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Endemic Lake Baikal sponges from deep water. 2: Taxonomy and Bathymetric Distribution

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Abstract

Unique samples of deep-water sponges of Lake Baikal were collected between 120 and 1450 m depth and their taxonomy and bathymetric distribution were studied. Based on morphological studies with scanning electron microscopy (SEM) and molecular analyses (CO1, ITS) we describe a new species, *Baikalospongia abyssalis* **sp. nov.** Spicule morphology of this new species is similar to *Palaeoephydatia* sp., a species previously known only from fossils in Late Pliocene (3.2−2.8 mya) sediments. Other sponge samples collected were identified as *Baikalospongia intermedia intermedia, B. intermedia profundalis, B. bacillifera, B. fungiformis, B. martinsoni* and *Swartschewskia papyracea*, all from the family Lubomirskiidae. Sponge specimens with giant spicules, identified as *B. fungiformis*, were found at great depths. *B.i. intermedia* and *B. i. profundalis* are dominating species at great depth. Light is a limiting factor for distribution of *Lubomirskia baicalensis*, possibly due to its symbiosis with photosynthetic protists. The current study extends our knowledge on the distribution boundaries of Lubomirskiidae at great depths.

Introduction

Lake Baikal is the deepest and the most ancient lake in the world with an estimated age of about 30 million years (Mats 1993). The lake is divided into three basins of similar size—the deepest of which is the Central Basin (maximum depth 1637 m), followed by the South Basin (1461 m) and the North Basin (904 m). The well-oxygenated hypolimnia of Lake Baikal is inhabitable for Metazoa at all depths up to the deepest point. The unique deep-water fauna of Baikal include endemic species of fish, crustaceans, platyhelminths and sponges (Mascay *et al.* 2002; Timoshkin 1995). Sponges of Lake Baikal are represented by two families, Lubomirskiidae Rezvoi, 1936 and Spongillidae Gray, 1867, with only the former endemic family inhabiting the greater depths.

Lubomirskiidae includes thirteen species and two subspecies (Efremova 2001, 2004; Itskovich *et al.* 2015a). According to Bazikalova (1945), the lake is divided into five vertical zones: littoral (0–5 m), sublittoral (5–150 m), transition zone (150–300 m), profundal (300–500 m), abyssal (500–1637 m). Most species of Lubomirskiidae are sublittoral but some inhabit the deeper zones (Masuda 2009). The current classification of Baikalian sponges is predominantly based on the morphology of their megascleres (among the other skeletal characters) but molecular analyses have suggested a need for revision (Itskovich *et al.* 2008, 2013, 2015a).

Most Baikalian sponge samples previously studied for taxonomy and biodiversity were collected by scuba diving from depths up to 40 meters. Therefore very little was known of deep-water sponges of Lake Baikal until recently. A few recent studies on deep-water specimens collected by either dredging, or by the deep diving submersible "*Pisces*", or by the remotely operated vehicle "SEA ROV" revealed that the deep-water sponge fauna is profoundly different from its shallow water counterpart, for example, collection of single specimens from the deep zone resulted in the description of a new subspecies, *B. intermedia profundalis* (Rezvoi 1936), and a new species, *Rezinkovia arbuscula* (Efremova *et al.* 2004). It was also revealed that *B. intermedia* showed the highest frequency among all species in the shallow zone and that Lubomirskiidae mostly inhabit depths of 10−20 m (Masuda 2009). Studies on stable isotopic signatures for Lake Baikal deep-water sponges also revealed that they

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assimilate carbon and nitrogen from environmental sources and microbial symbionts (Sitnikova *et al.* 2016). Nevertheless, studies on the vertical distribution of sponges in Lake Baikal are scarce (see Masuda *et al.* 1999, Masuda 2009, Bukshuk & Timoshkin 2013).

In 2008, expeditions in Lake Baikal were carried out with the use of the deep-water manned vehicles Mir-1 and Mir-2. During the dives between 120−1450 m, unique samples of deep-water sponges were collected and their habitats were studied. In a previous article we revealed new deep-water species and cryptic speciation within Lubomirskiidae based on molecular and spicule morphological analyses of ITS nuclear DNA and CO1 mitochondrial DNA (Itskovich *et al.* 2015a). In this study we describe this new species, *Baikalospongia abyssalis* sp. nov., with the morphological characters. We also analyze, for the first time, the vertical distribution of deep-water sponges in Lake Baikal. Furthermore we discuss factors responsible for bathymetric segregation of distribution of sponges in Lake Baikal.

