Complete genome sequence of *Arcticibacterium luteifluviistationis* SM1504\(^T\), a cytophagaceae bacterium isolated from Arctic surface seawater

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**Abstract**

*Arcticibacterium luteifluviistationis* SM1504\(^T\) was isolated from Arctic surface seawater and classified as a novel genus of the phylum *Bacteroides*. To date, no *Arcticibacterium* genomes have been reported, their genomic compositions and metabolic features are still unknown. Here, we reported the complete genome sequence of *A. luteifluviistationis* SM1504\(^T\), which comprises 5,379,839 bp with an average GC content of 37.20%. Genes related to various stress (such as radiation, osmosis and antibiotics) resistance and gene clusters coding for carotenoid and flexirubin biosynthesis were detected in the genome. Moreover, the genome contained a 245-kb genomic island and a 15-kb incomplete prophage region. A great percentage of proteins belonging to carbohydrate metabolism especially in regard to polysaccharides utilization were found. These related genes and metabolic characteristics revealed genetic basis for adapting to the diverse extreme Arctic environments. The genome sequence of *A. luteifluviistationis* SM1504\(^T\) also implied that the genus *Arcticibacterium* may act as a vital organic carbon matter decomposer in the Arctic seawater ecosystem.

**Keywords:** *Arcticibacterium luteifluviistationis*, Secondary metabolite biosynthesis, Stress resistance, Carbohydrate metabolism, Arctic

**Introduction**

As the third most abundant bacterial group in the seawater system, phylum *Bacteroidetes* plays a vital role in diverse oceanic biogeochemical processes [1]. It has been reported that phylum *Bacteroidetes* could mediate the degradation of HMW compounds especially in the respect of algal organic matter [2, 3]. Many heterotrophic microorganisms such as the SAR11 clade and marine *Gammaproteobacteria* grow partly due to phylum *Bacteroidetes*-derived organic products [4, 5]. Thus, phylum *Bacteroidetes* groups may play crucial roles in the nutrient utilization and cycling in the seawater ecosystem.

The family *Cytophagaceae*, currently comprising 31 genera, is one of the largest groups in the phylum *Bacteroidetes* [6]. The species in the family *Cytophagaceae* have been isolated from various habitats including freshwater river [7], seawater [8], permafrost soil [9] and even polar glacial till [10]. The genus *Arcticibacterium*, belonging to the family *Cytophagaceae*, accommodates only one recognized species: *A. luteifluviistationis* SM1504\(^T\) (=KCTC 42716\(^T\)=CCTCC AB 2015348\(^T\)) [11]. Strain SM1504\(^T\) was isolated from surface seawater of King’s Fjord, Arctic. However, to date, no genomes of the genus *Arcticibacterium* have been reported, their genomic compositions and metabolic pathways are still lacking. In the study, we reported the first genome sequence of the genus *Arcticibacterium* to better understand its survival strategy and ecological niche in the Arctic seawater.

**Organism information**

**Classification and features**

As the type strain of *A. luteifluviistationis* in the family *Cytophagaceae*, strain SM1504\(^T\) is a Gram-negative, aerobic, non-motile and rod bacterium (Fig. 1). The...
yellow-pigmented colony was found after incubation at 20 °C for 2 days on a TYS agar plate. The strain could utilize glycerol, D-xylose, D-glucose, D-fructose, dulcitol, inositol D-mannitol, D-sorbitol, N-acetylglucosamine, arbutin, aesculin, cellobiose, maltose, sucrose, trehalose, starch, turanose and potassium gluconate for energy and growth, which were summarized in Table 1. Then it hydrolyzed aesculin, gelatin, tyrosine, Tween 20, 40 and 60 but did not hydrolyze DNA, agar, casein, elastin, lecithin, starch, Tween 80. In addition, various enzymes such as alkaline phosphatase, esterase (C4), esterase lipase (C8), leucine arylamidase, valine arylamidase, cystine arylamidase, trypsin and glucosidase were produced for degrading organic matter [11].

