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Phylogeny of the freshwater lineages within the phyla Actinobacteria (Overview)

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ABSTRACT. This review presents molecular classification of freshwater Actinobacteria based on the phylogeny of the 16S rRNA gene. We show the classification of the entire phylum Actinobacteria and the taxonomic rank of freshwater lineages of Actinobacteria within this phylum. The discovery history of different groups of freshwater Actinobacteria is considered. We have systematized the information about the phylogeny of cultivated and uncultivated freshwater Actinobacteria and give their brief description. Data is provided on freshwater groups of Actinobacteria found in different ecotopes of Lake Baikal.

Keywords: 16S rRNA gene-based phylogeny, phylum Actinobacteria, freshwater lineages of Actinobacteria, Lake Baikal

1. Introduction

Phylum Actinobacteria is one of the largest taxonomic units in the domain Bacteria. It consists of gram-positive bacteria with a high G+C DNA content (from 51 to 70%) (Ventura et al., 2007). Actinobacteria have a diverse morphology, from coccoid (*Micrococcus spp.*), rod-coccoid (*Arthrobacter spp.*) forms to fragmenting hyphae (*Nocardia spp.*) and highly differentiated branched mycelium (*Streptomyces spp.*). This phylum is widespread, especially in soil, and it includes saprophytes (inhabitants of soil, vegetation, the gastrointestinal tract of animals and humans), symbionts and pathogens (Ventura et al., 2007). Actinobacteria are biotechnologically important producers of various biologically active substances that are widely used in industry, medicine and agriculture (Barka et al., 2016).

It has been long believed that actinobacteria isolated from water are of soil origin, and they do not develop in the aquatic environment, having inactive state in the form of spores (Goodfellow and Williams, 1983). The molecular methods independent of cultivation, mainly such as fluorescent cell labelling and PCR analysis of 16S rRNA gene sequences, revealed that uncultivated members of Actinobacteria are numerous and cosmopolitan inhabitants of freshwater ecosystems, constituting the dominant fraction of heterotrophic bacterioplankton (Glöckner et al., 2000; Zwart et al., 2002; Warnecke et al., 2004; Allgaier and Grossart, 2006; Newton et al., 2011). After evidence of the fundamental difference of freshwater bacterioplankton from soil and marine bacteria has accumulated, Actinobacteria are under the scrutiny of researchers as one of the main groups of the freshwater bacterial community (Methe´ et al., 1998; Rappe´ et al., 1999; Glöckner et al., 2000; Zwart et al., 2002).

This overview aimed to systematize the taxonomic data on uncultivated and cultivated freshwater Actinobacteria obtained from the phylogeny of the 16S rRNA gene.

2.1. Molecular classification of the phylum Actinobacteria

The phylogeny of the 16S rRNA gene divides Actinobacteria into six classes, such as Actinobacteria, Acidimicrobiia, Coriobacteriia, Nitriliruptoria, Rubrobacteria, and Thermoleophilia (Ludwig et al., 2012). According to this classification, the largest class Actinobacteria includes 15 orders, and other classes consist of one-two orders.

In the phylogenetic tree, there are two large clades within the class Actinobacteria. The first clade includes the orders Actinopolysporales, Corynebacteriales, Glycomycetales, Jiangellales, Micromonosporales, Propionibacteriales, and Pseudonocardiales. The second clade includes the orders Actinomycetales, Bifidobacteriales, Kineosporiales, and Micrococcales. The orders Catenulisporales, Streptomycetales, Streptosporangiales, and Frankiales are distinct genetically separated branches within the class Actinobacteria (Ludwig et al., 2012). Analysis of 100 whole-genome sequences of the main families and orders belonging to the class Actinobacteria divided the

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order Frankiales into four monophyletic orders, such as Frankiales, Geodermatophilales, Acidothermales, and Nakamurellales (Sen et al., 2014). The order Micrococcales is also polyphyletic and requires additional revision, but officially this cannot be done due to the insufficient number of whole genomes. Thus, at present, the class Actinobacteria includes 18 recovered orders.

