, due to a weak development or the absence of a choanosomal skeleton, infrequent spicule fusions and the absence of terminal ray branching in spicules (Reid, 2003a; Reiswig, 2002a). However, the absence of an expressed choanosomal skeleton is a common feature of thin-walled sponges independently of their affinities. For example, a number of early Palaeozoic reticulosans are attributed to the family Protospongiidae Hinde, 1887, which morphology corresponds entirely to the diagnosis of the order. On the contrary, Mesozoic representatives of the same order are distinguished either by variable dictyonal fussed skeletons (e.g. *Asociatella* Hurcewicz, 1985) or by thick-walled well-developed choanosomal skeletons (e.g. *Microstaura* Finks, 1960). Besides, not only the earliest reticulosans but even the latest ones differed drastically from the crown-group hexactinellids and, particularly, from their relatives from the order Amphidiscosida (Mehl, 1991; Reiswig, 2002b).

Nowadays, the understanding of both composition and definition of the order Reticulosa is highly diluted and the majority of former reticulosans are formally ascribed to hexactinellids (Mehl, 1991; Botting, Muir, 2018). By contrast, early Paleozoic non-reticulosan sponges possessing a developed choanosomal skeleton and expressed hypodermal spicules are discovered as well (Botting *et al*., 2018, 2020, 2023; Li *et al*., 2019; Luo, Reitner, 2019). They are opposed with the Reticulosa as possible crown-group or stem-group representatives of the Hexactinellida.

Representatives of the genus *Protospongia* Salter, 1864 have all the principal features of the order Reticulosa and the family Protospongiidae in particular (Carrera, Botting, 2008). They exemplify a regular orthogonal skeletal pattern (quadrules) resulted from a tip to tip obligate arrangement of stauractines of several size orders in vertical and horizontal series. In turn, smaller stauractines form a quadrule inside the area between the rays of larger ones dividing this square into four smaller squares and so on to the fourth order (Rigby, 1966; Finks, Rigby, 2004). All these stauractines form a single tangential layer of the skeleton. This feature is suggested to be the most primitive one of the reticulosans (Botting, Muir, 2018).

It is highly unlikely that *Protospongia* and similar sponges were the earliest hexactinellids because definite hexactines were discovered in the basal lower Cambrian (Chang *et al*., 2017, 2019). Stauractines appeared later on in the fossil record. Some early Cambrian protospongiids, such as *Paradiagoniella* Chen *et al*., 2015, had a minor number of oxeas and rare hexactines in addition to usual stauractines. *Diagoniella* Rauff, 1894 differs from *Protospongia* by diagonal orientation of quadrules (Rauff, 1894; Walcott, 1920). This insufficient morphological difference was a source of problem for identification of fragmental fossils (Rigby, Collins, 2004). Although *Diagoniella* had a developed rooting tuft of monaxons, this feature was not preserved in all instances (e.g. Dawson, Hinde, 1889; Rigby, Collins, 2004; Caron *et al*., 2010; Rigby *et al*., 2010).

Siberian intact reticulosans were extremely rarer and until now were restricted to a single specimen of *Diagoniella* sp. from the lower Cambrian Sinsk Formation (c. 513 Ma) of the middle Lena River (Ivantsov *et al.*, 2005). Until now, the same Sinsk Lagerstätte yields the only rich Cambrian set of intact spiculate poriferan skeletons of the Siberian Platform. Here we describe a new find of intact reticulosan sponge from the middle Cambrian of the south-eastern Siberian Platform. Despite a significant weathering of the fragile skeletal fragment, its relatively good preservation allows us to describe in tiny details its reticulation pattern.