The phylogenetic placement of strain SM1504T (based on complete 16S rRNA gene sequence) through neighbor-joining phylogenetic tree was identified (Fig. 2). It formed a distinct phylogenetic branch within the family Cytophagaceae and closely relatives were species of the genera Lacihabitans, Erticicia, Fluvimonas and Leadbetterella with low sequence similarities between 88.9 and 91.6%.

**Genome sequencing information**

**Genome project history**

Isolated from an extreme Arctic environment, *A. luteifluviostationis* SM1504T was selected for genome sequencing to elucidate the special abilities of adapting to diverse extreme stresses. We have accomplished the genome sequencing of strain SM1504T as reported in this paper. The complete genome data has been deposited in the GenBank database under the accession number CP029480.1. The project information and its association with MIGS are provided in Table 2 [12].

| MIGS ID | Property | Term | Evidence codea |
|---------|----------|------|----------------|
| MIGS-6  | Habitat  | seawater | TAS [11] |
| MIGS-6.3| Salinity | 0–4% NaCl (w/v) | TAS [11] |
| MIGS-22 | Oxygen requirement | Aerobic | TAS [11] |
| MIGS-15 | Biotic relationship | Free-living | NAS |
| MIGS-14 | Pathogenicity | Non-pathogen | NAS |
| MIGS-4  | Geographic location | King’s Fjord, Arctic | TAS [11] |
| MIGS-5  | Sample collection | 2014 | TAS [11] |
| MIGS-4.1| Latitude | Not reported | |
| MIGS-4.2| Longitude | Not reported | |
| MIGS-4.4| Altitude | Not reported | |

**Growth conditions and genomic DNA preparation**

*A. luteifluviostationis* SM1504T was cultivated in TYS broth at 20 °C. After cultivation for two days, genomic DNA for sequencing was extracted by using a commercial bacterial DNA isolation kit (OMEGA).

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Table 1 Classification and general features of *Arcticibacterium luteifluviostationis* SM1504T [12]

| MIGS ID | Property | Term | Evidence codea |
|---------|----------|------|----------------|
| Classification | Domain | Bacteria | TAS [28] |
| Phylum | Bacteroidetes | TAS [29, 30] |
| Class | Cytophagia | TAS [30, 31] |
| Order | Cytophagales | TAS [32, 33] |
| Family | Cytophagaceae | TAS [32, 34] |
| Genus | Arcticibacterium | TAS [11] |
| Species | Arcticibacterium luteifluviostationis | TAS [11] |
| Strain: | SM1504T | TAS [11] |
| Gram stain | Negative | TAS [11] |
| Cell shape | Rod | TAS [11] |
| Motility | Non-motile | TAS [11] |
| Sporulation | Not reported | |
| Temperature range | 4–30 °C | TAS [11] |
| Optimum temperature | 20 °C | TAS [11] |
| pH range; Optimum | 6.0–7.5; 6.5–7.0 | TAS [11] |
| Carbon source | glycerol, D-xylose, D-glucose, D-fructose, dulcitol, inositol D-mannitol, D-sorbitol, N-acetylglucosamine, arbutin, aesculin, cellobiose, maltose, sucrose, trehalose, starch, turanose and potassium gluconate | TAS [11] |

*aEvidence codes - TAS Traceable Author Statement, NAS Non-traceable Author Statement. These evidence codes are from the Gene Ontology project [35]*
Fig. 2 Neighbor-joining phylogenetic tree based on 16S rRNA gene sequences, showing the relationships of *Arcticibacterium luteifluviistationis* SM15044 and its taxonomic neighbors. *Rhodothermus marinus* DSM 42522 was used as the outgroup. Bootstrap values (> 70%) based on 1000 replicates are shown at nodes. Bar, 0.02 substitutions per nucleotide position.

