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Mucilaginibacter paludis gen. nov., sp. nov. and *Mucilaginibacter gracilis* sp. nov., pectin-, xylan- and laminarin-degrading members of the family *Sphingobacteriaceae* from acidic *Sphagnum* peat bog

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Two facultatively aerobic, heterotrophic bacteria capable of degrading pectin, xylan, laminarin and some other polysaccharides were obtained from the acidic *Sphagnum* peat bog Bakchar, in western Siberia, Russia, and were designated strains TPT18^T and TPT56^T. Cells of these isolates are Gram-negative, non-motile, long rods that are covered by large capsules. On ageing, they transform into spherical L-forms. Strains TPT18^T and TPT56^T are acido- and psychrotolerant organisms capable of growth at pH 4.2–8.2 (with an optimum at pH 6.0–6.5) and at 2–33 °C (with an optimum at 20 °C). The major fatty acids are iso-$C_{15:0}$, anteiso-$C_{15:0}$, iso-$C_{17:0}$ 3-OH and summed feature 3 (iso-$C_{15:0}$ 2-OH and/or $C_{16:1}\omega7c$); the quinones are MK-7 and MK-6. Comparative 16S rRNA gene sequence analysis revealed that the novel strains share 97 % sequence similarity and belong to the family *Sphingobacteriaceae*; however, they are related only distantly to members of the genera *Pedobacter* (91.8–93.3 % similarity) and *Sphingobacterium* (89.6–91.2 % similarity). The DNA G+C content of strains TPT18^T and TPT56^T is 42.4 and 46.1 mol%, respectively. The low DNA–DNA hybridization value (42 %) and a number of phenotypic differences between strains TPT18^T and TPT56^T indicated that they represent two separate species. Since the two isolates are clearly distinct from all currently described members of the family *Sphingobacteriaceae*, we propose a novel genus, *Mucilaginibacter* gen. nov., containing two novel species, *Mucilaginibacter gracilis* sp. nov. and *Mucilaginibacter paludis* sp. nov. The type strains of *Mucilaginibacter gracilis* and *Mucilaginibacter paludis* are respectively TPT18^T (=ATCC BAA-1391^T =VKM B-2447^T) and TPT56^T (=ATCC BAA-1394^T =VKM B-2446^T).

Representatives of the phylum *Bacteroidetes* are widely distributed in aquatic and terrestrial habitats and are especially proficient in degrading various biopolymers. These bacteria comprise a significant portion of the isolates obtained routinely from water and soil samples and are reasonably well represented in culture collections (Floyd *et al.*, 2005). However, in contrast to many other environments, little is known about members of the *Bacteroidetes* that inhabit acidic *Sphagnum* peat bogs. So far, taxonomically characterized members of the *Bacteroidetes* from this acidic habitat are represented by only four strains of gliding, xylanolytic and laminarinolytic bacteria that were identified as *Chitinophaga arvensicola* (Pankratov *et al.*, 2006). Here, we describe two more polysaccharide-degrading representatives of the phylum *Bacteroidetes* from acidic peat.

Strains TPT18^T and TPT56^T were isolated from a sample collected from 10–20 cm below the surface of the *Sphagnum* peat bog Bakchar, in the Tomsk region of

Abbreviation: EPS, extracellular polymeric substance.

The GenBank/EMBL/DDBJ accession numbers for the 16S rRNA gene sequences of *Mucilaginibacter gracilis* TPT18^T and *M. paludis* TPT56^T are AM490402 and AM490403.

