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EXPERIMENTAL ARTICLES

Spirosoma xylofaga sp. nov., an Oligotrophic Pleomorphic Bacterium from a Myco-Bacterial Community of Freshwater Ecosystems

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Abstract—A novel aerobic bacterial strain Z-0088 was assigned to the genus *Spirosoma* on the basis of 16S rRNA analysis; it was isolated from a bacterial community of moderately acidic (pH 5.0) dystrophic, slightly humified water formed by xylotrophic fungi grown on decaying spruce wood. The cells are nonmotile, gram-negative, straight or curved rods, 0.5–1.5 × 1.0–6.0 μm; they may also be toroidal. The cells are usually single but can form spiral filaments containing from 4 to 13 coils; their reproduction is by division. Strain Z-0088 is an organoheterotroph utilizing xylan, inulin, xylose, sucrose, and *N*-acetylglucosamine as organic growth substrates. The bacterium is oligotrophic (the optimum substrate concentration is 0.5 g/L). It is characterized by high sensitivity to NaCl concentration; growth was completely suppressed at 1% NaCl. The strain grows in a pH range of 3.8–7.5 with the optimum at pH 5.5–6.5. The temperature range for growth was 13–35°C with the optimum at 28°C. The DNA G+C base content was 50.2 mol %. The ecophysiological features of strain Z-0088, such as oligotrophic, mesophilic, moderate acidophilic properties, and sensitivity to NaCl, support its designation as a representative of ombrophilic dissipotrophs. The strain is assigned to a novel species *Spirosoma xylofaga* sp. nov.

Keywords: xylotrophic community, oligotrophic bacteria, dissipotrophs, dystrophic waters, acid tolerance, *Spirosoma xylofaga* sp. nov.

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A bacterium of specific morphology with ring- or horseshoe-shaped cells was first isolated in 1887 [1]. It was described as *Spirosoma* Migula in 1894, but was subsequently lost. A bacterium with the same properties was isolated and described in 1978 [2]. In 1984, the genus *Spirosoma* was assigned to the family *Spirosomaceae*, which included four genera: *Spirosoma, Flectobacillus, Runella*, and *Cyclobacterium* [3]. At present, the genus *Spirosoma* is included into the family *Flexibacteriaceae* (order *Sphingobacteriales*, class *Sphingobacteria*, type *Bacteroidetes*), together with the genera *Flectobacillus, Runella, Flexibacter, Meniscus, Microscilla, Sporocytophaga, Dyadobacter, Hymenobacter, Cytophaga*, and *Cyclobacterium*. [4]. All representatives of the genus *Spirosoma* are typical saprotrophs inhabiting water and silt of freshwater habitats, and rarely occurring in soils.

The goal of the present work was to study the ecophysiological features of strain Z-0088, a representative of a bacterial community from dystrophic, slightly humified water, and to designate the taxonomic position of a novel bacterium.

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MATERIALS AND METHODS

Subject of study and source of isolation. Strain Z-0088 was isolated from dystrophic, moderately acidic (pH 5.0) water of a microlysimeter, in which spruce wood was decayed by a community of xylotrophic fungi [5].

Medium composition and cultivation conditions. Strain Z-0088 was isolated on mineral medium containing Hutner's basal salt solution, 5 mL/L [5]; culture liquid after fungal growth, 10 mL/L; and yeast extract as a growth factor, 0.05 g/L (HCY medium). The culture liquid was obtained by cultivating *Aspergillus ustus, Trichoderma harzianum, Cladosporium* sp., *Penicillium* sp., and *Paecilomyces* sp. in Czapek mineral medium with xylose (2 g/L) as a substrate. Pure culture of strain Z-0088 was isolated from a dystrophic water sample by repeated culture plating onto solid medium (2% agar). To inhibit fungal growth during the isolation, nystatin (500000 U/L) was used.

Pure culture was maintained in liquid HCY medium containing Hutner's basal salt solution (20 mL/L), a vitamin mixture [5], xylose (0.5 g/L) as a substrate, and yeast extract (0.01 g/L). The medium conductivity was 930 μS.

