Mesonia oceanica sp. nov., isolated from oceans during the *Tara* Oceans Expedition, with a preference for mesopelagic waters

1.1 Author names

Teresa Lucena[1], Isabel Sanz-Sáez[2], David R. Arahal[1], Silvia G. Acinas[2], Olga Sánchez[3], Carlos Pedrós-Alió[4], Rosa Aznar[1] and María J. Pujalte[1]*

1.2 Affiliation

[1]Departamento de Microbiología y Ecología and Colección Española de Cultivos Tipo (CECT), Universitat de València, Valencia, Spain
[2]Departament de Biologia Marina i Oceanografia, Institut de Ciències del Mar, ICM-CSIC, Barcelona, Spain
[3]Departament de Genètica i Microbiologia, Facultat de Biociències, Universitat Autònoma de Barcelona, 08193 Bellaterra, Spain
[4]Department of Systems Biology, Centro Nacional de Biotecnología (CNB), CSIC, Madrid, Spain

1.3 Corresponding author

maria.j.pujalte@uv.es

1.4 Keyword

Mesonia, Mesonia oceanica, Flavobacteriaceae, marine bacteria, taxogenomics, mesopelagic zone

1.5 Repositories:

The accession number of *Mesonia oceanica* ISS653^T 16S rRNA gene sequence and draft genome are MH732189 and CABVMM01, respectively. The accession number of *Mesonia oceanica* ISS1889 16S rRNA gene is MN836382.

ABSTRACT

Strain ISS653^T, isolated from Atlantic seawater, is a yellow pigmented, non-motile, Gram-negative rod-shaped bacterium, strictly aerobic and chemoorganotrophic, slightly halophilic (1-15% NaCl) and mesophilic (4-37 ºC), oxidase and catalase positive and proteolytic. Its major cellular fatty acids are iso-$C_{15:0}$, iso-$C_{15:0}$ 2-OH, and iso-$C_{17:0}$ 3-OH; the major identified phospholipid is phosphatidylethanolamine and the major respiratory quinone is MK6. Genome size is 4.28 Mbp and DNA G+C content is 34.9 mol%. 16S rRNA gene sequence similarity places the strain among members of *Flavobacteriaceae,* with the types of *Mesonia phycicola* (93.2 %), *Salegentibacter mishustinae* (93.1 %) and *Mesonia mobilis* (92.9 %) as

closest relatives. Average Amino acid Identity (AAI) and Average Nucleotide Identity (ANI) indexes show highest figures with *M. mobilis* (81% AAI; 78.9% ANI), *M. phycicola* (76% AAI; 76.3% ANI), *M. maritima* (72 % AAI, 74.9 % ANI), *M. hippocampi* (64 % AAI, 70.8 % ANI) and *M. algae* (68% AAI; 72.2 % ANI). Phylogenomic analysis using the Up-to-date-Bacterial Core Gene set (UBCG) merges strain ISS653^T in a clade with species of the genus *Mesonia*. We conclude that strain ISS653^T represents a novel species in the genus *Mesonia* for which we propose the name *Mesonia oceanica* sp. nov., and strain ISS653^T (= CECT 9532^T = LMG 31236^T) as the type strain. A second strain of the species, ISS1889 (= CECT 30008) was isolated from Pacific Ocean seawater. Data obtained throughout the *Tara* Oceans expedition indicate that the species is more abundant in the mesopelagic dark ocean than in the photic layer and it is more frequent in the South Pacific, Indian and Atlantic oceans.

The genus *Mesonia* belongs to the *Flavobacteriaceae* [1], the bacterial family which includes the largest number of genera to date, 153 according to LPSN [2]. Marine members of the family *Flavobacteriaceae* play fundamental roles as complex organic matter degraders and in the nutrient turnover in oceans, where many of them are found in association with marine phytoplankton and algal live or detritic material [1, 3] and some display proteorodopsin-based photoheterotrophy [3]. The genus *Mesonia* was established in 2003 to accommodate a group of algal-associated marine bacteria that were different from *Salegentibacter* and other halophilic flavobacteria [4]. It currently contains eight species with validly published names, all of them isolated from marine environments and organisms: *Mesonia algae*, the type species [4], *M. mobilis* [5], *M. phycicola* [6], *M. ostreae* [7], *M. aquimarina* [8], *M. hippocampi* [9], *M. sediminis* [10] and *M. maritima* [11]. The genus is one of the many included in a recent phylogenomic study of the phylum *Bacteroidetes* [12] and has not been affected by the reclassifications therein proposed. From *Tara* Oceans expedition (2009–2013) [13] we have isolated in culture a large collection of marine bacteria from different oceanographic regions and depths [14]. Based on such isolation effort, here we present the description of a novel species in this family, based on the phenotypic, genomic and phylogenetic study of the strains ISS653^T and ISS1889.

Isolation

Strain ISS653^T was isolated in September 2012 from surface seawater at the North Atlantic Ocean (36°10'10.2"N 29°01'13.8"W). Sampling strategy and methodology have been described previously [13]. Briefly, the isolate was obtained by plating 100 µl of undiluted and 10x diluted seawater (pre-filtered by 200 µm and 20 µm meshes to remove large plankton) in Marine Agar 2216 plates (BD Diagnostics). Plates were incubated at room temperature (approximately 20ºC) in the dark until no more colonies appeared (10-30 days). Colonies that grew were streaked on agar plates in duplicate to ensure their purity and avoid contamination. The isolates were stored in the broth medium used with glycerol (25% v/v) in cryovials at -80ºC. The culture was regrown on Marine Agar 2216 (BD Diagnostics) at room temperature for 3 days. The strain has been maintained by lyophilisation at the Spanish Type Culture Collection (CECT) as CECT 9532^T (= LMG 31236^T) where part of the characterization was also conducted. A second strain of the species, ISS1889 (= CECT 30008), was isolated during the same expedition from surface seawater of the Eastern Pacific Ocean

(5°15'36.0"S 85°10'04.1"W). A study, including phenotypic, genomic and phylogenetic characterization of the strains was undertaken in order to define their taxonomic position.

16S RNA phylogeny

A partial (1328 bp) 16S rRNA gene sequence of strain ISS653^T was obtained after DNA extraction as reported previously [15] and deposited under the accession number MH732189. A BLAST search for the closely related taxa, based on this sequence, related the strain to the family *Flavobacteriaceae* and revealed spec ies of the genera *Salengentibacter*, *Mesonia*, *Zunongwangia* and *Gramella* species as its closest neighbours, with sequence similarities always lower than 93%. These values suggested that the strain represented a novel taxon. At a different stage, the nearly complete 16S rRNA gene sequence of strain ISS1889 (1425 bp) was obtained through already reported methods [15] and deposited under accession number MN836382. It was found to be identical to that of ISS653^T, suggesting that both strains could represent the same species.
The sequence (1530 bp) obtained from the genome draft of strain ISS653^T, described under the next heading, was subsequently used for determining similarity values with the type strains of closely related species [16] and also to reconstruct phylogenetic trees [17, 18] using ARB. Closest neighbours based on 16S rRNA sequence similarity, as determined by the Identifier tool of EzBiocloud [16] were: *Mesonia phycicola* (93.2 %), *Salegentibacter mishustinae* (93.1 %), *Mesonia mobilis* (92.9 %), *Mesonia maritima* (92.9 %), *Salegentibacter. salarius* (92.9 %) and *Mesonia aquimarina* (92.6 %). A phylogenetic tree based on 16S rRNA gene sequences is shown in Fig. 1. It places strains ISS653^T and ISS1889 in the clade formed by species of the genus *Mesonia*, as a sister clade. The low 16S rRNA gene similarities found and the position of the branch in the tree support the taxonomic novelty of the strains at the species level and even suggest that they might represent a novel genus in the family. However, genus boundaries are not defined as clearly as species on genomic and phylogenetic grounds and a careful evaluation of all genomic and phenotypic evidence is required for definition of a genus. We thus, explored some other indexes and phylogenetic approaches to decide whether strains ISS653^T and ISS1889 should be classified as representing a novel species of the genus *Mesonia* or as a novel genus in the family *Flavobacteriaceae.*

Genome Features

A draft genome of strain ISS653^T was obtained through whole genome sequencing at Centre Nacional d'Anàlisi Genòmica (CNAG) (https://www.cnag.crg.eu/) following procedures described previosuly [15]. The libraries were sequenced on HiSeq 2500 (HiSeq Rapid SBS Kit V2, Illumina) in paired-end mode 2×251+8+8 bp. Primary data analysis, image analysis, base calling and quality scoring of the run were processed using the manufacturer's software Real Time Analysis (RTA 1.18.66.3), followed by generation FASTQ sequence files. The reads were analysed for quality control using FASTQC, a common quality control tool developed by Babraham Bioinformatics to check raw sequencing data. After filtering, the remaining reads were assembled using SPAdes 3.9.0 software [19]. A plot, coverage versus length of the contigs, was performed to help in the choice of the parameters for contigs filtering. After

the filtration of contigs (minimal length 500 bp and coverage 10-50× kmer), evaluation of the final assembly against a reference genome was done with the software QUAST v4.3 [20]. The bioinformatic tool CheckM v1.0.7 [21] was used to assess the genome quality prior to annotation using Prokka v1.12 [22] and RAST v2.0 (Rapid Annotation using Subsystem Technology) [23]. The process of quality assessment of reads, read-processing, assembly and annotation with Prokka was carried out in Linux OS, other tools were accessed online. The minimal standards for the quality of genome sequences and how they can be applied for taxonomic purposes have been observed in this study [24].

