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PLANARIANS (PLATHELMINTHES, TRICLADIDA, DENDROCOELIDAE) OF BAIKAL ORIGIN IN THE BOGUCHANY RESERVOIR OF THE ANGARA RIVER

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Planarians of Baikal origin, subendemics, found in the Boguchany Reservoir, which is located more than 1000 km away from Lake Baikal, were described. The sampled specimens were referred to four genera. The genus *Bdellocephala* De Man 1875 was represented by the species *Bdellocephala angarensis* (Gerstfeldt 1858), *Archicotylus* Korotneff 1912 by the species *Archicotylus decoloratus* (Korotneff 1912), *Microarchicotylus* Timoshkin et Porfiriev 2015 by juvenile planarian specimens, and *Baikalobia* Kenk 1930 by the species *Baikalobia raddei* (Sabussov 1911). Of special interest is the finding of *B. raddei*, because this species has hitherto never been recorded in Lake Baikal. all previous reports having been confined to the mouth of Angara River. For many years, this latter fact was used to substantiate the hypothesis of a non-Baikal origin of all *Baikalobia* planarians. In this study, the phylogenetic analysis of *B. raddei*, as well as the planarians of the genera *Archicotylus*, *Microarchicotylus*, *Rimacephalus*, *Baikaloplana*, and *Bdellocephala*, was performed based on several regions of the ribosomal genes ITS1, 5.8S and ITS2. The morphological and physiological characteristics that enabled some Baikal planarians to leave the lake and get adapted to new ecological conditions is an area of further research.

Keywords: subendemics, rRNA, *Microarchicotylus* sp., *Archicotylus decoloratus*, *Bdellocephala angarensis*, *Baikalobia raddei*

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Freshwater triclads or planarians (Plathelminthes, Tricladida) is the characteristic component of the Baikal fauna. All Baikal planarians are endemic and collectively belong to the single family Dendrocoelidae, even though the water bodies around Lake Baikal are also inhabited by planarians of another family – Planariidae. This is a striking example of incompatibility of the Baikal fauna (Livanov, 1961; Porfirieva, 1977). Beyond the lake margins, certain species of Baikal planarians are known from the basins of the Angara and Yenisei Rivers (Rubtsov, 1928; Zabusova-Zhdanova, 1955; Golyshkina, 1963, 1966, 1969, 1970; Kozhov, 1972; Porfirieva, 1973, 1977). Previously, 12 planarian species of Baikal origin were described from the Angara River (Porfirieva, 1977). According to the recent biogeographic classification of aquatic and amphibiotic fauna of the Baikal region (Takhteev, 2009), all planarian species inhabiting the Boguchany Reservoir are Baikal subendemics, i.e., despite having been first described from Lake Baikal, they are not actually endemic to it.

The Baikal-Angara hydrobionts, including subendemic planarians, freely spread along the Angara River bed before the construction of the Angara chain of power plants and subsequent development of water reservoirs (Pleshanov, Takhteev, 2008). When the barriers emerged, the endemic hydrobionts of Baikal origin either disappeared or adjusted themselves to the new conditions (fast-flowing rivers – water reservoirs with nearly standing water) (Pleshanov, Takhteev, 2008), as well exemplified by the Boguchany Reservoir. This water reservoir appeared after the construction of the Boguchany power plant, which was first brought into operation in 2012, and lies 1400 km away from Lake Baikal along the Angara River area. In July 2016, a complex study of the Boguchany Reservoir, including phyto- and zoobenthos residing here, was performed as part of its biodiversity monitoring by Limnological Institute, Siberian Branch, Russian Academy of Sciences. The investigation of zoobenthic organisms also included the collection of flat worms, such as planarians. The sampled planarian specimens

