Emendation of the genus *Sphingomonas* Yabuuchi *et al.* 1990 and junior objective synonymy of the species of three genera, *Sphingobium*, *Novosphingobium* and *Sphingopyxis*, in conjunction with *Blastomonas ursincola*

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The 16S rDNA sequence similarities between the type strains of *Sphingomonas paucimobilis* and 32 other *Sphingomonas* species range from 90.2 to 99.6%. It might be possible to divide the genus into several new genera according to a dendrogram drawn from 16S rDNA sequence similarity. However, the phenotypic and biochemical information needed to define clusters of strains representing distinct genera within this group of organisms was not previously available. Although the cellular lipids of type strains of all 28 *Sphingomonas* species tested contained glucuronosyl-(1 → 1)-ceramide together with 2-hydroxymyristic acid, other molecular species of sphingoglycolipids were distributed randomly. *Sphingomonas natatoria* and *Sphingomonas ursincola*, bacteriochlorophyll *a*-containing, Gram-negative facultative phototrophs, belong to the cluster of the genus *Sphingomonas*. Other phototrophic *Porphyrobacter* and *Erythrobacter* species in the *Sphingomonadaceae* were classified into a cluster different from the genus *Sphingomonas*, as reported previously. None of the physiological and biochemical characteristics considered, including cellular lipids and fatty acid composition, provided evidence for the division of the current genus *Sphingomonas*. It is therefore concluded that the genus *Sphingomonas* should remain undivided at this time. The species of three recently proposed genera, *Sphingobium*, *Novosphingobium* and *Sphingopyxis*, in conjunction with *Blastobacter ursincola*, are junior objective synonyms of species of the genus *Sphingomonas*.

Keywords: glucuronosyl ceramide, 2-hydroxymyristic acid, bacteriochlorophyll *a*, alcapton

INTRODUCTION

Delineation of the genus *Sphingomonas* has been the subject of taxonomic discussion by various workers (Balkwill *et al.*, 1997; Hiraishi *et al.*, 2000; Kämpfer *et al.*, 1997; Stolz *et al.*, 2000; Takeuchi *et al.*, 1994,

2001). The recent detection of bacteriochlorophyll *a* from cells of *Blastomonas natatoria* DSM 3183^T and *puf* genes encoding proteins of the photosynthetic reactions detected by PCR (Hiraishi *et al.*, 2000) has raised new interest. Based on the results of DNA–DNA hybridization and phylogenetic analysis of 16S rDNA sequences of *B. natatoria* DSM 3183^T and *Erythromonas ursincola* DSM 9006^T, the latter species has been transferred to the genus *Blastomonas* in a

Abbreviation: SGL, sphingoglycolipid.

Table 1. History and growth conditions of type strains of 33 *Sphingomonas* species

Authorities are given for each name; these papers are not included in the reference list unless cited elsewhere.