The available genomes of type strains of genera of the family *Flavobacteriaceae* closely related to the novel taxon were retrieved from public databases. Table 1 shows their accession numbers and main characteristics.

The draft genome of strain ISS653^T has an estimated size of 4.28 Mbp. It is composed of 72 contigs with a N50 value of 251,300 nucleotides and final assembly coverage of 452×. CheckM results of contamination and completeness were 0.53 and 99.6 %, respectively. The assembly contains 4030 protein coding sequences and 45 RNA genes. Only one ribosomal RNA operon is detected and its 16S rRNA gene sequence is complete and 100% coincident with the partial sequence previously amplified (Sanger). The G+C molar content is 34.9 %. This genome is the largest one of all available genomes of members of the genus *Mesonia*, in fact, is about 1.0 Mbp larger than the one of *M. phycicola* (which had the maximum genome size recorded until now).

The presence of four copies of a CTnDOT-like transposon [25] is predicted from the four *Tra* regions (containing *TraJ*, *K*, *M*, *N*, *I* and *G* genes) identified as part of this Bacteroidetes-specific transposon. It is also present in the genomes of *M. maritima* (two copies) and *M. phycicola* (one copy).

Further exploration of annotated genome of strain ISS653^T allowed the prediction of some potential abilities of the strain, such as multiple degradative polysaccharide capabilities, a trait characteristic of several taxa in the family. Among them, carbohydrate active enzymes (CAZymes) predicted from the genome of strain ISS653^T account for pectate lyase (EC 4.2.2.2., two copies), polygalacturonase (EC 3.2.1.15), xylan β-1-4 xylosidase (EC 3.2.1.37), endo 1-4 β-xylanase, pectin estearase (EC 3.1.1.11), a pectin degradation protein, KdgF, rhamnogalacturonate acetyl estearase, endoglucanase, β-glucosidase (five copies), mucin desulfating sulfatase (two copies), phytase, glucan 1-4 α-glucosidase (two copies), a polysaccharide deacetylase, glycogen synthase, laminarinase, β-1-4 glucanase, hyaluronan synthase, oligogalacturonate lyase and neopullullanase (Table S2, available in the online version of the article).

Apart from these, it is also interesting to note the presence of genes coding for phosphatidylserine decarboxylase (in agreement with the presence of PE as major identified polar lipid) but also of cardiolipin synthase (although no DPG was detected among the identified polar lipids). A large CRISPR region and several Cas proteins are also encoded, as well as a type III restriction-modification system, and various gliding motility-associated ABC transporter permeases. Enzymes involved in carotene metabolism, as phytoene synthase, phytoene dehydrogenase, lycopene β-cyclase and β-carotene hydroxylase are also found. No rhodopsin-related enzymes are predicted.

The similarity between genomes was assessed using several indexes useful for species and genus delineation. Average Amino acid Identity (AAI) was calculated with the online server ANI/AAI-Matrix [26]. DNA-DNA hybridization (DDH) was estimated *in silico* with the Genome-to-Genome Distance Calculator (GGDC 2.1), using the BLAST method and

recommended formula 2 [27]; Average Nucleotide Identities, according to BLAST (ANIb) were determined in JSpeciesWS [28]. AAI and ANIb values among referenced genomes are presented in Table 2. ANI values confirm, as expected from 16S rRNA gene data, that strain ISS653^T does not belong to any of the compared species, since the figures obtained are always lower than 95 % (in fact, lower than 91 %). In silico DDH values for strain ISS653^T genome against *M. algae*, *M. hippocampi*, *M. maritima*, *M. mobilis*, and *M. phycicola* type strain genomes are 18.0 to 22.4 %, confirming that the strain does not belong to any of the mentioned species. AAI values to other *Mesonia* spp. are mostly over 70 %, but they range from 64 to 81 %, with 68% to the type species of the genus, *M. algae*. Finally, phylogenomic relationships among strain ISS653^T, members of *Mesonia* and other representatives of the family *Flavobacteriaceae* were explored with UBCG, based on the analysis of 92 universal bacterial core gene sequences [29]. The resulting trees, based on amino acid and nucleotide sequences are shown in Fig. 2 and Fig. S1, respectively. In both trees, ISS653^T forms a branch deeply embedded within the *Mesonia* clade; this branch shows the highest possible gene support index (GSI) value on the immediate nodes relating strain ISS653^T to *M. mobilis* and *M. phycicola*.

Ecology

Additionally, we explored the biogeography distribution of strain ISS653^T across oceans and depths by comparing the amplicon sequencing of the V4-V5 region of the 16S rRNA gene (16S iTAGs, primers 515F-Y and 926R [30]; sequenced by Illumina MiSeq platform (iTAGs) datasets from *Tara* Oceans [31]. We have been able to compare at 100% similarity the 16S rRNA gene sequences of ISS653^T and ISS1889 with zOTUs (zero-radius OYUs, i.e. Operational Taxonomic Units defined at 100% sequence similarity) denoted from high-throughput sequencing of the 16S rRNA of surface and mesopelagic samples (Fig. 3). The two strains were identical to one zOTU that based on rank abundance analysis (Fig. 4) belongs to the rare biosphere in the surface layer (0.0045% of the total reads) but to the mid-abundant biosphere (0.31%) in the mesopelagic. In addition, if we look the average of reads that were 100% identical to the mentioned strains per oceanographic region, the higher abundances were found in the mesopelagic samples of the South Pacific Ocean (Fig. 4) where ISS1889 was isolated. Interestingly, higher abundances were found in the mesopelagic layer, indicating probably a higher preference of these strains for aphotic layers.

Physiology and Chemotaxonomy

Phenotypic characterization included morphological, cultural, biochemical, physiological and nutritional screening and was performed by methods described previously [32]. *Mesonia algae* CECT 9441^T, *Salegentibacter salegens* CECT 9443^T, *Gramella echinicola* CECT 9439^T and *Zunongwangia profunda* CECT 9445^T were characterized in parallel for comparative purposes.

Flexirubin type pigmentation was tested according to the methods of Bernardet *et al*. (2002) [33]. In addition, analyses of cellulose degradation, nitrate reduction acid production from

carbohydrates in API 50CH/E, APIZYM and API 20NE profile were performed as described previously [15]. Transmission Electron Microscopy (TEM) and Scanning Electron Microscopy (SEM) observations of the morphology and ultrastructure also followed previously described procedures [15].

ISS653^T and ISS1889 were Gram-reaction negative, rod-shaped and non-motile, strictly aerobic and chemoorganoheterotrophic, oxidase and catalase positive. They were unable to grow anaerobically, either by carbohydrate fermentation or through nitrate reduction. The strains grew well on Marine Agar and Marine Broth 2216 (BD Diagnostics). Colonies on Marine Agar were yellow, round, with regular borders, with no indication of swarming or gliding. Temperature range for growth was 4 to 37 ºC (30 ºC for ISS1889), with optimum at 26-30 ºC. No growth was obtained at 40ºC. pH range was 5 to 8, with optimum at 6-8, very weak growth at 9 and 10 and no growth at 4 and below. The strains grew at total salinities of 1 to 15 %, optimally at 2-4 %, they did not grow at 0.5 % or less nor 18 % or higher salinities. The growth was strictly Na^+ -dependent. They are, thus, mesophilic, neutrophilic and slightly halophilic. They were able to hydrolyse gelatine and casein but the hydrolyses of Tween 80 (negative for ISS1889) and DNA were weak. Alginate, starch, cellulose and agar were not hydrolysed. Good growth was obtained on Baumann's Basal Medium with yeast extract (positive control of the carbon source screening) but it was negative with all the substrates used (D-ribose, L-arabinose, D-xylose, D-glucose, D-fructose, D-galactose, D-trehalose, D-mannose, L-rhamnose, maltose, D-cellobiose, lactose, sucrose, D-melibiose, amygdalin, salicin, N-acetyl-D-glucosamine, D-gluconate, D-glucuronate, D-galacturonate, D-saccharate, D-glycerol, D-mannitol, D-sorbitol, *myo*-inositol, acetate, pyruvate, propionate, butyrate, citrate, *t*-aconitate, 2 ketoglutarate, succinate, fumarate, malate, lactate, 3-hydroxybutyrate, glycine, L-leucine, L-alanine, L-glutamate, L-serine, L-arginine, L-tyrosine, L-treonine, L-aspartate, L-citrulline, L-ornithine, L-histidine, L-lysine, L-sarcosine and putrescine) suggesting that ISS653^T may have a growth factor requirement. ISS1889 was not tested for carbon source utilization in this medium. On the assimilation tests of API 20NE, both strains grew well with malate and, less conspicuously, on glucose, mannose, maltose, arabinose, mannitol, N-acetyl D-glucosamine, gluconate and adipate, but not on caprate or citrate; phenyacetate grow was positive only for ISS653^T. Both strains were positive for PNPG test (β-galactosidase activity) and esculin and gelatin hydrolysis, but negative for indole, arginine dihydrolase and urease. On APIZYM, both strains were positive for alkaline and acid phosphatases, leucine and valine arylamidases, and α- and β-glucosidases and were negative for other tests. Acid production from carbohydrates on API50CH/E strips was very scarce, with positive reaction only for aesculin hydrolysis and a slight acidification in D-glucose, D-mannose, amygdalin, salicin, D-cellobiose and maltose wells after 48 h incubation. Strain ISS1889 was almost identical except for the acid production from arbutin and 2-ketoglutarate (weak). They also showed slight differences in minor fatty acids (Table S1).