### Table 2 Project information

| MIGS ID | Property                      | Term                                                                 |
|---------|-------------------------------|----------------------------------------------------------------------|
| MIGS 31 | Finishing quality             | Complete                                                            |
| MIGS-28 | Libraries used                | Two genomic libraries: one Illumina library, one PacBio standard library |
| MIGS 29 | Sequencing platforms          | Illumina Hiseq 2500, PacBio RS                                      |
| MIGS 31.2 | Fold coverage               | 315x Illumina, 45x PacBio                                            |
| MIGS 30 | Assemblers                    | SOAPdenovo v. 2.04; HGAP v. 2.3.0                                   |
| MIGS 32 | Gene calling method           | Prodigal                                                           |
|         | Locus Tag                     | SM1504                                                              |
|         | Genbank ID                    | CP029480.1                                                           |
|         | GenBank Date of Release       | June 20, 2018                                                       |
|         | GOLD ID                       | Not registered                                                      |
|         | BIOPROJECT                    | PRJNA471374                                                          |
| MIGS 13 | Source Material Identifier    | KCTC 427165=CTCC AB 2015348                                      |
|         | Project relevance             | Environmental, microbes                                             |
Genome sequencing and assembly
Genome sequencing was performed on both the Illumina Hiseq and the PacBio RS sequencing platforms. 400-bp Illumina paired-end libraries and 20-kb PacBio libraries were constructed and sequenced yielding 315 × and 45 × average coverages, respectively (Table 2). About 1.69 Gb and 243 Mb data from the Illumina and PacBio sequencing were assembled using SOAPdenovo [13, 14] and HGAP [15]. The final assembly resulted in one scaffold.

Genome annotation
Coding gene sequences were predicted and annotated through Prodigal v2.6.3 [16] and RAST v2.0 [17]. Functional categorization and carbohydrate-active enzymes CAZy of the predicted genes were annotated against EggNOG and CAZy databases, respectively. Then rRNAs and tRNAs were predicted by RNAmmer v1.2 [18] and tRNAscan-SE v1.3.1 [19]. In addition, the CARD analyses were performed to find resistance genes. Genomic islands and secondary metabolite biosynthesis were predicted through IslandViewer 4 [20] and antiSMASH [21].

Genome properties
The total size of the genome of *Arcticibacterium luteifluviistationis* SM1504\(^T\) is 5,379,839 bp with an average GC content of 37.20% (Fig. 3). Total 4595 protein-coding genes (CDSs) were identified, which occupied 89.73% of the genome. Therein, 3045 CDSs were annotated with putative functions and 1550 CDSs matched hypothetical proteins (Table 3). Then 4 rRNAs and 36 tRNAs were found in the genome. CRISPR repeat, transmembrane helix, signal peptide and Pfam protein family predictions were

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**Table 3** Genome statistics

| Attribute                        | Value     | % of Total |
|----------------------------------|-----------|------------|
| Genome size (bp)                 | 5,379,839 | 100        |
| DNA coding (bp)                  | 4,827,135 | 89.73      |
| DNA G + C (bp)                   | 2,029,275 | 37.20      |
| DNA scaffolds                     | 1         | 100.00     |
| Total genes                      | 4635      | 100.00     |
| Protein coding genes             | 4595      | 99.14      |
| RNA genes                        | 40        | 0.86       |
| Pseudo genes                     | 0         | 0          |
| Genes in internal clusters       | NA        | NA         |
| Genes with function prediction   | 3045      | 65.70      |
| Genes assigned to COGs           | 3319      | 71.61      |
| Genes with Pfam domains          | 3617      | 78.04      |
| Genes with signal peptides       | 693       | 14.95      |
| Genes with transmembrane helices | 988       | 21.32      |
| CRISPR repeats                   | 4         | 0.09       |

*NA*, not applicable
done. In addition, distribution of genes into COG functional categories was shown in Table 4.

**Insights from the genome sequence**

**Adaption to diverse stresses**

Strain SM1504<sup>T</sup> genome owned two putative gene clusters for secondary metabolite biosynthesis. The cluster 1 belonged to terpene type - the largest group of natural products [22], matching the carotenoid biosynthesis. The cluster 2, affiliated to arylpolyene type, was predicted to produce flexirubin. Furthermore, we found that the yellow-pigmented strain SM1504<sup>T</sup> harbors a complete set of genes required for zeaxanthin biosynthesis (e.g., isopentenyl-diphosphate delta-isomerase, phytoene synthase, phytoene dehydrogenase, lycopene cyclase and beta-carotene hydroxylase), which was commonly detected in other species of the phylum *Bacteroidetes* [23, 24]. The pigment maybe help the strain to obtain energy and for cold adaption and ultraviolet light protection in the Arctic environments [25].