Strain	Received as	Source of isolation	Medium and incubation temperature (°C)*
<i>Sphingomonas adhaesiva</i> Yabuuchi <i>et al.</i> 1990 EY 4215 ^T	GIFU 11458 ^T	'Sterile' water used before surgery	Heart infusion agar, 30
<i>Sphingomonas alaskensis</i> Vancanneyt <i>et al.</i> 2001 EY 4374 ^T	DSM 13593 ^T	Sea-water sample from Gulf of Alaska	Tryptic soy agar, 30
<i>Sphingomonas aquatilis</i> Lee <i>et al.</i> 2001 KCTC 2881 ^T	KCTC 2881 ^T	Natural mineral water, Taejon, Korea	
<i>Sphingomonas aromaticivorans</i> Balkwill <i>et al.</i> 1997 EY 4296 ^T	IFO 16084 ^T	Terrestrial subsurface sediments	Tryptic soy agar, 30
<i>Sphingomonas asaccharolytica</i> Takeuchi <i>et al.</i> 1995 EY 4229 ^T	IFO 15499 ^T	Roots of <i>Malus</i> spp.	PYA, 26
<i>Sphingomonas capsulata</i> (Leifson 1962) Yabuuchi <i>et al.</i> 1990 EY 4216 ^T	GIFU 11526 ^T	Distilled water	Heart infusion agar, 26
<i>Sphingomonas chlorophenolica</i> Nohynek <i>et al.</i> 1996 EY 4219 ^T	ATCC 33790 ^T	Pentachlorophenol-contaminated soil	1/2 TSA
<i>Sphingomonas chungbukensis</i> Kim <i>et al.</i> 2000 EY 4375 ^T	JCM 11454 ^T	Freshwater sediment, Taejon, Korea	Difco nutrient agar, 30
<i>Sphingomonas cloacae</i> Fujii <i>et al.</i> 2001 EY 4361 ^T	JCM 10874 ^T	Sewage-treatment-plant water sample, Tokyo	Heart infusion agar, 30
<i>Sphingomonas echinoides</i> (Heumann 1962) Denner <i>et al.</i> 1999 EY 4340 ^T	JCM 10637 ^T	Plate contaminant	1/2 TSA, 30
<i>Sphingomonas herbicidovorans</i> Zipper <i>et al.</i> 1997 EY 4344 ^T	DSM 11019 ^T	Soil	Tryptic soy agar, 28
<i>Sphingomonas koreensis</i> Lee <i>et al.</i> 2001 EY 4376 ^T	JCM 11456 ^T	Natural mineral water, Taejon, Korea	Difco nutrient agar, 30
<i>Sphingomonas macrogoltabidus</i> Takeuchi <i>et al.</i> 1993 EY 4304 ^T	JCM 10192 ^T	Soil	Tryptic soy agar, 30
<i>Sphingomonas mali</i> Takeuchi <i>et al.</i> 1995 EY 4341 ^T	IFO 15500 ^T	Roots of <i>Malus</i> spp.	1/2 TSA, 30
<i>Sphingomonas natatoria</i> (Sly 1985) Yabuuchi <i>et al.</i> 1999 EY 4220 ^T	ATCC 35951 ^T	Freshwater swimming pool	PYA, 26
<i>Sphingomonas parapaucimobilis</i> Yabuuchi <i>et al.</i> 1990 EY 4213 ^T	GIFU 11387 ^T	Urine	Heart infusion agar, 30
<i>Sphingomonas paucimobilis</i> (Holmes <i>et al.</i> 1977) Yabuuchi <i>et al.</i> 1990 EY 2395 ^T	GIFU 2395 ^T	Hospital mechanical respirator	Heart infusion agar, 30
<i>Sphingomonas puitosa</i> Denner <i>et al.</i> 2001 EY 4370 ^T	DSM 13101 ^T	Eutrophic fountain water, Vienna, Austria	Tryptic soy agar, 30
<i>Sphingomonas pruni</i> Takeuchi <i>et al.</i> 1995 EY 4228 ^T	IFO 15498 ^T	Roots of <i>Prunus persica</i>	PYA, 26
<i>Sphingomonas rosa</i> Takeuchi <i>et al.</i> 1995 EY 4227 ^T	IFO 15208 ^T	Hairy roots of <i>Rosa</i> spp.	PYA, 26
<i>Sphingomonas roseiflava</i> Yun <i>et al.</i> 2000 EY 4345 ^T	JCM 99038 ^T	Plant (<i>Setaria viridis</i>)	Tryptic soy agar, 28
<i>Sphingomonas sanguinis</i> Takeuchi <i>et al.</i> 1993 EY 2397 ^T	GIFU 2397 ^T	Blood	Heart infusion agar, 30
<i>Sphingomonas stygia</i> Balkwill <i>et al.</i> 1997 EY 4297 ^T	IFO 16085 ^T	As <i>S. aromaticivorans</i> IFO 16084 ^T	Tryptic soy agar, 30
<i>Sphingomonas subarctica</i> Nohynek <i>et al.</i> 1996 EY 4251 ^T	DSM 10700 ^T	Biofilm of reactor inoculated with activated sludge	Tryptic soy agar, 28
<i>Sphingomonas suberifaciens</i> (van Burgen <i>et al.</i> 1990) Yabuuchi <i>et al.</i> 1999 EY 4204 ^T	JCM 8521 ^T	Corky root of lettuce	ATCC medium 1700, 26
<i>Sphingomonas subterranea</i> Balkwill <i>et al.</i> 1997 EY 4298 ^T	IFO 16086 ^T	As <i>S. aromaticivorans</i> IFO 16084 ^T	Tryptic soy agar, 30
<i>Sphingomonas taejonensis</i> Lee <i>et al.</i> 2001 EY 4377 ^T	JCM 11457 ^T	Natural mineral water, Taejon, Korea	Difco nutrient agar
<i>Sphingomonas terrae</i> Takeuchi <i>et al.</i> 1993 EY 4207 ^T	IFO 15098 ^T	Activated sludge	Tryptic soy agar
<i>Sphingomonas trueperi</i> Kämpfer <i>et al.</i> 1997 EY 4218 ^T	ATCC 12417 ^T	Soil	Tryptic soy agar, 26
<i>Sphingomonas ursincola</i> (Yurkov <i>et al.</i> 1997) Yabuuchi <i>et al.</i> 1999 EY 4250 ^T	DSM 9006 ^T	Freshwater cyanobacterial mat	NA, 26
<i>Sphingomonas wittichii</i> Yabuuchi <i>et al.</i> 2001 EY 4224 ^T	DSM 6014 ^T	Water from the River Elbe	TSA, 30
<i>Sphingomonas xenophaga</i> Stolz <i>et al.</i> 2000 EY 4343 ^T	DSM 6383 ^T	Water from the River Elbe	Tryptic soy agar, 28
<i>Sphingomonas yanoikuyae</i> Yabuuchi <i>et al.</i> 1990 EY 4208 ^T	GIFU 9882 ^T	Clinical specimen	Tryptic soy agar, 28

* Heart infusion agar and tryptic soy agar were from Difco. ATCC medium 1700 is *Rhizobium* medium. Other media are abbreviated as NA (0.5 g Bacto peptone, 0.3 g Bacto yeast extract and 1.5 g agar in 100 ml), 1/2 NA (0.25 g Bacto peptone, 0.15 g Bacto yeast extract and 1.5 g agar in 100 ml), PYA (1.0 g Bacto peptone, 0.2 g Bacto yeast extract, 0.2 g NaCl and 1.2 g agar in 100 ml) and 1/2 TSA (2.0 g Bacto tryptic soy broth and 1.5 g agar in 100 ml).

proposed new combination, *Blastomonas ursincola* (Yurkov *et al.* 1997) Hiraishi *et al.* 2000.

However, it had been proposed previously that *B. natatoria* DSM 3183^T and *Erythromonas ursincola* DSM 9006^T belong to the genus *Sphingomonas*, as *Sphingomonas natatoria* (Sly 1985) Yabuuchi *et al.* 1999 and *Sphingomonas ursincola* (Yurkov *et al.* 1997) Yabuuchi *et al.* 1999, by the study of polyphasic taxonomy (Yabuuchi *et al.*, 1999). The presence of bacteriochlorophyll *a* and facultative phototrophic ability are unlikely to indicate a close phylogenetic relationship in prokaryotes (Kondratieva *et al.*, 1992). Other phototrophic organisms, such as *Erythrobacter longus*, *Erythrobacter litoralis*, *Erythromicrobium ramosum* and *Porphyrobacter tepidarius* (Hanada *et al.*, 1997), are outside the genus *Sphingomonas*, but included in *Sphingomonadaceae* Kosako *et al.* 2000, according to the presence of glucuronosyl ceramide in their cellular lipids and phylogenetic analysis of 16S rDNA nucleotide sequences (Kosako *et al.*, 2000).