Fig. 3 displays SEM and TEM images of strain ISS653^T cells: they are regular straight rods with rounded ends, 0.5-0.6 × 0.9-1.5 µm in size, appearing singly or in pairs and showing the profile typical for a Gram-negative bacterium in TEM images. No appendages or internal structures were seen. Additional images are included in Fig. S2.

Fatty acid methyl esters were extracted from ISS653^T and ISS1889 biomass grown in Marine Agar at 26 ºC after 72 h incubation. Extracts were prepared according to standard protocols as described for the MIDI Microbial Identification System [34] at the CECT. Cellular fatty acid content was analysed by gas chromatography with an Agilent 6850 chromatographic unit, with the MIDI Microbial Identification System using the TSBA6 method [35] and identified

using the Microbial Identification Sherlock software package. Table S1 shows the cellular fatty acids detected in the two strains, that include iso-$C_{15:0}$, summed feature 3 and iso-$C_{17:0}$ 3-OH as major components, followed by iso-$C_{15:1}$ G, summed feature 9 ($C_{16:0}$ 10-methyl/iso-$C_{17:1}$ ω*9c*) and iso-$C_{15:0}$ 3-OH. An issue has been reported [36] about the peak names for summed feature 3 in flavobacteria that makes us believe it might correspond to iso-$C_{15:0}$ 2-OH, and so it is reported as such in the species description. The fatty acid profile of the strains closely resembles those of other *Mesonia* species and all the fatty acids present in percentages higher than 5% are found in similar amounts in the six species reported by [11]. Analysis of respiratory quinones and major polar lipids of ISS653^T were carried out by the Identification Service and Dr. Brian Tindall, DSMZ, Braunschweig. Germany. Detailed methods for the analyses have been reported previously [15]. MK6 was identified as the major quinone and phosphatidyl ethanolamine (PE) was the only identified polar lipid, among others detected (three unidentified lipids, two glycolipids and three aminolipids, Fig. S3). Both MK6 and PE are typical chemotaxonomic features of the genus *Mesonia*, present in all species so far described.

In summary, phylogenetic, genomic and phenotypic distinctiveness of the strains are indication of them representing, at least, a novel species, a novelty confirmed by 16S rRNA gene sequence similarity (less than 94 %) and ANI values (less than 95 %) exhibited between strain ISS653^T and the rest of the species of the genus *Mesonia* spp. and the neighboring taxa. In fact, the strains initially appeared to represent a novel genus in the family due to the low 16S rRNA gene similarity and to the topology of the 16S rRNA gene-based tree (Fig. 1). However, when considering genomic indexes, such as AAI, and the UBCG phylogenomic analysis, the relationship to their neighbors seems closer than anticipated by the 16S rRNA analysis: instead of representing a marginal and distant branch, ISS653^T merges in the core of the genus *Mesonia*. Its AAI values to other species of the genus *Mesonia* fall in the lower range of AAIs among congeneric species of *Flavobacteriaceae,* as, for example, species of the genus *Psychroflexus* spp. (62-91 % intragenus AAIs, data not shown). AAI has been used to define genus boundaries in the family, and particularly with the genus *Chryseobacterium* and related genera, in a recent paper [40]. These authors propose a cutoff value of 76% AAI for assignment of a novel species to an existing genus and consider that all type strain of congeneric species should present at least a 74% AAI to each other. By following this proposal, the novel species characterized in our study would constitute a novel genus, different from *Mesonia*, and this genus would encompass *M. mobilis* and *M. phycicola*. The species *M. hippocampi* and *M. maritima* should, in turn, be classified in two novel, different genera, while *M. algae* would be the only representative of the genus *Mesonia sensu stricto*. However, such major arrangements should wait until genome sequences for the type strains of all species of the genus *Mesonia* are available. For the time being, we consider the best option is to describe the novel species as a member of the genus *Mesonia*, provided that the genus does not become polyphyletic with this inclusion and that the novel species fits well with the genus description: the presence of iso-$C_{15:0}$ as major fatty acid, a genomic DNA G+C content of 34.9%, PE as the major identified polar lipid, MK-6 as the major respiratory quinone, the pigmentation type, the aerobic chemoorganotrophic metabolism, a positive responese for catalase, oxidase and alkaline phosphatase and the strict requirement of sodium for growth are features that qualify the strains as members of the genus *Mesonia*.

On the other hand, several traits shown in Table 3 allow to differentiate them phenotypically from any other *Mesonia* species.
In consequence, we propose a novel species of the genus *Mesonia*, with the name *Mesonia oceanica* and strain ISS653^T = CECT 9532^T = LMG 31236^T as the type strain.

Protologue

DESCRIPTION OF *MESONIA OCEANICA* SP. NOV.

Mesonia oceanica (o.ce.a'ni.ca, N.L. fem. adj. *oceanica*, of or pertaining to the ocean). Cells are Gram-reaction negative, rod-shaped, 0.5-0.6 µm × 0.9-1.5 µm and non-motile. Strictly aerobic and chemoorganotrophic; positive for catalase and oxidase. Colonies in Marine Agar medium are regular and yellow pigmented. Flexirubin-type pigments are not produced. Mesophilic, neutrophilic and slightly halophilic, with optima at: 26 ºC (range: 4-30 ºC, 40 ºC negative), 6-8 pH (range: 5-8, pH 4, negative, pH 9 and 10, weak) and 2-4 % total salinity (range: 1 to 15 %, 0.5 and 18 % negative). Requires sodium ions for growth. Nitrate is not reduced to nitrite or N_2. Hydrolyses esculin, casein, gelatin, Tween 80 (weakly) and DNA (weakly), but not alginate, cellulose (as filter paper) or agar. Indole production from tryptophan, arginine dihydrolase and uresase are negative. PNPG test (β-galactosidase) is positive in API 20NE. Assimilates malate, as well as glucose, mannose, maltose, arabinose, mannitol, N-acetyl D-glucosamine, gluconate and adipate, but not caprate or citrate on API 20NE. The type strain was unable to grow in minimal medium (Basal Medium) with any of 52 sole carbon and energy sources, but grew with yeast extract. The following carbohydrates are metabolised with weak acid production in aerobic API 50CH/E tubes: D-glucose, D-mannose, amygdalin, salicin, D-cellobiose and maltose. Enzymatic activities displayed on API ZYM are alkaline and acid phosphatases, leucine and valine arylamidases, and α- and β-glucosidases. Naphthol-AS-BI-phosphohydrolase, estearase and estearase lipase are weakly positive; lipase, cystine arylamidase, trypsin, α-chymotrypsin, α-galactosidase, β-galactosidase, β-glucuronidase, N-acetyl-β-glucosaminidase, α-mannosidase and α-fucosidase are negative. Major polar lipids are phosphatidyl ethanolamine (PE), two unidentified glycolipids, three unidentified aminolipids and three unidentified lipids. Major respiratory quinone is MK6. Major cellular fatty acids include iso-$C_{15:0}$, iso-$C_{15:0}$ 2-OH (although reported as summed feature 3 ($C_{16:1}$ *ω7c/ω6c*) and iso-$C_{17:0}$ 3-OH.
The type strain is ISS653^T (=CECT 9532^T =LMG 31236^T), which was isolated from surface seawater of the Atlantic Ocean during the *Tara* Oceans Expedition. Strain ISS1889 (=CECT 30008) is an additional strain of the species. The G+C DNA content of the type strain is 34.9 mol% and its genome size is 4.28 Mbp. The GenBank/EMBL/DDBJ accession numbers for the whole genome sequence and 16S rRNA gene of strain ISS653^T are CABVMM01 and MH732189, respectively.

