Genome-Based Classification of Strain 16-SW-7, a Marine Bacterium Capable of Converting B Red Blood Cells, as *Pseudoalteromonas distincta* and Proposal to Reclassify *Pseudoalteromonas paragorgicola* as a Later Heterotypic Synonym of *Pseudoalteromonas distincta*

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A strictly aerobic, Gram-stain-negative, rod-shaped, and motile bacterium, designated strain 16-SW-7, isolated from a seawater sample, was investigated in detail due to its ability to produce a unique α-galactosidase converting B red blood cells into the universal type blood cells. The phylogenetic analysis based on 16S rRNA gene sequences revealed that the strain 16-SW-7 is a member of the *Gammaproteobacteria* genus *Pseudoalteromonas*. The closest relatives of the environmental isolate were *Pseudoalteromonas distincta* KMM 638<sup>T</sup> and *Pseudoalteromonas paragorgicola* KMM 3548<sup>T</sup>, with the plural paralogous 16S rRNA genes of 99.87–100% similarity. The strain 16-SW-7 grew with 1–10% NaCl and at 4–34°C, and hydrolyzed casein, gelatin, tyrosine, and DNA. The genomic DNA G+C content was 39.3 mol%. The prevalent fatty acids were C<sub>16:1</sub>ω7c, C<sub>16:0</sub>, C<sub>17:1</sub>ω8c, C<sub>18:1</sub>ω7c, C<sub>17:0</sub> and C<sub>12:0</sub> 3-OH. The polar lipid profile was characterized by the presence of phosphatidylethanolamine, phosphatidylglycerol, two unidentified amino lipids, and three unidentified lipids. The major respiratory quinone was Q-8. The finished genome of the strain 16-SW-7 (GenBank assembly accession number: GCA_005877035.1) has a size of 4,531,445 bp and comprises two circular chromosomes L1 and S1, deposited in the GenBank under the accession numbers CP040558 and CP040559, respectively. The strain 16-SW-7 has the ANI values of 98.2% with KMM 638<sup>T</sup> and KMM 3548<sup>T</sup> and the DDH values of 84.4 and 83.5%, respectively, indicating clearly that the three strains belonged to a single species. According to phylogenetic evidence and similarity for the
INTRODUCTION

The genus *Pseudoalteromonas* was proposed by Gauthier et al. (1995) by splitting the genus *Alteromonas* into two genera due to its high level of heterogeneity. At the time of writing, the genus *Pseudoalteromonas* comprises 49 validly published species, including *Pseudoalteromonas haloplanktis* as the type species. Cells of the genus were described as Gram-stain-negative, aerobic, chemoorganotrophic, non-spore-forming, straight and curved rods or ovoid, those are motile by means of a single polar flagellum. All species of the genus were oxidase-positive, required a seawater base for growth, and did not accumulate poly-p-hydroxybutyrate. Subsequently, the genus was emended due to the newly obtained data, including the presence of polar, bipolar, or lateral flagella, gelatin and Tween 80 hydrolysis, glucose fermentation, and the ability of some strains to produce buds and prosthecæ (Ivanova et al., 2002a; Hwang et al., 2016; Beermann et al., 2017). In addition, the G+C content of DNA was extended up to 37–55 mol% (Park et al., 2016). Currently, the G+C content of the genomic DNA ranges from 34.8 mol% for *Pseudoalteromonas denitrificans* DSM 6059T (NCBI RefSeq: NZ_FOLO00000000.1) to 54.9 mol% for *Pseudoalteromonas aequariivorans* DB-2T (Park et al., 2016). Members of the genus *Pseudoalteromonas* are often isolated from different marine environments, including surface and deep seawater, sediments and sea ice samples, ascidians, coral, a surface slime of a puffer fish, mussels, brown and green algae, diatoms, and the halophyte plants (Bowman, 1998; Sawabe et al., 2000; Egan et al., 2001; Ivanova et al., 2002a,b; 2004; Romanenko et al., 2003a,b; Park et al., 2005; Matsuyma et al., 2013; Wu et al., 2017; Navarro-Torre et al., 2020). In this study, we characterized a non-pigmented strain 16-SW-7, isolated from seawater of the Okhotsk Sea. This strain is attracting the attention of researchers for its ability to convert B red blood cells into the universal type of blood cells (Bakunina et al., 1998; Balabanova et al., 2010). A preliminary study of the taxonomic position of the strain 16-SW-7, reclassify the species *P. paragorgicola* as a later heterotypic synonym of *P. distincta*, and specify the description of the species *P. distincta* based on the results of phylogenetic analysis, and genotypic and phenotypic characterization.