Microscopic investigations. Cell morphology was studied under an Amplival phase contrast microscope (Carl Zeiss, Germany) as well as under a JEM-100C electron microscope (JEOL, Japan); for electron microscopy, negatively stained preparations were used. The cells were stained with 1% uranyl acetate. To obtain ultrathin sections, the cells were fixed with glutaraldehyde, postfixed with osmic tetroxide in cacodylate buffer, and embedded in epoxide resins. Ultrathin sections were obtained with an LKB ultramicrotome (BROMMA, Sweden), stained with lead citrate, and then additionally contrasted with a 3% aqueous solution of uranyl acetate.

Determination of ecophysiological characteristics. The following growth substrates were tested: sugars (arabinose, xylose, glucose, fructose, galactose, mannose, lactose, maltose, sucrose, raffinose, xylan, cellobiose, rhamnose, and trehalose), alcohols (arabitol, glycerol, sorbitol, and mannitol), salts of organic acids (formate, acetate, butyrate, propionate, pyruvate, fumarate, succinate, oxalate, oxaloacetate, citrate, malate, and benzoate), primary alcohols (methanol and ethanol), amino acids (methylalanine, glutamate, leucine, cysteine, and aspartate), and methylamines.

The growth of bacteria was followed by measuring optical density (OD_{600}) of the cell suspension on a UNICO 2100 spectrophotometer (UNICO, United States) and by determination of respiration rate by monitoring the changes in carbon dioxide concentration in experimental bottles with the use of an INFRALIT-4 infrared CO_2 analyzer (GUNKALOR-DESAU, Germany).

The growth of bacteria was studied within a pH range from 3.0 to 8.0; pH was adjusted to 3.0–4.8 by acidifying the basal medium with 0.1 N HCl; pH values of 4.8–8.0 were obtained by addition of 0.05 M solutions of Na_2HPO_4 and KH_2PO_4 to the medium. The pH was measured on an Expert 001 pH/ion meter (Ekoniks-expert, Russia).

Growth temperature was studied in the range from 2 to 42°C.

The growth dependence on NaCl was determined in the concentration range of 0.2–30.0 g/L.

Electrical conductivity of the medium was measured with an H1 8733 conductometer (HANNA Instrument Srl., Italy)

The affinity of the pigment from strain Z-0088 to the group of carotenoids or xanthophylls was determined according to the described method [6, 7].

Catalase activity was assayed by monitoring the formation of oxygen bubbles on addition of a 3% hydrogen peroxide solution to the cells; the presence of oxidase was detected by changes in the colony pigmentation on addition of the REF-55635 reagent (BioMerieux, France).

The vitamin requirements of the strain were determined in the HCY medium containing a vitamin mixture [5]; the vitamin-free medium was used as the control.

The fatty acid composition of the lipids was determined by chromatographic analysis of the biomass of the the exponential-phase culture grown under optimal conditions using a Sherlok Microbial Identification System (MIDI, Inc., Newark, United States) according to the method [8]. Fatty acids were identified by their mass spectra on an AT-5971 SMART device (Agilent Technologies, United States).

Antibiotic resistance of the strain was assessed with the use of the test discs (Becton Dickinson and Co., United States).

Molecular genetic studies. DNA extraction was performed by the modified method of alkaline DNA isolation according to Birnboim and Doly [9] and Wizard-technology (Promega, United States). PCR amplification of the 16S rRNA gene fragments was carried out using the universal primer system [10]; amplification of the full-size copy of the 16S rRNA gene was performed using a pair of primers (8-27f)–1492r. Sequencing of the amplification products was carried out by the Sanger method [11] using a Big Dye Terminator v. 3.1 reagent kit (Applied Biosystems Inc., United States) on an ABI PRIZM 3730 analyzer (Applied Biosystems Inc., United States) in accordance with the manufacturer's instructions. Primary comparative analysis of the de novo obtained sequences with those deposited in the GenBank database was performed with the NCBI Blast program (http://www.ncbi.nlm.nih.gov/blast). The sequence editing was carried out using the BioEdit program (http://jwbrown.mbio.ncsu.edu/BioEdit/bioedit.html). The unrooted phylogenetic trees of the studied bacteria were constructed with the aid of the methods implemented in the TREECON software package [12].