AUTHOR STATEMENTS

1.6 Authors and contributors

Conceptualization: I.S.S., S.G.A. and M.J.P. Data curation, formal analysis and investigation: T.L., I.S.S., S.G.A., O.S. and M.J.P. Funding acquisition: S.G.A. and C.P.A. Project

administration and resources: D.R.A., S.G.A., R.A. and M.J.P. Supervision and writing original draft: M.J.P. All authors contributed to review and editing.

1.7 Conflicts of interest

The authors declare that there are no conflicts of interest.

1.8 Funding information

Sequencing was funded by grant CTM2016-80095-C2-1-R to CPA from the Spanish Ministerio de Economía y Competitividad. Additional funding was obtained by grant CTM2017-87736-R to SGA from the Spanish Ministerio de Economía y Competitividad. Other parts of this work received no specific grant from any funding agency.

1.9 Ethical approval

Not applicable

1.10 Consent for publication

Not applicable.

1.11 Acknowledgements

We thank our fellow scientists, the crew and chief scientists of the different cruise legs involved in *Tara* Oceans for collecting the culture samples used in this study. This is a *Tara* Oceans contributed paper number 105.

ABBREVIATIONS

CECT, Colección Española de Cultivos Tipo; LMG, Laboratorium voor Microbiologie, Universiteit Gent; ANI, Average Nucleotide Identity; DDH, DNA-DNA hybridization; AAI, Average Amino acid Identity; SCSIE, Servicio Central de Soporte a la Investigación Experimental; RAST, Rapid Annotation using Subsystem Technology; GGDC, Genome-to-Genome-Distance Calculator; BLAST, Basic Local Alignment Search Tool; UBCG, Up-to-date-Bacterial Core Gene; GSI, Gene Support Index; LTP, The All-Species Living Tree Project; NCBI, National Center for Biotechnology Information; PE, Phosphatidylethanolamine.

REFERENCES

1. **Bernardet JF.** *Flavobacteriaceae.* In Bergey's Manual of Systematics of Archaea and Bacteria. 2015. John Wiley & Sons, Inc. doi: 10.1002/9781118960608.fbm.00069
2. **Parte AC.** LPSN – List of prokaryotic names with standing in nomenclature (bacterio.net), 20 years on. *Int J Syst Evol Microbiol* 2018;68:1825–1829. doi: 10.1099/ijsem.0.002786

3. **Fernández-Gómez B, Richter M, Schüler M, Pinhassi J, Acinas SG *et al*.** Ecology of marine *Bacteroidetes:* A comparative genomics approach. *ISME J* 2013;7:1026–1037. doi: 10.1038/ismej.2012.169
4. **Nedashkovskaya OI, Kim SB, Han SK, Lysenko AM, Rohde M *et al.*** *Mesonia algae* gen. nov., sp. nov., a novel marine bacterium of the family *Flavobacteriaceae* isolated from the green alga *Acrosiphonia sonderi* (Kütz) Kornm. *Int J Syst Evol Microbiol* 2003;53:1967–1971.
5. **Nedashkovskaya OI, Kim SB, Zhukova NV, Kwak J, Mikhailov VV *et al.*** *Mesonia mobilis* sp. nov., isolated from seawater, and emended description of the genus *Mesonia*. *Int J Syst Evol Microbiol* 2006;56:2433–2436.
6. **Kang HS, Lee SD.** *Mesonia phycicola* sp. nov., isolated from seaweed, and emended description of the genus *Mesonia*. *Int J Syst Evol Microbiol* 2010;60:591–594.
7. **Lee SV, Lee MH, Yoon JH.** *Mesonia ostreae* sp. nov., isolated from seawater of an oyster farm, and emended description of the genus *Mesonia. Int J Syst Evol Microbiol* 2012;62:1804–1808.
8. **Choi A, Baek K, Lee H, Cho JC.** *Mesonia aquimarina* sp. nov., a marine bacterium isolated from coastal seawater. *Int J Syst Evol Microbiol* 2015;65:135–140.
9. **Kolberg J, Busse HJ, Wilke T, Schubert P, Kämpfer P *et al*.** *Mesonia hippocampi* sp. nov., isolated from the brood pouch of a diseased Barbour's Seahorse (*Hippocampus barbouri*). *Int J Syst Evol Microbiol* 2015;65:2241–2247.
10. **Wang FQ, Xie ZH, Zhao JX, Chen GJ, Du ZJ.** *Mesonia sediminis* sp. nov., isolated from a sea cucumber culture pond. *Antonie van Leeuwenhoek* 2015; 108, 1205–1212.
11. **Sung HR, Joh K, Shin KS.** *Mesonia maritimus* sp. nov., isolated from seawater of the South Sea of Korea. *Int J Syst Evol Microbiol* 2017;67:2574–2580.
12. **García-López M, Meier-Kolthoff JP, Tindall BJ, Gronow S, Woyke T *et al*.** Analysis of 1,000 type-strain genomes improves taxonomic classification of *Bacteroidetes. Front Microbiol* 2019;10:2083.
13. **Pesant S, Not F, Picheral M, Kandels-Lewis S, *et al*.** Open science resources for the discovery and analysis of *Tara* Oceans data. *Sci Data* 2015;2:150023. doi: 10.1038/sdata.2015.23
14. **Sanz-Sáez I, Salazar G, Lara E, Royo-Llonch M, Vaqué D *et al.*** Diversity patterns of marine cultivable bacteria along vertical and latitudinal gradients. *bioRxiv* 2019 doi: 10.1101/774992
15. **Lucena T, Arahal DR, Sanz-Saez I, Acinas SG, Sánchez O *et al*.** *Thalassocella blandensis* gen. nov., sp. nov., a novel member of the family *Cellvibrionaceae. Int J Syst Evol Microbiol* 2020;70:1231–1239. doi: 10.1099/ijsem.0.003906
16. **Yoon SH, Ha SM, Kwon S, Lim J, Kim Y *et al.*** Introducing EzBioCloud: A taxonomically united database of 16S rRNA and whole genome assemblies. *Int J Syst Evol Microbiol* 2017;67:1613–1617.
17. **Yarza P, Ludwig W, Euzéby J, Amann R, Schleifer K-H *et al.*** Update of the all-species living tree project based on 16S and 23S rRNA sequence analyses. *Syst Appl Microbiol* 2010;33:291–299.
18. **Ludwig W, Strunk O, Westram R, Richter L, Meier H *et al.*** ARB: a software environment for sequence data. *Nucl Acids Res* 2004;32:1363–1371.
19. **Nurk S, Bankevich A, Antipov D, Gurevich AA, Korobeynikov A *et al*.** Assembling genomes and mini-metagenomes from highly chimeric reads. In: Deng M., Jiang R., Sun

F., Zhang X. (eds) Research in Computational Molecular Biology. RECOMB 2013. Lecture Notes in Computer Science, vol 7821. Springer, Berlin, Heidelberg

