**Phaeobacter piscinae** sp. nov., a species of the *Roseobacter* group and potential aquaculture probiont

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**Abstract**

Four heterotrophic, antimicrobial, motile, marine bacterial strains, 27-4T, 8-1, M6-4.2 and S26, were isolated from aquaculture units in Spain, Denmark and Greece. All four strains produced the antibiotic compound tropodithietic acid, which is a key molecule in their antagonism against fish pathogenic bacteria. Cells of the strains were Gram-negative, rod-shaped and formed star-shaped aggregates in liquid culture and brown-coloured colonies on marine agar. The predominant cellular fatty acids were C18:ω7c, C18:ω0, C11 methyl C18:ω7c and C16:0 2-OH, and the polar lipids comprised phosphatidylglycerol, diphosphatidylglycerol, phosphatidylethanolamine, phosphatidylcholine, an aminolipid, a phospholipid and an unidentified lipid. The strains grew optimally at 31–33 °C. Growth was observed at a salt concentration between 0.5 and 5–6 % NaCl with an optimum at 2–3 %. The pH range for growth of the strains was from pH 6 to 8–8.5 with an optimum at pH 7. Based on 16S rRNA gene sequence analysis, the strains are affiliated with the genus *Phaeobacter*. The genome sequences of the strains have a DNA G+C content of 60.1 % and share an average nucleotide identity (ANI) of more than 95 %. The four strains are distinct from the type strains of the closely related species *Phaeobacter gallaeciensis* and *Phaeobacter inhibens* based on an ANI of 90.5–91.7 and 89.6–90.4 %, respectively, and an in silico DNA–DNA hybridization relatedness of 43.9–46.9 and 39.8–41.9 %, respectively. On the basis of phylogenetic analyses as well as phenotypic and chemotaxonomic properties, the isolates are considered to represent a novel species, for which the name *Phaeobacter piscinae* sp. nov. is proposed. The type strain is 27-4T (=DSM 103509T=LMG 29708T).

Bacteria affiliated with the *Roseobacter* group are widely distributed in marine environments and may represent up to 8 % of the surface water bacterioplankton [1–4]. They have been isolated from seawater, marine sediments, surfaces of marine organisms and hyper-saline ponds [5]. Close association and interaction with microalgae has been suggested due to their co-appearance in the marine environment [4, 6] and the ability of many strains to metabolize algal-derived dimethyl-sulfoniopropionate [5, 7]. Members of the *Roseobacter* group co-cultivated with microalgae in the laboratory were found to initially stimulate growth of the microalgae but subsequently led to algal decline [8–10]. In the case of strains belonging to the genus *Phaeobacter*, this activity may be due to the production of algicidal molecules, the roseobacticides [11]. Furthermore, all three species of the recently reclassified genus *Phaeobacter* [12] with validly published names, *Phaeobacter inhibens* [13, 14], *Phaeobacter gallaeciensis* [13, 15] and *Phaeobacter porticola* [16], produce the antibacterial compound tropodithietic acid (TDA), providing them with antagonistic activity against the fish pathogen *Vibrio anguillarum*. TDA-producing strains of the genus *Phaeobacter* have also been found as a dominant colonizer in aquaculture units [17–19]. These strains are therefore promising candidates as probionts for disease control in aquaculture industries. In the present study, we describe four strains isolated from different marine aquaculture units representing a novel species of the genus *Phaeobacter*.

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**Keywords:** Phaeobacter; Roseobacter group; aquaculture; tropodithietic acid; probiont.

**Abbreviations:** ANIb, average nucleotide identity by BLAST; MIC, minimal inhibitory concentration; OD600, optical density at 600 nm; TDA, tropodithietic acid.

The GenBank/EMBL/DDBJ accession numbers for the 16S rRNA gene sequences of the *Phaeobacter piscinae* strains 27-4T, M6-4.2, S26 and 8-1 are AJ536669.1, FJ014982.1, KT884056.1 and AJ536670.1, respectively. The genome accession numbers for *Phaeobacter piscinae* strains 27-4T, M6-4.2, S26 and 8-1 are CP010681-88, CP010643-49, JSWK01 and CP010767-75, respectively.

