Transfer of Pseudomonas pictorum Gray and Thornton 1928 to genus Stenotrophomonas as Stenotrophomonas pictorum comb. nov., and emended description of the genus Stenotrophomonas

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Abstract

A polyphasic taxonomic approach including analysis of phenotypic, physiological and genotypic characteristics, 16S rRNA gene sequence and DNA–DNA hybridization analysis was used to determine the most consistent affiliation of Pseudomonas pictorum. Pseudomonas pictorum ATCC 23328T exhibited phenotypic traits of members of the genus Stenotrophomonas including cellular fatty acid composition, quinone and limited range of substrates that could be used. Antibiotic susceptibility and physiological characteristics were determined. The DNA G+C content was 65.7 mol%. Phylogenetic analysis revealed that the type strains of Stenotrophomonas terrae, Stenotrophomonas humi, Stenotrophomonas nitritireducens and Stenotrophomonas acidaminiphila were the nearest relatives (16S rRNA gene sequence similarity of 98.0 to 98.8 %). All the other type strains of species of the genus Stenotrophomonas showed high 16S rRNA gene sequence similarities (96.8 to 97.2 %). DNA–DNA hybridizations revealed 31.0, 32.0, 43.3 and 43.6 % reassociation between Pseudomonas pictorum ATCC 23328T and the type strains of S. terrae, S. humi, S. nitritireducens and S. acidaminiphila, respectively. Our overall results indicate that Pseudomonas pictorum should be transferred to the genus Stenotrophomonas as a novel species of this genus, Stenotrophomonas pictorum comb. nov. Since the original description of the genus Stenotrophomonas was made with only one species (Stenotrophomonas maltophilia), an emendation of the genus description is proposed in order to match better with the characteristics of the eleven novel species assigned to this genus since then.

The first description of Pseudomonas pictorum proposed by Gray and Thornton [1] was a report of the phenotypic characteristics of cells and morphology of colonies. Over the years, phenotypic studies (cellular fatty acid composition, quinone type content of cells, polyamine pattern and esterase polymorphism) and phylogenetic analysis (16S rRNA gene sequences, gyrB sequence, full genome sequence) have clearly pointed out that Pseudomonas pictorum should rather be reclassified within the family Xanthomonadaceae lineage and that its closest relatives are species of the genus Stenotrophomonas [2–12]. As a consequence, the type strain of Pseudomonas pictorum has been included in several studies concerning the genomic and phenotypic diversity of the genus Stenotrophomonas in which this type strain was even sometimes presented as a member of Stenotrophomonas maltophilia, with which, however, it shows only 30 % DNA–DNA reassociation [4, 13, 14]. Despite this body of evidence and wide acceptance, Pseudomonas pictorum has still not been formerly assigned to the genus Stenotrophomonas. The aim of the present study was to determine the most consistent taxonomic position of Pseudomonas pictorum by a polyphasic taxonomic approach including analysis of phenotypic, physiological and genotypic (16S rRNA gene sequence similarities and DNA–DNA hybridization) properties and characteristics of this species. Since no other Pseudomonas pictorum strain than the type strain is presently available in public culture collections and all the accessible cultures of the type strain are derived from the strain deposited in the Czech collection of micro-organisms under the number CCM 284T, our study was limited to the type strain.

Cultures of all the type strains were prepared using nutrient broth media (3 g meat extract l–1, 5 g peptone l–1, 5 g yeast extract l–1). Unless otherwise indicated, cultures of microorganisms for performing phenotypic tests were prepared

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Abbreviations: CFA, cellular fatty acid; MICs, minimum inhibitory concentrations.
The GenBank/EMBL/DDBJ accession number for the 16S rRNA gene sequence of the type strain is AJ131116. Two supplementary figures and three supplementary tables are available with the online Supplementary Material.