20. **Gurevich A, Saveliev V, Vyahhi N, Tesler G.** QUAST: quality assessment tool for genome assemblies. *Bioinformatics* 2013;29:1072–1075.
21. **Parks DH, Imelfort M, Skennerton CT, Hugenholtz P, Tyson GW.** CheckM: assessing the quality of microbial genomes recovered from isolates, single cells and metagenomes. *Genome Res* 2015;25:1043–1055.
22. **Seemann T.** Prokka: rapid prokaryotic genome annotation. *Bioinformatics* 2014;30:2068–2069.
23. **Overbeek R, Olson R, Pusch GD, Olsen GJ, Davis JJ *et al*.** The SEED and the rapid annotation of microbial genomes using subsystems technology (RAST). *Nucleic Acids Res* 2014;42:D206–D214.
24. **Chun J, Oren A, Ventosa A, Christensen H, Arahal DR *et al*.** Proposed minimal standards for the use of genome data for the taxonomy of prokaryotes *Int J Syst Evol Microbiol* 2018;68:461–466.
25. **Bonheyo G, Graham D, Shoemaker NB, Salyers, AA.** Transfer region of a *Bacteroides* conjugative transposon, CTnDOT. *Plasmid* 2001;45,41–51.
26. **Rodriguez-R LM, Konstantinidis KT.** The enveomics collection: a toolbox for specialized analyses of microbial genomes and metagenomes. *PeerJ Preprints* 2016;4:e1900v1.
27. **Meier-Kolthoff JP, Auch AF, Klenk HP, Göker M.** Genome sequence-based species delimitation with confidence intervals and improved distance functions. *BMC Bioinformatics* 2013;14:60.
28. **Richter M, Rosselló-Móra R, Glöckner FO, Peplies J.** JSpeciesWS: a web server for prokaryotic species circumscription based on pairwise genome comparison. *Bioinformatics* 2015;32:929–931.
29. **Na SI, Kim YO, Yoon SH, Ha SM, Baek I, Chun J.** UBCG: Up-to-date bacterial core gene set and pipeline for phylogenomic tree reconstruction. *J Microbiol* 2018;56:281–285.
30. **Parada AE, Needham DM, Fuhrman JA.** Every base matters: assessing small subunit rRNA primers for marine microbiomes with mock communities, time series and global field samples. *Environ Microbiol* 2016;18:1403–1414.
31. **Ibarbalz FM, Henry N, Brandão MC, Martini S, Busseni G *et al.*** Global trends in marine plankton diversity across kingdoms of life. *Cell* 2019;179:1084–1097. doi: 10.1016/j.cell.2019.10.008
32. **Pujalte MJ, Lucena T, Rodriguez-Torres L, Arahal DR.** Comparative genomics of *Thalassobius* including the description of *Thalassobius activus* sp. nov and *Thalassobius autumnalis* sp. nov. *Front Microbiol* 2018;8:2645.
33. **Bernardet JF, Nakagawa Y, Holmes B.** Proposed minimal standards for describing new taxa of the family *Flavobacteriaceae* and emended description of the family. *Int J Syst Evol Microbiol* 2002;52:1049–1070. doi: 10.1099/00207713-52-3-1049.
34. **Sasser M.** Identification of bacteria by gas chromatography of cellular fatty acids, MIDI Technical Note 101. 1990. Newark: DE: MIDI Inc.
35. **MIDI.** Sherlock Microbial Identification System Operating Manual, version 6.1. 2008. Newark, DE: MIDI Inc.
36. **Montero-Calasanz MC, Göker M, Rohde M, Spröer C, Schumann P *et al*.** *Chryseobacterium oleae* sp. nov., an efficient plant growth promoting bacterium in the rooting induction of olive tree (*Olea europaea* L.) cuttings and emended descriptions of the genus *Chryseobacterium*, *C. daecheongense*, *C. gambrini*, *C. gleum*, *C. joostei*, *C.*

jejuense, *C. luteum*, *C. shigense*, *C. taiwanense*, *C. ureilyticum* and *C. vrystaatense*. *Syst Appl Microbiol* 2014;37:342–350. doi: 10.1016/j.syapm.2014.04.004

37. **Liang QY, Xu ZX, Zhang J, Chen GJ, Du ZJ.** *Salegentibacter sediminis* sp. nov., a marine bacterium of the family *Flavobacteriaceae* isolated from coastal sediment *Int J Syst Evol Microbiol* 2018;68:2375–2380.
38. **Li AZ, Han XB, Lin LZ, Zhang MX, Zhu HH**. *Gramella antarctica* sp. nov., isolated from marine surface sediment. *Int J Syst Evol Microbiol* 2018;68:358–363.
39. **Qin QL, Zhao DL, Wang J, Chen XL, Dang HY *et al*.** *Wangia profunda* gen. nov., sp. nov., a novel marine bacterium of the family *Flavobacteriaceae* isolated from southern Okinawa Trough deep-sea sediment. *FEMS Microbiol Lett* 2007;271:53–58.
40. **Nicholson AC, Gulvik CA, Whitney AM, Humrighouse BW, Bell ME, *et al*.** Division of the genus *Chryseobacterium*: Observation of discontinuities in amino acid identity values, a possible consequence of major extinction events, guides transfer of nine species to the genus *Epilithonimonas*, eleven species to the genus *Kaistella*, and three species to the genus *Halpernia* gen. nov., with description of *Kaistella daneshvariae* sp. nov. and *Epilithonimonas vandammei* sp. nov. derived from clinical specimens. *Int J Syst Evol Microbiol* 2020, doi: 10.1099/ijsem.0.003935 .

FIGURES AND TABLES

Fig. 1. Phylogenetic reconstruction based on the 16S rRNA gene using the Neighbor joining method. Sequence accession numbers are given in parentheses. Bar, number of substitutions per position.

Fig. 2. Phylogenetic tree generated with UBCG [29] by using amino acid sequences. The numbers at the nodes indicate the gene support index (GSI, maximal value is 92). Genome accession numbers are indicated in parentheses. Bar, 0.05 substitutions per position.

Fig. 3. Distribution of strains ISS653^{T} and ISS1889. (A). Rank abundance based on the number of reads per zOTU denoted from the 16S rRNA sequences. Color indicates the layer were the zOTUs come from: light-blue, surface; turquoise, mesopelagic. Orange circle and square indicate the position in the rank of the zOTU 100% identical to the two strains. (B). Heatmap indicating the average of reads 100% identical to the isolates per oceanographic region in surface and mesopelagic (Meso) samples. Lighter colors indicate lower number of reads, while strong indicate higher number of reads.

Fig. 4. SEM and TEM images of strain ISS653^{T}. Samples were gold sputter coated in order to visualize them with SEM Zeiss MERLIN Fe. Visualizations were done at the Microscopy service of the Universitat Autònoma de Barcelona (http://sct.uab.cat/microscopia/en/content/inici).

536 **Table 1.** Genomes used in the study and their main characteristics.

Strain	Accession number	Size (Mbp)	G+C (mol%)	Protein encoding genes	RNA encoding genes
Mesonia oceanica ISS653^T	GCF_902499555 (CABVMM01)	4.28	34.9	3854	45
Mesonia algae DSM 15361^T	GCF_003253545 (QKYV01)	3.09	33.1	2859	70
Mesonia mobilis DSM 19841^T	GCF_000423405 (AUHX01)	3.21	35.2	2875	46
Mesonia phycicola DSM 21425^T	GCF_900141885 (FQYY01)	3.23	31.4	2911	47
Mesonia maritima DSM 102814^T	jgi.1227497*	3.14	33.7	2946	67
Mesonia hippocampi DSM 29568^T	jgi.1220074*	2.59	34.5	2378	45
Salegentibacter salegens ACAM 48^T	GCF_900142975 (LT670848.1)	4.01	37.2	3415	58
Gramella echinicola DSM 19838^T	GCF_000423065 (AUHG01)	3.51	36.9	3112	50
Zunongwangia profunda SM-A87^T	GCF_000023465 (CP001650.1)	5.13	36.2	4270	60

537

538 *These sequence data were produced by the US Department of Energy Joint Genome
539 Institute (http://www.jgi.doe.gov/) in collaboration with the user community and are part of
540 The One Thousand Microbial Genomes Phase 4 Project (KMG-4) by M. Göker.
541

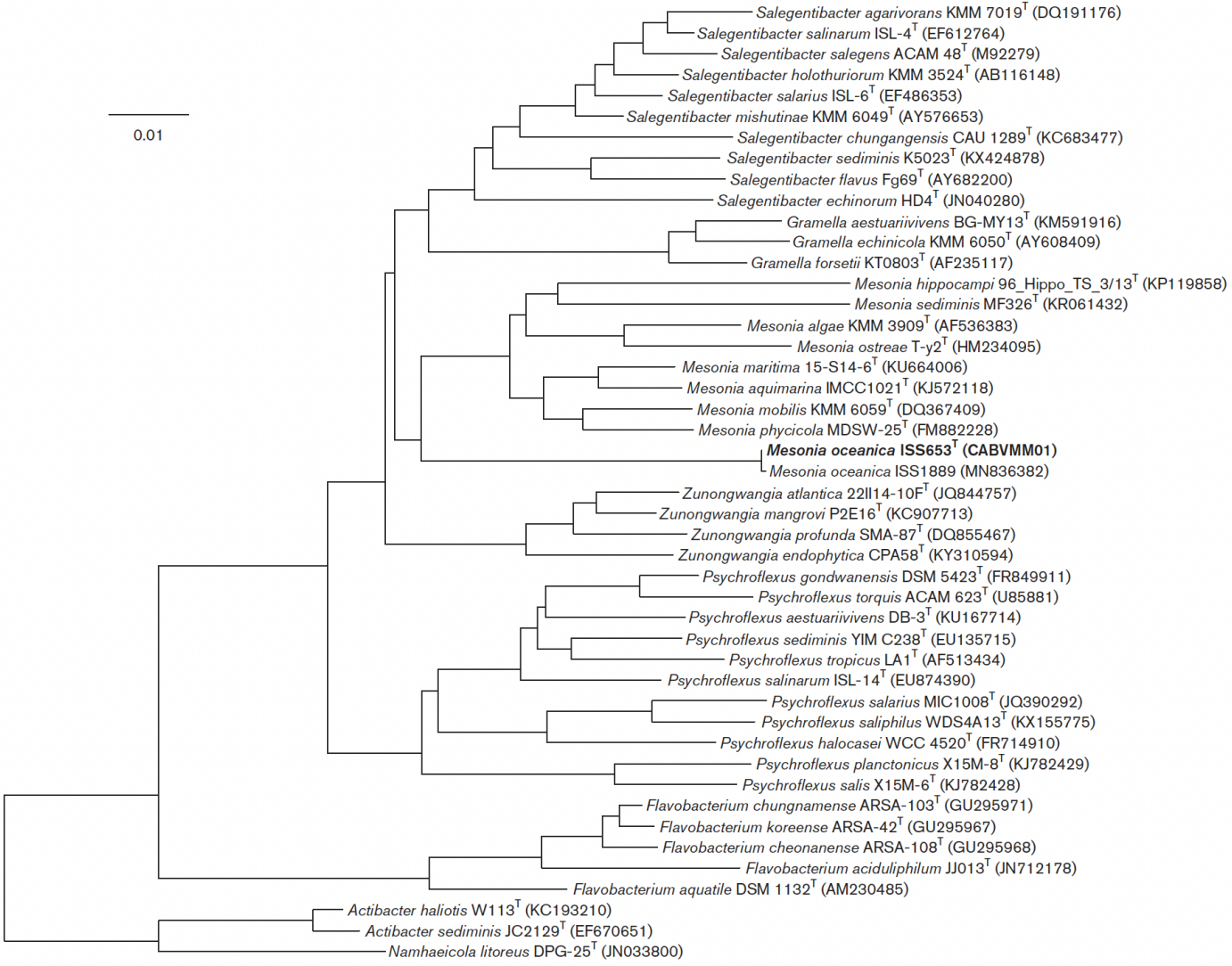
Table 2. Average Amino acid Identity (AAI, yellow cells) and Average Nucleotide Identity (ANIb, blue cells) indexes among genomes of type strains of *Flavobacteriaceae* species related to ISS653^T. Values relating *Mesonia oceanica* with all other species are shown in bold type.

