**INTRODUCTION**

A variety of microorganisms are used in industrial fermentation for production of enzymes, medicines, and other organic compounds. Those microorganisms are generally grown in high-nutrient medium containing large amounts of sugar, nitrogen, phosphorus, minerals, and other nutrients that are considered essential for their growth. Consequently, nutrient cost is an important factor when trying to achieve cost-effective fermentation. This has led to the development of several related technologies, including bioengineering of microorganisms so as to enhance their productivity and yield (Min, Hwang, Lim, & Jung, 2017), use of agricultural byproducts as carbon and mineral sources (Thomsen, 2005), and production of chemicals such as bioemulsifiers (Banat, Satpute, Cameotra, Patil, & Nyayanit, 2014), biofuels (Ho, Ngo, & Guo, 2014), and biosurfactants (Banat et al., 2014) from renewable substrates.

Oligotrophs are organisms that grow under conditions of low levels of nutrients but grow more slowly at high levels (Kuznetsov, Dubinina, & Lapteva, 1979). Consequently, oligotrophs have not been applied for industrial use. We suggest that production costs...
could be reduced if oligotrophs could be used for industrial fermentation, and therefore screened for oligotrophs that are unaffected by a high-nutrient condition. Here, we report the screening, isolation, and characterization of an oligotrophic bacterium from leaf soil, which is one kind of the compost and is accrued by fermenting the dry leaves. The isolate was named strain CCA6. This bacterium was capable of growth on poor-nutrient medium, and its growth was unaffected by high-nutrient mixtures. Moreover, physiological, chemotaxonomic, and phylogenetic analyses as well as average nucleotide identity (ANI) value analysis were performed to characterize strain CCA6. Based on the results of these analyses, we propose that strain CCA6 represents a novel species within the genus *Enterobacter*, for which the name *E. oligotrophica* sp. nov. is proposed.

## 2 | MATERIALS AND METHODS

### 2.1 | Bacterial isolation

Soil samples were collected from Higashi-Hiroshima city in Hiroshima prefecture, Japan. A 1.5% agar (Nacalai tesque, Kyoto, Japan) plate (pH 7.2), which contained sulfates (>0.4%), calcium (>0.1%), iron (>0.01%), and a few fatty acids and/or other minerals at concentrations <0.01% was used for isolation. After 1 ml of a 10% (w/v) soil wash solution was inoculated onto a plate, the plate was incubated for 2 days at 37°C. Thereafter, a single colony was successively re-streaked onto a new 1.5% agar plate at least three times to obtain a pure colony. The purified strain was then grown aerobically at 37°C in Nutrient Broth (Kyokuto, Tokyo, Japan) and preserved at −20°C as a suspension in Nutrient Broth supplemented with glycerol (30%, w/v).

### 2.2 | Physiological characterization

Growth of strain CCA6 in Nutrient Broth was evaluated at various temperatures (4–50°C), pH (4.0–10.5), and NaCl concentrations (1–7%, w/v), and in the presence of selected antibiotics (ampicillin, chloramphenicol, and kanamycin). The OD_{600}, which reflects cell growth, was measured by monitoring the difference between cellular and cell-free turbidity values using an Eppendorf BioSpectrometer (Eppendorf, Hamburg, Germany). Carbon source utilization was assessed using API 20E (bioMérieux, Marcy-l’Etoile, France) and API 50 CHE (bioMérieux, France) according to the manufacturer's instructions.