2.2. Discovery of freshwater Actinobacteria

Uncultivated freshwater Actinobacteria were first discovered in 1997 in the Adirondack Mountain Lakes of the USA (Hiorns et al., 1997). In the phylogenetic tree, they formed an ACK-4 cluster that is separate from other known cultivated actinobacteria. This group of Actinobacteria called hgcI was detected in great numbers in lakes Fuchskuhle (Germany) and Gossenkollesee (Austria) as well as in Lake Baikal (Russia) (Glöckner et al., 2000).

Zwart et al. (2002) showed that freshwater Actinobacteria are autochthonous and cosmopolitan, and he identified five proposed clusters typical of freshwater uncultivated Actinobacteria, which were combined into two large monophyletic groups. The first group, ACK-4 (Hiorns et al., 1997) or hgcI (Glöckner et al., 2000), included clusters ACK-M1 and Sta2-30 (Zwart et al., 2002). The second group of Actinobacteria called C111 (Urbach et al., 2001) included clusters Urk0-14, CL500-29 and Med0-06 (Zwart et al., 2002).

As a rule, the proposed cluster should contain at least two sequences that have at least 95% similarity and inhabit deep zones of at least two freshwater bodies. According to these conditions, the Luna cluster was the next sixth proposed cluster belonging to the typical freshwater bacteria (Hahn et al., 2003). The members of this cluster were widespread in various freshwater ecosystems of Europe, Asia and North America, and they contained cultivated members having ultramicrobacterial cell sizes (less than 0.1 μm^3) even when grown in a very rich medium. The isolated pure cultures had cells in the shape of a vibrio.

2.3. Phylogenetic lineages of freshwater Actinobacteria

Warnecke et al. (2004) first proposed a unified classification of freshwater Actinobacteria. Actinobacterial sequences obtained from various freshwater bodies were grouped into four phylogenetic clusters: acI, acII, acIII, and acIV. These phylotypes were stable in different tree reconstructions (neighbour joining, maximum parsimony and maximum likelihood), and they were separated from the soil and marine lineages of Actinobacteria.

The acI and acII clusters were typical autochthonous freshwater Actinobacteria, and the acIV cluster contained only sequences of uncultivated Actinobacteria from freshwater bodies, marine sediments and soil (Warnecke et al., 2004). The acI was separated into three subclusters: acI-A corresponding to the ACK-M1 cluster, acI-B corresponding to Sta2-30 (Zwart et al., 2002) and a new acI-C subcluster (Warnecke et al., 2004). In the acII cluster, the subclusters acII-B and acII-D were identified, corresponding to Luna-1 and Luna-2 (Hahn et al., 2003) and two new groups: acII-A (meromictic lake Sælenvannet, Norway) and acII-C (dystrophic lake Fuchskuhle, eutrophied water body in the Czech Republic and hot springs in New Zealand) (Warnecke et al., 2004). Sequences in the acIII cluster were obtained from chemocline of Lake Sælenvannet (Norway) and corresponded to the sequences of the cluster 2 identified in water of hypersaline soda lake (Humayoun et al., 2003). The acIV cluster was divided into the acIV-A subcluster corresponding to CL500-29 (Zwart et al., 2002) and the acIV-B subcluster (Warnecke et al., 2004).

Newton et al. (2011) supplemented and extended the previous classification by using his data and material accumulated in the databases. Nine freshwater lineages (acI, acTH1, acSTL, Luna1, acIII, Luna3, acTH2, acIV, and acV), including more than 40 clusters, were isolated in the phylum Actinobacteria. Phylogenetic lineages acI, acTH1, acSTL, Luna1, acIII, Luna3, and acTH2 belonged to the orders Actinomycetales and Micrococcales (class Actinobacteria), and the lineages acIV and acV – to the order Acidimicrobiales (class Acidimicrobiia) (Newton et al., 2011; Ludwig et al., 2012; Ghai et al., 2014). The 16S rRNA phylogeny of some freshwater actinobacteria is shown in the figure borrowed from Ghai et al. (2013).