On the basis of phylogenetic analysis of 16S rDNA sequences and polyamine profiles, Takeuchi *et al.* (2001) proposed that the genus *Sphingomonas* be classified into four genera, *Sphingomonas*, *Sphingobium*, *Novosphingobium* and *Sphingopyxis*. From a practical aspect, it is essential that any genus should not be delineated by phylogenetic analysis alone, but should also be distinguished by a combination of phenotypic tests that are performed easily in every microbiological laboratory. In this paper, we have examined the phenotypic characteristics of species currently assigned to the genus *Sphingomonas* (Yabuuchi *et al.* 1990) in relation to their phylogeny and found that there is no phenotypic evidence to support a proposal to split the species into four genera. We thus conclude that the genus *Sphingomonas* should remain undivided at this time.

METHODS

Bacterial strains. The history and growth conditions of the type strains of 33 *Sphingomonas* species are listed in Table 1. Two of them were isolated from clinical specimens, two from a hospital environment, one from a diseased plant and the remaining 28 were of environmental origin. Growth media and incubation temperatures for each type strain are also listed in Table 1.

16S rDNA sequences and phylogenetic analysis. Deposited data on 16S rDNA sequences of the type strains of 33 *Sphingomonas* species, two subspecies of *Zymomonas mobilis* as a representative member of *Sphingomonadaceae* and *Acetobacter aceti* as an outgroup organism were obtained from the DNA Database of Japan (DDBJ, Institute of Genetics, Shizuoka, Japan) and were used for phylogenetic analysis. Sequence accession numbers of bacterial strains used in this study are shown in Fig. 1. Phylogenetic analysis by 16S rDNA oligonucleotide sequences was performed as described previously (Kosako *et al.*, 2000). In brief, nucleotide substitution rates (K_{nuc} ; Kimura, 1980) were determined and a distance-matrix tree was constructed by the neighbour-joining method (Saitou & Nei, 1987) using the program CLUSTAL W (Thompson *et al.*, 1994). Alignment gaps and

unidentified base positions were excluded from the calculation. To evaluate the topology of the phylogenetic tree, a bootstrap analysis was performed (Yabuuchi *et al.*, 1999; Kosako *et al.*, 2000).

Phenotypic characterization and carbon assimilation. Phenotypic features were determined by the methods of Yabuuchi *et al.* (1990, 1999). Production of oxidative acids from sugars and polyalcohols was determined using OF basal medium (Difco), except for three strains, *Sphingomonas xenophaga* EY 4343^T, *Sphingomonas herbicidovorans* EY 4344^T and *Sphingomonas roseiflava* EY 4345^T, that were unable to grow in OF basal medium. To analyse these strains, cystine tryptic agar (Difco) was used. Assimilation tests were performed by using Biotype 100 and Biotype medium (bioMérieux) in accordance with the manufacturer's instructions. API 20NE (bioMérieux) was also used for characterization of organisms.

Production of homogentisic acid/alcapton/2,5-dihydroxy-phenylacetic acid. Culture supernatants of all bacterial strains used in the present study, including *Sphingomonas herbicidovorans* EY 4344^T and *Pseudomonas aeruginosa* ATCC 23268, standard producers of homogentisic acid (Yabuuchi & Ohyama, 1972), were tested for production of homogentisic acid during the metabolism of phenylalanine and tyrosine by using HPLC (Bory *et al.*, 1990; Mathieu *et al.*, 1997).

Antimicrobial susceptibility testing. Except for *Sphingomonas suberifaciens* EY 4204^T, *Sphingomonas pruni* EY 4228^T, *Sphingomonas asaccharolytica* EY 4229^T and *Sphingomonas mali* EY 4341^T, antimicrobial susceptibility testing was performed using Sensi-discs and Mueller-Hinton II plates (Difco) (Kosako *et al.*, 2000; Yabuuchi *et al.*, 1999, 2001). *Sphingomonas suberifaciens* EY 4204^T was tested using ATCC medium 1700 supplemented with 1.5% agar (Yabuuchi *et al.*, 1999). Peptone/yeast extract agar was used for growth of *Sphingomonas pruni* EY 4228^T and *Sphingomonas asaccharolytica* EY 4229^T and a 50% concentration of nutrient broth supplemented with 1.5% agar was used for *Sphingomonas mali* EY 4341^T.

Analysis of cellular lipids and fatty acids. Bacterial cells grown on agar media at optimal temperatures were harvested to analyse cellular lipids and fatty acids as described previously (Naka *et al.*, 2000; Yabuuchi *et al.*, 1990, 1999).

RESULTS AND DISCUSSION

Phylogenetic analysis

Fig. 1 shows a dendrogram derived from 16S rDNA oligonucleotide sequence similarity among the type strains of 33 *Sphingomonas* species and *Acetobacter aceti* as an outgroup micro-organism. From *Sphingomonas parapaucimobilis* to *Sphingomonas wittichii*, including *Sphingomonas paucimobilis*, the type species of the genus, it seems to form a single large branch. From *Sphingomonas chlorophenolica* to *Sphingomonas terrae*, 17 species are divided into three branches. The type strain of *Sphingomonas suberifaciens* belongs to the branch of *Sphingomonas chlorophenolica*. Both *Sphingomonas ursincola* and *Sphingomonas natatoria* are included in the *Sphingomonas chlorophenolica*–*Sphingomonas terrae* branch. Numerical analysis of 27 type strains of *Sphingomonas* species demonstrates that the members of three new genera proposed by

Fig. 1. Dendrogram based on phylogenetic analysis of 16S rDNA sequence of type strains of 33 *Sphingomonas* species. Nucleotide substitution rates (K_{nuc}) (Kimura, 1980) were determined using the program CLUSTAL W (Thompson *et al.*, 1994). The neighbour-joining method (Saitou & Nei, 1987) was used to reconstruct a phylogenetic tree from the distance matrices by using NJPLOT. Alignment gaps and unidentified base positions were excluded from the calculation and final analysis. To evaluate the topology of the phylogenetic tree, a bootstrap analysis was performed using 1000 bootstrapped trials. Bootstrap values are indicated at branching points.

Takeuchi *et al.* (2001) do not form solid clusters (Fig. 2). Our results do not support the proposal of the genus *Sphingomonas* and three new genera, *Sphingobium*, *Novosphingobium* and *Sphingopyxis*, on the basis of phylogenetic and chemotaxonomic analyses.