Material and methods

Deep-water sponge samples were collected by GOA Mir 1 and Mir2 during expeditions in Lake Baikal in August – September 2008. The collection sites (5 stations) are situated in the sublittoral (5–150 m), transition zone (150–300 m), profundal (300–500 m), abyssal (500–1637 m) zones as defined by Bazikalova (1945) of the Central Basin and South Basin from depths between 120 to 1450 m. Sixty samples of sponges were collected by a manipulator. All specimens were photographed and fixed in 96% ethanol. Species identifications were performed by morphological and molecular methods. Molecular analyses (ITS and CO1) comprised 17 samples with different morphological characteristics (see Itskovich *et al.* 2015a). Spicule and skeleton preparations were carried out as described previously (see Masuda *et al.* 1999, Efremova 2001) and were examined using Zeiss Axiovert light microscope and Philips SEM 525M scanning electron microscope. The shape and consistency of sponges, skeletal characters, the form and size of spicules and their variability in each sample were analyzed. Spicule sizes were determined by measuring 50 spicules from each sample.

Results and discussion

Systematics

Phylum Porifera Grant, 1836

Class Demospongiae Sollas, 1885

Subclass Heteroscleromorpha Cárdenas, Perez &Boury-Esnault, 2012

Order Spongillida Manconi & Pronzato, 2002

Family Lubomirskiidae Weltner, 1895

Genus *Baikalospongia* Annandale, 1914

***Baikalospongia abyssalis* sp. nov.**
Fig. 1.

Spongillina n.sp. Itskovich *et al.* 2015a: 127, Fig. 2.

Type material. Holotype: MIRY_2008_BS99; Paratype MIRY_2008_BS100. The holotype and paratype were collected on September 21, 2008 by GOA Mir 1 and Mir 2 at 750 m depth near the northwest coast of Lake Baikal 1 km south to the Olkhon Gate (52°57'35.4"N 106°53'36.3"E). Sponge samples were scraped off a rock, collected by a manipulator, and deposited in the collection of the Limnological Institute SB RAS, Irkutsk, Russia.

Type locality. Lake Baikal.