MATERIALS AND METHODS

Strain Isolation and Cultivation

The strain 16-SW-7 was isolated from a seawater sample collected near Island Paramushir (Kuril Islands), the Okhotsk Sea, during the 16th cruise of the Research Vessel Academician Oparin by plating 0.1 ml of seawater directly onto nutrient medium as described previously (Nedashkovskaya et al., 2007). After primary isolation and purification, the bacterium was cultivated at 28°C on the same medium or marine agar 2216 (Difco, bioMérieux, Pacific, Biosciences) and stored at −80°C in artificial seawater or marine broth (Difco, bioMérieux, Pacific, Biosciences) supplemented with 20% (v/v) glycerol. The strain 16-SW-7 was deposited in the collection of marine microorganisms (KMM) at the G.B. Elyakov Pacific Institute of Bioorganic Chemistry FEB RAS (Vladivostok, Russia), Korean Collection for the type cultures (KCTC) and VKM under deposit numbers KMM 701, KCTC 52772, and VKM B-2135 D, respectively. The type strains *P. distincta* KMM 638T (=ATCC 700518T) and *P. paragorgicola* KMM 3548T (=DSM 26439T) were obtained from the collection of marine microorganisms (KMM) and used as the reference strains for comparative taxonomic analysis.

Morphological, Biochemical, and Physiological Characterization

The physiological, morphological, and biochemical properties of the strain 16-SW-7 were studied using the standard methods. The novel isolate was also examined in the API 20E, API 20NE, API 50 CH, API 32 ID GN, and API ZYM galleries (bioMérieux, France) according to the manufacturer’s instructions, except that the inoculum was prepared using ASW (Bruns et al., 2001).

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and the galleries were incubated at 28°C. Gram-staining was performed as recommended by Gerhardt et al. (1994). Oxidative or fermentative utilization of glucose was determined on Hugh and Leifson’s medium modified for marine bacteria (Lemos et al., 1985). Catalase activity was tested by the addition of 3% (v/v) H₂O₂ solution to a bacterial colony and observation for the appearance of gas. Oxidase activity was determined by using tetramethyl-p-phenylenediamine. Degradation of agar, starch, casein, gelatin, chitin, DNA and urea and production of acid from carbohydrates, hydrolysis of Tween 80, nitrate reduction, production of hydrogen sulfide, acetoin (Voges-Proskauer reaction), and indole were tested according to standard methods (Gerhardt et al., 1994). The temperature range for growth was assessed on MA. Tolerance to NaCl was assessed in medium containing 5 g Bacto Peptone (Difco), 2 g Bacto Yeast Extract (Difco), 1 g glucose, 0.02 g KH₂PO₄, and 0.05 g MgSO₄.7H₂O per liter of distilled water with 0, 0.5, 1.0, 1.5, 2.0, 2.5, 3, 4, 5, 6, 8, 10, 12, 15, 17, 19, and 20% (w/v) of NaCl. Susceptibility to antibiotics was examined on MA plates at 28°C by the routine disk diffusion plate method. Disks were impregnated with the following antibiotics: ampicillin (10 µg), benzylpenicillin (10U), carbenicillin (100 µg), cefalexin (30 µg), cefazolin (30 µg), chloramphenicol (30 µg), erythromycin (15 µg), gentamicin (10 µg), kanamycin (30 µg), lincomycin (15 µg), nalidixic acid (30 µg), neomycin (30 µg), ofloxacin (5 µg), oleandomycin (15 µg), oxacillin (10 µg), polymyxin B (300 U), rifampicin (5 µg), streptomycin (30 µg), tetracycline (5 µg), and vancomycin (30 µg).

**Chemotaxonomic Characterization**

For whole-cell fatty acid and polar lipid analysis, the strains 16-SW-7, *P. distincta* KMM 668³ and *P. paragorgicola* KMM 3548¹ were grown under optimal physiological conditions for all strains (at 28°C for 24 h on MA). Cellular fatty acid methyl esters (FAMEs) were prepared according to the methods described by Sassar (1990), using the standard protocol of Sherlock Microbial Identification System (version 6.0, MIDI), and analyzed with the use of a GC-21A chromatograph (Shimadzu) equipped with a fused-silica capillary column (30 m × 0.25 mm) coated with Supelcowax-10 and SPB-5 phases (Supelco) at 210°C. FAMEs were identified by using equivalent chain-length measurements and comparing the retention times to those of authentic standards. The polar lipids of the strains studied were extracted using the chloroform/methanol extraction method of Bligh and Dyer (1959). Two-dimensional TLC of polar lipids was carried out on silica gel 60 F254 (10 cm × 10 cm; Merck) using chloroform/methanol/water (65: 25: 4, by vol.) in the first dimension, and chloroform/methanol/acetic acid/water (80: 12: 15: 4, by vol.) in the second dimension (Collins and Shah, 1984). For detection of the lipids, 10% sulfuric acid in methanol, molybdenum blue, ninhydrin, and a-naphthyl were applied. Isoprenoid quinones were extracted with chloroform/methanol (2:1, v/v) and purified by TLC, using a mixture of n-hexane and diethyl ether (85:15, v/v) as the solvent. Isoprenoid quinone composition of the strain 16-SW-7 was characterized by HPLC (Shimadzu LC-10A) using a reversed-phase type Supelcosil LC-18 column (15 cm × 4.6 mm) and acetonitrile/2-propanol (65:35, v/v) as a mobile phase at a flow rate of 0.5 ml min⁻¹ as described previously (Komagata and Suzuki, 1988).