Material and methods

The fossil sponge was picked up in the lower middle Cambrian Chaya Formation from the well-exposed outcrop of the Krasivaya Mountain on the right bank of the Maya River, a tributary of the Aldan River, immediately above the Ychchakyyt Creek mouth in the Republic of Sakha (Yakutia). The sponge-bearing stratum belongs to the lowermost *Anopolenus henrici* trilobite Zone of the local Mayan stage (Egorova *et al*., 1982). By trilobites, this zone is correlated with the middle Drumian Stage, Miaolingian Series of the International Chronostratigraphic Chart, approximately embracing the 504–502 million years interval (Naimark, Pegel, 2017; Korovnikov, Tokarev, 2018).

The host rock consists of dark grey thinly parallel laminated marls with abundant pyrite concretions. The bed yields calcareous carapaces of agnostoid stem crustaceans including intact ones, linguliformean phosphatic shells and hyolith calcareous conchs. By contrast with mostly brownish red and greyish green argillaceous marls of the upper Chaya Formation, the strata under discussion resemble closely underlying dark brown parallel laminated marls and limestones of the upper Inikan Formation.

The reticulate skeleton of the *Protospongia* sp. is preserved intact despite its primary fragile nature. A similarly complete preservation of thinly-bodied spiculate sponges is observed in the Chengjiang Lagerstätte of South China (Chen *et al*., 2015). In all cases a fast burial in soft fine-grained sediment, which, later on, has been not disturbed by bioturbators, is suggested (Gabbott *et al*., 2004; Zhao *et al*., 2012). Thus, the Siberian *Protospongia* sp. could be preserved in the same way. Pyrite and organic matter enrichment in addition to the fine mudstone structure is indicative for the formation of hosting strata under calm and low-oxic conditions.

The specimen is housed in the Borissiak Palaeontological Institute, Russian Academy of Sciences (PIN RAS), collection no. PIN RAS No. 5119/2001.

The skeletal fine morphology was examined by optical stereomicroscope Micromed MC-2-ZOOM. Macrophotographs were taken by a Canon EOS 80D equipped with a Canon MACRO EF-S 35 mm F/2.8. Final images were prepared with Photoshop version 23.1. Measurements of the spicule's length and diameter were carried out by ImageJ2 from Canon EOS 80D photos.

Systematics

Hexactinellida Schmidt, 1870
Order Reticulosa Reid, 1958
Superfamily Protospongioidea Hinde, 1887
Family Protospongiidae Hinde, 1887
Protospongia Salter, 1864

DIAGNOSIS. Subcylindrical, conical, to bowl-shaped or globular, thin-walled sponges, which skeletal net consists of uniformly spaced, diagonally, rectangularly or rhombically arranged stauractines or stauractine-based spicules. Intervening skeletal areas are covered with similarly oriented smaller stauractines forming together a descending order of quadrules.

TYPE SPECIES. *Protospongia fenestrata* Salter, 1864.

TYPE LOCALITY. Lingula Flags Formation, Menevian Group, St. David's Series (Miaolingian Series), Cambrian, Pembrokeshire, South Wales, U.K.

Protospongia sp.
Fig. 1.

DESCRIPTION. A single fragment of thin-walled reticulate skeleton 95 mm in height and 70 mm in width, composed of tangentially arranged stauractines. Stauractines are grouped in four size orders, which form quadrules of four descending sizes imparting the entire fossil a square pattern (Fig. 1A, B). First-order stauractines have uniformly tapering rays with a length from 5 to 8 mm (mean = 7.06; SD = 0.76; N = 17) and maximum ray diameter of 0.2–0.6 mm (mean = 0.28; SD = 0.11; N = 17). Sharp tips usually do not preserve. The largest stauractines express regular quincuncial pattern and form the first-order quadrules. Second-order stauractines have rays about 0.1–0.25 mm in diameter (mean = 0.24; SD = 0.1; N = 24) and 2.5–4.7 mm in length (mean = 3.39; SD = 0.51;