Phenotypic characteristics

Colonies of *Sphingomonas natatoria* EY 4220^T and *Sphingomonas ursincola* EY 4250^T, facultatively phototrophic organisms, were orange-coloured. At harvest, however, they gave a melted-chocolate-like colour. *Sphingomonas herbicidovorans* EY 4344^T produced water-soluble melanin-like pigment on heart infusion or tryptic soy agar plates. Grown slowly on Bactophenylalanine agar slants, *Sphingomonas herbicidovorans* EY 4344^T turned the medium pink from the surface. The culture supernatant of *Sphingomonas*

herbicidovorans EY 4344^T, but not other strains, contained alcapton/homogentisic acid (Mann, 1979). Because of its nutritional requirements, both API 20NE and Biotype 100 enabled us to estimate the assimilating ability of *Sphingomonas suberifaciens* EY 4204^T. A combination of certain phenotypic features was useful to differentiate strains at the species level, but not groups of strains at the generic level (Tables 2–4 and Fig. 2).

Distribution of sphingoglycolipids (SGLs) and major polyamines

Glucuronosyl-(1 → 1)-ceramide (SGL-1), but not galacturonosyl-(1 → 1)-ceramide (SGL-1'), was present in cellular lipids of all 28 strains tested (Table 5). Other SGLs (SGL-2, -3 and -4) and fatty acids, such as 2-OH 15:0 and 2-OH 16:0, could not contribute to the

Fig. 2. Numerical analysis of 27 type strains of *Sphingomonas* species. Numerical analysis was performed by using NTSYS-pc version 2 (Applied Biostatistics). The coefficient of simple matching was used for calculation and the dendrogram was depicted by UPGMA (Sneath & Sokal, 1973). *S.*, *Sphingomonas*. Genera in parentheses follow Takeuchi *et al.* (2001). *, Not included in Takeuchi *et al.* (2001).

division of the genus. Major polyamines detected were identified as spermidine and homospermidine (Hamana & Matsuzaki, 1993; Segers *et al.*, 1994; Stolz *et al.*, 2000; Takeuchi *et al.*, 1995).

Antimicrobial susceptibility of *Sphingomonas* species

All strains tested were susceptible (S) or showed an intermediate response (IM) to antimicrobials such as tetracycline, doxycycline and amikacin (Table 6). Meropenem, panipenem, amoxicillin/clavulanic acid, minocycline and imipenem exerted antimicrobial activity against most strains used in this study. *Sphingomonas suberifaciens* EY 4204^T, *Sphingomonas natatoria* EY 4220^T, *Sphingomonas roseiflava* EY 4345^T and *Sphingomonas paucimobilis* EY 2395^T were each susceptible to more than 30 of 36 discs. Although isolates from the clinical specimen and from the hospital environment were susceptible to fluoroquinolones, 12 strains originating from plants, soil and other sources were resistant to certain or all new fluoroquinolones tested. The type strains of *Sphingomonas pruni* and *Sphingomonas rosa* were resistant to more than 50 % of discs tested. Again, these results indicate that the pattern of antimicrobial susceptibility/resistance does not provide any convenient basis for subdividing the genus.

Phototrophic ability is distributed widely in prokaryotes and does not necessarily indicate a close phylogenetic relationship (Kondratieva *et al.*, 1992). *Sphingomonas natatoria* and *Sphingomonas ursincola* are closely related phylogenetically within the genus *Sphingomonas* (Yabuuchi *et al.*, 1999). Both *Sphingomonas ursincola* and *Sphingomonas natatoria* have been identified as phototrophs by HPLC analysis of photosynthetic pigments and genetic studies (Hiraishi *et al.*, 2000). In addition, flagella morphology is unlikely to be a key feature to distinguish a genus from others (Yabuuchi *et al.*, 1995). The presence of bacteriochlorophyll *a* is not a reason, in isolation, to exclude

two phylogenetically related and facultatively phototrophic species, *Sphingomonas natatoria* and *Sphingomonas ursincola*, from the genus *Sphingomonas*.

The division of the genus *Sphingomonas* into four genera has been proposed on the basis of sequence analysis of 16S rDNA, including signature sequences, and polyamine patterns (Busse & Auling, 1988; Hamana & Matsuzaki, 1993; Takeuchi *et al.*, 1995). More recently, similar methods were used to propose three new genera derived from the genus *Sphingomonas* (Takeuchi *et al.*, 2001). In the present study, we have examined 28 type strains of *Sphingomonas* species by phenotypic, biochemical and genetic analyses. We have shown that there is no phenotypic and phylogenetic evidence to support a proposal to divide the species into new genera. Therefore, we have concluded that the genus *Sphingomonas* should remain undivided at this time. The species of three recently proposed genera, *Sphingobium*, *Novosphingobium* and *Sphingopyxis*, in conjunction with *Blastobacter ursincola*, are junior objective synonyms of species of the genus *Sphingomonas*.

Emended description of the genus *Sphingomonas* Yabuuchi *et al.* 1990

Gram-negative, asporogenous rods or ovoid cells. Soma size is 0.7 × 1.4 µm, 0.4 × 0.9 µm (*Sphingomonas suberifaciens*) or 0.9 × 2.0 µm (*Sphingomonas ursincola*). Budding or asymmetric division is visualized by electron microscopy in two species (*Sphingomonas natatoria* and *Sphingomonas ursincola*). Bipolar staining in Gram stain (*Sphingomonas ursincola*) and rosette formation in some species. Usually single polar flagellum when motile. *Sphingomonas trueperi* is peritrichous. *Sphingomonas chlorophenolica*, *Sphingomonas cloacae*, *Sphingomonas xenophaga*, *Sphingomonas aromaticivorans*, *Sphingomonas subterranea*, *Sphingomonas capsulata*, *Sphingomonas stygia*, *Sphingomonas subarctica*, *Sphingomonas rosa*,

Table 2. Physiological and biological characteristics of 28 type strains of *Sphingomonas* species