Six supplementary figures and four supplementary tables are available with the online Supplementary Material.
Strains 27-4T and 8-1 were isolated from rotifers and a turbot larvae tank surface, respectively, from Spanish turbot rearing units in 2001 [18], M6-4.2 was isolated from the turbot larvae tank surface of a Danish turbot larval farm in 2006 [17], and S26 was isolated from a Greek sea bass aquaculture unit in 2013 [19]. The reference strains Phaeobacter inhibens DSM 16374T, Phaeobacter galacceiensis DSM 26640T, and strains Pseudophaeobacter arcticus DSM 23566T, Pseudophaeobacter leonis DSM 25627T, Leisingera caerulea DSM 24564T and Leisingera daeponensis DSM 23529T formally belonging to the genus Phaeobacter were obtained from the Leibniz-Institut DSMZ-German Collection of Microorganisms and Cell Cultures (Braunschweig, Germany); Leisingera aquaemixtae CECT 8399T was obtained from the Colección Española de Cultivos Tipo (Paterna, Spain), and ‘Phaeobacter (Pseudophaeobacter) marinintestinus’ JCM 19926, whose name has not yet been validly published, was obtained from the RIKEN BioResource Centre (Ibaraki, Japan). Phaeobacter porticola PP7T was kindly provided by Sven Breider (University of Oldenburg, Germany). Routinely, strains were cultivated on marine agar 2216 (MA; Difco) at 25 °C and pre-cultures were grown in 5 ml ½YTSS [per litre: 20 g sea salts (Sigma-Aldrich), 2 g yeast extract and 1.25 g tryptone] [20] in 15 ml culture tubes at 200 r.p.m. at 25 °C.

Motility was assessed using light microscopy (at ×1000 magnification). Cell morphology was studied by scanning electron microscopy (FEI Quanta 200F FEG in wet-STEM mode and FEI Helios, dual beam, in high vacuum). Gram testing, and determination of catalase and oxidase activity were performed with 3 % KOH [21], 3 % H2O2 [22] and the BBL DrySlide Oxidase kit (BD Diagnostics), respectively. Anaerobic growth was evaluated on MA with incubation at room temperature using an anaerobic jar and anaerobic atmosphere generation bags (Sigma-Aldrich).

Optimal growth conditions were determined for strains 27–4T, 8-1, M6-4.2, S26, DSM 26640T and DSM 16374T using cultures inoculated with 1 % (v/v) overnight pre-culture. The temperature range for growth was analysed in 10 ml ½YTSS in 100 ml Schott flasks incubated without shaking at 5, 6, 8, 10, 15, 37 and 45 °C. The temperature optimum was investigated in 200 μl ½YTSS in flat-bottom Nunc MicroWell 96-well plates (ThermoFisher Scientific) at 21, 23, 25, 27, 29, 31, 33, 35 °C. The salinity range and optimum for growth were analysed in 200 μl mineral medium [23] in flat-bottom Nunc MicroWell 96-well plates using 0, 0.5, 1, 2, 3, 4, 5, 6, 7, 8, 9, 10 % NaCl at 25 °C. The pH range and optimum for growth were analysed in 200 μl ½YTSS in flat-bottom Nunc MicroWell 96-well plates using 50 mM sodium acetate (pH 5.0–6.0), Tris/HCl (pH 6.5–9.0) or N-cyclohexyl-3-aminopropanesulfonic acid (CAPS) (pH 9.5–11.0) as buffer at 25 °C.

Physiological and biochemical characterization using API 20 NE strips (BioMérieux) and API ZYM strips (BioMérieux) was performed for all strains at 25 °C. Bacterial suspensions were performed in 2 % (w/v) sea salts (Sigma-Aldrich) using biomass grown overnight on MA at 25 °C, and inoculation was done in agreement with the instructions of the manufacturer. The ability to produce the antibacterial compound TDA was determined by inoculation of 1 % overnight pre-culture into 5 ml ½YTSS containing 5 mM FeCl3 in 50 ml Falcon tubes, with incubation of cultures for 72 h at 25 °C and subsequent extraction and chemical validation by ultra-HPLC/time-of-flight mass spectrometry (UHPLC-TOFMS) as described previously [19].