Detailed phenotypic characteristics of strains TPT18^T and TPT56^T are available as supplementary material with the online version of this paper.

western Siberia (56° 51′ N 82° 50′ E), by spread-plating of serially diluted peat suspension onto the surface of peat extract medium solidified with gellan gum (a polysaccharide from *Alteromonas* sp.; Fluka) (Dedysh *et al.*, 2006). Two highly distinctive types of either cream- or pink-coloured, raised, semi-transparent and slimy colonies developed on plates inoculated with the terminal dilutions of peat suspension. Both types of colonies were composed of rod-shaped bacteria that produced large amounts of an extracellular polymeric substance (EPS). Partial sequencing of the 16S rRNA genes from these two bacteria showed that they are affiliated with the *Bacteroidetes* and are only distantly related (89–91 % sequence similarity) to members of the genera *Pedobacter* and *Sphingobacterium.* Thus, the goal of our study was to determine the taxonomic position of the newly isolated strains and to examine their capacity to degrade various biopolymers under acidic conditions.

The isolates were maintained on tenfold-diluted agar medium R2A (Difco). All tests were carried out using medium MM1 containing (l^{-1} distilled water) 0.5 g glucose, 0.04 g $MgSO_4 . 7H_2O$, 0.02 g $CaCl_2 . 2H_2O$ and 0.1 g yeast extract. Cell morphology and cell life cycle were examined using cultures grown on agar medium MM1. Preparation of ultrathin sections was performed as described before (Kulichevskaya *et al.*, 2006). Growth of the novel strains under a variety of conditions, including temperatures of 2–37 °C, pH 4.0–9.0 and NaCl concentrations of 0.01–3.0 % (w/v), was examined using batch cultures grown in liquid medium MM1. The OD_{600} was measured in an Eppendorf BioPhotometer at 2 day intervals for 2 weeks. The range of potential growth substrates of the novel strains was examined by replacing glucose in medium MM1 with various carbon sources. The ability to degrade different biopolymers was examined by measuring the rate of CO_2 production in tightly closed 120 ml serum bottles containing 20 ml liquid medium MM1 with 0.05 % (w/v) of the corresponding polymer substrate for 1 month at 20 °C. Control incubations were run in parallel under the same conditions but without substrate. Fermentative utilization of carbohydrates was investigated as described for the Hugh–Leifson test (Gerhardt *et al.*, 1981). Susceptibility to antibiotics was determined on MM1 agar plates using discs (Oxoid) containing the following antibiotics: ampicillin (10 μg), gentamicin (10 μg), kanamycin (30 μg), neomycin (10 μg), novobiocin (30 μg), streptomycin (10 μg), chloramphenicol (30 μg) and lincomycin (10 μg).

Cell biomass for cellular fatty acid and isoprenoid quinone analyses and for DNA extraction was obtained from batch cultures grown in liquid MM1 medium at 24 °C for 1 week. Cellular fatty acid analysis was performed by the DSMZ Identification Service. Isoprenoid quinones were extracted according to Collins (1985) and analysed using an LCQ ADVANTAGE MAX tandem-type mass spectrometer and a Finnigan Mat 8430 ionization mass spectrometer. The DNA base composition of strains was determined by thermal denaturation using a Unicam SP1800 spectrophotometer at a heating rate of 0.5 °C min^{-1}. The G+C content was calculated according to Owen *et al.* (1969). PCR-mediated amplification of the 16S rRNA gene was performed using primers 9f and 1492r and reaction conditions described by Weisburg *et al.* (1991). 16S rRNA gene amplicons were purified using QIAquick spin columns (Qiagen) and sequenced on an ABI Prism 377 DNA sequencer (PE Applied Biosystems). Phylogenetic analysis was carried out using the ARB program package (Ludwig *et al.*, 2004).