2.4. Characterisation of uncultivated and cultivated representatives of phylogenetic lineages of freshwater Actinobacteria

The abundant and widespread actinobacterial groups in freshwater bodies are acI, acIV and Luna1 (Humbert et al., 2009; Newton et al., 2011; Parveen et al., 2011; Martinez-Garcia et al., 2012).

According to the classification of Newton et al. (2011), acI contains 13 clusters. One of the clusters includes ‘*Candidatus* Planktophila limnetica’, being the first proposed species of Actinobacteria, which was obtained in the mixed culture (Jezbera et al., 2009). Recently, pure cultures of Actinobacteria belonging to acI, which are related to the genera ‘*Candidatus* Planktophila’ and ‘*Candidatus* Nanopelagicus’, were obtained (Kang et al., 2017; Neuenschwander et al., 2018). These two genera formed a new family ‘*Ca.* Nanopelagicaceae’ as well as a new order ‘*Ca.* Nanopelagicales’ that formed in the phylogenetic tree a stable related group together with the orders Streptomycetales, Streptosporangiales and Acidothermales (Neuenschwander et al., 2018). ‘*Candidatus*’ status is given to genera and species until none of the freshwater groups is represented by a taxon with a reliably published name (Hahn, 2009). The genus ‘*Candidatus* Planktophila’ includes six species (‘*Ca.* Planktophila limnetica’, ‘*Ca.* Planktophila dulcis’, ‘*Ca.* Planktophila sulfonica’, ‘*Ca.* Planktophila versatilis’, ‘*Ca.* Planktophila lacus’, and ‘*Ca.* Planktophila vernalis’),

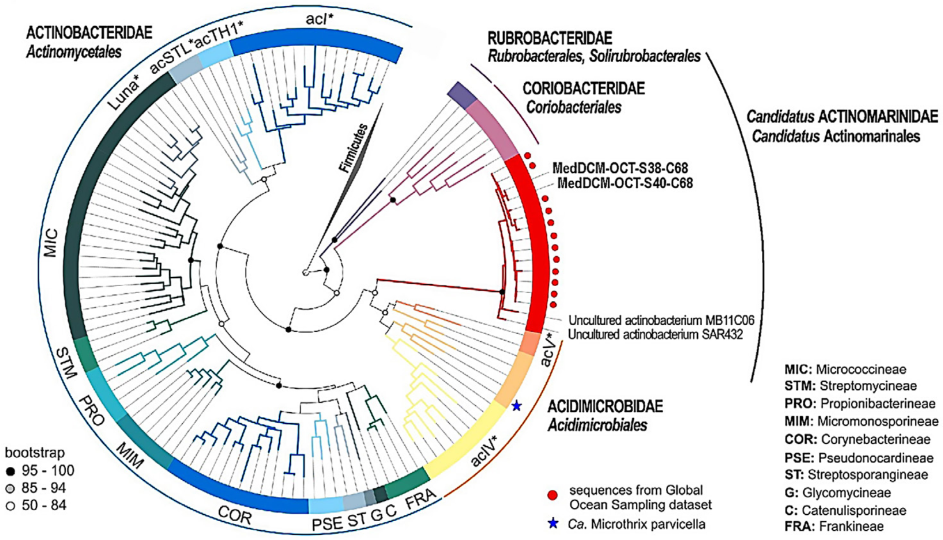

Fig. 16S rRNA phylogeny of some freshwater lineages in the context of the entire Actinobacteria phylum, with Firmicutes as the outgroup. Actinobacterial sub-classes are in bold uppercase and orders in bold italics. Sub-orders are shown in different colors in the tree and labeled (key is shown on bottom right). Freshwater actinobacterial clades are marked with black asterisk. Bootstrap values for all major branches are indicated by colored circles (see key bottom left) (Ghai et al., 2013).

and the genus *Candidatus* Nanopelagicus' – three species ('*Ca.* Nanopelagicus limnes', '*Ca.* Nanopelagicus hibericus'and '*Ca.* Nanopelagicus abundans'). The strains isolated from Lake Soyang (Korea) are two more new species: '*Ca.* Planktophila rubra' and '*Ca.* Planktophila aquatilis' (Kim et al., 2019).