Table 1. Planarian species used for phylogenetic analysis

Sampling site	Specimen designations	Sampling site
1. *Bdellocephala angarensis* (Gerstfeldt 1858)	Bd.a.B	Boguchany Reservoir
	Bd.a.11–13	Lake Baikal, Maloe More Strait
2. *B. melanocinerea* (Korotneff 1912)	Bd.m.1	Lake Baikal, Bol'shoi Ushkanii Island
3. *B. baikalensis* (Sabussov 1903)	Bd.b. Bd.b.1	Lake Baikal, Listvennichnyi Gulf
4. *Microarchicotylus stringulatus* (Korotneff 1912)	M.s.1–M.s.2	Lake Baikal, Listvennichnyi Gulf
	M.s.3	Lake Baikal, BPPP
5. *Rimacephalus pulvinar* (Grube 1872)	R.p.	Lake Baikal, Chivyrkuiskii Gulf
6. *Baikaloplana valida* (Korotneff 1912)	B.val.	Lake Baikal, Barguzinskii Gulf
7. *Archicotylus decoloratus* (Korotneff 1912)	A.d.1	Lake Baikal, Listvennichnyi Gulf
	A.d.2	Lake Baikal, Bol'shoi Ushkanii Island
8. *Baikalobia variegata* (Korotneff 1912)	B.v. B.v.1	Lake Baikal, Listvennichnyi Gulf
9. *B. copulatrix* (Korotneff 1912)	B.c.	Lake Baikal, Listvennichnyi Gulf
10. *B. raddei* (Sabussov 1911)	B.r.	Boguchany Reservoir
11. *B. elochinensis* (Porfiriev 2018)	E1	Lake Baikal, Cape Elokhin
12. *B. guttata* (Gerstfeldt 1858)	Zg1	Lake Baikal, Zagli-Nur
	EL1	Lake Baikal, Cape Elokhin
	PL1	Lake Baikal, Cape Berezovyi, Polygon
13. *Phagocata sibirica* (Sabussov 1903)	P.s.	Zhilishche Stream, Bol'shye Koty Village

were referred to the following four genera: *Bdellocephala*, *Archicotylus*, *Microarchicotylus*, and *Baikalobia*. All the genera, except *Bdellocephala*, are endemic to Lake Baikal based on their origin. *Bdellocephala* planarians are the only ones living in Palearctic water bodies.

The purpose of the research was to study the collected samples of triclads from the Boguchany Reservoir and to analyze the representatives of the Baikal and Boguchany fauna of planarians from the phylogenetic perspective.

MATERIALS AND METHODS

Planarians representing different species were collected by E.P. Zaytseva in July 2016 from the depth of 5–7 m in the Boguchany Reservoir. Histological sections were made following the standard protocol. The slides were stained according to Mallory (Romeis, 1953). Schematic reconstructions of the copulatory organ were performed using the serial photos obtained under the Axio Imager M2 Carl Zeiss microscope. The histological reconstructions were based on the medial sections of adult planarian specimens; the slides and samples are stored at the Department of Zoology and General Biology, Kazan Federal University (Table 1).

Phylogenetic analysis was carried out on Baikal planarians from six genera (12 species in total). The planarian specimen identified as a representative of the family Planariidae was taken as an outgroup. Species names and sampling sites are given in table. DNA extraction, PCR of the ITS1-5.8S-ITS2 ribosomal cluster region, and sequencing were performed as described previously (Porfiriev et al., 2018).

The nucleotide sequences were aligned using the MAFFT v. 7.42 (Katoh, Standley, 2013) offered by EMBL-EBI service (Madeira et al., 2019). The genetic distances were calculated in the MEGA v. 7 (Kumar et al., 2016) using the K2P model (Kimura, 1980); the phylogenetic relationships were analyzed with the help of NJ (Saitou, Nei, 1987) in the MEGA v. 7 and GTR + I + G model in the MrBayes v. 3.1.2 (Huelsenbeck, Ronquist, 2001). The significance of nodes in the tree was tested by posterior probability and bootstrap test (Felsenstein, 1985).

RESULTS

Genus ***Bdellocephala*** De Man 1875

M a t e r i a l: two series of sagittal sections (Bd1, Bd2), planarians sampled on July 7, 2016, sample № 8, Boguchany Reservoir, section 1, depth 5.8 m.