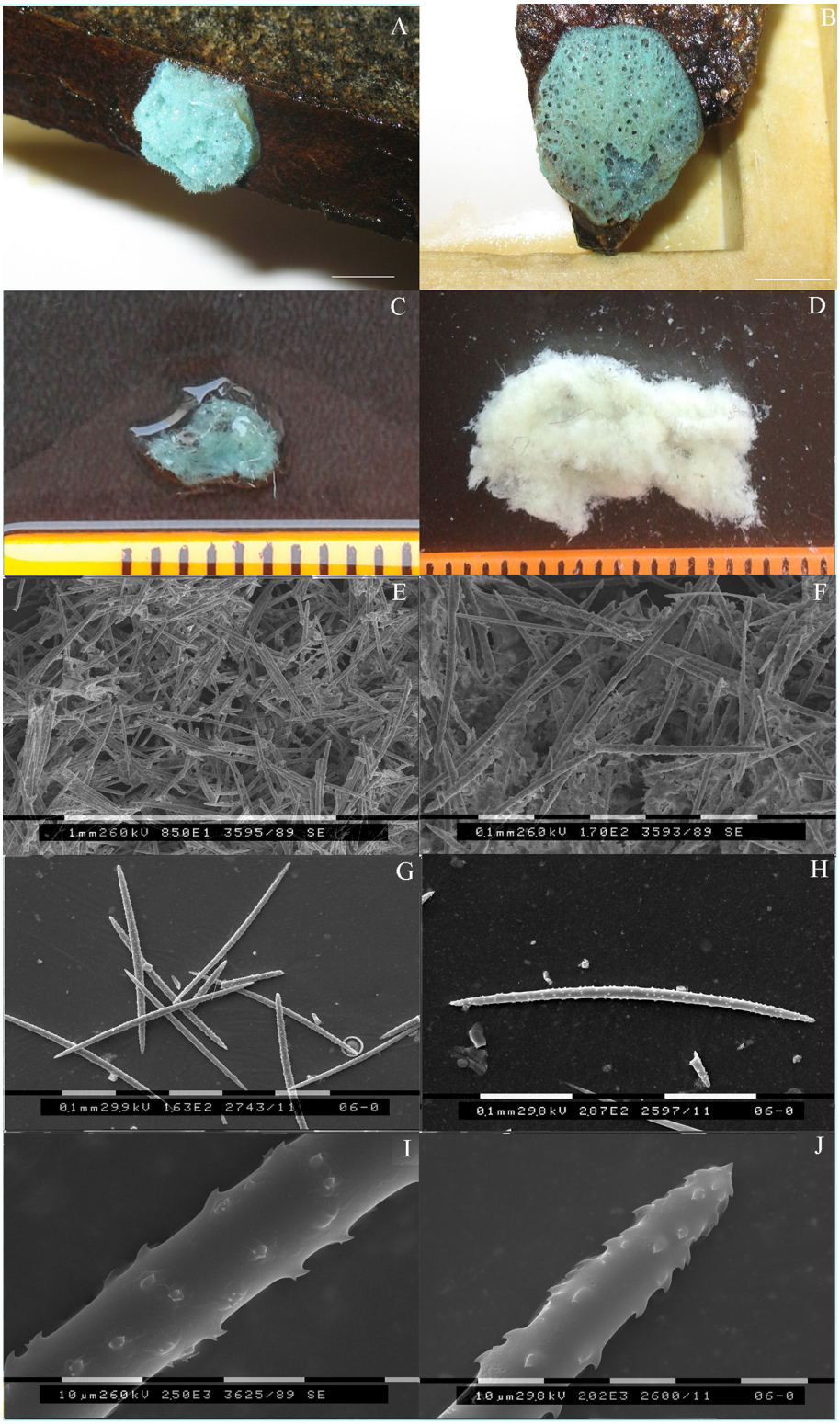

FIGURE 1. *Baikalospongia abyssalis* **sp. nov.** A: Holotype: BS99. Scale bar 1 cm. B: Paratype: BS 100. Scale bar 1 cm. C: fragment of holotype BS99 fixed in ethanol. Scale bar 1 mm. D: fragment of holotype BS99 fixed in formalin. Scale bar 1 mm. E,F: the skeleton of holotype BS99. Scale bars 1 mm and 100 µm. G–J: SEM photos of megascleres. Scale bars 100 µm and 10 µm.

Etymology. The name represents the abyssal depths of the Lake Baikal from which the samples were collected.

Diagnosis. Encrusting sponge. Consistency soft, not fragile. Megascleres very long and thin oxeas (length

370–470 μm, width 10–15 μm) covered with simple and polymorphic spines. Microscleres absent. Gemmules absent.

Description. Holotype: Encrusting sponge, 3 cm in diameter, 1.5 cm thick. Two fragments were collected of size 15 mm in diameter and 7 mm thick, and 5 mm in diameter, 2 mm thick. Consistency soft but not fragile. Color light blue in life and in the preserved state in ethanol and white in the preserved state in formalin. Surface uneven, rough. Oscula not seen in preserved specimen.

Megascleres very long and thin, slightly curved oxeas (length 370–470 μm, width 10–15 μm). Megascleres covered by simple and polymorphic spines located throughout the length of spicules, at the ends of spicules spines curved down (see Fig. 1).

Ectosomal and choanosomal skeleton indistinguishable. Skeleton anisotropic, with paucispicular primary fibres and rare cross bundles (Fig. 1). Variable amount of spongin. There are no spicular tufts on top of the main bundles.

Paratype: matching description above for holotype, Paratype is encrusting sponge 1 cm thick, 0.5 cm in diameter. A fragment was collected with size 15 mm in diameter and 7 mm thick. Color light blue in life and white in the preserved state in formalin.

Taxonomic remarks. *Baikalospongia abyssalis* **sp. nov.** belongs to the Baikalian endemic family Lubomirskiidae. This species differs from other Lubomirskiidae by very thin and long spicules, which are similar to the spicules of *Trochospongilla* sp. (family Spongillidae) from Lake Baikal (Efremova 2001) or the fossil genus *Palaeoephydatia* (Veynberg 2009). However, the molecular data clearly identified this species as Lubomirskiidae (Itskovich *et al.* 2015a).