To test the utilization of different carbon sources for growth, pre-cultures were grown overnight in 5 ml mineral medium [23] supplemented with 0.3 % casamino acids at 200 r.p.m. and 25 °C. Cells were washed twice in mineral medium without carbon source and were then inoculated to a starting optical density at 600 nm (OD600) of 0.01 in mineral medium containing the following carbon sources at a final concentration of 1 mM: DL-aspartic acid, L-asparaginase, D-glucose, L-glutamine, L-isoleucine, L-leucine, L-lysine, D-mannan, D-mannose, L-phenylalanine, raffinose, D-sorbitol, Tween 40 and Tween 80. Medium with each carbon source without addition of cells as well as medium without carbon source with addition of cells were used as negative controls. The cultures were incubated at 200 r.p.m. and 25 °C, and growth was determined by measuring OD600 after 1 week.

The cellular fatty acids of strains 27–4T, 8-1, M6-4.2, S26, Phaeobacter inhibens DSM 17395, DSM 26640T and DSM 16374T were analysed as methyl esters by gas chromatography. The analysis was performed using biomass grown for 24 h on MA at 25 °C and according to the instructions of the Microbial Identification System (MIDI). Respiratory lipiquiones and polar lipids were extracted after Tindall et al. [24] from freeze-dried cell material of strains 27–4T, 8-1 and M6-4.2 grown in marine broth 2216 (MB; Difco) at 25 °C. Respiratory lipoquinones were identified by HPLC using an RP18 column, and polar lipids were separated by two-dimensional TLC and identified based on their reaction with specific staining reagents [24].

Complete 16S rRNA gene sequences were extracted from the genome sequences using RNAmmer [25]. The genome accession numbers are given in Figs 1 and S4 (available in the online Supplementary Material). The 16S rRNA gene sequence of JCM 19926 (acc. no. KJ461690.1) was retrieved from NCBI due to the lack of a full genome sequence. To determine percentage similarities, the sequences were aligned using megablast [26]. For phylogenetic comparison, the 16S rRNA gene sequences were aligned using MUSCLE [27] and neighbour-joining and maximum-likelihood trees were generated with bootstrap values based on 1000 replicates in MEGA7 [28]. Comparison of average nucleotide identity based on BLAST (ANiB) was conducted using JSpeciesWS (http://jspecies.ribohost.com/jspeciesws/) [29]. A heatmap was generated in R using complete agglomeration clustering based on Euclidean distances. In addition, in silico DNA–DNA hybridization was carried out using the Genome-to-Genome Distance Calculator GGD 2.1 with formula 2 (http://ggdc.dsmz.de/distcalc2.php) [30, 31].
Experiments were done in three parallels. Forming units were quantified after 4–5.0, 5.5 or 6.0 mM CuCl₂ supplemented with 0.0, 0.5, 1.0, 1.5, 2.0, 2.5, 3.0, 3.5, 4.0, 4.5, 5.0, 5.5 or 6.0 mM CuCl₂ and incubated at 25°C. Antibiotic susceptibility was determined in 27-4, M6-4.2, S26, 8-1 and their closest relatives, obtained using the neighbour-joining method and compared with the maximum-likelihood method. Rhodovulum sulfidophilum DSM 1374ᵀ was used as an outgroup. The sequence alignment was performed with MUSCLE [27], and the reconstructions were generated using MEGA7 [28]. Support values (percentages) from 1000 bootstrap replicates are displayed above branches. Only values >50 % are shown at major nodes. Bar, 0.01 nucleotide substitutions per site. Filled circles indicate nodes also recovered reproducibly with the maximum-likelihood method.