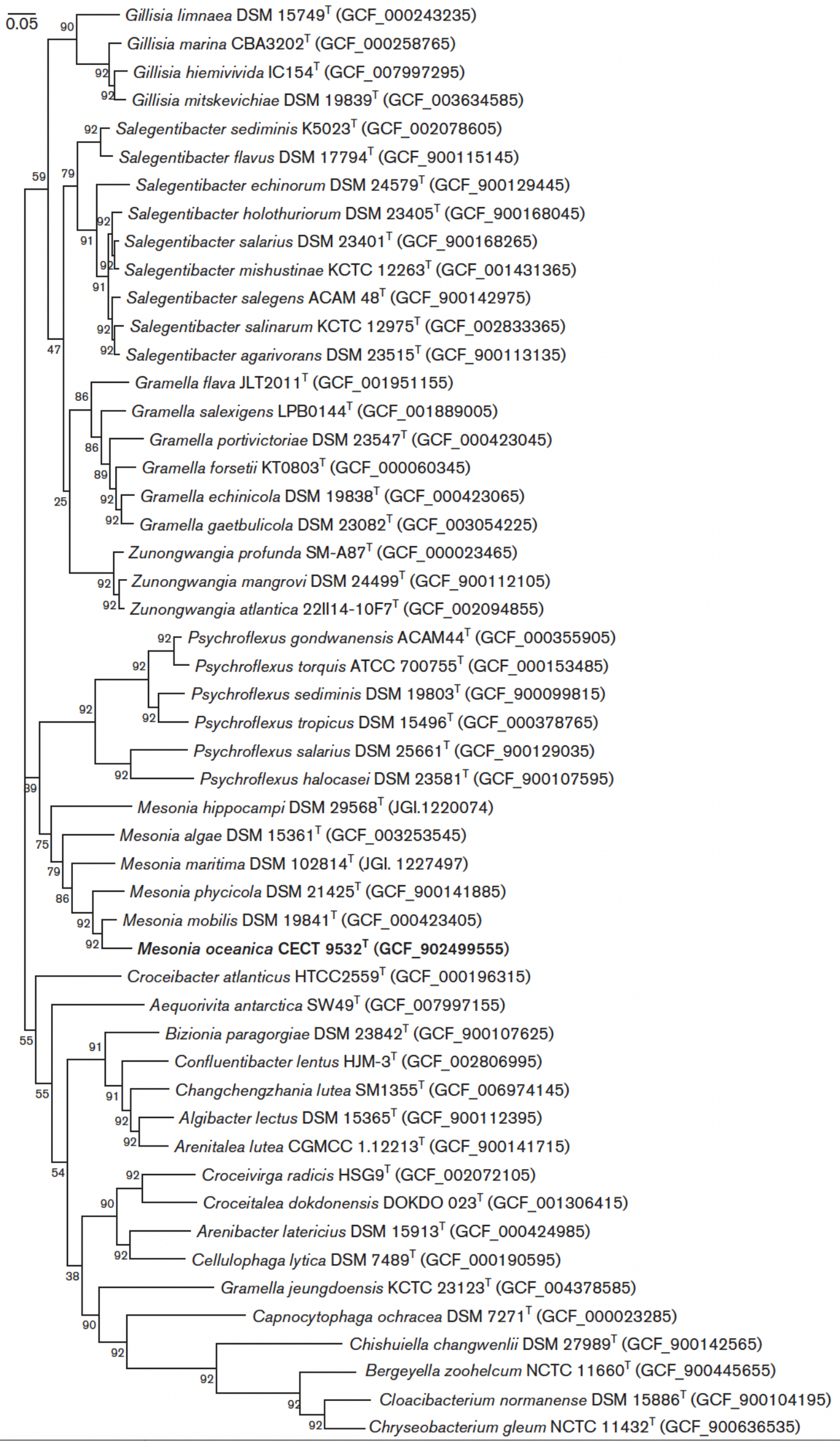
		1	2	3	4	5	6	7	8	9
1	*Mesonia oceanica* ISS653^T		**78.9**	**76.3**	**74.9**	**70.8**	**72.2**	**70.0**	**68.8**	**72.3**
2	*Mesonia mobilis* DSM 19841^T	**81**		78.4	74.4	70-9	72.4	69.7	68.6	70.7
3	*Mesonia phycicola* DSM 21425^T	**76**	80		73.4	71.5	73.5	69.6	68.9	70.0
4	*Mesonia maritima* DSM 102814^T	**72**	72	70		71.3	72.9	70.4	69.0	70.9
5	*Mesonia hippocampi* DSM 29568^T	**64**	65	65	65		71.0	69.1	68.2	68.9
6	*Mesonia algae* DSM 15361^T	**68**	70	70	70	65		69.5	68.8	69.6
7	*Salegentibacter salegens* ACAM 48^T	**63**	64	63	64	61	63		71.1	71.3
8	*Gramella echinicola* DSM 19838^T	**62**	63	63	63	61	63	70		70.2
9	*Zunongwangia profunda* SM-A87^T	**65**	64	63	64	60	62	68	67	

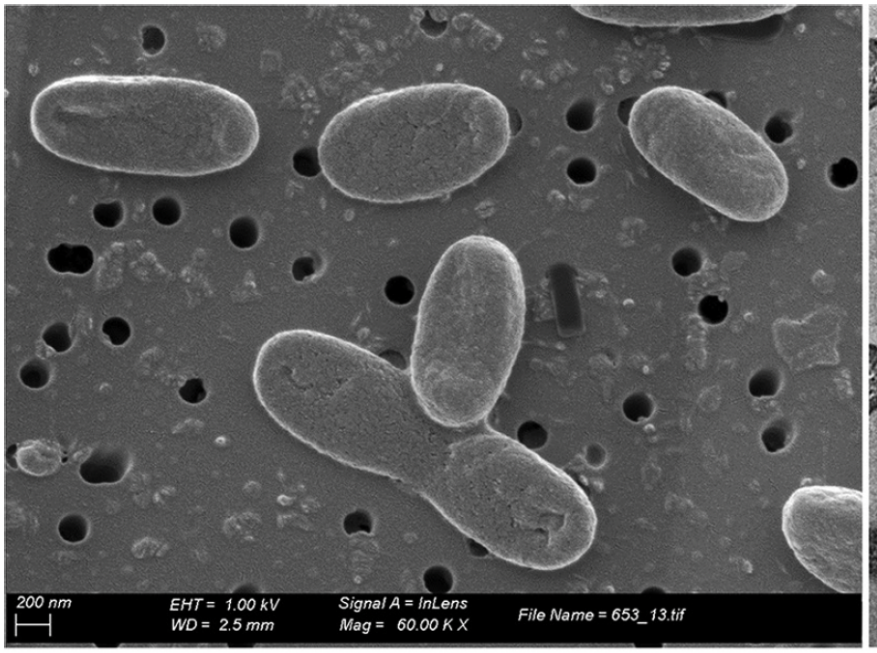
Table 3. Differential characteristics between strains ISS653^T and ISS1889 and its closest phylogenomic relatives. 1, *Mesonia oceanica* ISS653^T and ISS1889; 2, *M. algae* CECT 9441^T; 3, *M. mobilis* [5]; 4, *M. phycicola* [6]; 5, *M. ostreae* [7]; 6, *M. aquimarina* [8]; 7, *M. hippocampi* [9]; 8, *M. sediminis* [10]; 9, *M. maritima* [11]; 10, *Salegentibacter salegens* CECT 9443^T; 11, *Gramella echinicola* CECT 9439^T; 12*, Zunongwangia profunda* CECT 9445^T. All data from this study unless indicated. +: positive; - negative; nd: not determined; Y: yellow; W: white; Or: orange; G: gliding; Fl: flagellated. All strains were Gram-reaction-negative, aerobic, chemoorganotrophic bacteria, positive for oxidase, catalase, alkaline and acid phosphatases and leucine arylamidase; and negative for cellulose hydrolysis, α-galactosidase, β-glucuronidase, α-mannosidase and α-fucosidase.

