**Hymenobacter taeanensis** sp. nov., radiation resistant bacterium isolated from coastal sand dune

Ji Hee Lee · Jong-Hyun Jung · Min-Kyu Kim · Han Na Choe · Sangyong Lim

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**Abstract** An aerobic, Gram-stain-negative, non-motile, non-spore-forming, rod-shaped, and light pink-colored bacterial strain, designated TS19T, was isolated from a sand sample obtained from a coastal sand dune after exposure to 3 kGy of gamma radiation. Phylogenetic analysis based on the 16S rRNA gene sequences revealed that the isolate was a member of the genus *Hymenobacter* and was most closely related to *H. wooponensis* WM78T (98.3% similarity). Strain TS19T and *H. wooponensis* showed resistance to gamma radiation with D10 values (i.e., the dose required to reduce the bacterial population by tenfold) of 7.3 kGy and 3.5 kGy, respectively. The genome of strain TS19T consists of one contig with 4,879,662 bp and has a G + C content of 56.2%. The genome contains 3,955 protein coding sequences, 44 tRNAs, and 12 rRNAs. The predominant fatty acids of strain TS19T were iso-C15:0, summed feature 4 (iso-C17:1 and/or anteiso-C17:1 B), summed feature 3 (C16:1ω6c and/or C16:1ω7c), and C16:1ω5c. The major polar lipids were phosphatidylethanolamine, and one unidentified aminophospholipid. The main respiratory quinone was menaquinone-7. Based on the phylogenetic, physiological, and chemotaxonomic characteristics, strain TS19T represents a novel species, for which the name *Hymenobacter taeanensis* sp. nov. is proposed. The type strain is TS19T (= KCTC 72897T = JCM 34023T).

**Keywords** *Hymenobacter* · Coastal sand dune · Taxonomy · Gamma radiation · Phylogenetic analysis

**Introduction**

The genus *Hymenobacter* (*Hymenobacter roseosali-varius*, type species) was first proposed by Hirsch et al. (1998), and then emended by Buczolits et al. (2006), Reddy (2013), and Han et al. (2014). The genus *Hymenobacter*...
Hymenobacter was placed in the family Hymenobacteraceae, phylum Bacteroidetes (Munoz et al. 2016). The members of genus Hymenobacter have been isolated from natural environments, such as soil (Kim et al. 2008), freshwater (Kang et al. 2015), and air (Buczolits et al. 2006). These species have also been found in extreme conditions, e.g., glacial ice (Klassen and Foght 2011), Antarctic soil (Sedláček et al. 2019a, b), and arid land (Reddy and Garcia-Pichel 2013).

Extremophilic bacteria, including UV- and gamma radiation (γ-radiation)-resistant bacteria, have shown their potential applications in biotechnology, bioremediation, etc. (Gabani and Singh 2013; Orellana et al. 2018). For instance, Deinococcus, one of the most radiation-resistant bacteria, has gained great interest due to the extraordinary resistance to desiccation and oxidative stress as well as UV and γ-radiation and its potential application in various industries (Gerber et al. 2015; Jin et al. 2019). Since the Hymenobacter species was isolated from irradiated pork (Collins et al. 2000), UV and γ-radiation-resistant species have been isolated (Su et al. 2014; Lee et al. 2017, 2021; Sedláček et al., 2019b; Maeng et al., 2020). In addition, most species produce carotenoid pigments known to be effective reactive oxygen species scavengers, which have potential applications in biotechnology and biomedicine (Klassen and Foght 2008).

In the course of our study seeking novel radiation-resistant bacteria from sand sample collected from coastal dune, a Gram-stain-negative, light pink-colored, and rod-shaped bacterial strain, designated TS19^T was isolated and subjected to a detailed investigation using a polyphasic taxonomic approach.

Materials and methods

Isolation of bacterial strain and culture condition

Strain TS19^T was isolated from the sand sample obtained from Taean coastal dune, Republic of Korea (GPS position; site 1 33° 21′ 44″ N, 126° 32′ 00″ E). Prior to isolation, the sand sample was irradiated by γ-radiation (3 kGy). One gram of irradiated sand sample was mixed with saline solution and spread on R2A agar (MB cell) using the standard dilution plating technique. After plating, plates were incubated at 30 °C for 5 days. The isolate, light pink-pigmented strain, was routinely cultured on R2A agar and stored in glycerol (20%, w/v) at −70 °C. Reference strains H. wooponensis KCTC 32528^T and H. gelipurpurascens KACC 12069^T were purchased from the Korean Collection for Type Cultures (KCTC) and Korean Agricultural Culture Collection (KACC), respectively.