On solid media made with agar or gellan gum, strains $TPT18^T$ and $TPT56^T$ formed large (up to 1 cm in diameter), convex, circular, semi-transparent colonies of slimy consistency. The colony colour varied from cream to light orange for strain $TPT18^T$ and from light pink to reddish for strain $TPT56^T$. Cells of these strains were Gram-negative, non-spore-forming, non-motile rods that occurred singly, in pairs or in short chains and were covered with large capsules of EPS. Young (2–3 days old) cultures contained long cells (6–15 μm) (Fig. 1a, b); cells up to 40 μm in length were occasionally observed. On ageing, long cells divided by binary fission into several non-motile shorter (1.5–5 μm) cells. Cells of strain $TPT56^T$ were slightly thicker (0.5–0.8 μm) than cells of strain $TPT18^T$ (0.4–0.5 μm). Old cultures of both strains contained L-forms of cells (Fig. 1c). Morphologically, the L-forms appeared as spherical bodies of varying sizes (0.5–3 μm); some of them were granular and some contained vacuoles (Fig. 1d). After transfer to fresh medium, the L-forms reverted to normal vegetative cells that continued to grow as usual. Ultrathin sections of vegetative cells revealed the presence of numerous spherical outer-membrane vesicles, ranging in size from 50 to 240 nm (Fig. 1e, f). Also, small globular bodies bounded by bilayered membranes and resembling mesosome-like structures were observed in many cells of the novel isolates (Fig. 1e, f). The nature of these cell structures remains unclear.

The novel isolates from *Sphagnum* peat had an absolute requirement for the presence of growth factors (50–100 mg yeast extract l^{-1}) in cultivation media. Thus, utilization of a given carbon compound was assumed to have occurred when growth was distinctly improved in its presence compared with basal MM1 medium alone. The carbon compounds tested and the results are given in the two species descriptions (see below) or are shown in Supplementary Table S1 (available in IJSEM Online). Sugars were the preferred growth substrates. Strain $TPT18^T$ differed from strain $TPT56^T$ in its ability to utilize D-arabinose, D-raffinose and salicin and its inability to utilize *myo*-inositol and *N*-acetylglucosamine. Both novel isolates were able to hydrolyse pectin, laminarin, xylan, chondroitin sulfate, gellan gum, pullulan and starch.

Strains $TPT18^T$ and $TPT56^T$ grew in the pH range 4.2–8.2, with an optimum at pH 6.0–6.5. The temperature range for growth was 2–33 °C, with an optimum at 20 °C. Growth was inhibited completely at NaCl concentrations