RESULTS AND DISCUSSION

Cell morphology and ultrastructure. The cells of strain Z-0088 grown under optimal conditions were toroidal or horseshoe-shaped, single or in pairs (Figs. 1a, 1b, 2a, and 2b), nonmotile, 0.5–1.5 × 1.0–6.0 μm in size, had mucous capsules, formed no spores, and reproduced by division. The culture can contain S-shaped paired forms (Fig. 2a) or spiral filaments of 30–40 μm in length (Figs. 1c and 1d). Ultrathin sections of the cells of strain Z-0088 revealed the gram-negative structure of its cell walls (Fig. 2c). Cell morphology of the isolated bacterium was typical of all representatives of the genus *Spirosoma* (Table 1).

Cultural properties. When grown on HCY agar medium for ten days, strain Z-0088 formed rounded, opaque, slimy, viscous, bright yellow colonies (4–5 mm in diameter) with smooth edges and a plane profile.

Physiological properties. Stain Z-0088 was an obligately aerobic and mesophilic bacterium growing within a temperature range of 13–35°C with the opti-

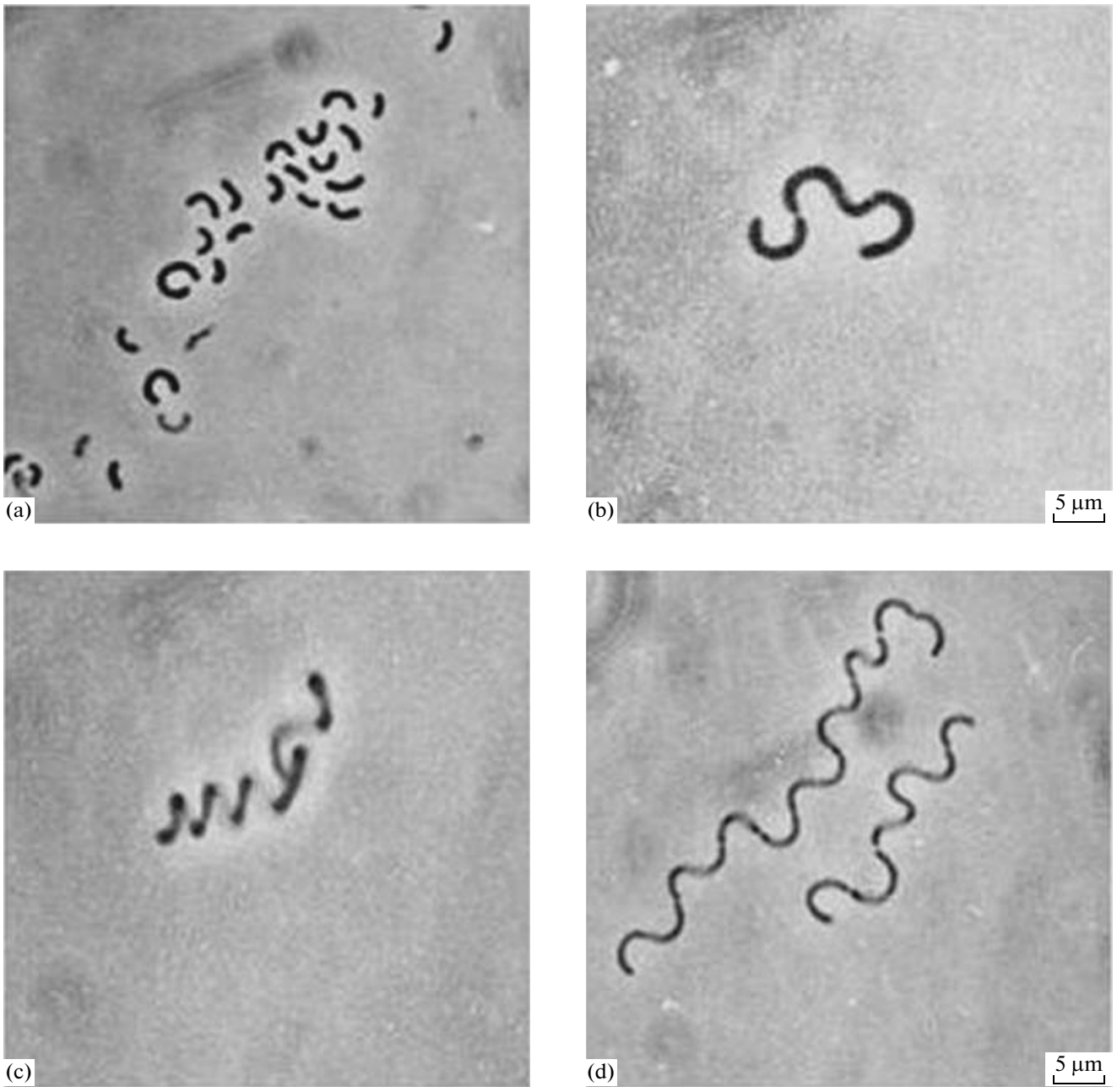

Fig. 1. Microphotographs of the cells of strain Z-0088, phase contrast.

mum at 28°C. The bacterium was moderately acidophilic and grew within a pH range of 3.8–7.5 with the optimum at pH 5.5–6.5. Unlike other members of the genus *Spirosoma*, which had the lower pH limit of 5–6 (Table 1) [12–14], strain Z-0088 was moderately acidophilic with a growth optimum at pH 5.5–6.5. NaCl concentration above 10 g/L inhibited cell growth, which is typical of all representatives of this genus [13–15].

The bacterium was obligately heterotrophic and utilized a limited range of organic compounds including xylan, inulin, xylose, sucrose, and *N*-acetylglucosamine. The strain was unable to utilize organic acids (acetate, succinate, citrate, malate, oxalate, and gluconate) and C_1 compounds. Unlike other members of the genus *Spirosoma*, the bacterium was not chemolithoautotrophic (Table 1). The optimum substrate concentration was 0.05% (Fig. 3).

Strain Z-0088, much like the other representatives of the genus *Spirosoma*, produced a bright yellow pigment [13–15]. The organism required vitamins and yeast extract (0.01 g/L) and was unable to grow on nitrogen-free medium. The strain was oxidase- and catalase-positive.