B. angarensis is the only representative of the genus *Bdellocephala* among the planarians collected from the Boguchany Reservoir. Since all the collected specimens were immature, they were identified based on

their external appearance. Subsequent phylogenetic analysis confirmed that these triclads belong to the species *B. angarensis* (see below). The species was earlier recorded in the Angara River near Irkutsk (Gerstfedt, 1858; Rubtsov, 1928), as well as in the area from the headwaters of the river up to the place where it flows into the Kat River (Golyshkina, 1970). Porfirieva (1977) described *B. angarensis* as the largest and most frequent planarian species in the Angara River. Zabusova-Zhdanova (1955) registered this species in the Yenisei River, 180 km above the mouth of the Angara River.

Genus ***Archicotylus*** Korotneff 1912

M a t e r i a l: three series of sagittal sections (dec1, dec2, dec3), planarians sampled on July 10, 2016, sample № 39, Boguchany Reservoir, section 4, depth 26 m.

Planarians of the genus *Archicotylus* were abundantly represented in the samples by the type species *A. decoloratus*. Based on their elongated and thin body, non-pigmented dorsal side, a pair of eyes, and copulatory organ structure, they were identified as *A. decoloratus*. The previous findings (Rubtsov, 1928) of this species were made in the Angara River near Irkutsk.

Genus ***Microarchicotylus*** Timoshkin et Porfiriev 2015

M a t e r i a l: two series of sagittal sections, planarians sampled on July 7, 2016, sample № 8, Boguchany Reservoir, section 1, depth 7 m, bottom substrate – gray sand without silt.

Based on the external features (dwarf forms, a pair of eyes, coloration of the dorsal side), these planarian forms were preliminary identified as belonging to the genus *Microarchicotylus*. Unfortunately, the samples contained only juvenile specimens, thereby making it impossible to identify them to the species level. The previous records of the type species of this genus, *Microarchicotylus stringulatus* (Korotneff 1912), were made in the Angara River near Irkutsk (Rubtsov, 1928).

Genus ***Baikalobia*** Kenk 1930

M a t e r i a l: four series of sagittal sections (cop1–cop4), planarians sampled on July 7, 2016, sample no. 7, Boguchany Reservoir, section 1, depth 5 m.

Based on the external (Fig. 1) and internal features, these triclads were identified as *B. raddei*. The dorsal body part of *B. raddei* is dark brown. The structure of the copulatory organ is characteristic of *B. raddei*: the canal of copulatory bursa runs alongside the copulatory organ; the latter has a single adenodactyl oriented posteriorly and slightly laterally, which is distinguishing for this species (Fig. 2). *B. raddei* was earlier found near the mouth of the Angara River, on stones in the offshore area and at small depths (Porfirieva, 1977). Therefore, our data suggest that the habitat range of this species is significantly larger.

Phylogenetic analysis

A total of 20 sequences were obtained for the ITS1-5.8S-ITS2 region (982–1217 bp). The sequences were deposited in the NCBI database under the accession numbers MK426771-MK426791. The analysis also included the sequences for *B. elochinensis* Porfiriev et Timoshkin 2018 (E1) and *B. guttata* (Gerstfeldt, 1858) (EL1) from our previous research (KY848669 and KY848669, respectively; Porfiriev et al., 2018). After the alignment, 903 positions were analyzed without indels; 401 positions were found to be informative. The genetic distances (*d*) within the non-endemic genus *Bdellocephala* and between the remaining endemic genera were in the range of 0.01–0.1 and 0.007–0.13, respectively. Therefore, the intraspecific differences in the genus *Bdellocephala* are generally at the same level as those between species of different genera of other Baikal planarians. If the sequences for *Bdellocephala* planarians are compared to the latter ones, the *d* values increase up to 0.35 on average. The genetic distances between *B. angarensis* planarians of Baikal and Boguchany origin were zero. *B. raddei* from the Boguchany Reservoir was closest to *B. copulatrix* ($d = 0.007$) among all Baikal planarians. Other representatives of this genus (*B. elochinensis*, *B. guttata*, and *B. variegata* (Korotneff 1912)) were more different from *B. raddei* ($d = 0.021$, 0.026, and 0.041, respectively).