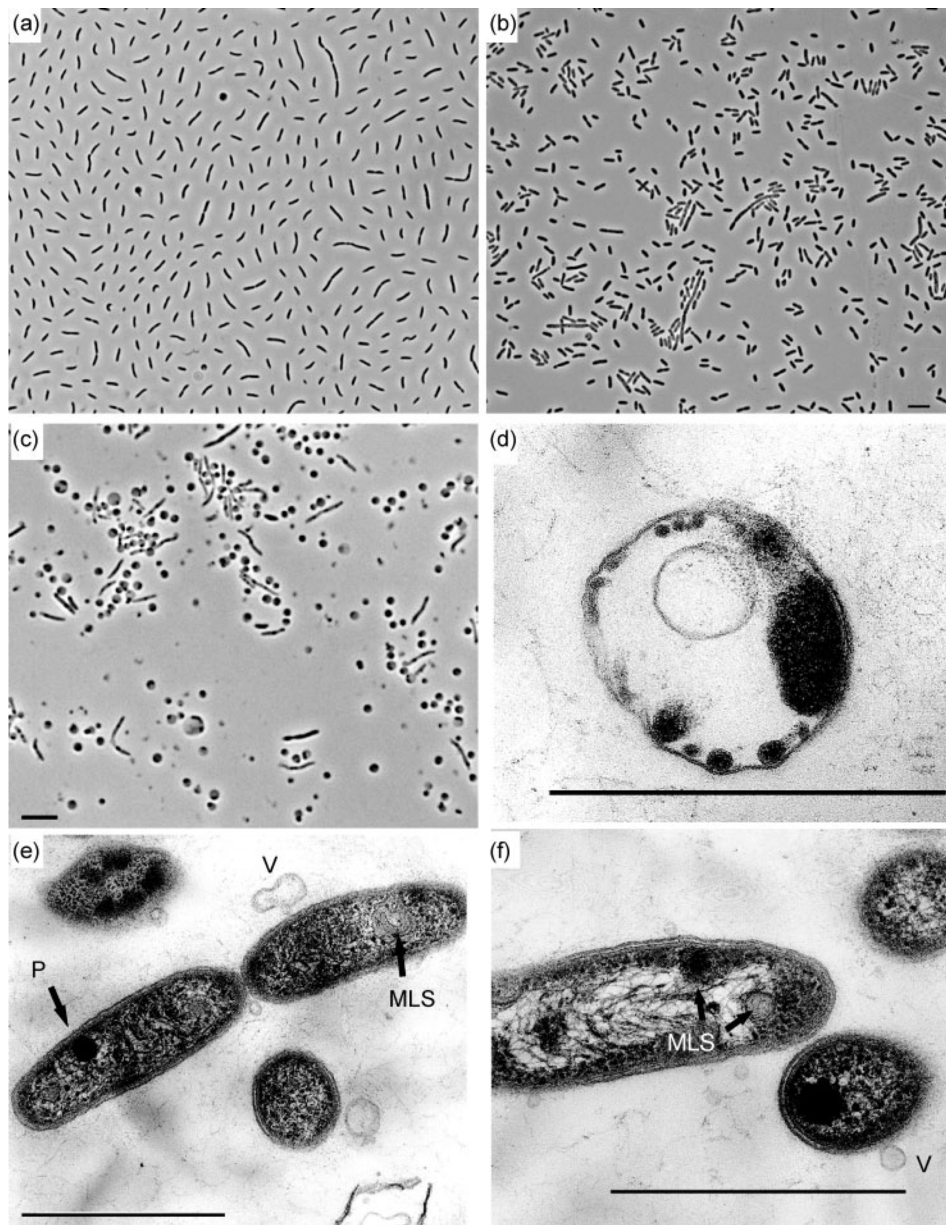

Fig. 1. (a–c) Phase-contrast micrographs of cells of strains TPT18^T (a) and TPT56^T (b) grown on MM1 medium for 3 days and L-forms of cells in a 2-week-old culture of strain TPT18^T (c). (d–f) Electron micrographs of ultrathin sections of vegetative cells (e, f) and an L-form of a cell (d) of strain TPT56^T. V, Outer-membrane vesicles; MLS, mesosome-like structures; P, polyphosphate granules. Bars, 5 μm [b (also applies to a), c] and 1 μm (d–f).

above 1.0 % (w/v). Both strains were resistant to ampicillin, gentamicin, kanamycin, neomycin and novobiocin and susceptible to streptomycin. Strain TPT18^T differed from strain TPT56^T in its susceptibility to lincomycin and resistance to chloramphenicol.

Both novel isolates contained menaquinone-7 (MK-7) as the predominant isoprenoid quinone and MK-6 as a minor component. The cellular fatty acid profiles of strains TPT18^T and TPT56^T had significant similarity to those of members of the family *Sphingobacteriaceae*. Similar to representatives of the genera *Pedobacter* and *Sphingobacterium*, the major fatty acids of the novel strains were iso-$C_{15:0}$, iso-$C_{17:0}$ 3-OH, iso-$C_{15:0}$ 2-OH and $C_{16:1}\omega7c$ (Table 1). However, the cellular fatty acid profiles of the novel isolates differed from those of *Pedobacter* and *Sphingobacterium* species by the presence of significant amounts of anteiso-$C_{15:0}$ (up to 21 % of the total fatty acids).

Table 1. Cellular fatty acid compositions (%) of strains TPT56[T] and TPT18[T] and representatives of the genera *Pedobacter* and *Sphingobacterium*

Data for *Pedobacter* and *Sphingobacterium* species were taken from Steyn *et al.* (1998), Kim *et al.* (2006), Gallego *et al.* (2006) and Yoon *et al.* (2006). −, Not detected; tr, trace (<1.0 %).

