Mesonia aestuariivivens sp. nov., isolated from a tidal flat

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Abstract
A Gram-negative, aerobic, non-flagellated and ovoid or rod-shaped bacterial strain (JHPTF-M18T), which was isolated from a tidal flat sediment in Republic of Korea, was taxonomically characterized. Strain JHPTF-M18T grew optimally at 25 °C, at pH 7.0–7.5 and in the presence of 2.0–3.0% (w/v) NaCl. 16S rRNA gene sequence analysis showed that strain JHPTF-M18T forms a phylogenetic lineage within the radiation comprising type strains of Mesonia species. The 16S rRNA gene of strain JHPTF-M18T shared sequence similarities of 97.7% with that of type strain of M. mobilis and 92.5–96.8% with those of type strains of the other nine Mesonia species. The DNA G+C content was 33.1% based on its genomic sequence. AAI, ANI and dDDH values between strain JHPTF-M18T and the type strains of M. mobilis, M. hitae, M. oceanica, M. phycicola and M. algae were 72.1–83.7%, 73.1–79.7% and 18.5–22.8%, respectively. Strain JHPTF-M18T was separated from recognized Mesonia species by its phenotypic properties together with the phylogenetic and genetic distinctiveness. Based on data presented in this study, strain JHPTF-M18T is considered to represent a novel species of the genus Mesonia. The name Mesonia aestuariivivens sp. nov. is proposed for JHPTF-M18T (=KACC 22185T = NBRC 115119T).

Keywords Tidal flat · Polyohasic taxonomy · Genome · Novel species · Mesonia aestuariivivens sp. nov

Abbreviations
ANI Average nucleotide identity
AAI Average amino acid identity
dDDH Digital DNA–DNA hybridization
GC Gas chromatography

Introduction
The genus Mesonia was created by Nedashkovskaya et al. (2003) with the assignment of Mesonia algae as the type species and belonged to the family Flavobacteriaceae of the phylum Bacteroidetes (Bernardet 2011). The genus Mesonia currently consists of ten species with validly published names at July 2022 (https://lpsn.dsmz.de/genus/mesonia; Parte 2018). Members of the genus Mesonia are known to be Gram-stain-negative, aerobic, catalase- and oxidase-positive and rod-shaped and to contain menaquinone-6 as predominant isoprenoid quinone, phosphatidylethanolamine as the major phospholipid identified and DNA G+C contents of 31.4–42.1 mol% (Kang and Lee 2010; Kolberg et al. 2015; Lee et al. 2012; Lucena et al. 2020; Nedashkovskaya et al. 2003, 2006; Zhou et al. 2021). Isolation sources of Mesonia species described so far include green alga, seaweed, seawater, diseased Barbour's Seahorse and sea cucumber culture pond (Kang and Lee 2010; Kolberg et al. 2015; Lee et al. 2012; Lucena et al. 2020; Nedashkovskaya et al. 2003, 2006; Wang et al. 2015). Recently, in the course of screening novel bacteria from a tidal flat at Seocheon on the Yellow Sea of Korean peninsula, many bacterial isolates have
been obtained followed by identified by 16S rRNA sequence analysis. Of these bacterial isolates, one strain (designated as JHPTF-M18\(^T\)) which showed the closest affiliation to members of the genus *Mesonia*, was selected for further taxonomic study. In this study, strain JHPTF-M18\(^T\) is characterized further using a polyphasic characterization.