Spicule dimensions of *Baikalospongia abyssalis* **sp. nov.** differ significantly from spicule dimensions of other Lubomirskiidae species with oxeas. Also spicules are covered with characteristic polymorphous spines with a few edges while other Lubomirskiidae species have simple spines. This species is placed under the genus *Baikalospongia* Annandale, 1914 based on the structure of the ectosomal skeleton in which there are no spicular tufts on top of the primary fibres (Rezvoi1936). According to Rezvoi (1936) the structure of the skeleton is diagnostic to determine the genera within Lubomirskiidae. Based on the differences in morphological features and sequences of CO1 and ITS (Itskovich *et al.* 2015a) our samples MIRY_2008_BS99, MIRY_2008_BS100 are considered to represent a novel species of the genus *Baikalospongia*, for which the name *Baikalospongia abyssalis* **sp. nov.** is proposed. Probably this is an exclusive deep-water species, as it has never been recorded from the shallow waters, despite numerous collections made in the littoral zone of Lake Baikal (Masuda 2009, Itskovich *et al.* unpubl.).

Taxonomy of other deepwater sponge samples

Sixty samples of deep-water sponges of Lake Baikal were collected at depths between 120 and 1450 m. All sponges were found on rocks and had white, yellow and blue colors.

Samples were classified into two genera, five species and one subspecies of the family Lubomirskiidae. Sponge samples were identified using scanning electron microscopy (SEM) as *Baikalospongia intermedia* Dybowsky, 1880*, B. intermedia profundalis* Rezvoj, 1936*, B. bacillifera* Dybowsky, 1880*, B. fungiformis* Makushok, 1927*, B. martinsoni* Efremova, 2004 and *Swartschewskia papyracea* Dybowski, 1880.

The analysis of the deep-water collection revealed samples with unusually large size of spicules. For example deep-water samples of *B. intermedia profundalis* (BS58, 78, 79, 80) and *B. fungiformis* (BS101) possess much larger spicule sizes then conspecifics of the shallow water (480–520 x 22–35μm vs. 330–470 x 20–25 μm for *B. intermedia profundalis* and 510–560 x 35–45 μm vs. 224–275 x 20–32 μm for *B. fungiformis*). Since, according to molecular data, these samples are not divergent from the other Lubomirskiidae (Itskovich *et al.* 2015a), they represent the first example of deep-water gigantism in freshwater sponges.

Distribution of sponges at great depths

Among samples collected at depths exceeding 120 m were predominantly *B. intermedia profundalis* (20 samples

from 550–1450 m), followed by *Baikalospongia intermedia intermedia* (13 samples from 120–300 m) and *B. fungiformis* (12 samples from 120–900 m) and *B. martinsoni* (11samples from 120–300 m). Far less numerous were *Baikalospongia abyssalis* **sp. nov.** (2 samples from 750 m), *B. bacillifera* (one sample from 250 m) and *Swartschewskia papyracea* (one sample from 120 m) (see Fig. 2). All collected samples belong to the lubomirskiid genera *Baikalospongia* Annandale, 1914 and *Swartschewskia* Makuschok, 1927. Species of *Lubomirskia* Dybowsky, 1880 and *Rezinkovia* Efremova, 2004 were not collected at these depths in our study and were not found at depth exceeding 120 m in previous studies (Efremova 2001, Masuda 2009) except for *L. abietina* (Sitnikova *et al.* 2016).