The inferred phylogenetic tree is shown in Fig. 3 (Fig. 3). All the studied planarians fall into two distinct clusters – the genus *Bdellocephala* and other endemic genera. The genus *Bdellocephala* is represented in our study by three species: *B. melanocinerea* (Korotneff 1912) and *B. angarensis*, including a specimen from the Boguchany Reservoir, are closely related; *B. baikalensis* (Sabussov 1903) forms a separate branch of this cluster. Another cluster contains several clades with high support values – *M. stringulatus*; the clade of giant planarians, including *B. valida* (Korotneff 1912) and *R. pulvinar* (Grube 1872); *A. decoloratus*; and planarians of the genus *Baikalobia*. The relationships between these clades are not clear. In the clade of Baikalobia, *B. raddei* found in the Boguchany Reservoir is closely related to *B. copulatrix*.

DISCUSSION

The findings of Baikal planarians outside the lake margins have been reported by a number of researches (Rubtsov, 1928; Zabusova-Zhdanova, 1955; Golyshkina, 1963, 1966, 1969, 1970; Kozhov, 1972; Porfirieva, 1973, 1977) during the 20th century. From this perspective, planarian species belonging to the genera *Baikalobia*, *Archicotylus*, and *Microarchicotylus*, which

Fig. 1. External appearance of *Baikalobia raddei*: *A* – dorsal view, *B* – ventral view.

were registered in the Boguchany Reservoir, are of special interest.

The migration of these triclads can be explained by the fact that the hydrochemical regime of the Angara River in the past was generally the same as that of Lake Baikal (low water temperatures, high concentrations of dissolved oxygen). The geological age of the Angara flow is estimated around 60000 years (Kononov, Mats, 1986): it can be taken as the time when the above-mentioned planarian species of Baikal origin must have distributed downstream along the river bed.

Particular attention should be paid to *B. raddei*, for which the morphological (Figs. 1, 2) and molecular (Fig. 3) data were obtained. *B. raddei* was first described by Zabusov (1911) from G.I. Radde's collection. However, the exact area of finding was not specified. It was only mentioned that the specimens were sampled in Eastern Siberia. Later, Porfirieva (1977) recorded this species near the headwaters of the Angara River, where it occurred regularly until the late 1960s (the latest sections of *B. raddei* are stored in the collection of the Zoological Museum of Kazan Federal University, the specimens were sampled in the mouth of the Angara River on June 3, 1969 by R. Mansurov). The problem of the origin of *B. raddei* is controversial. It has been still widely discussed whether *B. raddei* first appeared in the lake and then left it or its ancestor evolved in the river system after the migration. N.A. Porfirieva assumed that the ancestral form of all *Baikalobia* planarians resembled *B. raddei*, had a single adenodactyl (similarly to the modern species), and settled in Lake Baikal separately from other Baikal triclads (Porfirieva, 1977). Our molecular data suggest that *B. raddei* is similar to *B. copulatrix* with the number of adenodactyls ranging from 7 to 9, being unrelated to the ancestral form, from which all *Baikalobia* planarians were later derived (Fig. 3). Previously, it was revealed that *Baikalobia* planarians evolved from adenodactyl-deprived den-