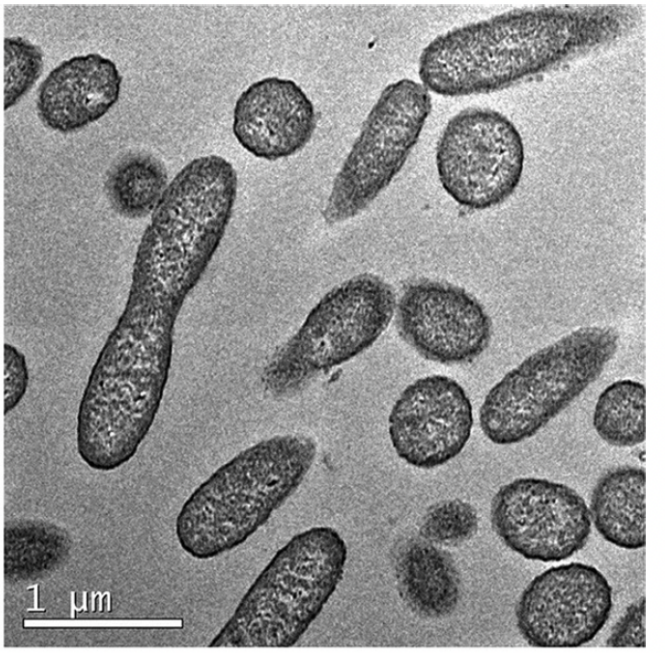
	1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**
Pigment colour	Y	Y	Y	Y	W	Y	Or	Y	Y	Y	Y	Y
Flexirubin	-	-	-	-	-	-	+	nd	-	-	-	-
Motility	-	-	+, G	-	-	-	-	-	+, Fl	-	+, G	-
Temp. range (ºC)	4-30	4-34	10-30	10-30	4-31	10-30	4-36	4-42	10-35	4-28	4-37	15-37
NaCl range (% w/v)	1-15	1-15	0.5-15	0.5-12	0-12	0.5-12	1-10	0.5-7	0.5-11	1-12	1-12	0.5-15
Hydrolysis of:												
Esculin	+	-	+	+	-	-	-	+	-	+	+	+
Casein	+	+	+	-	-	+	nd	nd	+	w	+	-
DNA	w	-	+	+	-	-	nd	nd	+	w	+	+
Tween 80	w	+	+	-	-	+	nd	+	+	-	-	+
Enzymatic activity (API ZYM)												
Valine arylamidase	+	+	+	+	+	+	-	+	+	+[a]	+[b]	+[c]
Trypsin	-	-	-	-	-	-	+	w	-	-[a]	w[b]	+[c]
β-Galactosidase	-	-	-	-	-	-	-	-	-	+[a]	-[b]	+[c]
α-Glucosidase	+	-	+	+	-	-	-	-	-	-[a]	+[b]	+[c]
β-Glucosidase	+	-	-	-	-	+	-	-	-	nd	w[b]	+[c]
G+C mol%	34.9	33.1	35.2	31.4	42.1[d]	41.4[d]	34.5	40.7[d]	33.7	37.2	36.9	36.2

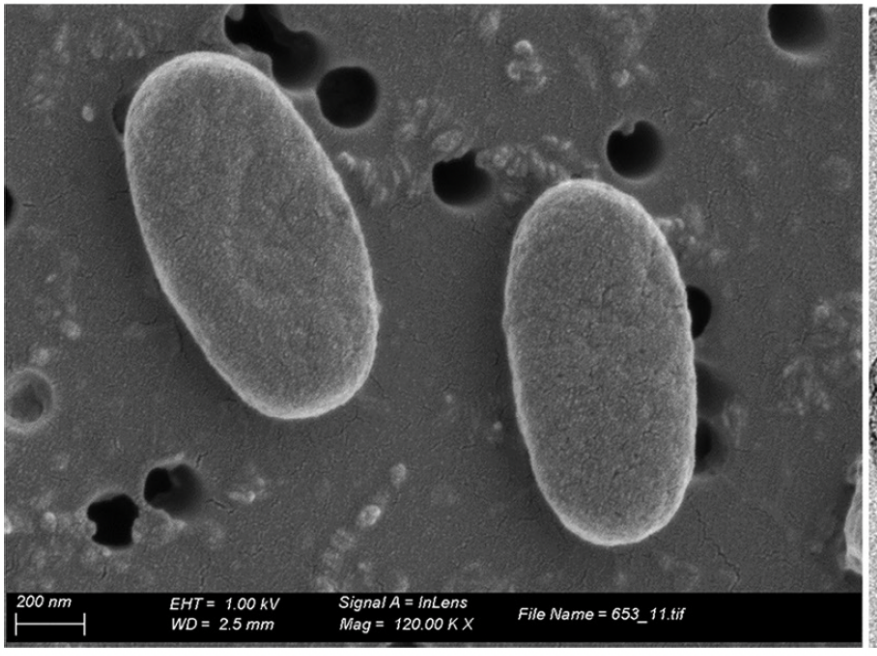
[a]data from [38]; [b]data from [39] ; [c]data from [40]; [d]determined by HPLC (all other values, from WGS)