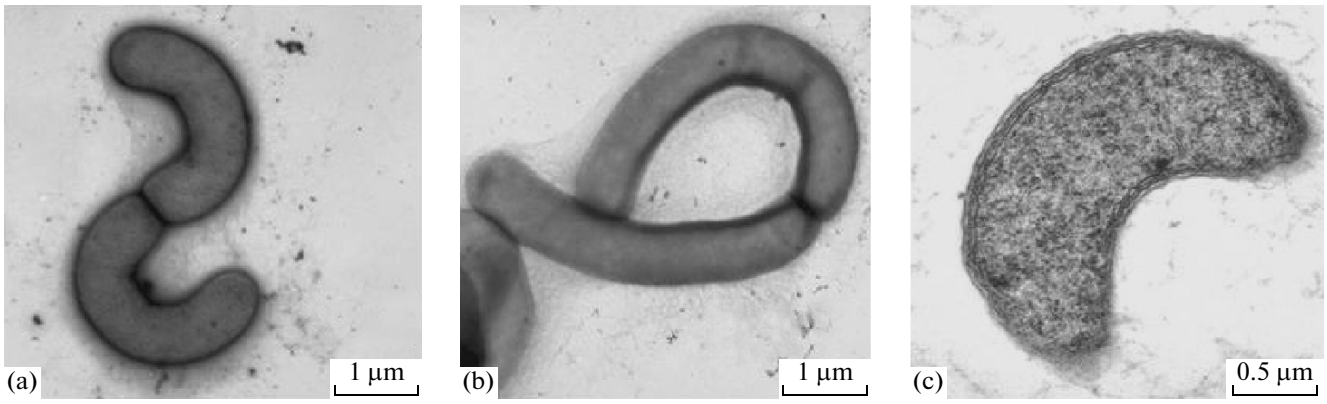

Fig. 2. Electron micrographs (a), (b) and ultrathin structure (c) of the cells of *Spirosoma* sp. strain Z-0088.

Antibiotic resistance. Strain Z-0088 was resistant to erythromycin, but sensitive to kanamycin, penicillin, novobiocin, gentamycin, streptomycin, chloramphenicol, and lincomycin.

Fatty acid content of the lipids. Fatty acid (FA) content and composition of the membrane lipids in strain Z-0088 were similar to those in other members of the genus *Spirosoma* (Table 2). The major FA were (% of the total): hexadecenoic ($C_{16:1\omega7}$), 30.51; 3-hydroxy-*iso*-pentadecanoic (3h-*iso*-$C_{15:0}$), 28.04; hexadecenoic ($C_{16:1\omega5}$), 10.01; hexadecanoic ($C_{16:0}$), 9.05; and *iso*-pentadecanoic (*iso*-$C_{15:0}$), 5.86. Strain Z-0088

Table 1. Differentiating characteristics of members of the genus *Spirosoma*

Characteristics	Z-0088	*S. linguale*	*S. panaciterrae*	*S. rigui*	*S. spitsbergense*
G+C base content, mol %	50.2	51–53	50.1	53.3	49.1
Oxidase	+	+	+	–	+
Catalase	+	+	+	+	+
Motility	–	N/D	–	Sliding	Sliding
Cell shape	Horseshoe-shaped	Horseshoe-shaped, filament formation	Rod-shaped	Rod-shaped, filament formation	Rod-shaped
NaCl sensitivity, %	0–1	0–1.25	0–1	0–1	0–1
Temperature range	13–35	5–39	15–42	4–37	4–30
pH range	3.8–7.5	N/D	5.0–9.0	6–11	6–9
Optimal pH	5.5–6.5	N/D	6.5–7.0	7	7
Optimal temperature, °C	28	20–30	30	30	25
Pigment	Yellow	Orange	Yellow	Yellow	Yellow
Oxygen requirement O_2	Aerobe	Aerobe	Aerobe	Facultative anaerobe	Aerobe
Glucosamine	+	–	+	–	N/D
Arabinose	+	–	+	–	N/D
Galactose	–	+	–	–	N/D
Glucose	+	–	+	+	N/D
Maltose	+	+	+	–	N/D
Mannose	+	+	+	–	N/D
Raffinose	+	+	–	–	N/D
Saccharose	+	+	+	–	N/D
Xylose	+	+	–	–	N/D

Note: N/D stands for “no data”.

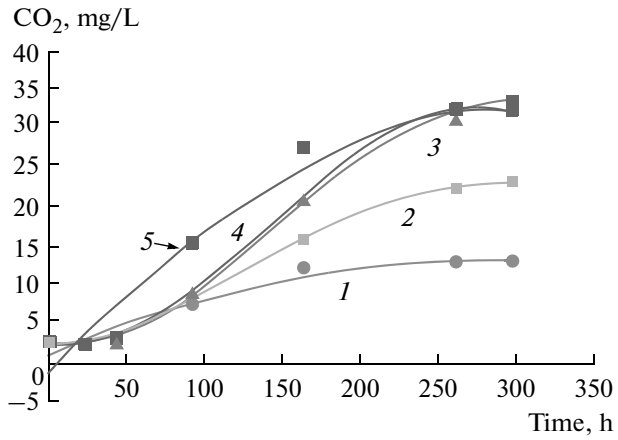

Fig. 3. Respiration rates of the Z-0088 cells grown at different xylose concentrations (%): control, without xylose (*1*); 0.05 (*2*); 0.1 (*3*); 0.5 (*4*); and 1.0 (*5*).

differed from other members of the genus *Spirosoma* by considerably higher (tenfold) content of 3-hydroxy-*iso*-pentadecanoic acid.