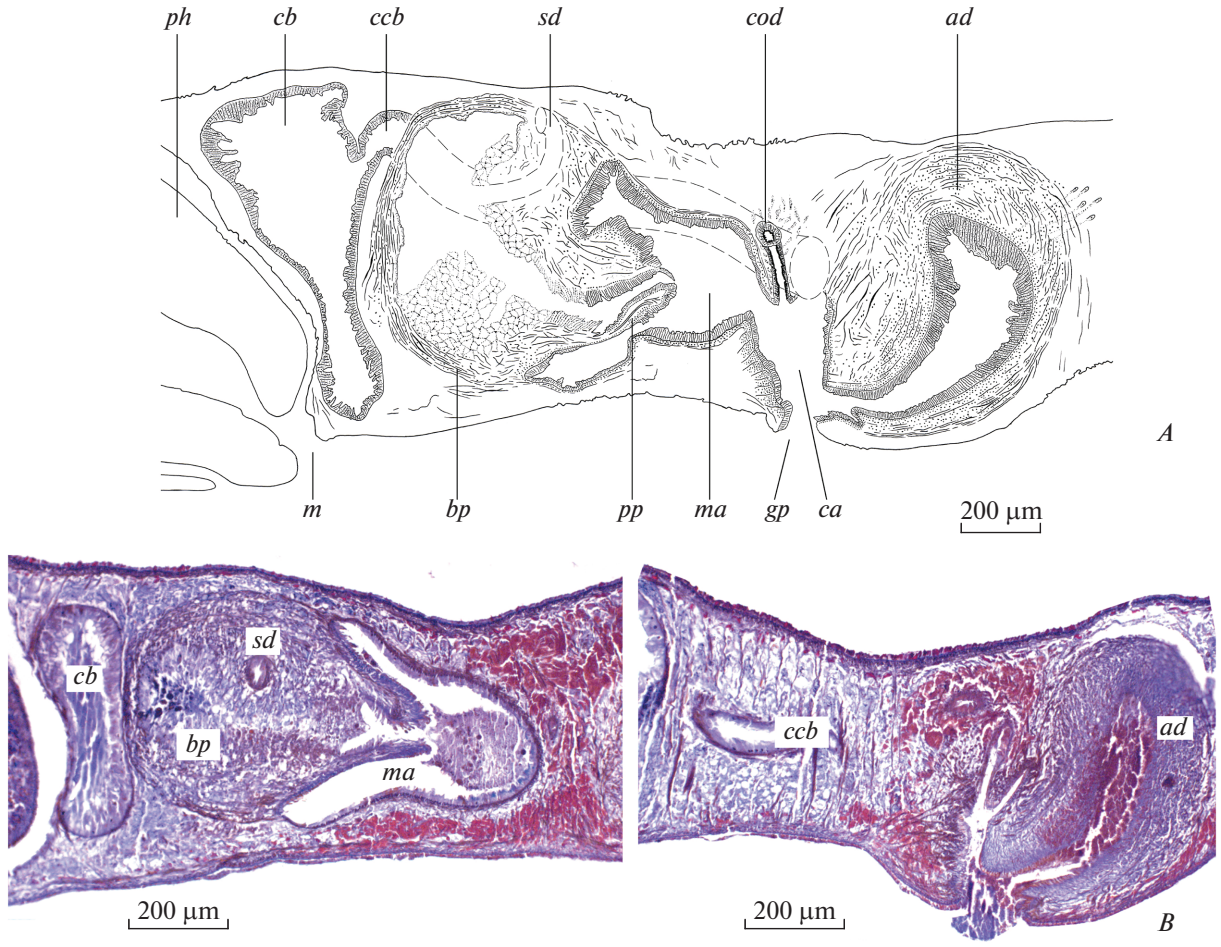

Fig. 2. *Baikalobia raddei*: *A* – copulatory organ reconstruction, *B* – a series of sagittal sections through copulatory organ.

drocoelids inside Lake Baikal (Kuznedelov et al., 1996).

Bdellocephala representatives inhabiting the same water body are widespread in the entire Palearctic region. The fact that the ITS1-5.8S-ITS2 sequences of *B. angarensis* of Baikal and Boguchany origin match each other perfectly (Fig. 3) can be attributed to the conservatism of the analyzed region of the ribosomal cluster, because there is no evidence of intraspecific polymorphism within it. Another reason can be the young age of *B. angarensis* population from the Boguchany Reservoir. The natural migration of *B. angarensis* from Lake Baikal along the Angara River bed probably ended after the Irkutsk HPS was commissioned in 1956.