**Whole-Genome Sequencing and Phylogenetic Analysis**

The genomic DNA of the strain *Pseudoalteromonas* sp. 16-SW-7 (=KMM 701 = KCTC 52772) was extracted from the cells grown on marine agar (25°C, 72 h), using a NucleoSpin microbial DNA kit (Macherey-Nagel, 54 Germany), and sequenced at Macrogen, Inc. (Seoul, South Korea). To construct libraries, the high-molecular-weight DNA (15 µg) was fragmented to generate 20-kb SMRTbell™ templates, and then, the fragments were annealed using a PacBio DNA polymerase binding kit and sequenced by the PacBio RS II platform (Pacific Biosciences, United States), with the use of PacBio version 4.0 sequencing kit with single-molecule real-time cells. Hierarchical Genome Assembly Process 3 (HGAP3) was used to perform de novo assembly of the PacBio reads for *Pseudoalteromonas* sp. 16-SW-7. The circular shape of the contigs was formed by testing the overlap ability of the contig ends. Because of the mapping reads against the assembled contigs and error correction using Quiver, the final sequence with the highest quality was generated.

The 16S rDNA gene and genome phylogenetic analyses were performed by the Type (Strain) Genome Server (TYGS), an automated high-throughput platform for state-of-the-art genome-based taxonomy (Meier-Kolthoff and Göker, 2019). The genome of the strain 16-SW-7 (GenBank accession: GCA_005877035.1) was compared against all types of strain genomes available in the TYGS database via the MASH algorithm, a fast approximation of intergenomic relatedness (Ondov et al., 2016), and the 10 types of strains with the smallest MASH distances were chosen. In addition, the set of 10 closely related type strains was determined via the 16S rDNA gene sequences, extracted from the genomes using RNAmer (Lagesen and Hallin, 2007), and BLASTed (Camacho et al., 2009) against the 16S rDNA gene of each of 14,309 type strains. This was used as a proxy to find the best 50 matching type strains, according to the bit score for the 16-SW-7 genome and to subsequently calculate precise distances using the Genome BLAST Distance Phylogeny approach (GBDP) under the algorithm “coverage” and distance formula d₅ (Meier-Kolthoff et al., 2013). These distances were finally used to determine the top 10 closest genomes of the type strains. For the phylogenomic inference, all pairwise comparisons among the set of genomes were conducted using GBDP and accurate intergenomic distances inferred under the algorithm “trimming” and distance formula d₅. One hundred distance replicates were calculated each. Digital DNA-DNA hybridization (DDH) values and confidence intervals were calculated using the recommended settings of the GGDC 2.1 (Meier-Kolthoff et al., 2013). The resulting intergenomic distances were used to infer a balanced minimum evolution tree with branch support via FastME 2.1.6.1 including SPR post-processing (Lefort et al., 2015). Branch support was inferred from 100 pseudo-bootstrap replicates each. The trees were rooted at the midpoint (Farris, 1972) and visualized with PhyD3 (Kreft et al., 2017). The type-based species...
clustering, using a 70% dDDH radius around each of the 13 type strains, was done as previously described (Meier-Kolthoff and Göker, 2019). Subspecies clustering was done using a 79% dDDH threshold as previously introduced (Meier-Kolthoff et al., 2014).

The whole-genome average nucleotide identity (ANI) values were calculated with the use of ChunLab’s ANI calculator (Yoon et al., 2017). The average amino acid identity (AAI) values were calculated by an AAI-profiler available at http://ekhidna2.biocenter.helsinki.fi/AAI (Medlar et al., 2018). Biosynthetic gene clusters (BGCs) were identified with antiSMASH version 5.1.1 (Medema et al., 2011). The whole-genome sequence analyses and comparative genomics of Pseudoalteromonas sp. 16-SW-7, P. paragorgicola KMM 3548T (GenBank accession: GCA_014918315.1), and P. distincta ATCC 700518T (GenBank accession: GCA_000814675.1) were additionally carried out using the high-performance computing servers Rapid Annotation of microbial genomes using Subsystems Technology (RAST; Overbeek et al., 2014), EzBioCloud (Yoon et al., 2017), and Integrated Microbial Genomes and Microbiomes (IMG/M) system (Chen et al., 2021).

RESULTS AND DISCUSSION

Morphological, Biochemical, and Physiological Characterization

The strain 16-SW-7 was shown to be a strictly aerobic, heterotrophic, Gram-stain-negative, and motile bacterium, which formed non-pigmented colonies on marine agar and required NaCl or seawater for growth. It was positive for cytochrome oxidase and catalase and hydrolyzed aesculin, casein, gelatin, Tweens 20, 40, and 80, DNA, and tyrosine (Table 1).

The strains 16-SW-7, P. distincta KMM 638T, and P. paragorgicola KMM 3548T shared many common phenotypic features, such as respiratory type of metabolism, motility by means of flagella, the presence of catalase, alkaline phosphatase, esterase lipase (C8), leucine arylamidase, valine arylamidase, acid phosphatase, and naphthol-AS-BI-phosphohydrolase activities (Table 1). They could not synthesize lipase (C14), N-acetyl-β-glucosaminidase, β-glucosidase, α-galactosidase, β-glucuronidase, α-mannosidase and α-fucosidase, hydrolyse agar, chitin, and urea and reduce nitrate to nitrite. However, the strain 16-SW-7 can be distinguished from its closest phylogenetic relatives by the several phenotypic traits, including the ability to form acid from D-rafinose, to produce hydrogen sulfide and cysteine arylamidase, trypsin and α-chymotrypsin, and to be resistant to ampicillin and vancomycin (Table 1). The above findings can extend the phenotypic characteristics those were reported for the species P. distincta (Romanenko et al., 1995; Ivanova et al., 2000, 2004) after justification of the placement of the strains 16-SW-7 and P. paragorgicola KMM 3548T in the species P. distincta.