**Materials and methods**

**Bacterial strains and culture conditions**

A tidal flat sediment was collected in July 2020 from Seocheon (36° 01’ 44.6" N, 126° 39’ 56.8" E) close to the Yellow Sea of Republic of Korea. The sample (about 1–2 g) was serially diluted with 0.85% (w/v) saline solution and spread on marine agar 2216 (MA; BD Difco). After incubation for 7 days at 25 °C, strain JHPTF-M18\(^T\) was isolated from the MA plates and streaked onto fresh MA. Strain JHPTF-M18\(^T\) was cultivated routinely on MA at 25 °C, and its cells suspended in a sterile solution containing 20% (w/v) glycerol were stored at –80 °C for long-term preservation. *Mesonia mobilis* KCTC 12708\(^T\) and *Mesonia algae* KCTC 12809\(^T\), which were used as experimental control strains, were obtained from the Korean Collection for Type Cultures (KCTC; South Korea). Cells of strain JHPTF-M18\(^T\) were obtained from culture grown for 3 days in marine broth 2216 (MB; BD Difco) at 25 °C, and they were used to extract DNA and to analyse isoprenoid quinones and polar lipids. Cell masses for cellular fatty acid analysis were obtained under the following conditions: 2, 3 and 5 days at 25 °C for strain JHPTF-M18\(^T\) and 3 days at 25 °C for *M. mobilis* KCTC 12708\(^T\) and *M. algae* KCTC 12809\(^T\).

**Sequencing and phylogenetic analysis of 16S rRNA gene**

Chromosomal DNA extraction was performed using a Wizard Genomic DNA isolation kit (Promega) according to the manufacturer’s instruction. The 16S rRNA gene amplification was performed as described previously (Yoon et al. 1997) using PCR in which 9F (5’-GAG TTT GAT CCT GGC TCA G-3’) and 1512R (5’-ACG GTT ACC TTG TTA CGA CTT-3’) were used. Sequencing of the 16S rRNA gene followed by phylogenetic analysis was carried out as described by Yoon et al. (2003). Similarity between 16S rRNA gene sequences was calculated using alignment obtained using Clustal W program.

**Genomic analysis**

A TruSeq DNA LT Sample Prep kit (Illumina) was used to prepare a library for genomic sequencing. The library was sequenced using Illumina MiSeq platform. Sequencing data were assembled with SPAdes (Bankevich et al. 2012). Contamination of genome sequence was assessed using Context16S (Lee et al. 2017). Library construction and sequencing were performed by Chunlab Inc. (Republic of Korea). Phylogenomic tree based on genomic sequences and tree based on AAIs were constructed with UBCG (Na et al. 2018) and EzAAI (Kim et al. 2021) in the EzBioCloud, respectively. The ANI value based on BLAST + was calculated using JSpecies WS (http://jspecies.ribolhost.com/jspeciesws/; Richter et al. 2015) or OrthoANI (Yoon et al. 2017) in EzBioCloud. The dDDH value was estimated using TYGS (https://tygs.dsmz.de/user_requests/new) with BLAST + in which the recommended formula 2 (Meier-Kolthoff et al. 2013) was used.

**Chemotaxonomic characterization**

Extraction and HPLC analysis of isoprenoid quinones were performed as described by Komagata and Suzuki (1987) and Park et al. (2014), respectively. Fatty acid analysis was performed as described by Park et al. (2014) using the standard MIDI protocol (Sherlock Microbial Identification System, version 6.2B), GC (Hewlett Packard 6890) and TSBA6 database of the Microbial Identification System (Sasser 1990). Extraction of polar lipids was carried out according to procedures described by Minnikin et al. (1984). They were separated by two-dimensional TLC using the solvent systems as described by Embley and Wait (1994). The TLC plates were sprayed with various reagents as described by Park et al. (2014), and individual polar lipids were visualized followed by identified with heating at 150 °C for 3 min.

**Morphological, cultural, physiological and biochemical characterization**

Cell shape, Gram reaction, pH range for growth, anaerobic growth, growth at various concentrations of NaCl, requirement for Mg\(^{2+}\) ions, hydrolysis of gelatin and urea, susceptibility to antibiotics were investigated as described by Park et al. (2014). Growth at 4, 10, 20, 25, 28, 30, 35, 37 and 40 °C was measured on MA to estimate the optimal temperature and temperature range for growth. Nitrate reduction and hydrolysis of aesculin and Tween 80 were investigated as described previously (Lányi 1987) using artificial seawater (Bruns et al. 2001) for the preparation of the media. Hydrolysis of other substrates was tested as described by Barrow and Feltham (1993) with the modification that MA
was used. Activity of catalase and oxidase was determined as described by Lányí (1987). The presence of flexirubin-type pigments was investigated as described previously (Bernardet et al. 2002; Reichenbach 1992). Spectral analysis of in vivo pigment absorption was performed as described previously (Jung et al. 2016). Other enzyme activities were determined using the API ZYM system (bioMérieux); the results were checked after incubation for 8 h at 25 °C. Acid production from carbohydrates was tested as described by Leifson (1963).