| TABLE 1 | Differential characteristics of strain CCA6 and phylogenetically related species |
|----------------|----------------------------------------------------------|
| **Characteristic** | **1** | **2** | **3** | **4** | **5** | **6** | **7** | **8** | **9** | **10** |
| **Carbon source utilization** | | | | | | | | | | |
| d-Sucrose | - | ++ | ++ | ++ | ++ | ++ | ++ | ++ | ++ | ++ |
| d-Melibiose | - | + | ++ | ++ | W | ++ | ++ | ++ | ++ | ++ |
| d-Turanose | - | + | + | - | W | + | - | W | + | + |
| l-Rhamnose | ++ | + | ++ | - | ++ | ++ | ++ | ++ | ++ | ++ |
| Inositol | - | + | ++ | ++ | - | W | W | + | ++ | ++ |
| Dulcitol | + | + | W | - | ++ | - | + | + | + | + |
| d-Sorbitol | ++ | ++ | ++ | ++ | W | ++ | ++ | ++ | ++ | ++ |
| Methyl-α-D-glucopyranoside | - | ++ | ++ | ++ | ++ | + | + | ++ | ++ | ++ |
| d-Arabinose | ++ | + | ++ | ++ | ++ | ++ | ++ | + | ++ | + |
| L-Fucose | ++ | + | + | ++ | ++ | + | ++ | W | - | + |
| d-Lyxose | ++ | ++ | W | ++ | + | ++ | ++ | + | ++ | + |
| Adonitol | + | + | + | - | W | W | ++ | - | + | + |
| d-Arabitol | - | + | + | - | W | W | ++ | - | + | + |
| 2-Keto gluconate | + | + | ++ | + | W | - | + | + | W | + |
| **Enzyme activity** | | | | | | | | | | |
| Arginine dihydrolase | + | + | ++ | ++ | ++ | ++ | ++ | - | ++ | ++ |
| Ornithine decarboxylase | + | + | ++ | ++ | ++ | ++ | ++ | - | ++ | ++ |
| Lysine decarboxylase | + | + | ++ | ++ | ++ | ++ | ++ | - | ++ | ++ |
| Esculin hydrolysis | + | + | ++ | ++ | ++ | ++ | ++ | - | ++ | ++ |
| Voges-Proskauer test | + | + | ++ | ++ | ++ | ++ | ++ | - | ++ | ++ |

Note. Strains: 1, strain CCA6; 2, *E. asburiae* ATCC 35953<sup>7</sup>; 3, *E. cloacae* subsp. *cloacae* ATCC13047<sup>7</sup>; 4, *E. cloacae* subsp. *dissolvens* ATCC 23373<sup>7</sup>; 5, *E. hormaechei* subsp. *hormaechei* ATCC 49162<sup>7</sup>; 6, *E. hormaechei* subsp. *hormaechei* DSM 16687<sup>7</sup>; 7, *E. hormaechei* subsp. *hormaechei* steigerwaltii DSM 16691<sup>7</sup>; 8, *E. hormaechei* subsp. *xiangfangensis* LMG 27195<sup>7</sup>; 9, *E. kobei* ATCC BAA-260<sup>7</sup>; 10, *E. ludwigii* EN-119<sup>7</sup>. ++, strong positive; +, positive; W, weak positive; −, not detected.
Voges–Proskauer (VP) test was carried out using RapiD 20E (bioMérieux). Enzyme activities were evaluated using API ZYM (bioMérieux).

2.3 Chemotaxonomic analyses

The cellular fatty acid composition of strain CCA6 was determined using Sherlock Microbial Identification System Version 6.0 (MIDI, Newark, DE) with TSBA6 database (MIDI). Using the method of Bligh and Dyer (1959), lipids were extracted from lyophilized cells of strain CCA6 and loaded onto a Sep-Pak Plus Silica cartridge (Waters, Milford, MA). The cartridge was then washed and the quinones were eluted. The quinones were quantified using an ACQUITY UPLC system (Waters) with an Eclipse Plus C18 column (Agilent technologies, Santa Clara, CA). The chromatographic conditions were as follows: mobile phase, methanol/isopropanol (3:1 v/v); flow rate, 0.5 ml/min; column oven temperature, 35°C. The quinone forms were identified as previously described (Tamaoka, Katayama-Fujimura, & Kuraishi, 1983).

2.4 Phylogenetic analysis based on 16S rRNA gene

After strain CCA6 was cultured aerobically for 6 hr at 37°C in Nutrient Broth, the cells were harvested by centrifugation, and their genomic DNA was extracted and purified using an illustra bacteria genomicPrep Mini Spin Kit (GE Healthcare, Chicago, IL) according to the manufacturer’s instructions. The 16S rRNA gene was amplified
FIGURE 1 Phylogenetic tree constructed from analysis of 16S rRNA gene sequences showing the relationships between strain CCA6 and the related type strains. The bar indicates a 0.02% nucleotide substitution rate. The tree was rooted using Xenorhabdus nematophila ATCC 19061T as the outgroup.
Figure 2
Phylogenetic tree reconstructed from analysis of the sequences of four housekeeping genes (atpD, gyrB, infB, and rpoB) and showing the relationships between strain CCA6 and the related type strains. The bar indicates a 0.1% nucleotide substitution rate. The tree was rooted using X. nematophila ATCC 19061T as the outgroup.
using KOD plus DNA Polymerase (TOYOBO, Osaka, Japan) with the bacterial universal primers 27f (5′-AGAGTTTGATCMTGGCTCAG-3′; Lane, 1991) and 1391r (5′-ACGGGCGGTGTGTRCA-3′; Turner, Pryer, Miao, & Palmer, 1999). After purifying the amplified PCR product using a Wizard SV Gel and PCR Clean-up System (Promega, Madison, WI), the purified product was cloned into pTA2 vector (TOYOBO) and sequenced. Sequence was then compared with reference sequences available in the GenBank/EMBL/DBJ databases.