Fatty acid	TPT56[T]	TPT18[T]	*Pedobacter*	*Sphingobacterium*
$C_{14:0}$	tr	tr	tr–1.6	0–3.2
$C_{14:0}$ 2-OH	tr	−	−	−
iso-$C_{13:0}$ 3-OH	tr	tr	−	−
iso-$C_{15:0}$	15.7	32.2	25.4–38.3	17.7–45.6
anteiso-$C_{15:0}$	21.1	5.8	tr–2.9	tr–2.6
$C_{15:1}\omega6c$	tr	1.2	tr–1.4	−
$C_{15:1}\omega5c$	−	tr	−	−
$C_{15:0}$	3.2	4.5	tr–1.6	−
iso-$C_{16:0}$	1.5	tr	−	−
$C_{16:1}\omega5c$	5.8	2.6	tr–4.5	0−1.5
$C_{16:0}$	3.1	tr	1.1–4.0	tr–7.8
iso-$C_{15:0}$ 3-OH	1.8	3.2	2.1–3.1	1.5–4.3
$C_{15:0}$ 2-OH	tr	tr	− or tr	−
iso-$C_{17:1}\omega9c$	tr	2.7	1.6–6.6	0−3.7
anteiso-$C_{17:1}\omega9c$	−	−	0–1.2	−
$C_{15:0}$ 3-OH	−	tr	−	−
iso-$C_{17:0}$	tr	tr	−	−
anteiso-$C_{17:0}$	4.5	−	−	−
$C_{17:1}\omega8c$	tr	1.5	−	−
$C_{17:1}\omega6c$	tr	tr	−	−
$C_{17:0}$	tr	tr	−	−
iso-$C_{16:0}$ 3-OH	tr	tr	−	−
$C_{16:0}$ 2-OH	−	−	− or tr	0−3.2
$C_{16:0}$ 3-OH	tr	tr	tr–4.5	0−6.3
iso-$C_{17:0}$ 3-OH	8.9	13.1	9.2–15.2	7.1–22.1
$C_{17:0}$ 2-OH	tr	tr	−	−
$C_{17:0}$ 3-OH	tr	tr	−	−
$C_{18:1}\omega9c$	tr	−	−	−
$C_{18:0}$	tr	−	−	−
Summed feature 3*	24.7	21.5	21.3–46.8	25.4–57.8

*Summed feature 3 contains iso-$C_{15:0}$ 2-OH and/or $C_{16:1}\omega7c$.

Comparative sequence analysis of the 16S rRNA gene placed strains TPT18[T] and TPT56[T] in the family *Sphingobacteriaceae*. However, they were only distantly related to members of the genera *Pedobacter* (91.8–93.3 % sequence similarity) and *Sphingobacterium* (89.6–91.2 % sequence similarity) (Fig. 2). The two strains shared a 16S rRNA gene sequence similarity of 97 %. The DNA G+C content of strains TPT18[T] and TPT56[T] was 42.4 and 46.1 mol%, respectively. A low DNA–DNA hybridization value (42 %) and a number of phenotypic differences between them indicated that they represent two separate species.

Since the novel isolates from *Sphagnum* peat possessed a number of characteristics that clearly distinguished them from the members of the genera *Pedobacter* and *Sphingobacterium* (Table 2), we propose a novel genus, *Mucilaginibacter* gen. nov., and two novel species, *Mucilaginibacter gracilis* sp. nov. and *Mucilaginibacter paludis* sp. nov., for strains TPT18[T] and TPT56[T].

Description of *Mucilaginibacter* gen. nov.

Mucilaginibacter (Mu.ci.la′gi.ni.bac′ter. L. n. *mucilago* -*inis* mucus; N.L. masc. n. *bacter* rod; N.L. masc. n. *Mucilaginibacter* mucus-producing rod).