Molecular genetic analyses. The DNA G+C content in strain Z-0088 was 50.2 mol %. Based on the results of 16S rRNA sequence analysis, strain Z-0088 was assigned to the genus *Spirosoma* and was most closely related to the species 'Spirosoma escalantus'; the similarity level was 97.8% (Fig. 4). This species was not validated or described. Among the validly described species, *S. linguale*, the type species of the genus *Spirosoma*, showed the highest similarity (96.6%) to strain Z-0088, although it differed considerably in fatty acid composition. Unlike *S. linguale*, strain Z-0088 contained hexadecenoic ($C_{16:1\omega7}$), octadecenoic ($C_{18:1\omega7}$), pentadecanoic ($C_{15:0}$), tetradecanoic ($C_{14:0}$), and octadecanoic ($C_{18:0}$) acids. Moreover, 3-hydroxy-*iso*-pentadecanoic (3h-*iso*-$C_{15:0}$) was the major fatty acid in strain Z-0088, whereas its amount in *S. linguale* was as low as 4.9% (Table 2). Unlike strain Z-0088, *S. linguale* was unable to utilize glucosamine, glucose, or arabinose as growth substrates, but grew on galactose (Table 1).

Strain Z-0088 is a typical representative of the genus *Spirosoma* and is similar in its ecophysiological characteristics to the bacterium *S. panaciterra*, which was isolated in 2009 from soil in South Korea [13]. The 16S rRNA gene sequence similarity between these strains was 92.7%. Both strains grew at a pH range shifted to a more acidic region and within a more narrow temperature range than the other representatives of this genus (Table 1). Both strains utilized *N*-acetylglucosamine and arabinose as a sole source of carbon and energy. Both strains were nonmotile and had a lower the DNA G+C content than the other representatives of this genus. However, these strains differed