1.0 (Pacific Biosciences, Menlo Park, CA), yielding SMRTbell libraries using a SMRTbell Template Prep Kit TUBE (Covaris, Brighton, UK), the resultant fragments were ligated to DNA/Polymerase binding kit P6 v2 (Pacific Biosciences), yielding were then bound to polymerases and sequencing primers using a (Agilent Technologies, Santa Clara, CA). The SMRTbell libraries of four housekeeping genes [atpD (β subunit of ATP synthase; 642 bp), gyrB (DNA gyrase; 743 bp), infB (translation initiation factor 2; 615 bp), and rpoB (β subunit of RNA polymerase; 637 bp)] from strain CCA6, was also reconstructed using the maximum-likelihood method with Tamura and Nei model (1993). The housekeeping genes of strain CCA6 and the related type strains are available in the GenBank/DBJ/EMBL databases.

2.5 | Multilocus sequence analysis based on housekeeping genes

Multilocus sequence analysis (MLSA) was performed using the method of Brady et al. (2008), Brady, Cleenwerck, Venter, Coutinho, and De Vos (2013) with some modifications. A phylogenetic tree of concatenated sequences (2,637 bp), including partial sequences of four housekeeping genes [atpD, gyrB, infB, and rpoB] from strain CCA6, was also reconstructed using the maximum-likelihood method with Tamura and Nei model (1993). The housekeeping genes of strain CCA6 and the related type strains are available in the GenBank/DBJ/EMBL/DBJ databases.

2.6 | Genome sequencing and ANI value analysis

The concentration and purity of the genomic DNA were measured using a NanoDrop ND-1000 spectrophotometer (Thermo Fisher Scientific, Waltham, MA) and a Quant-iT dsDNA BR assay kit (Invitrogen, Waltham, MA), respectively. After fragmenting the genomic DNA (20.9 μg) into approximately 20-kb pieces using g-TUBE (Covaris, Brighton, UK), the resultant fragments were ligated to SMRTbell sequencing adapters using a SMRTbell Template Prep Kit 1.0 (Pacific Biosciences, Menlo Park, CA), yielding SMRTbell libraries. The library size was measured using Agilent 2200 TapeStation (Agilent Technologies, Santa Clara, CA). The SMRTbell libraries were then bound to polymerases and sequencing primers using a DNA/Polymerase binding kit P6 v2 (Pacific Biosciences), yielding the sequencing templates. The concentration of the sequencing templates was calculated using Binding Calculator v2.3.1.1 (Pacific Biosciences), after which the templates were bound to MagBeads using a MagBead kit (Pacific Biosciences) and loaded onto SMRT Cells 8Pac v3 (Pacific Biosciences). Sequencing was then performed using PacBio RS II (Pacific Biosciences).

The raw data included 100,771 reads with 330 coverage and were assembled de novo using SMRT Analysis v2.3.0 (Pacific Biosciences; Chin et al., 2013) to filter the subreads. Genome annotation was performed using CRITICA (Badger & Olsen, 1999) and Glimmer2 (Delcher, Harmon, Kasif, White, & Salzberg, 1999). The tRNA and rRNA genes were detected using tRNAscan-SE (Lowe & Eddy, 1997) and BLASTN (Altschul, Gish, Miller, Myers, & Lipman, 1990), respectively. ANI values were calculated through pairwise genome comparison of whole-genome sequences of strain CCA6 and its related Enterobacter type strains using the ANI algorithm (Goris et al., 2007) implemented within OrthoANIu tools (Yoon, Ha, Lim, Kwon, & Chun, 2017).

The genome properties of type strains of Enterobacter, Klebsiella, Kosakonia, Lelliottia, Pluralibacter, Pseudescherichia, Pseudomonas, and Raoultella species are presented in Table A1.