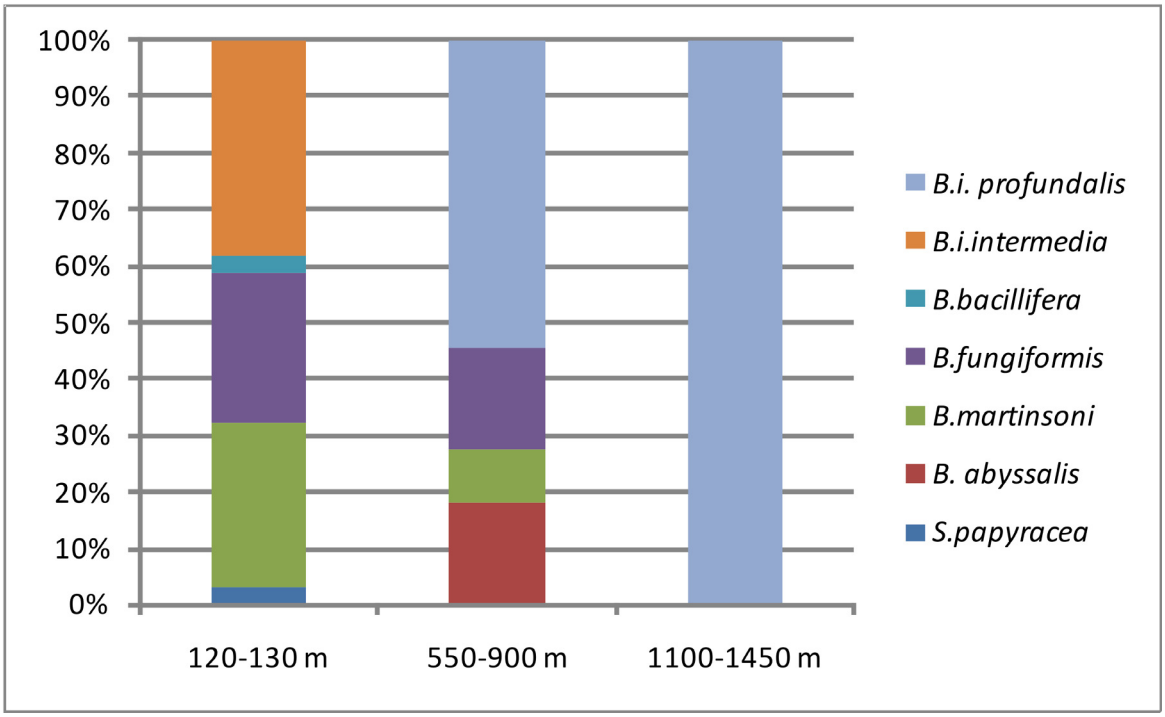

FIGURE 2. Vertical distribution of Lubomirskiidae in the Lake Baikal at depths of more than 120 m.

The present data extends our knowledge on distribution and habitats of Lubomirskiidae at greater depths of Lake Baikal. Sponges collected from the greatest depth (1450 m) were identified as *B. intermedia profundalis*. This subspecies was described based on a single specimen collected by dredging from depth of 889 m (Rezvoi 1936). Later, samples of *B. intermedia profundalis* were collected by the ROV *Pisces* from South Baikal and by dredging in the Centre and North Basins from depths at 150–540 m (Efremova 2004).This subspecies exclusively inhabits the deeper zones (Efremova 2004, Bukshuk&Timoshkin 2013). Our study reveals that *B. intermedia profundalis* can be found up to 1450 m depth and is the only subspecies at this depth.

Baikalospongia intermedia intermedia was second most abundant sponge collected from depths between 120–1200 m. This species is known to predominantly inhabit the shallow zone of Lake Baikal (Efremova 2001). However, samples of *B. intermedia intermedia* were collected from 420 m in the north-east of Lake Baikal in the estuary of Frolikha River, where sponges live in a symbiotic community with methanotrophic bacteria (Efremova *et al.* 1995). Molecular-phylogenetic studies revealed a highly diverse microbial community of Baikalian sponges (Kaluzhnaya *et al.* 2012, Kaluzhnaya & Itskovich 2014). Probably the successful settlements of *B. intermedia intermedia* and other species of *Baikalospongia* from both shallow and greater depths have been facilitated due to the ability to successful symbioses with both photosynthetic protists and chemosynthetic bacteria. It has been shown that the composition of the functionally important symbiotic community of deep-water sponges differs from that of the sponges from the littoral zone (Kaluzhnaya & Itskovich 2014). Deep-water sponges in Lake Baikal also participate in chemosynthetic food webs (Sitnikova *et al.* 2016).