Phylogenetic analysis of the 16S rRNA gene sequences demonstrated that strains 27-4ᵀ, M6-4.2, S26 and 8-1 form a separate cluster within the genus Phaeobacter (Fig. 1). The similarity that they share with Phaeobacter gallaeciensis DSM 26640ᵀ (99.66–99.86 %) is equivalent to the similarity that they have with Phaeobacter inhibens DSM 16374ᵀ (99.66–99.86 %). The strains are less similar to Phaeobacter portulica P97ᵀ (98.96–99.03 %) and ‘Phaeobacter marinintestinus’ JCM 19926 (96.40–96.48 %). The 16S rRNA gene sequence similarity between the strains and the most closely related type strains is comparable to that between Phaeobacter gallaeciensis DSM 26640ᵀ and Phaeobacter inhibens DSM 16374ᵀ (99.73 %). In the V4 and V5 region of the 16S rRNA gene [32], the four strains resemble either DSM 26640ᵀ (V4) or DSM 16374ᵀ (V5) (Fig. S3). A high similarity of 16S rRNA gene sequences despite a distinct genomic divergence has been described previously for the roseobacters [12].

According to the ANIb analysis, the genome sequences of strains 27-4ᵀ, M6-4.2, S26 and 8-1 share more than 95 % similarity, classifying them as representatives of the same species, while they are less than 95 % similar to Phaeobacter gallaeciensis DSM 26640ᵀ (90.7, 90.5, 90.8, 91.7 %, respectively) and Phaeobacter inhibens DSM 16374ᵀ (89.7, 89.6, 89.9, 90.4 %, respectively) (Fig. S4). The in silico DNA–DNA hybridization values to the other type strains are less than 46.9 % (Table S1), which is also far below the accepted threshold value for species delineation [31, 33]. The genome similarity among strains 27-4ᵀ, M6-4.2 and S26 is 85.1–
87.0%, while the similarity of these three strains to strain 8-1 is 64.7–64.9%.

The fatty acid profiles of 27-4T, M6-4.2, S26 and 8-1 were similar to those of DSM 26640T and DSM 16374T, with the dominant cellular fatty acids being C16:0 (47%), C12:0 (41%), C16:0 (35%) and C18:0 (15%) (Table S2). The polar lipid profile of all strains comprised phosphatidylglycerol, phosphatidylethanolamine, phosphatidylcholine, an aminolipid, a phospholipid and an unidentified lipid, which were also present in Phaeobacter gallaeciensis DSM 26640T, Phaeobacter inhibens DSM 16374T and Phaeobacter porticola [13, 16] (Fig. S5). In contrast to the other species of the genus Phaeobacter, strains 27-4T, 8-1 and M6-4.2 additionally contained diphasatidylglycerol, while lacking an unidentified lipid. Strains 27-4T and M6-4.2 additionally contained a phospholipid. The sole respiratory lipoquinone of all strains was Q10, which is generally dominant in bacteria of the Roseobacter group.

Growth of 27-4T, M6-4.2 and S26 occurred at a temperature range of 10 to 35°C (15–35°C for 8-1). After 1 week of incubation, they did not grow at 8 or 37°C. They grew optimally at 31–33°C (Table 1). The elevated optimal growth temperature distinguished the strains from the most closely related species (Freese and others, unpublished). They demonstrated a C12 fatty acid as dominant cellular fatty acid, while less efficient in using α-ketobutyric acid and L-homoserine in comparison with the type strains and other strains of the species Phaeobacter gallaeciensis and Phaeobacter inhibens. Furthermore, the strains differed in their utilization of D-

Table 1. Differential phenotypic and genotypic properties of 27-4T, M6-4.2, S26, 8-1 and the closely related type strains of species of the genus Phaeobacter