16S rRNA gene sequencing and phylogenetic analysis

Bacterial DNA preparation, PCR amplification, and sequencing of the 16S rRNA gene were carried out as described previously (Chun and Goodfellow 1995). Identification of phylogenetic neighbors and calculation of pairwise 16S rRNA gene sequence similarities were achieved using the EzBioCloud server (www.ezbiocloud.net). Multiple sequence alignments were performed using the CLUSTAL_W program (Thompson et al. 1994) integrated into the BioEdit version 7.2 software (Hall 1999). Phylogenetic analysis was performed using the software package MEGA version 7 (Kumar et al. 2016). Phylogenetic trees were inferred using the neighbor-joining (Saitou and Nei 1987), maximum-likelihood (Felsenstein 1993), and maximum-parsimony (Fitch 1971) algorithms. Evolutionary distances of the neighbor-joining algorithm were computed using the Kimura’s two-parameter model (Kimura 1980). The robustness of the topology in the neighbor-joining phylogenetic tree was evaluated by bootstrap analysis based on 1,000 resamplings (Felsenstein 1985).

γ-Radiation-resistant analysis

To determine survival rate after exposure to γ-radiation, strain TS19^T, H. wooponensis KCTC 32528^T, H. gelipurpurascens KACC 12069^T, and Deinococcus radiodurans R1^T (positive control) were grown to early stationary phase and irradiated at room temperature using a ^60^Co-gamma irradiator (AECL, IR-79; MDS Nordion International Co., Ltd.) with doses of 3, 6, 9, 12 kGy at Advanced Radiation Technology Institute in Republic of Korea. Following irradiation, the strains were serially diluted tenfold and then spotted on R2A agar plates. The plates were incubated at 30 °C for 3 days and the numbers of
colony-forming units (c.f.u.) of strains were determined, and the survival rate was calculated.

Genomic analysis

Genomic DNA of strain TS19T was extracted using a G-spin™ Genomic DNA Extraction Kit (iNtRON) following the manufacturer’s instructions. Whole genome sequencing of the isolate was performed using PacBio RSII single-molecule real-time (SMRT) sequencing technology (Pacific Biosciences) at Macrogen Co., Ltd. De novo assembly was performed using the Hierarchical Genome Assembly Process version 3 (HGAP3) (Chin et al. 2013). After the whole genome was assembled, genes were identified and annotated by Prokka pipeline version 1.13 (Seemann 2014). Gene functions were then annotated using the eggNOG database (Huerta-Cepas et al. 2016).

The DNA G + C content was calculated directly from the genome sequence. The average nucleotide identity (ANI) was used to compare strain TS19T and related type species genome sequences. The ANI value was calculated by ANI calculator using the OrthoANIu algorithm (https://www.ezbiocloud.net/tools/ani) (Yoon et al. 2017). The digital DNA-DNA hybridization (dDDH) analysis was estimated using Genome-to-Genome Distance Calculator (GGDC) (https://ggdc.dsmz.de/distcalc2.php) (Meier-Kolthoff et al. 2013).