Baikalospongia fungiformis was described from 533 m depth based on a specimen with blue color (Rezvoi 1936) and is considered to be aeurybathic species (Efremova 2001). In our collections, this species was found between 120–900 m depth and some specimens likewise displayed the characteristic blue color, which might be the

result of copper assimilation from the substrate (Kaluzhnaya & Itskovich 2014).

The maximum depth recorded for *B. martinsoni* was 150 m (Efremova 2001). We extend here the known vertical distribution of this species up to 900 m depth. We also report *Swartschewskia papyracea* for the first time from the depth of 120 m. It is interesting that this species keeps its white color even in shallow water and preferably grows on the underside of rocks with low exposure to light.

It is interesting that the consistency of the sponge body apparently does not seem to correlate with depth. *Baikalospongia i. intermedia* and *B. i. profundalis* have soft and fragile consistency while *B. bacillifera* and *B. fungiformis* are hard and strong due to thick speculation and low amounts of spongin. We found that both hard and soft species successfully inhabit the deep zone up to 900 m. In previous studies it was shown that species with different body consistency can inhabit the zone up to 40 m depth (Masuda 2009). Lubomirskiidae have not been found in depths of less then 1 m as the strong wave action has damaging effect on the sponge bodies, while in greater depths wave action is rather insignificant (Masuda 2009).

In general, the study of vertical distribution of Lake Baikal sponges is important for understanding their ecology and evolution and to review their taxonomy with an integrative approach. The current study on the deep-water sponge fauna of Lake Baikal now indicates that the richness of species composition decreases with increasing water depth (Fig.2). The different species composition of sublittoral, littoral and deeper zones indicates a bathymetric segregation of sponges in Lake Baikal. Bathymetric segregation in other ancient lakes such as Lake Tanganyika or Malawi relates to differences in temperature, amount of oxygen, light and pressure at different depths (Martin 1998, Schön & Martens 2004). In Lake Baikal, oxygen is excluded from factors responsible for a bathymetric segregation because its water column is oxygenated to about the same level down to the deepest point (Martin 1998). However, in the deeper zones of Lake Baikal absence of sunlight, constant low water temperatures (near 3.2–3.5°C), high pressure, accumulation of organic sediments in the bottom layer and the presence of hydrocarbons at great depths (Namsaraev *et al.* 2006, Pavlova *et al.* 2008) may offer conditions suitable for some sponges.

Lubomirskiidae, in shallow waters, live in symbiosis with photosynthetic unicellular algae and cyanobacteria; therefore lack of light could probably be the limiting factor at great depths. In the shallow waters of Lake Baikal most of the sponges were green in color, mostly due to the chlorophyll containing photosynthetic symbionts, while all specimens collected from deep-water samples were white or bluish in color. Some of the samples collected from deep-water had green conspecifics in the littoral (*B. i. intermedia, B. fungiformis*), which indicates that the photosynthetic symbiosis may not be obligate for these species. However, species such as *Lubomirskia baicalensis* (Pallas, 1773) and the other species of *Lubomirskia* Dybowsky, 1880, which are usually abundant in shallow water (Masuda 2009), were not recorded during our deep-water sampling, potentially due to their obligatory symbiosis with photosynthetic microorganisms that demand greater light.

The second stenobathic taxon, *B. intermedia profundalis*, is not found in the littoral zone as opposed to *L. baicalensis* (Efremova 2001, Bukshuk & Timoshkin 2013).The water temperature in the lake at depth below 250 m is a constant 3.3–4.3°C but the top 250–300 m layer of water has temperature fluctuations (Shimaraev *et al.* 1994). Temperature fluctuations are most pronounced at depths 0–25 m (Kozhova & Izmest'eva 1998). During warming up periods in summer, water temperatures at 10 m can reach 12–13°C in some places (Timoshkin *et al.* 2009). Probably the deep-water Lubomirskiidae originated from its shallow-water lineages when the abyssal was colonized by sponges (Itskovich *et al.* 2015a). *Baikalospongia i.profundalis* may have lost its ability to adapt to temperature stress due to its evolution in environment with stable temperature. In this context interspecific variability in the mechanisms of stress adaptation has been demonstrated in three endemic Lake Baikal sponge species (*B. bacillifera, B. i. intermedia* and *S. papyracea*, see Itskovich *et al.* 2015b) but additional ecological studies are needed to understand this observed bathymetric separation.

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