Results and discussion

Phylogenetic analysis based on 16S rRNA gene sequence

The almost complete 16S rRNA gene sequence of strain JHPTF-M18T determined in this study had a continuous stretch of 1448 nucleotides, corresponding to positions 28–1491 (95%) of the Escherichia coli 16S rRNA sequence. In the neighbour-joining phylogenetic tree based on 16S rRNA gene sequences, strain JHPTF-M18T fell within the clade comprising the type strains of the other Mesonia species except for M. hitae and M. oceanica, and particularly joined the type strain of M. mobilis by a bootstrap resampling value of 70.4% (Fig. 1). Strain JHPTF-M18 shared the highest 16S rRNA gene sequence similarity value (97.7%) to M. mobilis KCTC 12708T. It also shared 92.9–96.8% 16S rRNA gene sequence similarities with the type strains of the other Mesonia species. These sequence similarities indicated that strain JHPTF-M18T might be a member of species different from recognized Mesonia species according to the values (98.7%) recommended for delineation of a bacterial species by Stackebrandt and Ebers (2006) and Kim et al. (2014).

Genomic features

The genome size of strain JHPTF-M18T obtained from the assembly of sequencing reads was 3,328,752 bp with a sequencing depth of coverage of 482.93X. The genomic sequence of strain JHPTF-M18T contained 73 contigs with N50 length of 192,421 bp. The complete 16S rRNA gene sequence extracted from the genomic data using ContEst16S (Lee et al. 2017) was found to be identical.
to respective 16S rRNA gene information previously obtained by Sanger sequencing. This indicated that strain JHPTF-M18T and its genomic data were not mislabelled and did not originate from any source of contamination (Chun et al. 2018). Based on its genomic sequence data, the DNA G+C content of strain JHPTF-M18T was 33.1%, a value in the range reported for Mesonia species (Lucena et al. 2020). The genome of strain JHPTF-M18T had 2,967 protein-coding genes, within the range reported for Mesonia mobilis DSM 19841T (2,897), Mesonia hitae R32T (3,535), Mesonia oceanica ISS653T (3,789), Mesonia physicola DSM 21425T (2,939) and Mesonia algae DSM 15361T (2,828). The genomic sequence of strain JHPTF-M18T was shown to have 4 rRNA-encoding genes with one 5S, one 16S and two 23S rRNAs, whereas those of the type strains of M. mobilis, M. hitae, M. oceanica, M. physicola and M. algae have rRNA-encoding genes of 5–10. UBCG phylogenomic tree based on genomic sequences showed that strain JHPTF-M18T form a cluster with the type strains of Mesonia species and Paramesonia marina (Fig. S1). Strain JHPTF-M18T had AAI values of 83.7, 81.2, 81.1, 80.2 and 72.1% to M. mobilis DSM 19841T, M. hitae R32T, M. oceanica ISS653T, M. physicola DSM 21425T and M. algae DSM 15361T, respectively, and less than 70.0% to members of other genera. The genomic sequence data of strain JHPTF-M18T had ANI values of 79.7, 78.8, 78.2, 78.0 and 73.1% and dDDH values of 22.8, 21.5, 21.5, 21.2 and 18.5% to those of the type strains JHPTF-M18T were similar to those of the type strains of M. algae in that phosphatidyethanolamine is the only major phospholipid identified and one unidentified lipid is major component, but distinguished from that of the type strain of M. algae by the absence of one unidentified glycolipid as a major component (Fig. S2).