Phenotypic and biochemical characterisation

Growth on various standard bacteriological media was tested using R2A agar, nutrient agar (NA; Difco), tryptic soy agar (TSA; Difco), Luria–Bertani agar (LB; MBcell), marine agar (MA; Difco) and tryptone glucose yeast agar (TGY; 5 g tryptone, 3 g yeast extract, 1 g glucose and 15 g agar in 1 l distilled water). Growth temperature (at 4, 10, 15, 20, 25, 30, 37, 40, or 45 °C) was tested on R2A agar. The pH range for growth was determined in R2A broth adjusted to pH 4–11 (at 1 pH intervals) using 100 mM acetate buffer (pH 4–5), 100 mM MES (pH 6), 100 mM HEPES (pH 7–8), 100 mM CHES (pH 9–10), 100 mM CAPS (pH 11). The requirement and tolerance of NaCl [final concentration: 0, 0.5, 1, 2, 3, 4, or 5% (w/v)] for growth was tested on R2A agar. Anaerobic growth was tested on R2A agar in a jar containing AnaeroGen (Thermo Scientific), which works as an oxygen absorber and CO₂ generator, for up to 14 days at 30 °C. Cell morphology was observed by transmission electron (Tecnai 12, FEI) microscopy. Cell motility was performed with 0.3% semi-solid R2A agar (Tittsler and Sandholzer 1936), and gliding motility was assessed by examining wet mounts of a 48 h R2A broth culture under phase-contrast microscopy (ICC50, Leica) (Bernardet et al. 2002). The Gram reaction was determined by using the Gram staining method and the KOH method (Powers1995). Catalase and oxidase activities were determined using 3% (v/v) hydrogen peroxide and 1% (w/v) tetramethyl-p-phenylenediamine (Kovacs 1956), respectively. Carotenoid pigments were extracted with methanol, and the absorption spectrum at 200–800 nm (at 0.5 nm intervals) was recorded using a UV/Vis spectrophotometer (OPTIZEN POP, Mecasys) (Klassen and Foght 2008). Hydrolysis of casein [2% (w/v) skimmed milk], carboxymethyl cellulose (CMC; 0.5%, w/v), starch (0.2%, w/v), Tween 20 (1%, v/v) and Tween 80 (1%, v/v) and decomposition of L-tyrosine (0.5%, w/v) were tested using R2A agar according to (Smibert et al. 1994). DNase activity was determined using DNase test agar (Difco). Other biochemical tests, enzyme activities, and utilization of carbohydrates were evaluated using the API 20NE and API ZYM kits (bioMérieux) following the manufacturer’s instructions.

Chemotaxonomic characterisation

For cellular fatty acid analysis, strain TS19T and reference strains were grown on R2A agar for 3 days at 30 °C. Extraction of fatty acid methyl esters (FAME) and separation by gas chromatography (GC) were performed using the Instant FAME method of the Microbial Identification System (MIDI) version 6.1 and the TSBA6 database (Sasser 1990). For analyses of polar lipids and isoprenoid quinone, cells of strain TS19T grown in R2A broth for 3 days at 30 °C were harvested and freeze dried. Polar lipids were extracted using standard procedures. Extracted polar lipids were separated by two-dimensional thin-layer chromatography (TLC) using TLC silica gel 60F254 (Merck). Chromatograms were developed in the first dimension with a mixture of chloroform/methanol/water (65:25:4 by volume) and in the second dimension with chloroform/acetic acid/methanol/water (80:18:12:5 by volume) (Da Costa et al. 2011).
Isoprenoid quinones were extracted and analysed by high-performance liquid chromatography (HPLC) (Collins 1985).

**Results and discussion**

**Phylogenetic analysis**

The 16S rRNA gene sequence (1433 bp) of strain TS19\(^T\) was obtained (GenBank accession no. MN911321). The sequence comparison using the EzBioCloud server indicated that our isolate was closely related to members of the genus *Hymenobacter*. Strain TS19\(^T\) showed the highest 16S rRNA gene sequence similarity to *H. woopenensis* WM78\(^T\) (98.3%), followed by *H. gelipurpurascens* Txg1\(^T\) (97.3%). Sequence similarity with other members of the genus *Hymenobacter* was less than 97.0%.

The neighbor-joining phylogenetic tree (Fig. 1) showed that strain TS19\(^T\) formed a distinct branch within the *Hymenobacter*. The two species that had highest 16S rRNA gene sequence similarity with the strain TS19\(^T\) were grouped with high bootstrap values. Strain TS19\(^T\) and two type species were also clustered in maximum-likelihood and maximum-parsimony algorithm trees (Fig. S1). The phylogenetic analysis revealed strain TS19\(^T\) to be closely related to *H. woopenensis* and *H. gelipurpurascens*, which were selected and used as reference species.

**γ-Radiation-resistant analysis**

After exposure to 3, 6, 9, and 12 kGy γ-radiation, strain TS19\(^T\) showed 45.6, 11.1, 7.5, and 2.3% cell survival, respectively, yielding a D\(_{10}\) of 7.3 kGy (Fig. 2). Interestingly, of the two closely-related species, while *H. woopenensis* KCTC 32528\(^T\) was somewhat resistant to gamma radiation (D\(_{10}\) = 3.5 kGy), *H. gelipurpurascens* KACC 12069\(^T\) did not grow at a γ-radiation dose of 3 kGy (Fig. 2). Further research, such as a genome comparison between species, is needed to define radiation-resistance determinants of TS19\(^T\).