Gram-negative, non-spore-forming, non-motile rods that occur singly, in pairs or in short chains and produce large amounts of EPS. Cells undergo a cyclic shape change during culture development. Young cultures contain long cells (6–15 μm, sometimes up to 40 μm in length). On ageing, long cells divide by binary fission into several non-motile shorter (1.5–5 μm) cells. Old cultures contain L-forms of cells, which revert to normal vegetative cells after transfer to fresh medium. Cells produce numerous outer-membrane vesicles. Colonies are large (3–10 mm in diameter), convex, circular, semi-transparent and slimy. The colony colour on tenfold-diluted medium R2A varies from cream to light orange and reddish. Flexirubin-type pigments are absent. Oxidase- and catalase-positive. Chemo-organotrophic facultative aerobes. Sugars are the preferred growth substrates. Capable of fermenting glucose and sucrose. Cannot utilize melibiose, melezitose, cellulose, chitin, heparin or aesculin. Hydrolyse pectin, xylan, laminarin, chondroitin 6-sulfate, gellan gum, pullulan and starch. Do not produce H_2S from thiosulfate or indole from tryptophan. Capable of growth at pH 4.2–8.2 and at 2–33 °C. NaCl inhibits growth at concentrations above 1 % (w/v). Major fatty acids are iso-$C_{15:0}$, anteiso-$C_{15:0}$, iso-$C_{17:0}$ 3-OH and summed feature 3 (iso-$C_{15:0}$ 2-OH and/or $C_{16:1}\omega7c$); the quinones are MK-7 and MK-6. The G+C content of the DNA varies between 42.4 and 46.1 mol%. Member of the family *Sphingobacteriaceae*. Strains have been isolated from acidic wetlands, specifically *Sphagnum* peat bogs. The type species is *Mucilaginibacter paludis*.

Description of *Mucilaginibacter paludis* sp. nov.

Mucilaginibacter paludis (pa.lu′dis. L. gen. n. *paludis* of a swamp, of a marsh, of a bog).

The description is as for the genus with the following additional traits. Cells are 0.5–0.8 μm wide. Colony colour varies from light pink to reddish. Utilizes D-cellobiose, D-fructose, D-galactose, sodium D-galacturonate, sodium D-gluconate, D-glucose, D-lactose, leucrose, maltose, D-rhamnose, sucrose, trehalose, D-xylose, D-mannose, *myo*-inositol and *N*-acetylglucosamine. Does not utilize acetate, adonitol, arabitol, arbutin, butyrate, capronate, citrate, D-arabinose, D-melezitose, D-melibiose, D-raffinose, dulcitol, fumarate, inulin, malate, mannitol, propionate, pyruvate, salicin, sorbitol, succinate or valerate. Capable of fermenting glucose and sucrose. Hydrolyses chondroitin 6-sulfate,

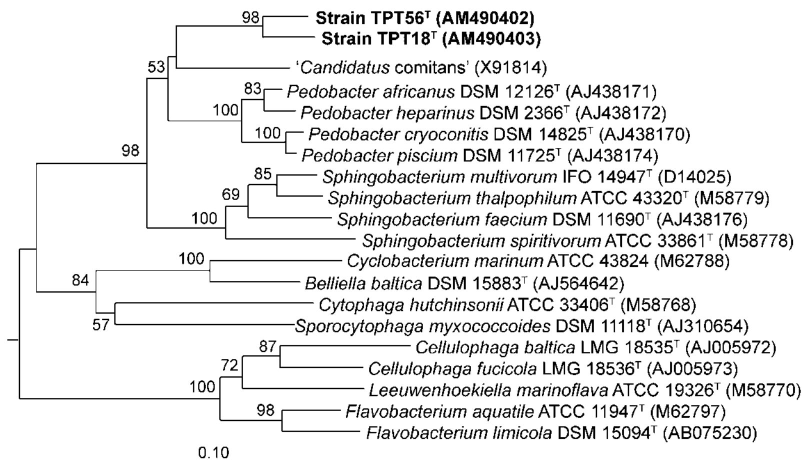

Fig. 2. 16S rRNA gene-based neighbour-joining tree showing the phylogenetic positions of strains TPT18^T and TPT56^T in relation to members of the genera *Pedobacter* and *Sphingobacterium* and some other representative members of the phylum *Bacteroidetes*. Bootstrap values (1000 data resamplings) >50 % are shown. The sequence of *Chlorobium limicola* UdG 6040 (GenBank accession no. Y10642) was used as an outgroup (not shown). Bar, 0.1 substitutions per nucleotide position.