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under aerobic conditions at 35°C, pH 7. All analyses were performed at least in duplicate. For phenotypic and biochemical characteristic determination as well as DNA–DNA hybridization experiments, we worked with *Pseudomonas pictorum* ATCC 23328<sup>T</sup>. The 16S rRNA sequence used for the phylogenetic analysis corresponds to that of *Pseudomonas pictorum* LMG 981<sup>T</sup> (GenBank accession number AJ131116; 1502 positions used). All the other type strains of species of the genus *Stenotrophomonas* used during this study were obtained from public culture collections. The culture collection references of these type strains are listed in Table S1 (available in the online Supplementary Material). The phylogenetic analysis was performed as described by Assih et al. [7] except that this time the MEGA software (version 5.2; http://www.megasoftware.net) and the Muscle algorithm were used to align the 16S rRNA sequences. This analysis revealed that the closest relatives were the type strains of *Stenotrophomonas humi*, *Stenotrophomonas terrae*, *Stenotrophomonas nitritireducens* and *Stenotrophomonas acidaminiphila* with similarity levels of 98.8, 98.8, 98.6 and 98.0%, respectively. All the other type strains of species of the genus *Stenotrophomonas* showed high 16S rRNA gene sequence similarities ranging from 96.8 to 97.2% (Fig. 1). *Pseudomonas pictorum* ATCC 23328<sup>T</sup> cannot be assigned to *Stenotrophomonas daejeonensis*, *Stenotrophomonas koreensis*, *Stenotrophomonas maltophilia* or *Stenotrophomonas pavanii* since they share less than 97% 16S rRNA gene sequence similarity [15, 16]. Recently, a 16S rRNA gene sequence similarity of 98.2% has been proposed as the new cut-off point above which DNA–DNA reassociation experiments should be necessary for testing the genomic uniqueness of a novel isolate [17–19]. Based on this criteria, *Pseudomonas pictorum* could not be assigned to *Stenotrophomonas chelatiphaga*, *Stenotrophomonas rhizophila* or *Stenotrophomonas ginsengisoli* with which it shares 97.1 to 97.2% 16S rRNA gene sequence similarity. Therefore, DNA–DNA tests were performed only with the four type strains sharing at least 98% 16S rRNA gene sequence similarities.

The DNA–DNA hybridizations with *S. acidaminiphila* CIP 106456<sup>T</sup> and *S. nitritireducens* DSM 12575<sup>T</sup> were done by the DSMZ using the spectroscopic method as described elsewhere [20–24] while the DNA–DNA hybridizations with *S. humi* CCUG 54881<sup>T</sup> and *S. terrae* CCUG 54880<sup>T</sup> were determined by the BCCM/LMG using the microplate method developed by Ezaki et al. [25] with the

![Phylogenetic Dendrogram](image-url)

**Fig. 1.** 16S rRNA gene sequence phylogenetic dendrogram showing the position of *Pseudomonas pictorum* LMG 981<sup>T</sup> among the representative members of the genus *Stenotrophomonas*. Bar, 2 nucleotide substitutions per 100 nucleotides. Numbers (percentages) at nodes correspond to bootstrap values based on 1000 resamplings. Sequence accession numbers are indicated in parentheses.
modifications implemented by Goris et al. [26] and Cleenwerck et al. [27]. These tests revealed that *Pseudomonas pictorum* ATCC 23328\(^T\) hybridized at 31.0±2.3 % with *S. humi* CCUG 54881\(^T\), at 32.0±10 % with *S. terrae* CCUG 54880\(^T\), at 43.6 % with *S. acidaminiphila* CIP 106456\(^T\) and at 43.3 % with *S. nitritireducens* DSM 12575\(^T\). These values are consistent with the 70 % cut-off limit for species delineation. The 16S rRNA gene sequence analysis coupled to the DNA−DNA hybridization with the closest relatives showed that *Pseudomonas pictorum* belongs to the genus *Stenotrophomonas* but that it cannot be assigned to any of the species of the genus *Stenotrophomonas* with names with valid standing in nomenclature described so far. As a consequence, the most consistent alternative seems to be the affiliation of *Pseudomonas pictorum* as a distinct novel species of the genus *Stenotrophomonas*. Such conclusion is in line with results pointed out by several authors [6, 11] including one study based on the analysis of the full genome of *Pseudomonas pictorum* [12].