The isolated strains of the genus '*Ca.* Planktophila' and the genus '*Ca.* Nanopelagicus' are aerobic free-living motionless photoheteotrophs. They have a very small cell size (from 0.012 to 0.061 μm3), streamlined genome (from 1.16 to 1.46 Mb), genome with low G + C content (less than 50%), and carry genes for actinorhodopsins (Kang et al., 2017; Neuenschwander et al., 2018; Kim et al., 2019).

The acIV lineage is divided into four monophyletic clusters (acIV-A, acIV-B, acIV-C, and acIV-D) and six subclusters (Newton et al., 2011). It consists of uncultivated actinobacterial sequences obtained from various environments and includes cultivated strains of Actinobacteria, such as the strain *Ilumatobacter fluminis* YM22-133 isolated from the sediments of the estuary of the Kuiragawa River (Japan) (Matsumoto et al., 2009) and the strain *Aquihabitans daechungensis* CH22-21 (family *Iamiaceae)* isolated from the water reservoir Daechung (Korea) (Jin et al., 2013). These strains are aerobic free-living motionless chemoorganotrophs with a high G + C DNA content (68-72%).

Analysis of the metagenomic sequences obtained from various lakes and estuaries indicated that the genomes acI and acIV have a low G + C DNA content, from 42 to 50% (Ghai et al., 2012). Although Actinobacteria are characterized as organisms with a high of G + C DNA content, both types of Actinobacteria together inhabit freshwater bodies.

The Luna1 lineage consists of four clusters, one of which, Luna1-A2, is the most numerous in the database of sequences (Hahn, 2009). New species of the isolated Actinobacteria belonging to this lineage and having '*Candidatus*' status formed two Luna clusters. The name Luna originates from the name of Lake Mondsee (Moon Lake, Austria), from which the first strains of freshwater Actinobacteria with selenoid morphology (vibrio) were isolated (Hahn et al., 2003; Newton et al., 2011).

The first cluster Luna-1 (the Luna1 lineage) included strains with red pigments, such as '*Ca.* Rhodoluna lacicola', '*Ca.* Planktoluna difficilis', '*Ca.* Aquiluna rubra', '*Ca.* Rhodoluna limnophila', '*Ca.* Rhodoluna planktonica', and '*Ca.* Limnoluna rubra', as well as one strain with yellow pigment, '*Ca.* Flaviluna lacus' (Hahn, 2009). Based on phylogenetic, phenotypic and chemotaxonomic features, the obtained '*Ca.* Rhodoluna lacicola' strain is a new species *Rhodoluna lacicola* of the new genus *Rhodoluna* within the family Microbacteriaceae and order Micrococcales (Hahn et al., 2014). Another IMCC13023 strain belonging to '*Ca.* Aquiluna rubra' was first isolated from seawater; then the similar 16S rRNA gene sequences with 99% homology were also found in freshwater bodies (Kang et al., 2012). Unlike other known members of the family Microbacteriaceae, the strains *Rhodoluna lacicola* and IMCC1302 have ultra-micro sizes, a reduced genome (1.43 and 1.359 Mb, respectively) and low content of GC base pairs in DNA (51.5-51.7%) (Kang et al., 2012; Hahn et al., 2014). The remaining strains from the Luna-1 cluster had the *Candidatus* status because they were obtained only in mixed culture with other non-actinobacterial strains (Hahn, 2009).

The second cluster Luna-2 (the acIII lineage) included only strains with yellow pigments, which had an unknown species status (Hahn et al., 2003).