A total of 150 resistance genes were found to encode 24 kinds of antibiotics (such as gentamicin, kanamycin, tetracycline and streptomycin), which was consistent with the experimental antibiotic susceptibility results [11]. The genes encoding heat shock proteins dnaK and cold shock protein cspA were detected in the genome. In line with this, SM1504<sup>T</sup> had a wider growth temperature ranges (4–30 °C) [11]. Besides, the genome harbored several genes coding for catalase and superoxide dismutase to assist the strain at cellular and molecular levels in dealing harsh radiation in the Arctic. Dozens of genes related to osmotic stress (such as choline and betaine uptake and betaine biosynthesis) and carbon starvation responses were discovered in the *A. luteiflaviiatationis* genome, which would endow cells with tolerance to hyperhaline and oligotrophic environments.

As another feature, a 245-kb genomic island coding for 208 genes was predicted. Therein, 9 genes encoded proteins related to gluclide biosynthesis, such as aslipopoly saccharide core biosynthesis glycosyltransferase (lpsD), UDP-glucose dehydrogenase and capsular polysaccharide synthesis enzyme (Cap8C). In addition, the presence of transposases, integrases and mobile element proteins indicated that gene transfer has occurred in the *A. luteiflaviiatationis* SM1504<sup>T</sup> genome [26]. Also, phage tail fiber proteins were predicted, which was in line with the

### Table 4

| Code | Value | %age | Description |
|------|-------|------|-------------|
| J    | 148   | 3.19 | Translation, ribosomal structure and biogenesis |
| A    | 0     | 0    | RNA processing and modification |
| K    | 180   | 3.88 | Transcription |
| L    | 121   | 2.61 | Replication, recombination and repair |
| B    | 0     | 0    | Chromatin structure and dynamics |
| D    | 17    | 0.37 | Cell cycle control, Cell division, chromosome partitioning |
| V    | 68    | 1.47 | Defense mechanisms |
| T    | 154   | 3.32 | Signal transduction mechanisms |
| M    | 273   | 5.89 | Cell wall/membrane biogenesis |
| N    | 3     | 0.06 | Cell motility |
| U    | 29    | 0.63 | Intracellular trafficking and secretion |
| O    | 129   | 2.78 | Posttranslational modification, protein turnover, chaperones |
| C    | 201   | 4.34 | Energy production and conversion |
| G    | 229   | 4.94 | Carbohydrate transport and metabolism |
| E    | 211   | 4.55 | Amino acid transport and metabolism |
| F    | 68    | 1.47 | Nucleotide transport and metabolism |
| H    | 83    | 1.79 | Coenzyme transport and metabolism |
| I    | 85    | 1.83 | Lipid transport and metabolism |
| P    | 224   | 4.83 | Inorganic ion transport and metabolism |
| Q    | 45    | 0.97 | Secondary metabolites biosynthesis, transport and catabolism |
| R    | 0     | 0    | General function prediction only |
| S    | 1080  | 23.30 | Function unknown |
| -    | 1286  | 27.75 | Not in COGs |

The total is based on the total number of protein coding genes in the genome.
analysis by PHAST [27] that a 15-kb incomplete prophage region could encode phage tail fiber proteins in the genome.

Degradation and utilization of carbohydrates

Totally, 3319 (71.61%) genes could be assigned a COG function, of which the wall/membrane/envelope biogenesis (5.89%), carbohydrate transport and metabolism (4.94%) and inorganic ion transport and metabolism (4.83%) were enriched (Table 4). The high percentage of proteins related to carbohydrate transport and metabolism suggested that the strain SM1504T could use various carbohydrates. On the other hand, the analyses from dbCAN showed that strain SM1504T possessed 341 genes which encoded carbohydrate metabolism enzymes, including 69 carbohydrate esterases (11 families), 125 glyco-side hydrolases (46 families), 62 glycosyltransferases (22 families), 17 polysaccharide lyases (6 families), 12 auxiliary activities (3 families) and 56 carbohydrate-binding modules (15 families). Therein, a variety of enzymes are related to the degradation of macromolecular polysaccharides (e.g., xylanase, chitinase, mannanase, alpha amylase, endogluccanase, glucoamylase and alginate lyase) derived from marine macroalgae and phytoplankton. Those polysaccharases could hydrolyze a variety of macromolecular polysaccharides into small molecules that can be absorbed and metabolized by strain SM1504T and other microorganisms in the seawater [4, 5].