As for the evolution of other Baikal planarians, our phylogenetic reconstruction based on the ITS1-5.8S-ITS2 region is generally consistent with that one for the short 18S rRNA fragment (Kuznedelov et al., 1996, 2000) and the actin gene region (Koroleva et al., 2013). Two large clusters can be distinguished – *Bdellocephala* (cluster I) and other Baikal planarians (cluster II), among which the above-described *Baikalobia* form a separately evolving clade (Fig. 3). The highest similarity was observed between *B. copulatrix*, *B. raddei, B. elochinensis*, and *B. guttata*, whereas *B. variegata* holds a basal position in this genus. The giant *B. valida* (the largest freshwater planarian in the world reaching 20–40 cm in length (Timoshkin, 1994)) and *R. pulvinar* planarians living in deep waters nested in a separate clade close to other small planarians of cluster II, which again confirms the hypothesis that giant planarians originated from small-sized littoral forms (Porfirieva, 1977; Timoshkin, 1994). Some giant planarians have creeping folds and numerous compound suckers; they are also characterized by a more complex structure of the muscular-glandular sac and copulatory organ (Porfirieva, 1977; Timoshkin, 1994). It is interesting that *M. stringulatus*, which is characterized by "dwarfness" (5–6 mm in length), bright coloration, and specific structure of the copulatory organ (Porfiriev, Timoshkin, 2016), resides in the same cluster (Fig. 3). Such diverse morphological features could have occurred in the process of evolution as result of