Chemotaxonomic Characterization

The fatty acid profiles of the strains 16-SW-7, P. distincta KMM 638T, and P. paragorgicola KMM 3548T were similar (Table 2). The predominant fatty acids (>5% of the total fatty acids) of the strain 16-SW-7 and its closest relatives were C₁₆:₀ α₇c (29–32.1%), C₁₆:₁ (15.4–18.2%), C₁₇:₁ o8c (11.7–17.9%), C₁₈:₁ ω7c (5.2–11%), C₁₇:₀ (5.8–10.3%), and C₁₃:₀ 3-OH (4.8–7.5%). The composition of other fatty acids presented in Table 2 was also similar except that the strain 16-SW-7 contained higher proportions of C₁₄:₀, C₁₂:₀, and iso-C₁₆:₀, and lower proportions of C₁₅:₁ o8c, C₁₂:₀ 3-OH, and C₁₃:₀ 3-OH. These values were consistent with the results of phylogenetic analysis and confirmed the affiliation of the strains studied to the same species. The polar lipid profile of the strain 16-SW-7 was characterized by the presence of phosphatidylethanolamine, phosphatidylglycerol, two unidentified amino lipids, and three unidentified lipids (Table 2 and Supplementary Figure 1). It was similar to that of P. paragorgicola KMM 3548T and it can be distinguished from another relative, P. distincta KMM 638T, by the presence of unknown lipids L1 and L2. The nearest neighbors of the strains under study, Pseudoalteromonas aliena LMG 22059T and Pseudoalteromonas fuliginea KMM 216T, distinguished from them by the presence of unknown phospholipids and unknown aminophospholipid and two unknown glycolipids, respectively (Machado et al., 2016; Zhang et al., 2016). The main respiratory quinone of the strains under study was ubiquinone Q-8 that is consistent with those reported for the members of the family Pseudoalteromonadaceae (Ivanova et al., 2004).

16S rRNA Genes and Phylogenomic Analysis

The analysis of the 16S rRNA gene sequence of the strain 16-SW-7 (GenBank accession number: OL587468) in the EzTaxon database application (Yoon et al., 2017) revealed 100% similarity with Pseudoalteromonas arctica A 37-1-2T (CP011026) and Pseudoalteromonas elyakovii KMM 162T (AF082562), and 99.9% similarity with P. distincta KMM 638T (JWIG01000030) and P. paragorgicola KMM 3548T (AY040229). However, the 16S rRNA gene sequences obtained by the Sanger method are recommended to be compared with the genome sequences, as well as the use of overall genome data for the taxonomy of prokaryotes, such as average nucleotide identity (ANI) and digital DDH (dDDH) and relatedness between the strains and type of strain of a species (Chun et al., 2018). The closed genome of 16-SW-7 was found to contain nine full-length sequences of 16S rRNA genes with 99.87–100% similarity between each other (Table 3). The multiple 16S rRNA genes seem to be a characteristic of the type species of the family Pseudoalteromonadaceae, including P. distincta KMM 638T and P. paragorgicola KMM 3548T (Table 3). Among the nine 16S rRNA genes found in the genome of P. distincta KMM 638T (=ATCC 700518T), only one—the length-comparable gene in a contig 30—was extracted for the analysis, probably due to an incomplete genome sequencing (GenBank WGS accession: JWIG00000000.1). In the P. paragorgicola KMM 3548T genome, two 16S rRNA genes were completely sequenced among three found (GenBank WGS accession: AQHE00000000.1).

The whole-genome sequence of the strain 16-SW-7 was 4,531,445 bp, with a G+C content of 39.3 mol% and comprised of...
two circular chromosomes L1 and S1, deposited in the GenBank under the accession numbers CP040558 and CP040559, respectively (assembly accession: GCA_000814675.1). The genome size of P. distincta genome size of respectively (assembly accession: GCA_005877035.1). The two circular chromosomes L1 and S1, deposited in the GenBank under the accession numbers CP040558 and CP040559, respectively (assembly accession: GCA_000814675.1). The genome size of P. distincta genome size of respectively (assembly accession: GCA_005877035.1). The genome size of P. paragorgicola KMM 3548T =DSM 26439T was 4,322,351 bp, with the G+C content of 43.8 mol%. In comparison, the genome size of P. distincta KMM 638T (GenBank assembly accession: GCA_014918315.1) was 4,532,748 bp and the G+C content of 39.2 mol% (Supplementary Table 1). The GBDP phylogenomic tree is consistent with the branching patterns, observed for only the strains 16-SW-7 and P. paragorgicola KMM 3548T =DSM 26439T in the 16S rRNA gene sequence-based tree, generated by TYGS, because of the use of the P. distincta KMM 638T (=ATCC 700518T) gene with lower identity (Table 3, Figure 1, and Supplementary Figure 2).