gellan gum, laminarin, pectin, pullulan, starch and xylan but not alginate, CM-cellulose, cellulose, chitin, aesculin, fucoidan, heparin or lichenan. Produces acid from cellobiose, fructose, galactose, glucose, lactose, maltose, rhamnose, sucrose, xylose, mannose, laminarin and xylan. Optimal growth at 20–25 °C and at pH 6.0–6.5.

The type strain is strain TPT56^T (=ATCC BAA-1394^T =VKM B-2446^T), which was isolated from the *Sphagnum* peat bog Bakchar in the Tomsk region of western Siberia.

Description of *Mucilaginibacter gracilis* sp. nov.

Mucilaginibacter gracilis (gra′ci.lis. L. masc. adj. *gracilis* slender or thin).

The description is as for the genus with the following additional traits. Cells are 0.4–0.5 µm wide. Colony colour varies from creamy to yellowish or light orange. Utilizes D-arabinose, D-galactose, D-glucose, D-xylose, D-lactose, maltose, D-rhamnose, D-raffinose, salicin, sucrose, trehalose, D-fructose, D-cellobiose and pyruvate but not *N*-acetylglucosamine, D-melibiose, D-melezitose, L-sorbose, acetate, butyrate, valerate, gluconate, capronate, malate, propionate, succinate, fumarate, citrate, adonitol, arabitol, arbutin, dulcitol, inulin, mannitol, *myo*-inositol, sorbitol, mannose or sodium D-galacturonate. Capable of fermenting glucose and sucrose. Hydrolyses chondroitin 6-sulfate, gellan gum, laminarin, pectin, pullulan, starch and xylan but not alginate, CM-cellulose, cellulose, chitin, aesculin, fucoidan, heparin or lichenan. Produces acid from D-galactose, D-glucose, D-xylose, maltose, sucrose, trehalose, D-fructose, D-cellobiose, laminarin and xylan but not from mannose. Optimal growth at 18–22 °C and at pH 5.8–6.2.

The type strain is strain TPT18^T (=ATCC BAA-1391^T =VKM B-2447^T), which was isolated from the *Sphagnum* peat bog Bakchar in the Tomsk region of western Siberia.

Table 2. Major characteristics that distinguish *Mucilaginibacter* gen. nov. and the genera *Pedobacter* and *Sphingobacterium*

Data for *Pedobacter* and *Sphingobacterium* species were taken from Steyn *et al.* (1998), Shivaji *et al.* (2005), Vanparys *et al.* (2005), Hwang *et al.* (2005), Kim *et al.* (2006), Gallego *et al.* (2006) and Yoon *et al.* (2006).

Characteristic	*Mucilaginibacter*	*Pedobacter*	*Sphingobacterium*
Relation to oxygen	Facultatively aerobic	Strictly aerobic	Facultatively aerobic
Copious EPS production	+	−	−
L-forms of cells in old cultures	+	−	−
Growth at pH 4.5	+	−	−
Growth at >1 % NaCl	−	+	+
Hydrolysis of heparin	−	+	−
Acid production from melibiose	−	−	+
Assimilation of D-melezitose	−	−	+
anteiso-$C_{15:0}$ as a major fatty acid	+	−	−
Quinone(s)	MK-7, MK-6	MK-7	MK-7
DNA G+C content (mol%)	42–46	36–45	37–44

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