Additional biochemical characteristics provided by our study were the cellular fatty acid (CFA) composition and DNA G+C content (mol%) of *Pseudomonas pictorum* ATCC 23328\(^T\). The CFA compositions of the type strains of all the species with validly published names assigned presently to the genus *Stenotrophomonas* were redetermined at the DSMZ using the Sherlock Microbial Identification system (MIDI) and standard MIDI procedures for strain cultivation (24 h at 28 °C in trypticase soy broth supplemented with 15 g agar l \(^{-1}\)). The CFA profiles obtained were compared by unweighted arithmetic average clustering to those of all the species of the genera *Pseudomonas*, *Pseudoxanthomonas* and *Xanthomonas* having names with valid standing in nomenclature at present in the MIDI TSBA6 library using MIDI proprietary software that discloses the results in the form of a dendrogram. The CFA profiles for each species in the MIDI TSBA6 library correspond to the average profile of several strains including the type strain. The major fatty acids of *Pseudomonas pictorum* ATCC 23328\(^T\) were iso-C\(_{15:0}\) (24.2 %), anteiso-C\(_{15:0}\) (8.1 %), iso-C\(_{17:1}\)\(ω9c\) (7.5 %), C\(_{16:0}\) (6.7 %), iso-C\(_{14:0}\) (6.1 %) and iso-C\(_{15:1}\) \(F\) (5.5 %). Up to 15 CFAs were always present in the CFA profile determined for the type strains of all the species of the genus *Stenotrophomonas* and in the cell fatty acid pattern of *Pseudomonas pictorum* ATCC 23328\(^T\) (Table S2 and genus description). The unresolved CFA mixture iso-C\(_{15:0}\) 2-OH/ C\(_{16:1}\)\(ω7c\) was also present in the CFA composition determined for all the strains included in our study (Table S2). The three CFAs (iso-C\(_{11:0}\), iso-C\(_{11:0}\) 3-OH and iso-C\(_{13:0}\) 3-OH) identified by Yang et al. [28] as characteristic of the genera *Stenotrophomonas* and *Xanthomonas* were detected in the CFA pattern of *Pseudomonas pictorum* ATCC 23328\(^T\) (Table S2).

Other fatty acids present at a level of more than 1 % in most of the type strains of species of the genus *Stenotrophomonas* tested were: iso-C\(_{11:0}\) (3.4–6.4 %), iso-C\(_{11:0}\) 3-OH (1.3–3.3 %), C\(_{14:0}\) (1.2–13.5 %), iso-C\(_{15:1}\) \(F\) (1.1–20.0 %), iso-C\(_{15:0}\) (17.1–38.1 %), anteiso-C\(_{15:0}\) (1.8–18.1 %), iso-C\(_{16:0}\) (1.2–11.9 %), C\(_{16:0}\) (1.2–6.7 %) and iso-C\(_{17:1}\)\(ω9c\) (2.2–13.5 %). The comparison by unweighted arithmetic average clustering of the CFA profile of *Pseudomonas pictorum* ATCC 23328\(^T\) showed that *S. terrae* CCUG 54880\(^T\) and *S. humi* CCUG 54881\(^T\) were the two type strains with the closest CFA profiles (Fig. S1), which is in line with the 16S rRNA gene sequence phylogeny (Fig. 1) and gyrB sequence analysis [11]. The CFA average clustering clearly showed also that *Pseudomonas pictorum* ATCC 23328\(^T\) does not cluster with the species of the genus *Pseudomonas* but rather with those belonging to the family *Xanthomonadaceae* lineage (Fig. S2). Within this lineage, the species of the genus *Stenotrophomonas* did not, however, form a homogeneous separate cluster from the members of the genus *Xanthomonas* and other related species (e.g. species of the genus *Pseudoxanthomonas*). This indicates that CFA is not an adequate discrimination tool among the different genera of this lineage.