Strains are arranged in the order of the dendrogram in Fig. 1. *Sphingomonas paucimobilis* is the type species of the genus. Strains (*S.*, *Sphingomonas*): 1, *S. chlorophenolica* EY 4219^T; 2, *S. herbicidovorans* EY 4344^T; 3, *S. yanoikuyae* EY 4208^T; 4, *S. cloacae* EY 4361^T; 5, *S. xenophaga* EY 4343^T; 6, *S. suberifaciens* EY 4204^T; 7, *S. aromaticivorans* EY 4296^T; 8, *S. subterranea* EY 4298^T; 9, *S. capsulata* EY 4216^T; 10, *S. stygia* EY 4297^T; 11, *S. subarctica* EY 4251^T; 12, *S. rosa* EY 4227^T; 13, *S. macrogoltabidus* EY 4304^T; 14, *S. terrae* EY 4207^T; 15, *S. ursincola* EY 4250^T; 16, *S. natatoria* EY 4220^T; 17, *S. parapaucimobilis* EY 4213^T; 18, *S. roseiflava* EY 4345^T; 19, *S. sanguinis* EY 2397^T; 20, *S. paucimobilis* EY 2395^T; 21, *S. pituitosa* EY 4370^T; 22, *S. trueperi* EY 4218^T; 23, *S. mali* EY 4341^T; 24, *S. pruni* EY 4228^T; 25, *S. asaccharolytica* EY 4229^T; 26, *S. adhaesiva* EY 4215^T; 27, *S. echinoides* EY 4340^T; 28, *S. wittichii* EY 4224^T. For *S. herbicidovorans*, *S. xenophaga* and *S. roseiflava*, Bacto CTA medium was used rather than Bacto OF basal medium. Data for the presence of nostoxanthin were taken from Jenkins *et al.* (1979). Data for the presence of bacteriochlorophyll *a* were taken from Yurkov *et al.* (1997) and Hiraishi *et al.* (2000). Oxidative acid production was tested using Bacto OF basal medium. Characters are scored as: +, positive reaction within 3 days; (+), positive reaction after more than 4 days; –, negative reaction; ND, no data; NG, no growth.

Characteristic	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28
Colony colour*	–	Y	(Y)	GW	Y	–	Y	Y	Y	Y	–	–	(Y)	(Y)	O	O	Y	PY	Y	Y	Y	Y	LY	Y	Y	Y	Y	(Y)
Nostoxanthin	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	+	+	ND	+	ND	ND	ND	ND	+	ND
Motility	–	+	+	–	–	+	–	–	–	–	–	–	+	+	–	–	–	–	+	+	+	+	+	–	–	+	+	+
Flagellation†	–	ND	1P	–	–	1P	–	–	–	–	–	–	1P	1P	–	1P	1P	–	1P	1P	1P	Peri	ND	–	–	1P	1P	1P
Oxidase (Kovacs)	+	–	–	–	+	+	+	+	–	+	+	–	+	+	+	–	–	–	–	–	+	–	+	+	+	–	–	+
Bacteriochlorophyll <i>a</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	+	–	–	–	–	–	–	–	–	–	–	–	–
Hydrolysis of:																												
Aesculin	+	+	+	+	+	+	+	+	+	+	+	+	+	+	(+)	+	+	+	+	+	+	+	+	+	+	+	+	+
Gelatin	+	+	–	–	–	–	+	+	–	+	+	–	+	+	+	–	–	–	+	+	–	–	–	–	–	–	+	+
Starch	–	–	–	–	–	–	+	–	+	–	–	–	+	–	+	+	+	+	+	+	+	–	–	(+)	+	+	+	–
Tween 80	–	–	–	–	+	–	–	–	+	–	–	–	+	–	+	+	+	+	+	+	+	–	+	+	+	+	–	–
Citrate (Simmons)	+	–	+	–	–	–	–	–	–	–	+	–	+	(+)	–	–	–	–	–	+	–	–	–	–	–	–	+	–
DNase	+	–	–	–	–	–	+	+	+	+	+	+	–	+	–	(+)	–	–	–	–	–	(+)	+	NG	NG	–	–	–
Phenylalanine deaminase	–	–	–	–	+	–	–	–	+	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–	–	–
Acylamidase	–	–	–	–	–	–	–	–	–	–	(+)	–	–	–	–	–	–	–	–	–	–	–	–	NG	NG	–	+	+
Alcapton production	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Oxidative acid from:																												
Glucose	+	+	+	–	+	NG	+	+	+	+	+	(+)	+	–	(+)	–	–	+	+	+	+	+	+	–	(+)	+	+	+
Maltose	–	+	+	(+)	+	NG	+	+	+	+	+	+	+	–	+	+	–	+	+	+	–	+	+	+	+	+	+	+
Sucrose	+	–	+	–	(+)	NG	+	+	+	+	+	+	+	–	+	+	+	+	+	+	+	+	–	–	–	+	+	+
D-Ribose	–	–	+	–	–	NG	+	+	+	–	+	(+)	(+)	+	–	+	–	–	–	–	–	–	–	–	–	–	–	+
Xylose	+	+	+	–	+	NG	+	+	+	+	–	–	+	–	–	–	(+)	+	+	+	–	+	+	+	(+)	+	+	+
Dulcitol	+	(+)	–	–	+	NG	+	+	–	NG	(+)	NG	–	+	+	+	–	–	–	–	–	(+)	+	–	+	–	–	–
Sorbitol	–	–	–	–	–	NG	–	–	–	+	(+)	–	+	+	–	–	–	–	–	–	–	–	–	(+)	–	–	+	+
Mannitol	+	(+)	–	–	–	NG	+	+	–	+	+	–	–	+	+	+	–	–	–	–	–	(+)	–	–	+	–	–	+
Inositol	–	–	–	–	–	NG	–	–	–	+	–	–	–	–	–	+	–	–	–	–	(+)	–	+	–	–	–	–	–
Adonitol	+	(+)	–	–	–	NG	+	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–	–	–	–	–	–	–

* Y, Deep yellow; O, orange; PY, pink-yellow; LY, lemon-yellow; (Y), yellowish after 3 or more days at room temperature.