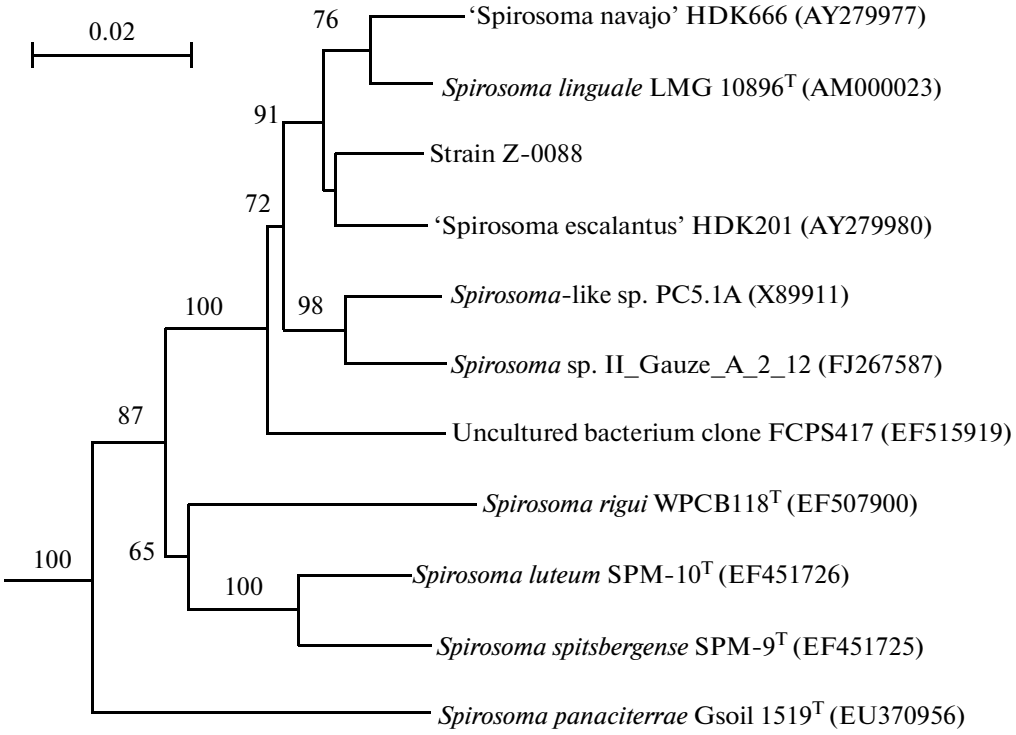

Fig. 4. Phylogenetic tree demonstrating the phylogenetic position of strain Z-0088 among members of the genus *Spirosoma*.

Table 2. Composition of fatty acids (%) in different members of the genus *Spirosoma*

Fatty acids	Z-0088	*S. panaciterrae*	*S. rigui*	*S. linguale*	*S. luteum*, *S. spitsbergense*
Hexadecenoic $C_{16:1\omega7}$	30.51	–	45.6	–	43.0–48.2
3-Hydroxy-*iso*-pentadecanoic 3h-*iso*-$C_{15:0}$	28.04	–	2.6	4.9	N/D
Hexadecenoic $C_{16:1\omega5}$	10.01	33.4	18.5	17.5	19.1–21.3
Hexadecenoic $C_{16:0}$	9.50	5.2	8.8	7.2	6.7–7.3
iso-Pentadecanoic *iso*-$C_{15:0}$	5.86	15.1	9.5	7.6	2.6–5.7
anteiso-Pentadecanoic *anteiso*-$C_{15:0}$	3.81	1.9	1.3	<1	N/D
3-Hydroxy-*iso*-heptadecanoic 3h-*iso*-$C_{17:0}$	2.55	3.2	3.5	6.5	4.7–6.0
3-Hydroxy-pentadecanoic 3h-$C_{15:0}$	1.87	N/D	N/D	N/D	N/D
iso-Heptadecenoic *iso*-$C_{17:0:1\omega8}$	1.40	N/D	N/D	N/D	N/D
Octadecenoic $C_{18:1\omega7}$	1.10	–	1.5	–	
Tridecanoic $C_{13:0}$	1.04	N/D	N/D	N/D	N/D
iso-Heptadecanoic *iso*-$C_{17:0}$	1.02	N/D	N/D	N/D	N/D
Pentadecanoic $C_{15:0}$	0.54	2.7	–	–	2.7
3-Hydroxy-hexadecanoic 3h-$C_{16:0}$	0.49	–	2.8	4.7	–