Conclusions

The genomic analyses showed that the strain SM1504T could adapt to extreme Arctic seawater environments, such as high solar radiation, cold temperature and high salinity. Besides, it may act as a vital macromolecular polysaccharide decomposer and would play an important role in organic carbon cycling in the Arctic seawater ecosystem.

Abbreviations

CARD: Comprehensive antibiotic resistance database; CAZy: Carbohydrate-active enzymes; CRISPR: Clustered regularly interspaced short palindromic repeats; HMW: High molecular weight; MIGS: Minimum information on the genome sequence; RAST: Rapid annotation using subsystem technology; TYS: Tryptone-yeast extract-sea salt

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Authors’ contributions

YL and PW conducted the main tasks, including experiments, genomic analysis and manuscript writing. XHG and YRD performed phylogenetic analysis. QLQ provided technical support for this study. XYZ and XLC helped to revise the manuscript. All authors read and approved the final manuscript.

Competing interests

The authors declare that they have no competing interests.

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References

1. Fernández-Gómez B, Richter M, Schüler M, Pinhassi J, Acinas SG, González JM, et al. Ecology of marine Bacteroidetes: a comparative genomics approach. The ISME Journal. 2013;7:1026.

2. GPP R, Margarete S, FB M, Christin B, Hanno T, Jost W, et al. Genomic content of uncultured Bacteroidetes from contrasting oceanic provinces in the North Atlantic Ocean. Environ Microbiol. 2012;14:52–66.

3. Sun C, Fu G-Y, Zhang C-Y, Hu J, Xu L, Wang R-J, et al. Isolation and complete genome sequence of Algibacter alginitolyticus sp. nov., a novel seaweed-degrading Bacteroidetes bacterium with diverse putative polysaccharide utilization loci. Appl Environ Microbiol. 2016;82: 2975–87.

4. WT J, David W, Emilie L, Flavia E, DM Z, RM J, et al. The role of planktonic Flavobacteria in processing algal organic matter in coastal East Antarctica revealed using metagenomics and metaproteomics. Environ Microbiol. 2013;15:302–17.

5. Bunse C, Pinhassi J. Marine Bacterioplankton seasonal succession dynamics. Trends Microbiol. 2017;25:494–505.

6. Imhoff JF. The Family Chlobiobacteriaceae. In: Rosenberg E, DeLong EF, Lory S, Stackebrandt E, Thompson F. (eds) The Prokaryotes. Berlin, Heidelberg: Springer; 2014. p. 501.

7. Shiu S-Y, Chen Y-S, Shiu Y-W, Chen W-M. Flavimonas palidiflavis gen. nov., sp. nov., a new member of the family Cytophagaceae isolated from a freshwater river. Int J Syst Evol Microbiol. 2013;63:3861–7.

8. Kang JY, Chun J, Choi A, Cho J-C, Jahng KY. Nibrella saemangeumensis gen. nov., sp. nov., a novel member of the family Cytophagaceae, isolated from seawater. Int J Syst Evol Microbiol. 2013;63: 4508–14.

9. Finster KW, Herbert RA, Lomstein BA. Spirosoma spiribegensense sp. nov. and Spirosoma luteum sp. nov., isolated from a high Arctic permafrost soil, and emended description of the genus Spirosoma. Int J Syst Evol Microbiol. 2009;59:839–44.

10. Chang X, Jiang F, Wang T, Kan W, Qu Z, Ren L, et al. Spirosoma arcticum sp. nov., isolated from high Arctic glacial till. Int J Syst Evol Microbiol. 2014;64: 2233–7.