**Chemotaxonomic characteristics**

The predominant isoprenoid quinone detected in strain JHPTF-M18T was menaquinone-6 (MK-6), at a peak area ratio of approximately 95%, consistent with the results shown in the genus Mesonia (Lucena et al. 2020; Nedashkovskaya et al. 2003). The major fatty acids (> 10% of the total fatty acids in all growth phases) found in strain JHPTF-M18T were iso-C₁₅:₀, iso-C₁₇:₁ 3-OH and summed feature 3 (C₁₆:₁ω7c and/or C₁₆:₁ω6c) (Table S1). The major polar lipids detected in strain JHPTF-M18T were phosphatidyethanolamine and two unidentified lipids; minor amounts of eight other unidentified lipids, two unidentified aminolipids and one unidentified aminophospholipid were also present (Fig. S2). The polar lipid profile of strain JHPTF-M18T was similar to that of the type strain of M. algae in that phosphatidyethanolamine is the only major phospholipid identified and one unidentified lipid is major component, but distinguished from that of the type strain of M. algae by the absence of one unidentified glycolipid as a major component (Fig. S2).

**Morphological, cultural, physiological and biochemical characteristics**

Strain JHPTF-M18T had no flagellum and did not reduce nitrate. The genes involved in flagella biosynthesis and nitrate reduction were not retrieved from genomic data by “NCBI Prokaryotic Genome Annotation Pipeline”. Strain JHPTF-M18T showed catalase and oxidase activities which could also be confirmed by the presence of relevant genes retrieved from “NCBI Prokaryotic Genome Annotation Pipeline”. Strain JHPTF-M18T could not hydrolyse casein and susceptible to tetracycline, whereas the type strains of M. mobilis and M. algae hydrolysed casein and resistant to tetracycline (Table 1). Sonicated in vivo extracts of strain JHPTF-M18T showed absorption peak maxima at 454 and 480 nm, indicating the presence of carotenoids. Strain JHPTF-M18T was susceptible to carbenicillin (100 μg), chloramphenicol (100 μg), lincomycin (15 μg), oleandomycin (15 μg) and tetracycline (30 μg), but resistant to ampicillin (10 μg), cephalothin (30 μg), gentamicin (30 μg), kanamycin (30 μg), neomycin (30 μg), novobiocin (5 μg), penicillin G (20 IU), polymyxin B (100 IU) and streptomycin (50 μg). Phenotypic characteristics of strain JHPTF-M18T are given in the species description, Table 1 and Fig. S3.

**Conclusion**

Combined results obtained from the phylogenetic, genomic and chemotaxonomic analyses made it reasonable to assign strain JHPTF-M18T as a member of the genus Mesonia (Fig. 1; Figs. S1 & S2; Table S1). Strain JHPTF-M18T was distinguished from the type strains of M. mobilis and M. algae by differences in several phenotypic characteristics, including hydrolysis and acid production from some substrates, activity of some enzymes and susceptibility to some antibiotics (Table 1). Based on the polyphasic taxonomic data presented, strain JHPTF-M18T is considered to represent a novel species of the genus Mesonia, for which we propose the name Mesonia aestuariivivens sp. nov.
Table 1 Differential characteristics of strain JHPTF-M18\textsuperscript{T} and the type strains of Mesonia mobilis and Mesonia algae

| Characteristic                  | 1          | 2          | 3          |
|--------------------------------|------------|------------|------------|
| Hydrolysis of                  |            |            |            |
| Aesculin                       | +          | +          | –          |
| Casein                         | –          | +          | –          |
| Acid production form           |            |            |            |
| D-Glucose                      | –          | +          | –          |
| Maltose                        | –          | +          | –          |
| D-Mannose                      | –          | +          | –          |
| Susceptibility to              |            |            |            |
| Ampicillin                     | –          | W          | +          |
| Cephatholin                    | +          | –          | +          |
| Tetracycline                   | +          |  –         | –          |
| Enzyme activity (API ZYM)      |            |            |            |
| α-Glucosidase                  | –          | +          | –          |
| β-Glucosidase                  | –          | –          | +          |
| DNA G+C content (%)\textsuperscript{a} | 33.1       | 35.1       | 33.1       |