anteiso-heptadecenoic *anteiso*-$C_{17:1\omega6}$	0.45	N/D	N/D	N/D	N/D
3-Hydroxy-tetradecanoic 3h-$C_{14:0}$	0.35	N/D	N/D	N/D	N/D
iso-Hexadecanoic *iso*-$C_{16:0}$	0.31	N/D	N/D	N/D	N/D
Hexadecenoic $C_{17:1\omega6}$	0.28	N/D	N/D	N/D	N/D
Tetradecanoic $C_{14:0}$	0.26	1.6	1.3	–	N/D
Octadecenoic $C_{18:1\omega9}$	0.18	N/D	N/D	N/D	N/D
3-Hydroxy-*anteiso*-heptadecanoic 3h-*anteiso*-$C_{17:0}$	0.17	N/D	N/D	N/D	N/D
Octadecanoic $C_{18:0}$	0.15	–	1.2	–	
Tetradecenoic $C_{14:1\omega5}$	0.12	N/D	N/D	N/D	N/D

Note: N/D stands for “no data”.

significantly in the fatty acid composition of the membrane lipids. Unlike *S. panaciterrae*, strain Z-0088 contained hexadecenoic ($C_{16:1\omega)7}$), 3-hydroxy-*iso*-pentadecanoic (3h-*iso*-$C_{15:0}$), 3-hydroxy-hexadecanoic (3h-$C_{16:0}$), octadecenoic ($C_{18:1\omega7}$), and octadecanoic ($C_{18:0}$) acids; moreover, hexadecenoic ($C_{16:1\omega7}$) and 3-hydroxy-*iso*-pentadecanoic (3h-*iso*-$C_{15:0}$) were the major acids. The amount of hexadecenoic ($C_{16:1\omega5}$) acid in strain Z-0088 was threefold lower than that in *S. panaciterra* (Table 2).