However, the species-specific gene clusters for the strains 16-SW-7, P. paragorgicola KMM 3548T =DSM 26439T, and P. distincta KMM 638T (=ATCC 700518T) were identical, indicating that the three strains belonged to a single species (Figure 1 and Supplementary Figure 2). The ANI calculator in EzBioCloud, based on the use of OrthoANIu algorithm (Lee et al., 2016), showed the similar high ANI values (98.04–98.2%) for the strain 16-SW-7 and the reference strains P. distincta KMM 638T and P. paragorgicola KMM 3548T (Supplementary Table 2), which are higher than the species-level cutoff value of 95–96% (Richter and Rosselló-Móra, 2009). According to the TYGS results, the dDDH (d4) values between the 16-SW-7 genome
and genomes of *P. distincta* and *P. paragorgicola* were 84.4 and 83.5%, respectively (Supplementary Table 3), that are sufficiently higher than the suggested species boundary of 70% (Wayne et al., 1987). The proteome-wide sequence search results, implemented by a web server AAI-profiler (Medlar et al., 2018), showed 98.6% (87% matched proteins) and 98.8% (85.9% matches) average amino acid identity (AAI) of the strain 16-SW-7 with *P. distincta* and *P. paragorgicola*, which are higher than 85% proposed as a threshold for delimitation of a species (Goris et al., 2017).

The target count for *P. paragorgicola* proteins showed 98.8 and 98.5% AAI (83.5 and 83.1% matches) against the proteins of *Pseudoalteromonas* sp. 16-SW-7 and *P. distincta*, respectively. The calculated genetic similarities are presented in Supplementary Tables 1–3. These values support the proposed affiliation of the three strains to a single species of the genus *Pseudoalteromonas*.

### Genome Features and Comparative Genomics

The core-gene content (about 3200 genes according to EzBioCloud) and coding sequences (CDSs) similarity confirmed the affiliation of the strains 16-SW-7 and *P. paragorgicola* KMM 3548 to the species *P. distincta* (Supplementary Figures 3, 4 and Supplementary Tables 4–6). They include genes for use of some common mechanisms to respond to high salt stress, such as a high-affinity choline and betaine uptake system (Supplementary Table 4, Column 1: lines 769, 898, 1257, 2699, 3969–3974), the doubled genes for the glutamate synthase small and large subunits (Supplementary Table 4, Column 1: lines 1761, 3562, 2003, 2033), K⁺ transporters Trk H/A (Supplementary Table 4, Column 1: lines 3064, 3069), other ABC transporters/permeases, and transcription factors (Fu et al., 2014). However, analysis of the subsystem features, annotated by RAST, indicated the presence of some individual functions for the strains 16-SW-7, *P. distincta* KMM 638 (=ATCC 700518), and *P. paragorgicola* KMM 3548 (Table 4).

The RAST comparative genomics revealed 242 and 426 strain-specific CDSs (singletons) in the strain 16-SW-7 against the strains KMM 638 (=ATCC 700518) and KMM 3548, respectively, most of which encoded hypothetical proteins, and only 40 and 50 genes, respectively, had a function (Supplementary Table 4). Meanwhile, 1378 and 1229 CDSs of KMM 638 (=ATCC 700518) and KMM 3548, respectively, had 100% identity with the CDSs of 16-SW-7 (Supplementary Table 5). In the genome of the strain KMM 3548, 1259 identical CDS and 481 singletons were found vs. the strain KMM 638 (ATCC 700518), and 420 singletons vs. the strain 16-SW-7 (Supplementary Table 6). All three strains putatively have xylan and xylose degradation specialization, but differ from each other by exopolysaccharide and lipopolysaccharide biosynthesis pathways (Table 4 and Supplementary Tables 4, 6), which are known to be responsible for serotypes in clinical bacterial strains (Balabanova et al., 2020). Thus, the strain 16-SW-7 exclusively contains the doubled genes encoding for GDP-mannose mannosyl hydrolase, phosphomannomutase, and several sugar and glycosyltransferases, as well as the low-identical capsular polysaccharide synthases (up to 78–79%) of the type strain KMM 638 (ATCC 700518): A, B, C, D, UDP-glucose 4-epimerase, lipid carrier: UDP-N-acetylglactosaminyltransferase, O-antigen acetylace, N-acetyleneuraminicid cytidyllytransferase (sialic acid synthesis), polysaccharide deacetylase, dTDP-4-dehydroshamnose reductase, and specific lipoproteins which are absent in KMM 3548 (Supplementary Tables 4, 6). Meanwhile, KMM 3548 includes many genes for rhamnosyltransferases, some of which are similar only to KMM 638 (ATCC 700518), and related hydrolases, lipoproteins, and capsular polysaccharide synthesis and export systems (Supplementary Table 6). In addition, 16-SW-7 and KMM 3548 (ATCC 700518) differ from KMM 3548 by some genes responsible for xanthine and glucosamine metabolism, carbon starvation, catechol pathway, and phosphate metabolism (Supplementary Table 4, Column 1: lines 3684–3691). Contrarily, the strain KMM 3548 has almost all genes found in the strains 16-SW-7 and ATCC 700518, but mostly distinguishes from them by the large number of mobile elements, transposases, integrases, chaperone proteins of heat shock (HptG), components of fatty acid synthases, enlarged pectin degradation system, and hypothetical proteins of unknown function (Supplementary Table 6). In general, the different level of identity and numbers of the genes for motility functions, metal resistance, TonB-related receptors, transporters, beta-lactamases, bactericins, signal transduction (sensors, receptors, transporters, enzymes), mobile elements, and DNA repair systems reflect eco-physiological diversity and different adaptive lifestyles of the free-living 16-SW-7, and host-associated KMM 3548 and KMM 638 (ATCC 700518) (Table 4 and Supplementary Tables 4–6). Indeed, KMM 638.