† 1P, Polar mono; Peri, peritrichous.

Table 3. Selected features of the assimilation profiles of type strains of 28 *Sphingomonas* species obtained by Biotype 100

See Table 2 for identities of strains. +, Positive growth by substrate assimilation; –, substrate not assimilated. Final reading was performed after 7 days cultivation at 30 °C. The following compounds were not assimilated by any of the 28 type strains tested: dulcitol, L(+)-sorbitol, D(+)-arabitol, L(–)-arabitol, D-sorbitol, adonitol, hydroxyquinoline β -glucuronide, L(+)-tartrate, 3-phenylpropionate, *m*-coumarate, trigonelline, histamine, DL- α -amino-*n*-valerate, histidine, ethanolamine, malonate, 3-*o*-methyl D-glucopyranose, tryptophan.

Substrate	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28
D-Galacturonate	–	–	–	–	–	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	+	–	–	–	–
Phenylacetate	–	–	–	–	–	–	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	+
2-Oxoglutarate	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–	+	–	–	–	+	–	–	–	–	+	–	–
2-Keto-D-gluconate	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–	+	–	–	–	–	–	–	–	–	–	–	–
Benzoate	–	–	–	–	–	–	–	–	–	+	+	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
D(–)-Tartrate	–	–	–	–	–	–	–	–	–	–	–	–	+	+	–	–	–	–	–	–	+	–	–	–	–	–	–	–
D-Mannitol	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–	–	–	–	+	–	–	+
Citrate	–	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	+	–	–	–	–	+	–	–	+
L-Alanine	+	–	–	–	–	–	+	+	–	–	+	–	–	+	–	+	–	–	–	–	+	–	–	–	+	+	–	–
D(+)-Xylose	–	–	+	+	+	–	+	+	+	–	+	+	–	–	–	+	+	+	+	+	+	+	+	+	–	–	–	+
L(–)-Malate	+	+	+	–	+	–	–	–	+	–	+	–	–	+	–	–	+	+	–	+	+	+	+	–	+	+	+	+
L-Glutamate	+	–	+	+	–	–	+	+	+	+	+	–	+	+	–	+	+	–	+	+	+	+	+	+	+	+	–	+
α -L-Rhamnose	–	+	+	–	–	–	+	+	+	–	+	+	–	–	–	–	+	–	–	–	–	–	–	–	–	–	–	–
Succinate	–	–	+	–	+	–	–	–	+	+	+	+	–	–	–	–	+	+	+	+	+	+	–	–	+	+	–	+
D(+)-Mannose	–	–	+	–	–	–	+	+	+	–	–	+	–	–	+	–	+	–	+	+	+	+	–	+	+	+	+	+
Lactulose	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	+	+	+	–	–	–	–	–	–	–
D-Glucosamine	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–	–	–	–	–	+
Betaine	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–	–	–
Glutarate	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	+	–	–	–

Table 4. Results of API 20NE tests on type strains of 28 *Sphingomonas* species

See Table 2 for identities of strains. All 28 type strains were positive for the Zn-dust test and negative for the nitrite test, indole production from tryptophan, acid from glucose under mineral oil, arginine dihydrolase, urease and assimilation of D-mannitol. PNPG, *p*-Nitrophenyl β -D-galactopyranosidase.

Substrate or test	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28
Aesculin	+	+	+	*	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	*
PNPG	+	+	+	-	+	+	+	+	+	+	+	+	+	-	-	-	+	+	+	+	+	+	+	+	+	+	-	-
Assimilation of:																												
Glucose	+	+	+	+	+	-	+	+	+	+	+	+	+	-	-	+	+	+	+	+	+	+	+	+	+	+	+	-
L-Arabinose	-	-	+	+	+	-	-	+	+	+	+	+	-	-	-	+	+	+	+	+	+	+	+	+	+	+	+	-
D-Mannose	+	-	-	+	-	-	+	+	+	-	+	-	-	-	-	-	+	-	+	+	-	+	+	-	+	+	+	-
N-Acetyl glucosamine	-	-	+	+	-	-	+	-	+	-	+	+	-	-	-	-	+	-	+	+	+	+	+	+	+	+	+	-
Maltose	-	-	+	+	+	-	+	+	+	+	+	+	-	+	+	+	+	+	+	+	+	+	+	+	+	+	+	-
Gluconate	-	-	+	+	-	-	-	-	+	-	-	-	-	-	-	-	+	+	+	+	+	-	+	-	-	-	+	-
n-Capric acid	+	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-
Adipic acid	-	-	-	+	-	-	-	-	-	-	+	-	-	-	-	+	-	-	-	+	+	-	-	-	-	-	-	-
DL-Malic acid	-	+	+	+	+	-	-	-	-	-	+	-	-	+	-	-	+	+	+	+	+	+	-	-	-	+	+	-
Citrate	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	+	-	-	-	-	-	-	-	-
Phenylacetate	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+

* Negative on API 20NE, but positive on aesculin agar slants and Biotype 100.

Table 5. Selected cellular components characteristic for type strains of 28 *Sphingomonas* species

See Table 2 for identities of strains. All 28 type strains tested were positive for SGL-1 and ubiquinone 10. All 28 type strains tested were negative for 3-hydroxy fatty acids. tr, Less than 1 %; —, not detected; ND, no data; CPA, cyclopropanoic acid.