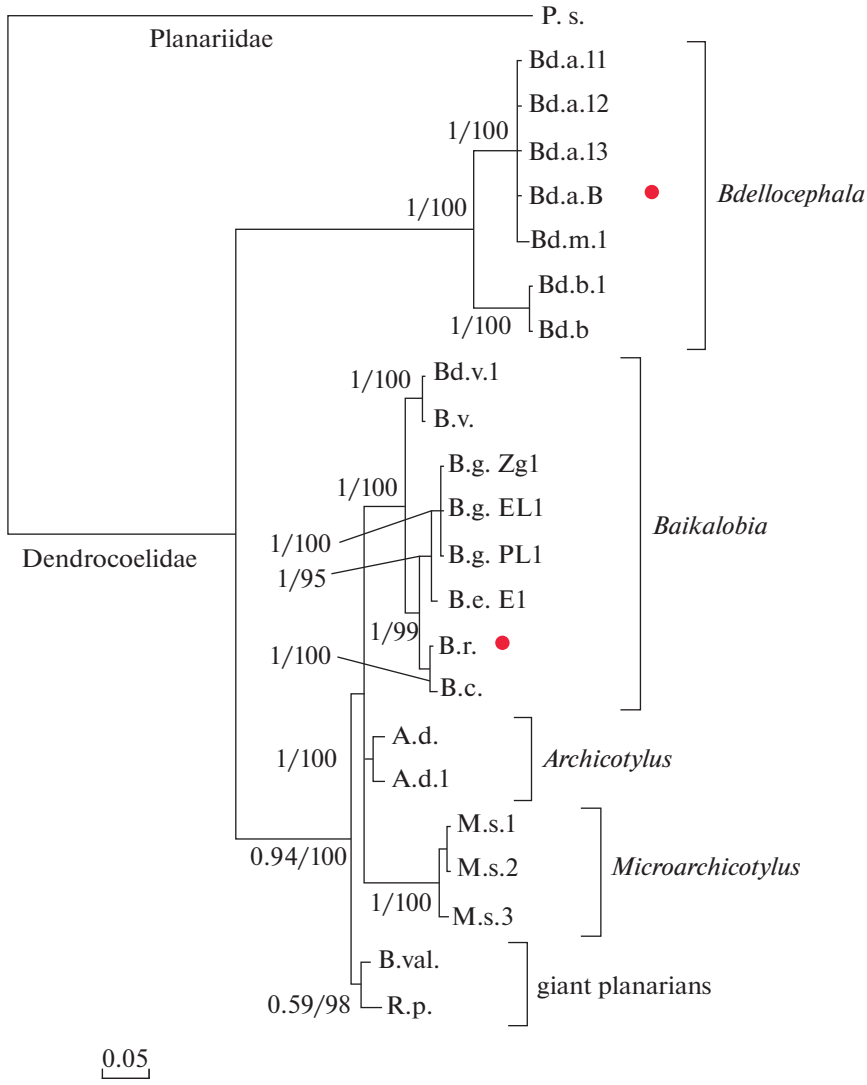

Fig. 3. Phylogenetic tree of Baikal planarians reconstructed from the sequences of the ribosomal cluster ITS1-5.8S-ITS2 (903 bp). The individuals found in the Boguchansky reservoir are marked with a circle. The nodes of the tree indicate the values of a posteriori probability (MrBayes v.3.1.2) and bootstrap test (MEGA 7). The nodes without values have low support. The scale bar shows genetic distances. Full names of species are given in Table 1.

adaptive or non-adaptive radiation (Czekanski-Moir, Rundell, 2019).

Since the morphological evolution of Baikal planarians proceeded in different directions, new planarian species – capable of expanding their habitat range beyond the lake – emerged, as seen in the case with the subendemics of Baikal origin. Despite the construction of the Angara chain of power plants, a barrier hampering the distribution of Baikal endemics downstream of the river, the populations of subendemics from Lake Baikal are still resitered in the Boguchany Reservoir.

Abbreviations in figures: *ad* – adenodactyl, *bp* – bulb of penis, *ca* – common atrium, *cb* – copulatory bursa, *ccb* – canal of copulatory bursa, *cod* – common oviduct, *gp* – gonopore, *m* – mouth, *ma* – male atrium, *ph* – pharynx, *pp* – penis papilla, *sd* – seminal duct.

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ПЛАНАРИИ (PLATHELMINTHES, TRICLADIDA, DENDROCOELIDAE) БАЙКАЛЬСКОГО ПРОИСХОЖДЕНИЯ В БОГУЧАНСКОМ ВОДОХРАНИЛИЩЕ РЕКИ АНГАРА

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Описаны планарии байкальского происхождения. Субэндемики обнаружены в Богучанском водохранилище, расположенном более чем в 1000 км от озера Байкал. Отобранные образцы были отнесены к четырем родам. Род *Bdellocephala* De Man 1875 был представлен видом *Bdellocephala angarensis* (Gerstfeldt 1858), род *Archicotylus* Korotneff 1912 – видом *Archicotylus decoloratus* (Korotneff 1912), род *Microarchicotylus* Timoshkin et Porfiriev 2015 – ювенильными экземплярами планарий, род *Baikalobia* Kenk 1930 – видом *Baikalobia raddei* (Sabussov 1911). Особый интерес представляет находка *B. raddei*, поскольку этот вид никогда ранее не был обнаружен в озере Байкал, а все предыдущие места находок были ограничены устьем реки Ангара. В течение многих лет последний факт использовался для обоснования гипотезы о небайкальском происхождении всех байкальских планарий. В этом исследовании филогенетический анализ *B. raddei* и планарий родов *Archicotylus*, *Microarchicotylus*, *Rimacephalus*, *Baikaloplana* и *Bdellocephala* был выполнен на основе нескольких областей рибосомных генов (ITS1, 5.8S, ITS2). Морфологические и физиологические характеристики, позволившие некоторым байкальским планариям покинуть озеро и адаптироваться к новым экологическим условиям, являются областью дальнейших исследований.

Ключевые слова: субэндемики, рРНК, *Microarchicotylus* sp., *Archicotylus decoloratus*, *Bdellocephala angarensis*, *Baikalobia raddei*