Strains: 1, JHPTF-M18\textsuperscript{T}; 2, M. mobilis KCTC 12708\textsuperscript{T}; 3, M. algae KCTC 12089\textsuperscript{T}. Data of column 1 obtained from this study and data of columns 2 and 3 obtained from Lee et al. (2012). +, positive reaction; −, negative reaction; w, weakly positive reaction. All strains are rod-shaped and positive for activity of catalase and oxidase; hydrolysis of gelatin and Tween 80; susceptibility to carbenicillin, chloramphenicol, lincomycin and oleandomycin; and activity of alkaline phosphatase, esterase (C4), esterase lipase (C8), leucine arylamidase, valine arylamidase, cystine arylamidase, cysteine arylamidase, acid phosphatase and naphthol-AS-BI-phosphohydrolase. All strains are negative for Gram-staining; production of flexirubin-type pigments; nitrate reduction; hydrolysis of hypoxanthine, xanthine, starch and urea; acid production from L-arabinose, D-cellobiose, D-fructose, D-galactose, lactose, D-melezitose, melibiose, D-raffinose L-rhamnose, D-ribose, sucrose, D-trehalose, D-xylene, myo-inositol, D-mannitol and D-sorbitol; susceptibility to gentamicin, kanamycin, neomycin, novobiocin, penicillin G, polymyxin B and streptomycin; and activity of lipase (C14), trypsin, α-chymotrypsin, α-galactosidase, β-galactosidase, β-glucuronidase, N-acetyl, β-glucosaminidase, α-mannosidase and α-fucosidase.

\textsuperscript{a}Data obtained from genomic sequences

Description of Mesonia australivivis sp. nov.

Mesonia australivivis (aes.tu.a.r.i.vi’vens. L. neut. n. aes-tuarium tidal flat; L. pres. part. vivens living; N.L. part. adj. aestuarivivis living in a tidal flat).

Cells are ovoid or rod-shaped measuring approximately 0.2–0.4 μm in diameter and 0.3–3.0 μm in length. Gram-staining reaction is negative. Spores are not formed. No flagellum is found. Non-motile by gliding. Colonies on MA are circular, slightly convex, smooth, glistening, vivid yellow in colour and 0.5–1.0 mm after incubation for 3 days at 25 °C. Grows optimally at 25 °C and pH 7.0–7.5. Growth occurs at 4 and 37 °C but not at 40 °C, and occurs at pH 5.5 but not at pH 5.0. Growth occurs in the presence of 0.5–14.0% (w/v) NaCl with an optimum of approximately 2.0–3.0% (w/v) NaCl. Mg\textsuperscript{2+} ions are not required for growth. Anaerobic growth does not occur on MA and on MA supplemented with nitrate. Catalase- and oxidase-positive. Nitrate is not reduced to nitrite. Aesculin, gelatin, Tween 80 and L-tyrosine are hydrolysed, but casein, hypoxanthine, starch, urea and xanthine are not. Flexirubin-type pigments are not produced. Carotenoid pigments are produced. Acid is not produced from L-arabinose, D-cellobiose, D-fructose, D-galactose, D-glucose, lactose, maltose, D-mannose, D-melezitose, melibiose, L-rhamnose, D-raffinose, D-ribose, sucrose, D-trehalose, D-xyllose, myo-inositol, D-mannitol and D-sorbitol. In assays with the API ZYM system, activities of alkaline phosphatase, esterase (C4), esterase lipase (C8), leucine arylamidase, valine arylamidase, cystine arylamidase, acid phosphatase, naphthol-AS-BI-phosphohydrolase and -glucosidase are present, but activities of other enzymes are absent. The predominant menaquinone is MK-6. The major fatty acids (> 10% of total fatty acids) are iso-C\textsubscript{15:0} 3-OH and summed feature 3 (C\textsubscript{16:1} ω7c and/or C\textsubscript{16:1} ω6c). The major polar lipids are phosphatidylethanolamine and two unidentified lipids. The DNA G+C content of the type strain is 33.1% (from genome sequence data).

The type strain, JHPTF-M18\textsuperscript{T} (= KACC 22185\textsuperscript{T} = NBRC 115119\textsuperscript{T}), was isolated from a tidal flat sediment collected from Sacheon on the Yellow Sea, South Korea.

The GenBank/EMBL/DDBJ accession number for the 16S rRNA gene sequence and GenBank accession number for the whole genome shotgun sequence of strain JHPTF-M18\textsuperscript{T} are MW364546 and JAHWDF000000000, respectively.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s00203-022-03146-8.

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Declarations

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

Ethical approval This article does not contain any studies with human participants or animals performed by any of the authors.

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