The DNA guanine-plus-cytosine content (G+C, mol%) of the bacterial DNA of *Pseudomonas pictorum* ATCC 23328\(^T\) was determined by the BCCM/LMG using the HPLC technique [29]. The value reported is the mean value of three independent analyses of the same DNA sample. The DNA G+C content (mol%) of *Pseudomonas pictorum* ATCC 23328\(^T\) found during this study was 65.7 mol%, which is within the range of values (64.0–69.2 mol%) reported for the other species of the genus *Stenotrophomonas* [30] (Table 1) and is identical to the value reported earlier by de Vos et al. [31]. The two previous experimental values are in agreement with the DNA G+C content (66.0 mol%) calculated from the full sequence of *Pseudomonas pictorum* JCM 9942\(^T\) by Patil et al. [12].

Procedures for determination of general phenotypic characteristics for *Pseudomonas pictorum* were as described elsewhere [7, 32, 33]. Our results of phenotypic characterization were partially consistent with those reported by Gray and Thornton [1] and the general characteristics given by Palleroni and Bradbury [34] and Palleroni [35] for the genus *Stenotrophomonas*. The overall results of phenotypic characterization are given in the genus and species descriptions and in Table 1. *Pseudomonas pictorum* could be easily distinguished from the other species of the genus *Stenotrophomonas* by the colour of its colonies on nutrient agar (data not shown) and from its closest relatives, *S. humi*, *S. terrae*, *S. nitritireducens* and *S. acidaminiphila*, by its ability to assimilate gentiobiose and D-lyxose but not L-proline or L-serine. Motility and fructose utilization were the common properties shared by *Pseudomonas pictorum* and its closest relatives pertaining to genus *Stenotrophomonas* (Table 1). The disc diffusion technique as described by Thierry et al. [33] was used to evaluate the susceptibility of the type strain of *Pseudomonas pictorum* towards a set of medical antibiotics. Our data showed that *Pseudomonas pictorum* ATCC 23328\(^T\) presented low MICs (minimum inhibitory concentrations) to 14 of the 16 antibiotics tested and was only apparently resistant to cefalotin, a first generation cephalosporin, and amoxicillin that both act on penicillin glycosynthase.
Table 1. General phenotypic characters and DNA G+C content (mol%) of the type strain of *Pseudomonas pictorum* and those of type strains of species of the genus *Stenotrophomonas* having names with standing in nomenclature

Taxa: 1, *Pseudomonas pictorum* ATCC 23328; 2, *Stenotrophomonas humi*; 3, *Stenotrophomonas terrae*; 4, *Stenotrophomonas nitritireducens*; 5, *Stenotrophomonas acidaminiphila*; 6, *Stenotrophomonas ginsengisoli*; 7, *Stenotrophomonas chelatiphaga*; 8, *Stenotrophomonas rhizophila*; 9, *Stenotrophomonas dajeonensis*; 10, *Stenotrophomonas maltophilia*; 11, *Stenotrophomonas koreensis*; 12, *Stenotrophomonas pavani*; +, Positive; −, negative; w, weakly positive; v, variable; nr, not reported. All the species are Gram-reaction-negative, oxidase-positive and catalase-positive. The following substrates were not utilized by *Pseudomonas pictorum* D:

<table>
<thead>
<tr>
<th>Characteristic</th>
<th>1(^a)</th>
<th>2(^b)</th>
<th>3(^b)</th>
<th>4(^c)</th>
<th>5(^c)</th>
<th>6(^c)</th>
<th>7(^c)</th>
<th>8(^d)</th>
<th>9(^b)</th>
<th>10(^f)</th>
<th>11(^f)</th>
<th>12(^f)</th>
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<tbody>
<tr>
<td>Morphology of colonies</td>
<td>Circular</td>
<td>Smooth, irregular</td>
<td>Smooth, round</td>
<td>NR</td>
<td>Circular</td>
<td>Glossy, circular</td>
<td>Smooth, convex, shiny</td>
<td>Yellowish</td>
<td>Yellowish</td>
<td>White, greyish or pale yellow</td>
<td>Smooth, glistening, entire margin</td>
<td>Smooth, convex, non-glossy</td>
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<tr>
<td>Colour of colonies</td>
<td>Yellow-orange</td>
<td>Light yellow</td>
<td>Beige</td>
<td>Yellow</td>
<td>Pale yellow</td>
<td>Yellow</td>
<td>Yellow</td>
<td>Yellowish</td>
<td>Yellowish</td>
<td>White, greyish or pale yellow</td>
<td>Smooth, glistening, entire margin</td>
<td>Smooth, convex, non-glossy</td>
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<tr>
<td>Motility</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
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<td>+</td>
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<td>Acid production from glucose</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>−</td>
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<td>Aesculin hydrolysis</td>
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<td>−</td>
<td>w</td>
<td>v</td>
<td>+</td>
<td>−</td>
<td>−</td>
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<td>+</td>
<td>+</td>
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<td>Gelatin hydrolysis (Protease)</td>
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<td>w</td>
<td>−</td>
<td>+</td>
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<td>Amylase (starch hydrolysis)</td>
<td>v</td>
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<td>−</td>
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<td>Nitrate reduction to nitrite</td>
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<td>−</td>
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<td>Nitrite reduction</td>
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<td>−</td>
<td>−</td>
<td>+ (to N(_2)O)</td>
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<td>NR</td>
<td>NR</td>
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<td>Nutritional spectrum</td>
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<td>D-Glucose</td>
<td>+</td>
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<td>−</td>
<td>+</td>
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<td>D-Fructose</td>
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<td>NR</td>
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<td>+</td>
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<td>+</td>
<td>−</td>
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<td>−</td>
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<td>NR</td>
<td>NR</td>
<td>v</td>
<td>NR</td>
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<td>D-Lyxose</td>
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<td>+</td>
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<td>L-Histidine</td>
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<td>−</td>
<td>−</td>
<td>v</td>
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<td>NR</td>
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<td>L-Proline</td>
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<td>w</td>
<td>w</td>
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<td>L-Alanine</td>
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<td>NR</td>
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<td>L-Serine</td>
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<td>−</td>
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<td>Acetate</td>
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<td>w</td>
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<td>Propionate</td>
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<td>−</td>
<td>w</td>
<td>v</td>
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<td>NR</td>
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<td>−</td>
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<td>DL-Lactate</td>
<td>−</td>
<td>+</td>
<td>v</td>
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**Pseudomonas pictorum** ATCC 23328\(^1\) was, however, susceptible to the six other antibiotics tested working with the same mechanism (Table S3).

Phylogenetic differences between the type strain of **Pseudomonas pictorum** and any of the type strains of species of the genus *Stenotrophomonas* are supported by phenotypic and biochemical differences. The overall results of the present study together with past analyses [2–7, 11, 12, 131, 31, 36] support that *Pseudomonas pictorum* should be transferred to the genus *Stenotrophomonas* as a novel species of this genus, *Stenotrophomonas pictorum* comb. nov. An emended description of the genus *Stenotrophomonas* is, therefore, proposed in order to take into account new taxonomic data available through the description of several novel species assigned to this genus since its creation by Palleroni and Bradbury [34].