![Fig. 1 A neighbor-joining tree based on 16S rRNA gene sequences showing the phylogenetic position of strain TS19\(^T\) and related strains of the genus *Hymenobacter*. Evolutionary distances, generated using the Kimura two-parameter model, are based on 1359 unambiguously aligned nucleotides. Bootstrap values greater than 60% (1000 resamplings) for nodes conserved among neighbor-joining analyses are shown. Closed circles indicate that the corresponding nodes were also recovered in trees generated with the maximum-parsimony and maximum-likelihood algorithms. Opened circles indicate branches of the tree that were also recovered using the maximum-parsimony algorithm. *Pontibacter actiniarum* KMM 6156\(^T\) (AY989908) was used as an outgroup. Bar, 0.01 substitutions per nucleotide position](image-url)
Genomic analysis

SMRT sequencing of strain TS19T resulted in single chromosomal contig with 4,879,662 bp (GenBank accession no. NZ_CP053538), which was smaller than those of the two related species H. woopenensis (GenBank accession no. NZ_SRKZ01000000; 6,015,946 bp) and H. gelipurpurascens (GenBank accession no. NZ_FYEW01000000; 5,060,617 bp). The ANI values between TS19T and the related species H. woopenensis and H. gelipurpurascens were 83.3% and 80.2%, whereas the dDDH values were 26.5% and 23.7%, respectively. Because ANI cutoff of 95–96% and DDH cutoff of 70% are generally used for microbial species definition, TS19T can represent distinct species (Yoon et al. 2017; Meier-Kolthoff et al. 2013).

The genome of strain TS19T contained 3,955 protein coding sequences (CDSs), 44 pseudogenes, 44 tRNA genes, and 12 rRNA genes (4 copies each of 5S, 16S, 23S). The DNA G + C content of strain TS19T was 56.2 mol%, which is within the range of 55–70 mol% reported for the genus Hymenobacter (Han et al. 2014). Of 3,955 coding genes, 3,606 genes were assigned to COG of proteins (Table S1). COG functional classification showed that TS19T had 113 genes (3.1%) associated with DNA replication and repair (Table S1). D. radiodurans has an extraordinary resistance to gamma radiation, which is attributable to efficient DNA repair systems. One of the characteristics of D. radiodurans DNA repair machinery is a relatively high number of DNA glycosylases for the base excision repair (BER) pathway (Timmins and Moe 2016). TS19T encoded 11 DNA glycosylases, which is comparable to 12 glycosylases encoded from D. radiodurans. D. radiodurans possesses two nucleotide excision repair (NER) pathways for repair of UV-induced DNA damage, the UvrABC- and UvsE-dependent pathways (Lim et al. 2019). Interestingly, TS19T genome contained not only UvrABC (three UvrA homologs) and UvsE but also photolyase PhrB and SplB for the direct reversal of UV-induced damage. TS19T encoded components for the RecFOR-mediated homologous recombination (HR) like D. radiodurans, together with RecA, RecJ, SSB (single-stranded DNA binding protein), UvrD, and three RecQs. Strain TS19T was equipped with various antioxidant enzymes, such as three catalases including one manganese (Mn)-catalase, two Mn superoxide dismutases, alkyl hydroperoxide reductase complex AhpCD, two BCP (bacterioferritin comigratory protein)-type thiol peroxidases, etc. The enzymes involved in bacillithiol (BSH) synthesis (2 copies each of bshA and bshB and 1 copy of bshC) were detected in the genome, suggesting that TS19T possibly produces BSH as low-molecular weight thiol.