The ecophysiological features of strain Z-0088 (its oligotrophy and acid tolerance) are in agreement with its adaptation to acidic, low-mineral dystrophic freshwaters poor in organic substances.

On the constructed phylogenetic tree, strain Z-0088 fell into a cluster with the unvalidated *Spirosoma* species ‘S. escalantus’ with a low level of the 16S rRNA gene sequence similarity (97.8%) and a low significance of the branching order as determined by bootstrap analysis (42%), which indicated an uncertain position of the studied strain within the cluster formed by *S. linguale* and unvalidated species ‘S. navajo’ and ‘S. escalantus’. The levels of the 16S rRNA gene sequence similarity of the species within this cluster (96.6–97.8%) reliably differed from those in the neighboring clusters (92.7–94.6%). According to the present concepts, these levels of the 16S rRNA gene sequence similarity between strain Z-0088 and the species *S. linguale*, ‘S. navajo’, and ‘S. escalantus’ makes it possible to classify strain Z-0088 within the genus *Spirosoma* as a new species *Spirosoma xylofaga* sp. nov. (Fig. 4).

Description of Spirosoma xylofaga sp. nov.

Xy.lo.'fa.ga.—L. n. fem. *xylon*, wood, *faga* L. fem. adj., eating, *Xylofaga* N.L. fem. adj. Wood-eating.

The organism belongs to the genus *Spirosoma*, which is included into the family *Flexibacteriaceae* (order *Sphingobacteriales*, class *Sphingobacteria*, type

Bacteroidetes). The cells are gram-negative, rod-shaped, curved, 0.5–1.5 × 1.0–6.0 μm in size, nonmotile, single or in pairs, can form spiral filaments; they reproduce by division. Colonies on HCY agar medium are rounded (up to 5 mm in diameter), flat with a smooth surface and even edges, mucous, opaque with a dense consistency, and bright yellow in color. The pH range for growth is 3.8–7.5 with the optimum at 5.5–6.5. The bacterium is a mesophile growing within a temperature range from 13 to 35°C with the growth optimum at 28°C. The cells are tolerant to NaCl concentrations not exceeding 1%. The organism is an aerobe and an obligate heterotroph; the main growth substrates are xylan, inulin, xylose, saccharose, and *N*-acetylglucosamine; the optimum substrate concentration is 0.05%. The bacterium cannot grow on organic acids (acetate, succinate, citrate, malate, oxalate, or gluconate) or on nitrogen-free medium; requires vitamins and yeast extract (0.1 g/L). The organism is unable to utilize C_1-compounds and to grow chemolithoautotrophically. The organism is catalase- and oxidase-positive.

The major FA include (%): 3-hydroxy-*iso*-pentadecanoic (3h-*iso*-$C_{15:0}$), 28.04; hexadecenoic ($C_{16:1\omega5}$), 10.01; hexadecanoic ($C_{16:0}$), 9.05; hexadecenoic ($C_{16:1\omega7}$), 30.51; and *iso*-pentadecanoic (*iso*-$C_{15:0}$), 5.86. The DNA G+C content is 50.2 mol %. The type strain is resistant to erythromycin, but sensitive to kanamycin, penicillin, novobiocin, gentamycin, streptomycin, chloramphenicol, and lincomycin.

The organism was isolated from acidic (pH 5.0) freshwater formed by a xylotrophic fungal community grown on decaying wood.

The type strain is Z-0088 (VKM B-2749).

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