Cellular component	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28
Fatty acids (%):																												
16:1 ω 9c	7	5	14	3	22	13	16	11	2	18	6	17	29	4	9	5	3	13	3	2	1	1	tr	ND	ND	4	1	6
17:0 CPA	tr	1	tr	—	tr	6	12	11	2	4	—	tr	tr	45	10	1	2	3	tr	—	9	—	20	3	32	4	ND	tr
2-OH 14:0	10	14	14	13	10	13	10	10	16	18	17	11	7	2	9	8	17	16	28	18	20	13	5	14	3	18	23	10
2-OH 15:0	—	—	—	—	—	2	4	3	tr	3	—	—	—	13	—	—	tr	—	—	—	—	—	—	2	15	—	—	—
2-OH 16:1	—	—	tr	—	—	tr	—	—	—	—	—	—	—	—	tr	6	—	—	—	—	—	—	—	—	—	—	—	—
2-OH 16:0	1	3	2	—	—	tr	—	—	tr	—	7	—	4	tr	2	4	tr	—	—	—	—	—	3	2	—	—	—	—
Lipids:																												
SGL-1'	—	—	+	+	—	—	—	—	—	—	—	—	+	+	—	—	—	—	—	—	—	—	—	—	—	—	—	+
Other SGL(s)*	—	—	—	—	—	—	—	—	+	+	—	+	—	—	—	—	+	—	+	+	+	+	+	+	+	+	+	—
Major polyamines:†																												
Spermidine	+ ^a	+ ^a	+ ^a		+ ^b	+ ^a	+ ^a	+ ^a	+ ^a	+ ^a	+ ^a	+ ^a	+ ^a	+ ^a	+ ^{c,d}	+ ^a					+ ^c				+ ^a	+ ^a	+ ^a	
Homospermidine									+ ^c					+ ^d			+ ^a		+ ^a	+ ^a		+ ^a	+ ^a	+ ^a	+ ^a	+ ^a	+ ^a	

* Other SGL(s) represents SGL-2, -3 or -4.

† Data were taken from: *a*, Takeuchi *et al.* (2001); *b*, Stolz *et al.* (2000); *c*, Busse & Auling (1988); *d*, Segers *et al.* (1994); *e*, Hamana & Matsuzaki (1993).

Table 6. Antimicrobial susceptibility testing of 28 type strains of *Sphingomonas* species determined by the Kirby–Bauer method

See Table 2 for identities of strains. Abbreviations: AMPC, amoxicillin; CVC, clavulanic acid; S, susceptible; IM, intermediate; R, resistant. Except for the combinations AMPC/CVC and sulfamethoxazole/trimethoprim, discs contained a single agent.

Antimicrobial agent (mg/disc)	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28
AMPC/CVC (20/10)	S	S	S	IM	S	S	S	S	S	S	S	S	IM	S	S	S	S	S	S	S	S	S	S	R	S	S	S	S
Amoxicillin (25)	S	R	S	R	R	S	S	S	S	S	S	R	R	S	S	S	R	S	R	S	R	S	S	R	S	S	S	S
Penicillin G (10)	S	R	S	R	R	S	S	R	S	S	S	R	R	S	S	S	R	R	R	S	R	R	R	R	S	R	S	S
Ampicillin (10)	S	R	S	R	R	S	S	S	S	S	S	R	R	S	S	S	R	S	R	S	R	S	S	R	S	S	S	S
Piperacillin (100)	S	R	R	R	R	S	S	S	IM	S	S	R	R	S	S	S	R	R	R	R	R	R	R	R	S	IM	S	S
Cefoperazon (75)	S	R	S	R	R	S	S	S	IM	S	S	R	R	S	S	S	R	R	R	S	R	R	R	R	R	S	S	IM
Moxalactam (30)	R	R	R	S	R	S	R	R	IM	S	R	R	R	R	R	R	R	R	R	R	S	R	R	IM	IM	R	S	R
Cefaclor (30)	S	R	S	S	S	S	IM	IM	S	S	R	S	R	IM	S	S	R	S	R	S	IM	S	S	R	S	S	S	S
Ceftazidime (30)	S	S	S	R	S	S	S	S	S	S	IM	R	R	S	S	S	R	S	R	S	R	IM	R	S	S	S	S	S
Flomoxef (30)	S	S	R	R	S	S	S	S	S	S	IM	R	R	R	IM	IM	R	S	R	S	R	R	R	IM	R	R	S	S
Cefazolin (30)	R	R	R	R	R	S	R	R	S	S	R	R	R	S	R	S	R	S	R	R	R	R	R	R	R	R	S	S
Cefmetazole (30)	S	S	R	S	S	S	R	R	S	S	R	R	R	R	IM	IM	R	S	R	R	S	R	R	R	S	IM	S	S
Cefotaxime (30)	S	S	S	S	S	S	S	S	S	S	S	S	R	S	S	S	R	S	R	S	S	IM	S	IM	S	S	S	S
Meropenem (10)	S	S	S	R	S	S	S	S	S	S	IM	R	R	IM	S	S	S	S	S	S	R	S	S	S	IM	S	S	S
Aztreonam (30)	R	IM	R	S	IM	R	IM	S	R	S	S	S	R	R	R	IM	R	R	R	IM	S	R	R	R	S	R	R	R
Imipenem (10)	S	S	S	R	S	S	S	S	S	S	S	S	S	S	S	S	S	S	IM	S	R	S	S	S	S	S	S	S
Carumonam (30)	R	R	R	S	IM	S	S	S	R	S	IM	S	R	R	R	R	IM	R	S	S	S	R	R	S	S	R	R	S
Panipenem (10)	S	S	S	S	S	S	S	S	S	S	IM	R	S	S	S	S	S	S	S	S	S	IM	S	S	S	S	S	S
Gentamicin (10)	S	S	S	S	S	S	S	S	S	S	S	S	S	S	R	S	S	S	S	S	S	S	S	S	S	S	S	S
Amikacin (30)	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S
Dibekacin (30)	S	S	S	R	S	S	S	S	S	S	S	S	S	S	R	S	S	S	S	S	S	S	S	S	S	S	S	S
Clarithromycin (15)	R	S	S	R	S	S	S	S	S	S	S	S	R	S	S	S	S	S	S	S	IM	S	S	R	IM	S	S	R
Roxithromycin (15)	R	S	R	R	IM	IM	IM	S	R	S	R	IM	IM	R	R	S	S	S	S	S	IM	R	R	R	IM	R	R	R
Erythromycin (15)	R	S	IM	S	IM	S	IM	IM	IM	S	IM	IM	S	IM	IM	S	S	S	S	S	S	IM	R	R	S	R	R	R
Tetracycline (30)	S	S	S	S	IM	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	IM
Doxycycline (10)	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S
Minocycline (30)	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	R	S	S	R	S	S	S	S
Polymyxin B (300)	S	S	S	S	S	S	S	R	IM	R	S	R	S	S	IM	IM	IM	S	R	IM	R	R	R	R	R	R	R	IM
Norfloxacin (10)	S	S	IM	R	S	R	R	R	R	R	R	R	S	IM	IM	S	R	S	S	IM	R	R	R	R	R	R	R	R
Trimethoprim (5)	R	R	R	S	R	R	R	R	R	R	R	R	R	R	R	R	R	S	R	R	S	R	R	R	R	R	R	R
Ciprofloxacin (5)	S	S	S	S	S	S	R	R	R	R	R	R	R	S	S	S	S	S	S	S	IM	IM	R	IM	R	IM	S	R
Ofloxacin (5)	S	S	S	S	S	S	R	R	R	R	R	R	R	S	IM	S	S	S	S	S	S	IM	S	R	R	IM	S	R
Tosufloxacin (5)	S	S	IM	S	IM	S	R	R	R	R	R	R	S	IM	IM	R	S	S	S	S	S	S	IM	S	IM	IM	R	R
Levofloxacin (5)	S	S	S	S	S	S	IM	R	S	R	R	R	S	S	IM	S	S	S	S	S	S	S	S	S	R	S	R	R
Sparfloxacin (5)	S	S	S	S	S	S	R	IM	IM	S	R	R	S	S	IM	S	S	S	S	S	S	S	S	S	S	S	R	R
Sulfamethoxazole/trimethoprim (23·8/1·25)	S	R	S	S	R	S	IM	R	S	R	R	R	S	R	R	S	S	S	S	S	IM	R	S	R	S	R	IM	R
Summary:																												
Number of agents resisted	8	11	9	14	9	3	9	12	8	8	13	21	16	9	9	4	16	5	16	5	12	14	16	19	9	12	9	13
Percentage resisted	22	31	25	39	25	8	25	33	22	22	36	58	44	25	25	11	44	14	44	14	33	39	44	53	25	33	25	36
Number scored as S+IM	28	25	27	22	16	33	27	24	28	28	23	15	20	27	27	32	20	31	20	31	24	22	20	17	27	24	27	23