Phenotypic and biochemical characterisation

Cells were observed to be Gram-stain-negative, non-motile, non-spore-forming, aerobic, and rod shaped (0.8–1.2 × 2.0–4.5 μm in size; Fig. S2). Strain TS19T grew on R2A agar and TGY but not on NA, TSA, LB, or MA. The strain was able to grow with 0–1.0% (w/v) NaCl, at pH 6–8 (optimally at pH 7) and at 10–37 °C (optimally at 25–30 °C). Colonies were observed to be irregular with undulate margin, light pink-colored, and 2–5 mm in diameter after incubation on R2A agar for 3 days, but colonies were observed to be circular with entire margin, orange-pink colored when grown on TGY agar. The strain was found to be positive for catalase, but negative for oxidase. Carotenoid pigment was produced, with absorbance spectral peaks at 478 nm. Casein, CMC, esculin, gelatin, and starch were hydrolysed, but arginine, DNA, Tween 20, Tween 80, and L-tyrosine were not. There are several
phenotypic characteristics such as the assimilation of mannitol, gluconate, and N-acetyl-glucosamine, and not hydrolysis of DNA and Tween 80 that differentiate between strain TS19T and phylogenetically related species. The detailed results of physiological and biochemical analyses are given in Table 1.

Table 1 Phenotypic characteristics that differentiate strain TS19T from phylogenetically related Hymenobacter species

| Isolation source | Soil | Fresh water | Soil |
|------------------|------|-------------|------|
| Growth at 4 °C   | –    | –           | +    |
| 37 °C            | +    | +           | –    |
| 1% NaCl          | –    | –           | +    |
| Oxidase          | –    | –           | +    |
| Hydrolysis of CMC | +    | –           | –    |
| DNA              | –    | +           | +    |
| Tween20          | –    | +           | –    |
| Tween80          | –    | +           | +    |
| Enzyme activity (API ZYM) | + | – | – |
| β-Glucosidase    | +    | –           | –    |
| Assimilation (API 20NE) |
| Glucose          | +    | +           | –    |
| Arabinose        | +    | +           | –    |
| Mannose          | +    | +           | –    |
| Mannitol         | +    | –           | +    |
| N-Acetyl-glucosamine | + | – | – |
| Maltose          | +    | +           | –    |
| Gluconate        | +    | –           | –    |
| DNA G + C content (mol%) | 56.2 | 56.1 | 57.0 |

Strains: 1, Strain TS19T; 2, H. wooponensis KCTC 32528T; 3, H. gelipurpurascens KACC 12069T. These data were from this study unless otherwise indicated. +, Positive; –, negative. All strains were positive for aerobic metabolism, catalase activity, carotenoid pigment production, hydrolysis of casein, esculin, and gelatin, and enzyme activity of alkaline phosphatase, acid phosphatase, cystine arylamidase, esterase (C4), esterase lipase (C8), N-acetyl-β-glucosaminidase, α-glucosidase, leucine arylamidase, naphthol-AS-BI-phosphohydrolase, and valine arylamidase. All strains were negative for indole production, nitrate reduction, hydrolysis of arginine, urea, and L-tyrosine, enzyme activity of α-chymotrypsin, α-fucosidase, α-galactosidase, β-galactosidase, β-glucuronidase, lipase (C14), α-mannosidase, and trypsin, and assimilation of adipate, caprate, citrate, malate, and phenyl-acetate.

Table 2 Fatty acid composition of strain TS19T and related Hymenobacter species

| C16:0 | 1 | 2 | 3 |
|-------|---|---|---|
| 3.6   | 36.5 | 3.2 | 16.1 |
| 33.2  | 3.4  | 1.6  |
| 5.4   | 8.5  | 4.0  | 6.3  |
| 6.3   | 7.8  | 2.3  |
| 10.5  | 9.2  | 17.2 |
| C16:1 ω5c | Tr | – | 1.9 |

Strains: 1, Strain TS19T; 2, H. wooponensis KCTC 32528T; 3, H. gelipurpurascens KACC 12069T. All data from this study. –, Not detected; Tr, trace (<1%).

Chemotaxonomic characterisation

The cellular fatty acid profile of strain TS19T is described in Table 2. The predominant fatty acids (> 10.0% of total fatty acids) were iso-C15:0 (33.2%), summed feature 4 (iso-C17:1 I and/or anteiso-C17:1 B) (13.7%), summed feature 3 (C16:1 ω6c and/or C16:1 ω7c) (13.1%) and C16:1 ω5c (10.5%), which were similar to those of related species. However, strain TS19T contained higher proportion of summed feature 3 and summed feature 4 compared with related species. The predominant polar lipid were phosphatidylethanolamine, and one unidentified aminophospholipid; a smaller amount of one unidentified aminophospholipid, two unidentified amino lipids, one unidentified phospholipid and two unidentified lipids were also detected but glycolipid was not detected (Fig. S3). The polar lipid pattern of strain TS19T was similar to that of the two reference type

Strains: 1, Strain TS19T; 2, H. wooponensis KCTC 32528T; 3, H. gelipurpurascens KACC 12069T. All data from this study. –, Not detected; Tr, trace (<1%).