**EMENDED DESCRIPTION OF THE GENUS **

*Stenotrophomonas*

The etymology, morphology and biochemical properties are as indicated in the genus description [34, 35]. Additional or modified properties are as follows: reduction of nitrate to nitrite is variable; oxidase reaction is variable; Tween 80, gelatin and starch hydrolysis are variable; species are nonmotile or motile by means of a single polar flagellum or several polar flagella; some species may grow anoxically using nitrate as an alternate electron acceptor; colonies are white, beige, greyish, yellowish, pale yellow, light yellow, orange-yellow or yellow on common solid media; colonies are smooth, glistening and often circular; growth is not accompanied by odour on common solid media but odour could develop on some media. The CFAs are of the iso/anteiso type with iso-\(C_{15:0}\) normally clearly predominating. The other predominating fatty acids present are iso-\(C_{11:0}\), anteiso-\(C_{15:0}\) and iso-\(C_{17:1}\). Other CFAs usually or always present in cells are \(C_{10:0}\), iso-\(C_{11:0}\), \(3\)-OH, iso-\(C_{13:0}\), \(C_{12:0}\), \(3\)-OH, iso-\(C_{14:0}\), \(C_{14:0}\), iso-\(C_{15:1}\), \(F\), \(C_{15:0}\), iso-\(C_{16:0}\), \(C_{16:0}\) and iso-\(C_{17:0}\). DNA G+C content is 64.0–69.2 mol%. Members of the genus are widely distributed in nature. The type species is *Stenotrophomonas maltophilia*.

**DESCRIPTION OF STENOTROPOMONAS PICTORUM COMB. NOV.**

*Stenotrophomonas pictorum* (pic.to’rum). L. gen. pl. n. pictorum of painters; here, intended to mean of the Picts, named after the Picts, a Scottish tribe.

Exhibits all of the characteristics of the members of the genus. Cell size: 0.5–0.8×1.5–3\(\mu\)m. Colonies are yellow and circular on trypticase soy agar. On nutrient agar, colonies are orange-yellow or yellow. Cells are positive for catalase, aesculin hydrolysis and ‘Tween 80 esterase but negative for urease, indole production, ONPG, Simmons’ citrate, lysozyme and ornithine decarboxylase, arginine dihydrolase, DNase and proteolysis. Oxidase and starch hydrolysis are variable. Nitrate is reduced but not nitrite. Polyamines: spermidine (major), cadaverine...
and spermine (minor). Quinone type: Q8. A limited range of substrates can be utilized (11 of 99 tested) including D-glucose, D-fructose, D-mannose, maltotriose, maltose, gentiobiose, D-lyxose, N-acetyl-D-glucosamine, L-histidine, L-alanine and phenol. Acid is produced from D-glucose (dextrose) and maltose. Cholesterol is depleted when grown on bovine calf serum but not used as a sole carbon source in mineral medium. Substrates not used are listed in Table 1. No growth was observed at 4°C or 41°C. Susceptible to the antibiotics ticarcillin, piperacillin, piperacillin + tazobactam, imipenem, cefotaxime, ceftazidime, tobramycin, amikacin, gentamicin, netilmicin, colistin, amoxicillin, piperacillin + tazobactam, imipenem, cefotaxime, ceftazidime, tobramycin, amikacin, gentamicin, netilmicin, colistin, trimethoprim + sulfamethoxazole, ofloxacin and ciprofloxacin; resistant to amoxicillin and cefalotin. All the CFAs characteristic of the genus *Pseudomonas* are present. Predominant fatty acids are, by decreasing order of abundance, iso-C₁₅:₀ anteiso-C₁₅:₀, iso-C₁₇:₁ω9c, C₁₆:₀, iso-C₁₄:₀ and iso-C₁₅:₁ F.

The type strain is ATCC 23328T (= CCM 284T = CCUG 1823T = CIP 103273T = DSM 19282T = JCM 9942T = LMG 981T = NCIMB 9152T = VKM 1240T), originally isolated from soil. The DNA G+C content of the type strain is 65.7 mol%. The GenBank/EMBL/DDBJ accession number for the 16S rRNA gene sequence of the type strain is AJ131116.

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**Conflicts of interest**
The authors declare that there are no conflicts of interest.

**References**