Sphingomonas ursincola, *Sphingomonas natatoria*, *Sphingomonas roseiflava*, *Sphingomonas pruni* and *Sphingomonas asaccharolytica* are non-motile, since they do not show spreading growth on 0.3 % semi-solid agar plates. Strictly aerobic. Metabolism is respiratory, but not fermentative. Cells of *Sphingomonas ursincola* and *Sphingomonas natatoria* contain bacteriochlorophyll *a* and these species are facultative photo-organotrophs. Colony colour varies from species to species, for instance, deep-yellow, orange, lemon-yellow or non-pigmented. The deep-yellow pigment of *Sphingomonas paucimobilis* is reported to be a carotenoid, nostoxanthin, rather than a xanthomonadin. This pigment was also found in *Sphingomonas* [*Pseudomonas*] *echinoides* (Denner *et al.*, 1999) and *Sphingomonas sanguinis* [*Pseudomonas paucimobilis*] (Jenkins & Starr, 1985; Starr *et al.*, 1977). In certain cases, pigmentation differs depending on the medium used. Colonies of some non-pigmented strains such as *Sphingomonas yanoikuyae* become lemon-yellow after more than 3 days incubation at room temperature. The type strain of *Sphingomonas herbicidovorans* produces alcapton via accumulation of homogentisic acid, as observed in pyromelanogenic strains of *Pseudomonas aeruginosa* (Gessard, 1891; Mann, 1979; Yabuuchi & Ohya, 1972).

Catalase is produced. Oxidase-positive with a few exceptions. The type strain of *Sphingomonas herbicidovorans* produces alcapton from phenylalanine (Zipper *et al.*, 1996) and a water-soluble melanin-like brown pigment is produced in peptone media. Respiratory quinone is ubiquinone 10. SGL-1 and 2-hydroxymyristic acid, but not 3-hydroxy fatty acids, are found in cellular lipids of all 28 species examined. Major long-chain bases of SGL-1 are C-18:0, C-20:1 and C-21 cyclopropane. SGL-1' exists in cellular lipids of *Sphingomonas yanoikuyae*, *Sphingomonas macroglabridus*, *Sphingomonas terrae*, *Sphingomonas wittichii* and *Sphingomonas cloacae*. The chemical structure, function and distribution of SGLs of *Sphingomonas* species have been reported from other members of the *Proteobacteria* (Kawahara *et al.*, 1999). The type strain of *Sphingomonas herbicidovorans* represents the second bacterial species in which homogentisic acid accumulates through metabolic defects in phenylalanine and tyrosine metabolism.

At the time of writing, the 33 species listed in Table 1 are assigned to the genus *Sphingomonas*. The 'Bacterial Nomenclature Up to Date' web site at the DSMZ (<http://www.dsmz.de>) should be referred to for further information.

Isolated from a wide variety of natural and artificial environments. Some are pathogenic for humans or lettuce. The plant-pathogenic species *Sphingomonas suberifaciens* is susceptible to 33 of 36 Sensi-discs; clinical and hospital-environment isolates are susceptible to fluoroquinolones, whereas species from other sources, especially from soil, are generally resistant to various kinds of antimicrobial agents. Strains of

species with optimal growth temperatures of 26 or 28 °C are unlikely to be human pathogens, although organisms in the natural environment that are resistant to various kinds of antimicrobials are potential human pathogens. Strains of certain species metabolize dioxins (Wittich *et al.*, 1992; Nohynek *et al.*, 1995, 1996) and other chlorophenol derivatives (Wittich *et al.*, 1992). The G + C content of DNA ranges from 59 to 67 mol % (HPLC). The type species is *Sphingomonas paucimobilis* (Holmes *et al.* 1977) Yabuuchi *et al.* 1990.

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