### TABLE 2 Fatty acid composition (%) of the strain 16-SW-7 and closely related strains of the genus *Pseudoalteromonas*.

| Fatty acids   | 1    | 2  | 3    |
|--------------|------|----|------|
| Saturated    |      |    |      |
| C₁₂:₀       | 2.8  | tr | tr   |
| C₁₄:₀       | 3.9  | tr | 1.3  |
| C₁₆:₀       | 2.5  | 4.7| 3.0  |
| C₁₈:₀       | 18.2 | 15.4| 16.0 |
| C₁₇:₀       | 6.1  | 10.3| 5.8  |
| C₁₈:₀       | 1.9  | 1.8 | 1.4  |
| Unsaturated  |      |    |      |
| C₁₅:₁ω₈C    | 2.7  | 4.3 | 4.9  |
| C₁₆:₁ω₇C    | 30.6 | 29.0| 32.1 |
| C₁₇:₁ω₈C    | 11.7 | 17.9| 15.3 |
| C₁₈:₁ω₇C    | 11.0 | 5.2 | 7.5  |
| Branched     |      |    |      |
| iso-C₁₆:₀    | 1.0  | tr | tr   |
| Hydroxy      |      |    |      |
| C₁₂:₀ 3-OH  | 4.8  | 6.3 | 7.5  |
| C₁₃:₀ 3-OH  | tr   | 1.2 | 1.0  |

Strains: 1, 16-SW-7; 2, *P. distincta* KMM 638; 3, *P. paragorgicola* KMM 3548. All data are from the present study. Major components (≥5.0%) are highlighted in bold. tr, trace amount (<1.0%).

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TABLE 3 | The 16S rRNA gene sequences content and similarity for the strains Pseudoalteromonas sp. 16-SW-7, P. distincta ATCC 700518T, and P. paragorgicola KMM 3548T.

| IMG homolog* | NCBI homolog genome locus_tag (16S rRNA gene) | Identity % | Identity/length | Genome ID | Genome name | Contig/length | Coordinates/strand |
|--------------|---------------------------------------------|------------|-----------------|-----------|-------------|---------------|------------------|
| 2888223316  | FFU37_04590 (OL587469)                      | 100.00     | 1536/1536       | CP040558  | Pseudoalteromonas sp. 16-SW-7 | 1(L1)/3735685 | 1023946..1025481/+ |
| 2888222433  | FFU37_00210 (OL587468)                      | 100.00     | 1536/1536       | CP040558  | Pseudoalteromonas sp. 16-SW-7 | 1(L1)/3735685 | 48439..49974/+    |
| 2888226108  | FFU37_18380 (OL587475)                      | 99.94      | 1535/1536       | CP040559  | Pseudoalteromonas sp. 16-SW-7 | 2(S1)/795760  | 37599..377134/+   |
| 2888225489  | FFU37_15325 (OL587473)                      | 99.94      | 1535/1536       | CP040558  | Pseudoalteromonas sp. 16-SW-7 | 1(L1)/3735685 | 3416198..3417733/− |
| 2888225372  | FFU37_14755 (OL587472)                      | 99.94      | 1535/1536       | CP040558  | Pseudoalteromonas sp. 16-SW-7 | 1(L1)/3735685 | 3277653..3279188/− |
| 2888225547  | FFU37_15610 (OL587474)                      | 99.87      | 1534/1536       | CP040558  | Pseudoalteromonas sp. 16-SW-7 | 1(L1)/3735685 | 3477632..3479167/+ |
| 2888225264  | FFU37_14215 (OL587471)                      | 99.87      | 1534/1536       | CP040558  | Pseudoalteromonas sp. 16-SW-7 | 1(L1)/3735685 | 3172769..3174304/− |
| 2888222403  | FFU37_00060 (OL587467)                      | 99.87      | 1534/1536       | CP040558  | Pseudoalteromonas sp. 16-SW-7 | 1(L1)/3735685 | 16934..18469/+    |
| 2888224778  | FFU37_11820 (OL587470)                      | 99.74      | 1533/1536       | CP040558  | Pseudoalteromonas sp. 16-SW-7 | 1(L1)/3735685 | 2652584..2654119/− |
|             | OT16_19995                                | 99.94      | 1542/1543       | JWGO1000030 | P. distincta strain ATCC 700518T | C30/180150 | 175393..176935/+ |
|             | PPAR_aR004                                | 99.87      | 1522/1524       | AQHE01000014 | P. paragorgicola DSM 3548T | 14/767276 | 187495..189018/+ |
|             | PPAR_aR007                                | 100.00     | 1524/1524       | AQHE01000021 | P. paragorgicola DSM 3548T | 21/300025 | 298305..299828/+ |

*From the alignment on query gene of the strain 16-SW-7 under the IMG/M database accession number 2888222433 (FFU37_00210/OL587468), implemented by Top IMG Isolate RNA hits or NCBI BLAST to get top RNA homologs.