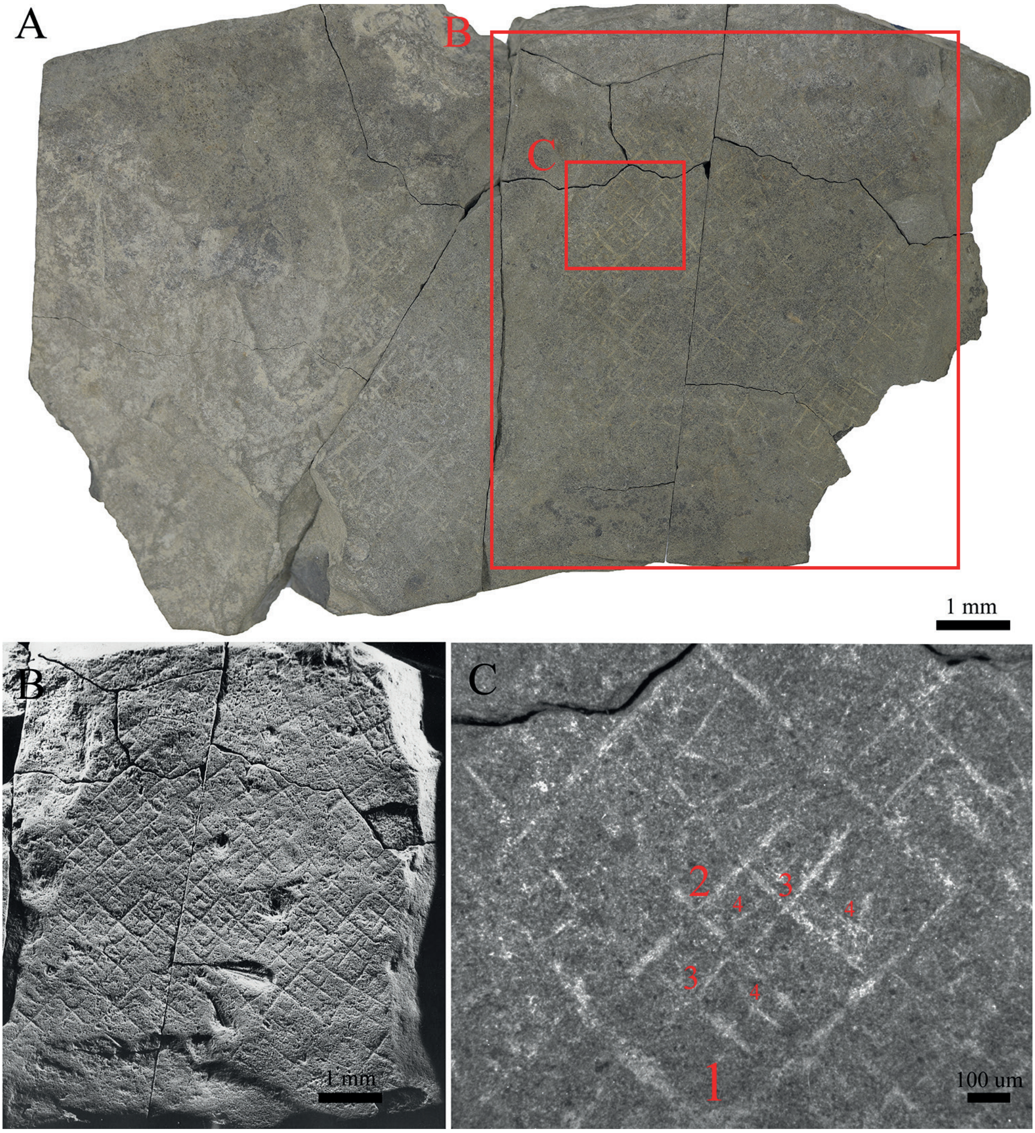

Fig. 1. *Protospongia* sp.*,* PIN RAS No. 5119/2001, Maya River, Krasivaya Mountain, Republic of Sakha (Yakutia), Chaya Formation, Drumian Stage, Miaolingian Series, middle Cambrian. A — general view, enlarged areas are ensquared. B — same specimen covered with ammonium chloride showing a minor inclination of first-order stauractines in a distal direction. C — enlarged area showing stauractines of four orders depicted as 1, 2, 3 and 4 respectively, numerals are placed about the center of each spicule.
Рис. 1. *Protospongia* sp.*,* ПИН РАН № 5119/2001, р. Мая, гора Красивая, Республика Саха (Якутия), чайская свита, друмский ярус, мяолинский отдел, средний кембрий. A — общий вид, прямоугольниками обведены увеличенные участки. B — тот же образец, покрытый хлоридом аммония и демонстрирующий небольшой наклон рядов ставрактин первого порядка к периферии. C — увеличенный участок скелета со ставрактинами четырёх порядков, помеченных вблизи перекрестия каждой спикулы цифрами 1, 2, 3 и 4 соответственно.

N = 24). Third-order ones are mostly well-preserved and have rays of 0.1–0.3 mm in maximum diameter (mean = 0.16; SD = 0.048; N = 48) and 1.2–3.0 mm in length (mean = 1.83; SD = 0.48; N = 48); fourth-order stauractines bear rays of 0.09–0.15 mm in diameter (mean = 0.12; SD = 0.02; N = 20) and of 0.6–2.3 mm in length (mean = 1.3; SD = 0.37; N = 20). All quadrules have a square shape, first-order ones are 8–12 mm wide, second-order — 4–6 mm wide, third-order — 2–3 mm wide and the fourth-order — 0.5–2 mm wide (Fig. 1C). All preserved stauractines are arrangement in parallel rows to the presumable sponge axis.

REMARKS. Neither diactines, no other spicules are detected in the specimen.