<table>
<thead>
<tr>
<th>Characteristic</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
<th>5</th>
<th>6</th>
<th>7</th>
</tr>
</thead>
<tbody>
<tr>
<td>DNA G+C content (mol%)</td>
<td>60.09</td>
<td>60.10</td>
<td>60.10</td>
<td>60.13</td>
<td>59.42</td>
<td>60.00</td>
<td>58.55</td>
</tr>
<tr>
<td>Growth at 10°C</td>
<td>+</td>
<td>+</td>
<td>(+)</td>
<td>–</td>
<td>–</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Temperature optimum (°C)</td>
<td>33</td>
<td>33</td>
<td>31</td>
<td>31</td>
<td>29</td>
<td>31</td>
<td>20–28</td>
</tr>
<tr>
<td>Salinity range for growth (%)</td>
<td>0.5–5.0</td>
<td>0.5–5.0</td>
<td>0.5–6.0</td>
<td>0.5–5.0</td>
<td>0.5–5.0</td>
<td>0.5–6.0</td>
<td>0.5–5.0</td>
</tr>
<tr>
<td>C8 esterase lipase</td>
<td>–</td>
<td>+</td>
<td>+</td>
<td>(–)</td>
<td>(+)</td>
<td>+</td>
<td>ND</td>
</tr>
<tr>
<td>Raffinose</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
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<td>–</td>
</tr>
<tr>
<td>N-Acetylglutamate</td>
<td>++</td>
<td>+</td>
<td>ND</td>
<td>++</td>
<td>+</td>
<td>+</td>
<td>ND</td>
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<tr>
<td>Carnitine</td>
<td>++</td>
<td>++</td>
<td>ND</td>
<td>++</td>
<td>++</td>
<td>+</td>
<td>ND</td>
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<tr>
<td>D-Lactic acid methyl ester</td>
<td>(+)</td>
<td>+</td>
<td>ND</td>
<td>+</td>
<td>++</td>
<td>+</td>
<td>ND</td>
</tr>
<tr>
<td>p-Glucosamine</td>
<td>+</td>
<td>+</td>
<td>ND</td>
<td>+</td>
<td>(+)</td>
<td>+</td>
<td>ND</td>
</tr>
<tr>
<td>p-Hydroxyphenylacetic acid</td>
<td>++</td>
<td>+</td>
<td>ND</td>
<td>+</td>
<td>(+)</td>
<td>+</td>
<td>ND</td>
</tr>
<tr>
<td>Acetoacetic acid</td>
<td>–</td>
<td>–</td>
<td>ND</td>
<td>–</td>
<td>(–)</td>
<td>(+)</td>
<td>ND</td>
</tr>
<tr>
<td>Minimum inhibitory concentration of copper (mM)</td>
<td>2.0</td>
<td>2.5</td>
<td>ND</td>
<td>3.5</td>
<td>2.5</td>
<td>0.5</td>
<td>ND</td>
</tr>
</tbody>
</table>

Strains: 1, 27-4T; 2, M6-4.2; 3, S26; 4, 8-1; 5, Phaeobacter gallaeciensis DSM 26640T; 6, Phaeobacter inhibens DSM 16374T; 7, Phaeobacter porticola P97T. All data were determined experimentally in this study apart from the temperature optimum of P97T [16] and the utilization of N-acetylglutamate, carnitine, D-lactic acid methyl ester, D-glucosamine, p-hydroxyphenylacetic acid and acetoacetic acid (Freese and others, unpublished). ++, Strongly positive; +, positive; (+), weakly positive; –, negative; ND, not determined.
lactic acid methyl ester and D-glucosamine in comparison
with *P. gallaeciensis* DSM 26640<sup>T</sup> and utilized carnitine and
p-hydroxyphenylacetic acid better than *Phaeobacter inhibens* DSM 16374<sup>T</sup>.