Summed features represent two or three fatty acids that cannot be separated by the Microbial Identification system. Summed feature 1 comprises iso-C15:1 H and/or C13:0 3-OH; summed feature 3 comprises C16:1 ω6c and/or C16:1 ω7c; summed feature 4 comprises iso-C17:1 I and/or anteiso-C17:1 B.
Strains, in which the major polar lipids are phosphatidylethanolamine and unidentified aminophospholipid. The main respiratory quinone of strain TS19T was menaquinone-7, which was also the main quinone of the genus *Hymenobacter* (Buczolits et al. 2006).

**Taxonomic conclusion**

Phylogenetic tree analysis, based on 16S rRNA gene sequences, revealed that strain TS19T was grouped in the genus *Hymenobacter*. Moreover, strain TS19T and two closely related species *H. woonponsis*, and *H. gelipurpurascens*, which were grouped one clade in the two types of phylogenetic tree. However, the genotypic, phenotypic, chemotaxonomic, and gamma radiation-resistant analyses presented in this study clearly show that the strain differs from the two closely related species. The physiological characteristics of strain TS19T and the reference species are summarized in Table 1. On the basis of phylogenetic, genomic, physiological, and chemotaxonomic characterization, we suggest that strain TS19T represents a novel species of the genus *Hymenobacter*, for which the name *Hymenobacter taeanensis* sp. nov. is proposed.

**Description of Hymenobacter taeanensis** sp. nov.

*Hymenobacter taeanensis* sp. nov. (tae-an-en’sis. N.L. masc. adj. taeanensis: of or belonging to Taean, Republic of Korea, the geographical origin of the type strain of the species.).

Cells are observed to be Gram-stain-negative, non-motile, non-spore-forming, aerobic, and rod shaped, approximately 0.8–1.2 μm in diameter and 2.0–4.5 μm in length. Colonies are observed to be irregular, undulate, light pink-colored, and 2–5 mm in diameter after incubation on R2A agar for 3 days, but colonies are observed to be circular, entire, orange-pink colored when grown on TGY agar. Growth occurs on R2A and TGY, with 0–1.0% (w/v) NaCl (optimally 0%), at pH 6–8 (optimally pH 7) and at 10–37 °C (optimally 25–30 °C). Strain TS19T tolerated to gamma radiation with a D10 value of 7.3 kGy. Strain is found to be positive for catalase activity, but negative for oxidase activity. Carotenoid pigment is produced with absorbance spectral peaks at 478 nm. Cells are confirmed to be positive for hydrolysis of casein, CMC, esculin, gelatin, and starch. Cells are confirmed to be negative for reduction of indole and nitrate, and hydrolysis of arginine, DNA, Tween 20, Tween 80, and L-tyrosine. The predominant fatty acids (> 10%) are iso-C15:0, summed feature 4 (iso-C17:1 I and/or anteiso-C17:1 B), summed feature 3 (C16:1 ω6c and/or C16:1 ω7c), and C16:1 ω5c. The major polar lipids are phosphatidylethanolamine, one unidentified aminophospholipid and main respiratory quinone is menaquinone-7. The type strain is TS19T (= KCTC 72897 T = JCM 34023 T), isolated from sand in the Republic of Korea. Its genome is 4.9 Mb with the DNA G + C content of 56.2 mol%, which contained 3,955 CDSs. The GenBank accession number for the 16S rRNA gene sequence and the genome sequence of strain TS19T are MN911321 and NZ_CP053538, respectively.

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**Availability of data and materials** The complete genome sequence of strain TS19T generated during the current study has been deposited in GenBank with the accession codes, https://ncbi.nlm.nih.gov/nuccore/NZ_CP053538. The 16S rRNA gene sequence also is available in the GenBank repository, https://ncbi.nlm.nih.gov/nuccore/MN911321.

**Declarations**

**Conflicts of interest** The authors have no conflicts of interest declare that are relevant to the content of this article.

**Ethical approval** Not applicable.

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