The maximum ray length of stauractines of the first- and second-orders is definitely underestimated due to the erosion of the specimen, which is preserved on an exposed bedding surface. Spicule imprints are visible only. Imprints of the fine tips of stauractines rays usually are absent. This does not allow understanding of the type tip to tip connection between rays. The first-order stauractine arrangement is not exactly orthogonal as the spicule rows decline from a regular pattern to 10–15^{0} (Fig. 1B). A post-mortem spicule displacement can be ruled out because such a deformation would be expressed in an irregular displacement among stauractines of different sizes. Also, the upper right half of the fragment has a sign of graduate incline of the skeletal net. First-order spicules together can form the subcylindrical or obconical profile like in *Protospongia conica* Rigby *et al.*, 1998 (Rigby, Harris, 1979; Rigby *et al.*, 1998), but this spicule arrangement is not resulted in such a well-expressed pattern. On the contrary, *Lantianospongia palifera* Xiao *et al.*, 2005 displays a clear deviation of the stauractine arrangement from rectangular pattern in its basal half but quadrules themselves are drastically deformed (Xiao *et al.*, 2005). Besides, the rays of some adjacent first and second-order stauractines are partially overlapped with each other along the last third of their length. A similar overlapping was observed in *Protospongia hicksi* Hinde, 1888, but it is mostly derived from an overall juxtaposition of stauractines of different size groups on each other and from a ray length oversizing an average quadrule width (Rigby, 1966).

The *Protospongia* skeletal fragment from the Maya River is similar in spicule size range with fragmental specimens of *Protospongia* from the middle Cambrian Burgess Shale and the Marjum Formation from western North America, which have been attributed to *P. hicksi*, but it lacks stauractines of the fifth order (Rigby, 1966; Rigby, Collins, 2004). A possible fragment of *P. hicksi* from the Silurian Ballytoohy Formation (the Clare Island, Ireland) has up to six size groups of spicules and as twice as bigger first-order stauractines (Rushton, Phillips, 1973).