FIGURE 1 | Tree inferred with FastME 2.1.6.1 from GBDP distances calculated from genome sequences by the TYGS server (Lefort et al., 2015). The branch lengths are scaled in terms of GBDP distance formula d5. The numbers above the branches are GBDP pseudo-bootstrap support values >60% from 100 replications, with an average branch support of 92.7%. The tree was rooted at the midpoint (Farris, 1972). The square labels colored by the same color indicate the genomes with the same species (light lilac) and subspecies (dark lilac) gene clusters, G+C content (white), and delta statistics: Pseudoalteromonas_GCF_005877035.1 (the strain 16-SW-7), P. distincta ATCC 700518T, and P. paragorgicola DSM 26439T form one phylogenomic clade separated from other species of the genus.
| Category                                | Subcategory                                                                 | Subsystem                                                                 | Function                                                                                                           | A | B | C |
|----------------------------------------|------------------------------------------------------------------------------|----------------------------------------------------------------------------|-------------------------------------------------------------------------------------------------------------------|---|---|---|
| Amino acids and derivatives            | Lysine, threonine, methionine, and cysteine                                  | Methionine biosynthesis (MB)                                               | Homoserine O-acetyltransferase (EC 2.3.1.31), MB subpathway                                                     | + | - | - |
| Amino acids and derivatives; protein    | Arginine; urea cycle; polyamines                                              | Urea decomposition; GSE family of P-loop GTPases                          | Urea ABC transporter, ATPase protein UntD, UntE, UntB, UntC; Urease accessory proteins UreD, UreE, UreF, UreG; Urease alpha, beta, and gamma subunits (EC 3.5.1.5) | - | + | - |
| Carbohydrates                          | Monosaccharides                                                             | Mannose Metabolism                                                         | GDP-mannose mannol hydrolyase (EC 3.6.1), Phosphomannomutase (EC 5.4.2.8)                                      | + | - | - |
| Cell wall and capsule                  | Capsular and extracellular polysaccharides                                   | Rhamnose containing glycans; dTDP-rhamnose synthesis                     | Alpha-1,2(1,3)-L-rhamnosyltransferase (EC 2.4.1), polysialic acid transporter KpsM; dTDP-4-dehydrorhamnose 3,5-epimerase (EC 5.1.3.13) and reductase (EC 1.1.1.133); dTDP-rhamnosyltransferase RfbF | - | + | - |
| DNA metabolism                         | DNA repair                                                                  | DNA repair, bacterial RecBCD pathway                                       | RecD-like DNA helicase Atu2026 (exodeoxyribonuclease V)                                                        | + | - | - |
| DNA metabolism                         | DNA repair                                                                  | DNA repair, bacterial                                                      | DNA-cytosine methyltransferase (EC 2.1.1.37), modulates gene expression, a component of bacterial restriction-modification systems | + | - | - |
| DNA metabolism                         | No subcategory                                                              | Restriction-modification system                                            | Type III restriction-modification system methylation and helicase subunits (EC 2.1.1.72), host-protective DNA methylation | - | - | + |
| DNA metabolism                         | No subcategory                                                              | Restriction-modification system                                            | Putative DNA-binding protein in cluster with Type I restriction-modification system                             | - | + | - |
| Fatty acids, lipids, and isoprenoids   | No subcategory                                                              | Polyhydroxybutyrate metabolism                                             | D-beta-hydroxybutyrate permease (utilization of poly-HB, glutonate)                                            | + | - | - |
| Membrane transport                     | Protein secretion system, Type II                                           | Widespread colonization island                                             | Fip plus assembly protein, pilin Fip                                                                          | - | + | - |
| Membrane transport; virulence and defense | Cation transporters; resistance to toxic compounds                           | Copper transport system; Cu2+ + homeostasis                                | Copper resistance proteins CopC, CopD, CopB; multicopper oxidase                                               | - | + | - |
| Nucleosides and nucleotides            | Detoxification                                                               | Housecleaning nucleoside triphosphate pyrophosphatases                    | Deoxyuridine 5'-triphosphate nucleotidohydrolase (EC 3.6.1.23), remove dUTP for preservation of genetic integrity for growth and virulence | - | + | - |
| Regulation and cell signaling          | Programmed cell death and toxin-antitoxin systems                          | Phd-Doc, YdcE-YdcD toxin-antitoxin (programmed cell death) systems         | Death on curing protein, doc toxin [mimicker of aminoglycoside antibiotic hygromycin B (HygB), increase in mRNA half-life] | - | - | + |
| Regulation and cell signaling          | No subcategory                                                              | DNA-binding regulatory proteins, strays                                    | Aromatic hydrocarbon utilization transcriptional regulator CatR (LysR family)                                 | - | - | + |
| Regulation and cell signaling          | No subcategory                                                              | Orphan regulatory proteins                                                 | Sensor kinase CitA, DpsB (EC 2.7.3.-), involved in anaerobic citrate catabolism in response to anaerobic conditions | - | + | - |
| Stress response                        | Cold shock                                                                  | Cold shock, CspA family of proteins                                       | Cold shock protein CspD                                                                                            | - | - | + |
| Stress response                        | Osmotic stress                                                              | Choline and betaine uptake and betaine biosynthesis                       | GbcA glycine betaine demethylase, transporter OpuD [utilization of quaternary ammonium compounds at high osmolalities (kidneys)] | - | + | - |
| RNA metabolism                         | RNA processing and modification                                              | Ribonucleases in bacillus                                                  | Metallo-beta-lactamase family protein, RNA-specific                                                             | - | + | - |
strain 16-SW-7 is affiliated to the species *P. distincta*. Moreover, the high similarities in the genomic sequences and phenotypic characteristics found between the species *P. distincta* and *P. paragorgicola* places them in the same species. Therefore, it is proposed to reclassify the species *P. paragorgicola* as a later heterotrophic synonym of *P. distincta* in accordance with the rules of priority of prokaryotic names, governed by the International Code of Nomenclature of Bacteria (Parker et al., 2019), and to emend the description of the species *P. distincta*.