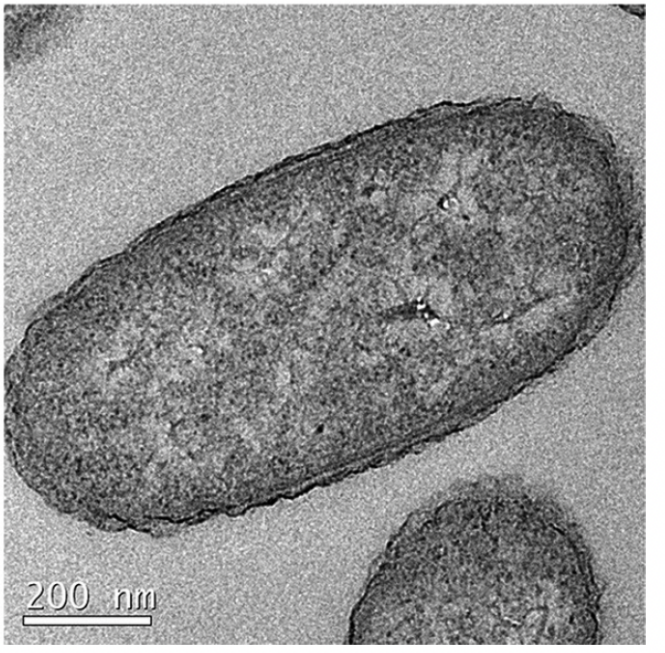

0.01
Salegentibacter agarivorans KMM 7019T (DQ191176)
Salegentibacter salinarum ISL-4T (EF612764)
Salegentibacter salegens ACAM 48T (M92279)
Salegentibacter holothuriorum KMM 3524T (AB116148)
Salegentibacter salarius ISL-6T (EF486353)
Salegentibacter mishutinae KMM 6049T (AY576653)
Salegentibacter chungangensis CAU 1289T (KC683477)
Salegentibacter sediminis K5023T (KX424878)
Salegentibacter flavus Fg69T (AY682200)
Salegentibacter echinorum HD4T (JN040280)
Gramella aestuariivivens BG-MY13T (KM591916)
Gramella echinicola KMM 6050T (AY608409)
Gramella forsetii KT0803T (AF235117)
Mesonia hippocampi 96_Hippo_TS_3/13T (KP119858)
Mesonia sediminis MF326T (KR061432)
Mesonia algae KMM 3909T (AF536383)
Mesonia ostreae T-y2T (HM234095)
Mesonia maritima 15-S14-6T (KU664006)
Mesonia aquimarina IMCC1021T (KJ572118)
Mesonia mobilis KMM 6059T (DQ367409)
Mesonia phycicola MDSW-25T (FM882228)
Mesonia oceanica ISS653T (CABVMM01)
Mesonia oceanica ISS1889 (MN836382)
Zunongwangia atlantica 22II14-10FT (JQ844757)
Zunongwangia mangrovi P2E16T (KC907713)
Zunongwangia profunda SMA-87T (DQ855467)
Zunongwangia endophytica CPA58T (KY310594)
Psychroflexus gondwanensis DSM 5423T (FR849911)
Psychroflexus torquis ACAM 623T (U85881)
Psychroflexus aestuariivivens DB-3T (KU167714)
Psychroflexus sediminis YIM C238T (EU135715)
Psychroflexus tropicus LA1T (AF513434)
Psychroflexus salinarum ISL-14T (EU874390)
Psychroflexus salarius MIC1008T (JQ390292)
Psychroflexus saliphilus WDS4A13T (KX155775)
Psychroflexus halocasei WCC 4520T (FR714910)
Psychroflexus planctonicus X15M-8T (KJ782429)
Psychroflexus salis X15M-6T (KJ782428)
Flavobacterium chungnamense ARSA-103T (GU295971)
Flavobacterium koreense ARSA-42T (GU295967)
Flavobacterium cheonanense ARSA-108T (GU295968)
Flavobacterium aciduliphilum JJ013T (JN712178)
Flavobacterium aquatile DSM 1132T (AM230485)
Actibacter haliotis W113T (KC193210)
Actibacter sediminis JC2129T (EF670651)
Namhaeicola litoreus DPG-25T (JN033800)

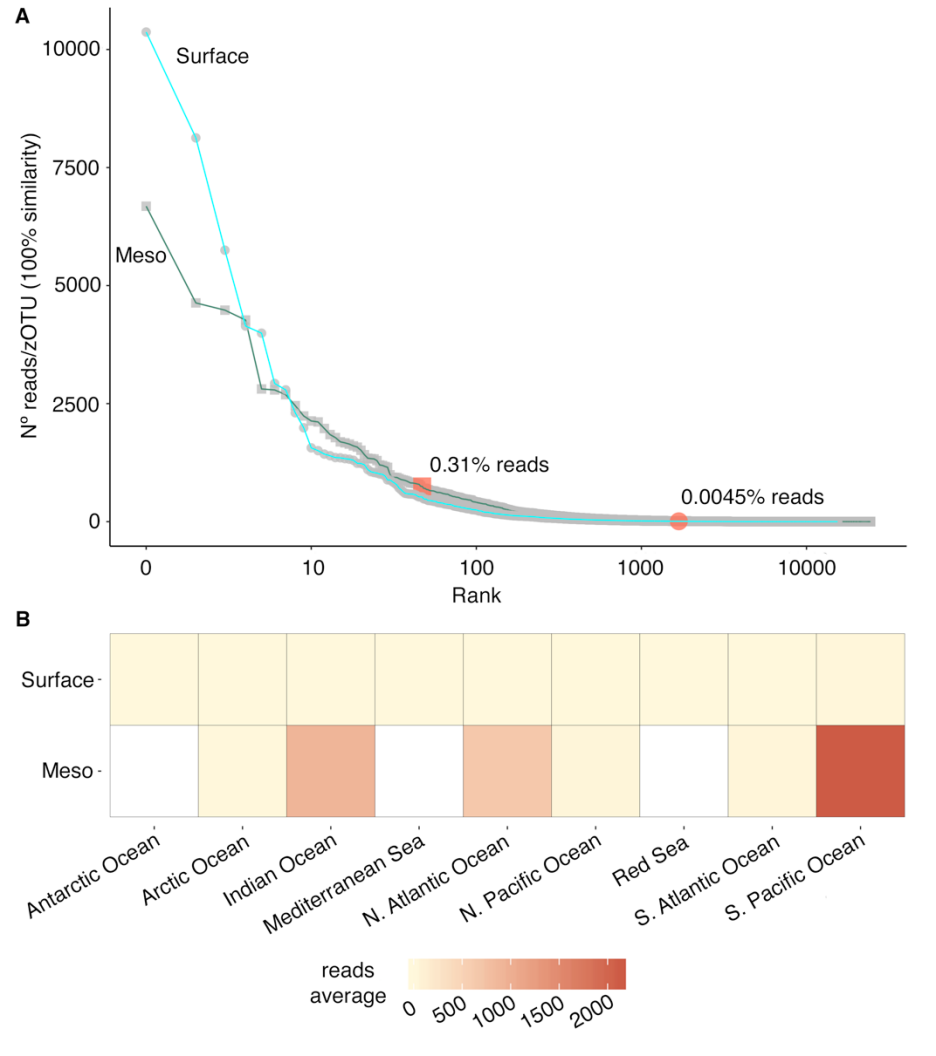

0.05
Gillisia limnaea DSM 15749T (GCF_000243235)
Gillisia marina CBA3202T (GCF_000258765)
Gillisia hiemivivida IC154T (GCF_007997295)
Gillisia mitskevichiae DSM 19839T (GCF_003634585)
Salegentibacter sediminis K5023T (GCF_002078605)
Salegentibacter flavus DSM 17794T (GCF_900115145)
Salegentibacter echinorum DSM 24579T (GCF_900129445)
Salegentibacter holothuriorum DSM 23405T (GCF_900168045)
Salegentibacter salarius DSM 23401T (GCF_900168265)
Salegentibacter mishustinae KCTC 12263T (GCF_001431365)
Salegentibacter salegens ACAM 48T (GCF_900142975)
Salegentibacter salinarum KCTC 12975T (GCF_002833365)
Salegentibacter agarivorans DSM 23515T (GCF_900113135)
Gramella flava JLT2011T (GCF_001951155)
Gramella salexigens LPB0144T (GCF_001889005)
Gramella portivictoriae DSM 23547T (GCF_000423045)
Gramella forsetii KT0803T (GCF_000060345)
Gramella echinicola DSM 19838T (GCF_000423065)
Gramella gaetbulicola DSM 23082T (GCF_003054225)
Zunongwangia profunda SM-A87T (GCF_000023465)
Zunongwangia mangrovi DSM 24499T (GCF_900112105)
Zunongwangia atlantica 22II14-10F7T (GCF_002094855)
Psychroflexus gondwanensis ACAM44T (GCF_000355905)
Psychroflexus torquis ATCC 700755T (GCF_000153485)
Psychroflexus sediminis DSM 19803T (GCF_900099815)
Psychroflexus tropicus DSM 15496T (GCF_000378765)
Psychroflexus salarius DSM 25661T (GCF_900129035)
Psychroflexus halocasei DSM 23581T (GCF_900107595)
Mesonia hippocampi DSM 29568T (JGI.1220074)
Mesonia algae DSM 15361T (GCF_003253545)
Mesonia maritima DSM 102814T (JGI. 1227497)
Mesonia phycicola DSM 21425T (GCF_900141885)
Mesonia mobilis DSM 19841T (GCF_000423405)
Mesonia oceanica CECT 9532T (GCF_902499555)
Croceibacter atlanticus HTCC2559T (GCF_000196315)
Aequorivita antarctica SW49T (GCF_007997155)
Bizionia paragorgiae DSM 23842T (GCF_900107625)
Confluentibacter lentus HJM-3T (GCF_002806995)
Changchengzhania lutea SM1355T (GCF_006974145)
Algibacter lectus DSM 15365T (GCF_900112395)
Arenitalea lutea CGMCC 1.12213T (GCF_900141715)
Croceivirga radicis HSG9T (GCF_002072105)
Croceitalea dokdonensis DOKDO 023T (GCF_001306415)
Arenibacter latericius DSM 15913T (GCF_000424985)
Cellulophaga lytica DSM 7489T (GCF_000190595)
Gramella jeungdoensis KCTC 23123T (GCF_004378585)
Capnocytophaga ochracea DSM 7271T (GCF_000023285)
Chishuiella changwenlii DSM 27989T (GCF_900142565)
Bergeyella zoohelcum NCTC 11660T (GCF_900445655)
Cloacibacterium normanense DSM 15886T (GCF_900104195)
Chryseobacterium gleum NCTC 11432T (GCF_900636535)


200 nm
EHT = 1.00 kV
WD = 2.5 mm
Signal A = InLens
Mag = 60.00 K X
File Name = 653_13.tif


1 µm


200 nm
EHT = 1.00 kV
WD = 2.5 mm
Signal A = InLens
Mag = 120.00 K X
File Name = 653_11.tif


200 nm


A
10000
7500
5000
2500
0
Nº reads/zOTU (100% similarity)
Surface
Meso
0.31% reads
0.0045% reads
0
10
100
1000
10000
Rank
B
Surface
Meso
Antarctic Ocean
Arctic Ocean
Indian Ocean
Mediterranean Sea
N. Atlantic Ocean
N. Pacific Ocean
Red Sea
S. Atlantic Ocean
S. Pacific Ocean
reads
average
0
500
1000
1500
2000