Siberian *Protospongia* is significantly larger than the other known representatives of the genus. It shows a close morphological similarity including a spicule size order with the Silurian *Protospongia columbiana* Rigby *et al.*, 1998. However, the skeleton of *P. columbiana* consists of hexactines, some of which has projecting rays appearing as prostalia (Rigby *et al.*, 1998). Also, the Siberian sponge differs from the lower Cambrian *P. gracilis* Xiao *et al.*, 2005 and the Silurian *P. conica* Rigby et Harris, 1979 by a more regular arrangement of quadrules and from *P. gracilis* by a less pronounced elongation of vertical rays in stauractines. *P. spina* Rigby et Mehl, 1994 has an unusual morphology, which is expressed in a ray curvature of marginal spicules and their overall oblique shape (Rigby, Harris, 1979; Rigby *et al.*, 1998; Xiao *et al.*, 2005). Its affinities with *Asthenospongia* Rigby *et al.*, 1981 is not excluded (Mehl *et al.*, 1993; Botting, 2004).

OCCURRENCE. Maya River, above the Ychchakyyt Creek mouth, the Krasivaya Mountain section, Republic of Sakha (Yakutia), Chaya Formation, Mayan stage (Drumian Stage), Miaolingian Series, “middle” Cambrian.

Discussion

The overall body shape of the Siberian *Protospongia* is difficult to outline due to the absence of a definite border between the sponge body and the hosting rock. However, the parallel orientation of quadrules to sponge axis is a plausible skeletal morphology. A sponge reconstruction with diagonally arranged stauractines to the body axis would be resulted in a skeleton of enormous size, which never has been released in *Diagoniella*. For instance, the entire *Diagoniella* sp. from the Sinsk Formation is several times smaller rather than the present *Protospongia* fragment (Ivantsov *et al.*, 2005). A similar size difference is observed with *D. cyathiformis* Dawson in Dawson et Hinde, 1889 from the Burgess Shale, in which the stauractines are four times smaller, despite of a gradation of quadrule on four size orders as in the Siberian *Protospongia* (Dawson, Hinde, 1889; Rigby, Collins, 2004). Middle Cambrian *D. magna* Rigby *et al.*, 2010 from the Drum Mountains (western USA) is the largest in the genus, but it does not reach a comparable size (Rigby *et al.*, 2010).

Despite a similarity of the Siberian *Protospongia* to other distinct representatives of the genus, this sponge additionally hints at the genus paraphyly and minor role of the Protospongioidea in origins of the Hexactinellida (Mehl, 1991;

Finks, Rigby, 2004). The type species *Protospongia fenestrata* was established on fragments, which seems to be pieces of a thin-walled skeleton with a rectangular arrangement of spicules (Salter, 1864). Better preserved specimens of the middle Cambrian *P. hicksi* from western Utah lack fused spicules and the prevalence of stauractines over hexactines (Rigby, 1966). However, a presence of hexactines detected in Silurian *P. columbiana, P. conica,* early Cambrian *P. gracilis* and other relatively complete skeletons of the same genus and forming a genuine part of regular orthogonal skeletal network, thus, contradicts to the present diagnosis of the genus (Rigby *et al*., 1998; Rigby, Collins, 2004; Xiao *et al*., 2005). *P. hicksi*, *P. fenestrata* and the new Siberian sponge are related species, which form a separate group within the *Protospongia* and deserve their own generic affiliation if more complete specimens will be discovered. In fact, they do not fit to the morphological concept of the Protospongiidae. Hardly, they can be regarded as ancestral protospongiids either. The dominance of hexactines and low organized skeletal network lacking spicule fusion can be a feature of a common ancestor of the Protospongiidae and the stem-group Hexactinellida as a whole (Rigby, Collins, 2004; Botting, Muir, 2018). Early Cambrian *Triticispongia* Mehl et Reitner in Steiner *et al*., 1993 and *Sanshapentella tentoriformis* Yun *et al.*, 2022 further highlight this contradiction and, in fact, could be the most basal Protospongiidae, from which *Protospongia* had derived (Steiner *et al.*, 1993; Yun *et al.*, 2022).

In summary, the group of solely stauractine-bearing sponges including *P. hicksi, P. fenestrata* and the Siberian *Protospongia* may be considered as a different genus within the family Protospongiidae.

Compliance with ethical standards

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

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