### Emended Description of the Species *Pseudoalteromonas distincta* (Romanenko et al. 1995) Ivanova et al. 2000

The description of the species *Pseudoalteromonas distincta* is as given by Romanenko et al. (1995) and Ivanova et al. (2000, 2002a) with the following modifications and amendments. Cells are Gram-stain-negative, non-spor-forming, strictly aerobic rods, motile by means of a single polar or four to seven lateral flagella. On marine agar, colonies are non-pigmented or slightly orange colored. They can produce diffusible melanin-like pigments. Cells are catalase- and oxidase-positive. They require Na⁺ ions or sea water for growth. Growth occurs in media with 0.5–10% NaCl. Temperature for growth ranges from 4 to 34°C. Aesculin, gelatin, Tween 20, 40, and 80, DNA, alginate, and tyrosine are hydrolyzed but agar, chitin, CM-cellulose, and urea are not hydrolyzed. Hydrolysis of casein and starch is strain dependent. Acid is formed from sucrose but not from L-arabinose, D-fructose, D-mannose, D-melibiose, L-rhamnose, D-ribose, D-trehalose, *N*-acetylglucosamine, and glycero. Some strains can produce acid from D-cellulose, D-galactose, D-glucose, D-lactose, maltose, D-raffinose, D-xylene, and D-mannitol and utilize citrate. In API 32GN gallery, they are positive for D-glucose, maltose, sucrose, D-mannitol, sodium acetate, sodium citrate, L-alanine, L-serine, L-proline, glycogen, propionic acid, valeric acid, and capric acids. Assimilation of inositol, sodium malonate, lactic acid, D-ribose, 3-hydroxybutyric acid, itaconic acid, potassium-2-keto-gluconate, L-histidine, and salicin is variable. In API ZYM gallery, alkaline phosphatase, esterase lipase (C8), leucine arylamidase, valine arylamidase, acid phosphatase, and naphthol-AS-BI-phosphohydrolase activities are present but lipase (C14), α-galactosidase, β-galactosidase, β-glucuronidase, α-glucosidase, β-glucosidase, *N*-acyl-β-glucosaminidase, α-mannosidase, and α-fucosidase activities are absent. Esterase (C4), cysteine arylamidase, trypsin, and α-chymotrypsin can be produced. Nitrate is not reduced to nitrite. Acetoin and indole are not produced. Production of hydrogen sulde is strain dependent. The predominant fatty acids (>5% of the total fatty acids) were C16:1, C16:0, C17:0, C18:1, C17:0, C18:0, and C12:0 3-OH. The polar lipid profile was characterized by the presence of phosphatidylethanolamine, phosphatidylglycerol, two unidentified amino lipids, and three unidentified lipids. The major respiratory quinone is ubiquinone Q-8. The genomic DNA G+C content is 39.2–39.3 mol%. The genome size is
4.3–4.5 Mb. The type of strain is KMM 638\(^T\) (=ATCC 700518\(^T\)), isolated from a marine sponge collected at a depth of 350 m near the Komandorskie Islands, Russia. The GenBank/EMBL/DDBJ accession number for the genome of the type of strain is GCA_000814675.1.

**DATA AVAILABILITY STATEMENT**

The datasets presented in this study can be found in online repositories. The names of the repository/repositories and accession number(s) can be found in the article/Supplementary Material.

**AUTHOR CONTRIBUTIONS**

ON and LB contributed to conception and designed of the study. ON, S-GK, LB, and NZ performed the experimental works.

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**SUPPLEMENTARY MATERIAL**

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmicb.2021.809431/full#supplementary-material

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