With respect to their antibiotic susceptibility, strains 27-4<sup>T</sup>, M6-4.2 and 8-1 clustered separately from *Phaeobacter gallaeciensis* DSM 26640<sup>T</sup>, *Phaeobacter inhibens* DSM 16374<sup>T</sup> and DSM 17395, although differences were often small (Fig. S6). The strains were strongly sensitive to linezolid (30 µg), imipenem (10 µg) and four cephalosporines and resistant to lincomides [clindamycin (10 µg), lincomycin (15 µg)] and glycopeptides [teicoplanin (30 µg), vancomycin (30 µg)]. Interestingly, the strains of the proposed species *Phaeobacter piscinae* sp. nov. tested differed strongly in their susceptibility to penicillins. Strain 27-4<sup>T</sup> was strongly sensitive, strain 8-1 was mostly resistant and M6-4.2 was heteroresistant whereas most cells were sensitive, but some showed a clear resistance. The response of the *Phaeobacter piscinae* sp. nov. strains to mezlocillin (either median inhibition zone: 42.8 mm, range: 36–44 mm or 0 mm, 0–0 mm) also differed distinctly from that of the *Phaeobacter inhibens* strains (27 mm, 25.5–29.5 mm) and *Phaeobacter gallaeciensis* DSM 26640<sup>T</sup> (31.5 mm, 30.5–32.5 mm). The strains of the proposed species *Phaeobacter piscinae* sp. nov. tested demonstrated a similar level of resistance to copper as *Phaeobacter gallaeciensis* DSM 26640<sup>T</sup> [minimal inhibitory concentration (MIC)=2.5 mM CuCl₂], but higher resistance than *Phaeobacter inhibens* DSM 16374<sup>T</sup> and DSM 17395 (MIC=0.5 mM CuCl₂) (Table 1), which may indicate an adaptation to anthropogenic aquaculture systems. Based on the genomic analyses and biochemical characterization, strains 27-4<sup>T</sup>, M6-4.2, S26 and 8-1 are distinct from the closest phylogenetically described neighbours *Phaeobacter gallaeciensis* DSM 26640<sup>T</sup> and *Phaeobacter inhibens* DSM 16374<sup>T</sup>. According to the whole-genome phylogeny together with the phenotypic data presented herein, specifically the temperature optimum, use of carbon sources and copper susceptibility, strains 27-4<sup>T</sup>, M6-4.2, S26 and 8-1 should be classified as members of a novel species within the genus *Phaeobacter*, for which the name *Phaeobacter piscinae* sp. nov. is proposed due to its presence in aquaculture facilities.

**DESCRIPTION OF PHAEOBACTER PISCINAE SP. NOV.**

*Phaeobacter piscinae* (pis.ci’nae. L. gen. n. piscinae of a fish pond, aquaculture).

Cells are Gram-reaction-negative and rod shaped (0.7–1.1 x 1.7–2.4 µm). Motile by means of a single polar flagellum. Colonies on marine agar (MA) are circular with regular edges, raised and light brown to brown in colour after 3 days of incubation at 25 °C. Growth occurs at 10 (15 for strain 8-1) to 35 °C, but not at 8 or 37 °C. The cells grow optimally at 31–33 °C. The salinity range for growth is 0.5 to 5–6 % with an optimum at 2–3 %. Cells grow at a pH range of pH 6.5–8.5 with optimal growth at pH 7.0. No anaerobic growth on MA. Catalase- and oxidase-positive. Negative for nitrate reduction, indole production, arginine dihydrolase, urease, protease, cystine arylamidase, trypsine, chymotrypsine, naphthol-AS-BI-phosphohydrolase, N-acetyl-β-glucosaminidase, α-mannosidase and α-fucosidase. Positive for α- and β-glucosidase and β-galactosidase, alkaline phosphatase, C4 esterase, C14 lipase, and leucine and valine arylamidase. L-Asparagine, D-glucose, L-glutamine, L-leucine, L-lysine, D-mannose, L-phenylalanine, D-sorbitol and Tween 80 are utilized. D-Mannan and raffinose are not utilized. Produces tropodithietic acid. Copper-resistant (MIC=2.0–3.5 mM). The major cellular fatty acids are C₁₈:₁ω₇c and C₁₆:₀. The sole lipoquinone is Q10. The polar lipid profile comprises phosphatidylglycerol, diphosphatidylglycerol, phosphatidyl-
ethanolamine, phosphatidylcholine, an aminolipid, a phospholipid and an unidentified lipid.

The type strain, 27-4<sup>T</sup> (=DSM 103509<sup>T</sup>=LMG 29708<sup>T</sup>), was isolated from a Spanish turbot-rearing unit. The DNA G+C content of the type strain is 60.1 %.

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**Conflicts of interest**

The authors declare that there are no conflicts of interest.

**References**


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