Other lineages of freshwater Actinobacteria are minor and found only in some water bodies. The acV lineage is associated with bacteria isolated from soil, and it clusters with the soil group SoilII + III. The acSTL, acTH1 and acTH2 lineages do not have cultivated representatives and consist of clones obtained from the water of Lake Stechlin in Germany (acSTL) and Lake Taihu in China (acTH1 and acTH2) (Wu et al., 2007; Newton et al., 2011). Luna3 is closely related to other Luna groups but still also consists of uncultivated representatives.

In addition to the above, new groups of photoheterotrophic planktonic Actinobacteria were identified within the already known freshwater lineages. These Actinobacteria had a reduced small genome (1.16-1.32 Mb) and different G+C content (from 44 to 61%) as well as possessed proteorhodopsins and actinorhodopsins (Ghai et al., 2014). These are the acMicro group in the acIII lineage (order Actinomycetales) and the acAcidi group in the order Acidimicrobiales.

2.5. Phylogenetic groups of freshwater Actinobacteria in Lake Baikal

In Lake Baikal, phylum Actinobacteria is one of the dominant groups (Parfenova et al., 2013; Zakharova et al., 2013; Gladkikh et al., 2014; Krasnopeev et al., 2016; Kurilkina et al., 2016; Bashenkhaeva et al., 2017; Cabello-Yeves et al., 2018; Kulakova et al., 2018), comprising approximately 30% of bacterioplankton (Parfenova et al., 2013; Bashenkhaeva et al., 2015; Mikhailov et al., 2015) and during spring blooming of phytoplankton – up to 57% of the bacterial community in the water column (Mikhailov et al., 2019), up to 14% of the microbial community of the endemic sponge *Lubomirskia baikalensis* (Gladkikh et al., 2014) and up to 44% of bacterial community in the lake sediments (Zemskaya et al., 2015).

Glöckner (2000) first discovered freshwater Actinobacteria in Lake Baikal. Molecular approach enabled identifying in the water column the species *Planktophila limnetica* (acI) typical of bacterioplankton (Parfenova et al., 2013; Gladkikh et al., 2014), the orders Actinomycetales and Acidimicrobiales as well as other unclassified Actinobacteria (Mikhailov et al., 2015; 2019). The genus *Planktophila* and the order Acidimicrobiales were found in all species of healthy Baikal sponges (Seo et al., 2016), and the representatives of the genera *Ilumatobacter* and *Iamia* (acIV) were identified in diseased sponges *L. baicalensis* and *Baicalospongia intermedia* (Krasnopeev et al., 2016). In the sub-ice waters, there were Actinobacteria of the genus *Ilumatobacter* (acIV) (Bashenkhaeva et al., 2015), freshwater acI ones, the acAcidi group, the family Acidimicrobiaceae and other unclassified Actinobacteria (Bashenkhaeva et al., 2017; Cabello-Yeves et al., 2018). Actinobacterial sequences of the genus *Ilumatobacter* were also detected in the deep near-bottom layers in the lake (Zakharova et al., 2013). In gas- and oil-bearing sediments, Actinobacteria belonging to the acI (family Sporichteaceae, hgcI group) and acIV (family Acidimicrobiaceae) were identified (Zemskaya et al., 2015).

To date, no strain of the known freshwater lineages of Actinobacteria has been isolated from Lake Baikal.

3. Conclusion

Therefore, over two past decades since the discovery of the first freshwater Actinobacteria, nine monophyletic freshwater lineages belonging to the classes Actinobacteria and Acidimicrobia within the phylum Actinobacteria have been identified. Pure and mixed cultures of Actinobacteria belonging to different freshwater lineages, such as acI, acIV, Luna1, and acIII, have been obtained. Another new order, '*Ca.* Nanopelagicales', within the class Actinobacteria has been proposed. The presented unified classification is not final and is being supplemented. Further studies to identify new phylogenetic groups of actinobacteria in freshwater environments and to isolate and cultivate new previously uncultivated representatives of freshwater Actinobacteria are promising, necessary and important because they form the basis for subsequent ecological research on the role of freshwater Actinobacteria in the natural habitat.

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