11. Li D-D, Peng M, Wang N, Wang X-J, Zhang X-Y, Chen X-L, et al. Arctibacterium luteflavuslactis gen. nov., sp. nov., isolated from Arctic seawater. Int J Syst Evol Microbiol. 2017;67:664–9.

12. Field D, Garrity G, Gray T, Morrison N, Selengut J, Sterk P, et al. The minimum information about a genome sequence (MIGS) specification. Nat Biotechnol. 2008;26:541–7.

13. Li R, Li Y, Kristiansen K, Wang J. SOAP: short oligonucleotide alignment program. Bioinformatics. 2008;24:713–4.

14. Li R, Zhu H, Ruan J, Qian W, Fang X, Shi Z, et al. De novo assembly of human genomes with massively parallel short read sequencing. Genome Res. 2010;20:265–72.

Note
15. Chin C-S, Alexander DH, Marks P, Klammer AA, Drake J, Heiner C, et al. Nonhybrid, finished microbial genome assemblies from long-read SMRT sequencing data. Nat Methods. 2013;10:10563.

16. Hyatt D, Chen G-L, LoCascio PF, Land ML, Larimer FW, Hauser LJ. Prodigal: prokaryotic gene recognition and translation initiation site identification. BMC Bioinformatics. 2010;11:119.

17. Aziz RK, Bartels D, Best AA, De Jongh M, Disz T, Edwards RA, et al. The RAST server: rapid annotations using subsystems technology. BMC Genomics. 2008:9:75.

18. Lagesen K, Hallin P, Rødland EA, Staerfeldt HH, Rognes T, Ussery DW. RNRammer: consistent and rapid annotation of ribosomal RNA genes. Nucleic Acids Res. 2007;35:3100–8.

19. Avni D, Biberman Y, Meyuhas O. The 5′ terminal Oligopyrimidine tract confers translational control on top Mnas in a cell type-and sequence context-dependent manner. Nucleic Acids Res. 1997;25:995–1001.

20. Bertelli C, Laird MR, Williams KP, Simon Fraser University research computing group, Lau BY, Hoag D, et al. IslandViewer 4: expanded prediction of genomic islands for larger-scale datasets. Nucleic Acids Res. 2017;45:30–5.

21. Weber T, Bliñ K, Duddela S, Krug D, Kim HJ, Brucocleri R, et al. antiSMASH 3.0—a comprehensive resource for the genome mining of biosynthetic gene clusters. Nucleic Acids Res. 2015;43:237–43.

22. Zhao B, Liao L, Yu Y, Chen B. Complete genome of Brachybacterium sp. P6-10-X1 isolated from deep-sea sediments of the Southern Ocean. Mar Genomics. 2017;35:27–9.

23. Hameed A, Shahnaz M, Huang H-C, Lai W-A, Lin S-Y, Stothard P, et al. Complete genome sequence of Stenotrophomonas maltophilia CC-SAMT-1, a flavobacterium isolated from coastal surface seawater. Mar Genomics. 2018;37:21–5.

24. Klassen JL. Phylogenetic and evolutionary patterns in microbial carotenoid biosynthesis are revealed by comparative genomics. PLoS One. 2010;5:e1257.

25. Mueller DR, Vincent WF, Bonilla S, Laurion I. Extremotrophs, extremophiles and broadband pigmentation strategies in a high arctic ice shelf ecosystem. FEMS Microbiol Ecol. 2005;53:73–87.

26. Oh J, Choe H, Kim BK, Kim KM. Complete genome of a coastal marine bacterium Muricauda lutaonensis KCTC 22339T. Marine Genomics. 2015;23:51–3.

27. Zhou Y, Liang Y, Lynch KH, Dennis JJ, Wishart DS. PHAST: A Fast Phage Search Tool. Nucleic Acids Res. 2011;39:347–52.

28. Woese CR, Kandler O, Wheelis ML. Towards a natural system of organisms: proposal for the domains archaea, bacteria, and Eucarya. Proc Natl Acad Sci. 1990;87:4576–9.

29. Krieg N, Sneath PHA. Approved lists of bacterial names. Int J Syst Bacteriol. 1980;30:225–420.