3 | RESULTS AND DISCUSSION

3.1 | Isolation of strain CCA6

To obtain oligotrophic microorganisms, filtrates were prepared from several soil samples and plated onto 1.5% agar (pH 7.2) without a carbon source or other medium components. After incubation for 2 days at 37°C, a single colony was obtained from the leaf soil filter. A purified colony was then obtained through standard dilution plating on the same plates and was named strain CCA6. Although high-nutrient mixtures suppress the growth of some oligotrophic bacteria (Ohta, 2000; Ohta & Taniguchi, 1988), strain CCA6 showed a higher rate of growth, similar to that of Escherichia coli MG1655, when cultured in Nutrient Broth or LB media (Figure A1). By contrast, E. coli MG1655 did not grow on a 1.5% agar (pH 7.2). These results suggest we had successfully isolated the desired oligotroph.

3.2 | Morphological and physiological characterization

Cells of strain CCA6 were Gram-negative, motile, rod-shaped and non-sporulating. Colonies grown on Nutrient Broth plates were circular, smooth, glistening, light yellow, and 5.0 mm in diameter after incubation overnight at 37°C. When we examined the effect of culture temperature and pH, we found that the strain was capable of growing at temperatures between 10 and 45°C, but no growth was seen at 4 or 50°C (Figure A2a). The strain also grew effectively at pHs between 4.5 and 10.0, but growth rates were sharply lower at pHs below 4.0 or above 10.5 (Figure A2b). The strain was tolerant to 6% (w/v) NaCl (Figure A2c) and was resistant to ampicillin, but chloramphenicol and kanamycin inhibited its growth.

Strain CCA6 showed a broad range of enzyme activities, including acid phosphatase, N-acetyl-β-D-glucosaminidase, alkaline phosphatase, cystine aminopeptidase, esterase lipase (C8), α-galactosidase, β-galactosidase, α-glucosidase, β-glucosidase, leucine aminopeptidase, α-mannosidase, naphthol AS-BI phosphate, trypsin, and valine aminopeptidase. By contrast, strain CCA6 did not exhibit α-chymotrypsin, esterase (C4), α-fucosidase, β-glucuronidase, or lipase (C14) activity. These results suggest that strain CCA6 is capable of catabolizing a variety of different carbon sources. Culture with different carbon sources revealed that CCA6 was able to utilize the following compounds as a carbon source for growth:
We have isolated a Gram-negative, non-sporulating, rod-shaped bacterium from leaf soil collected in Japan, which was designated strain CCA6. 16S rRNA gene sequence analysis revealed that strain CCA6 presented as a member of the family Enterobacteriaceae. (Figure 1). Moreover, MLSA based on partial sequences of the atpD, gyrB, infB, and rpoB gene showed clear separation between strain CCA6 and the related Enterobacter type strains (Figure 2). The ANI values between strain CCA6 and the related Enterobacter type strains were in the range of 79.75–88.02%, which was clearly below the cutoff of 95–96% for prokaryotic species delineation as established by Richter and Rosselló-Mora (2009).

4 | CONCLUSION

We have isolated a Gram-negative, non-sporulating, rod-shaped bacterium from leaf soil collected in Japan, which was designated strain CCA6. 16S rRNA gene sequence analysis revealed that strain CCA6 presented as a member of the family Enterobacteriaceae. (Figure 1). Moreover, MLSA based on partial sequences of the atpD, gyrB, infB, and rpoB gene showed clear separation between strain CCA6 and the related Enterobacter type strains (Figure 2). The ANI values between strain CCA6 and the related Enterobacter type strains were in the range of 79.75–88.02%, which was clearly below the cutoff of 95–96% for prokaryotic species delineation as established by Richter and Rosselló-Mora (2009).
4.1 | Description of *E. oligotrophica* sp. nov

*Enterobacter oligotrophica* (o.li.goтроphi.ca. Gr. adj. oligos little; Gr. adj. trophikos nursing, tending or feeding; N.L. fem. adj. oligotrophica eating little, referring to a bacterium living on low-nutrient media).

Cells are aerobic, Gram-negative, non-sporulating, and rod-shaped (1.0–2.0 μm × 4.0–5.0 μm). Colonies are circular, smooth, glistening, light yellow, and grow to 5.0 mm in diameter on Nutrient Broth plates after incubation for 24 hr at 37°C. Growth is observed in poor-nutrient medium, and growth is unaffected by high-nutrient medium. The VP test is negative. The major cellular fatty acids are C₁₆:0 and sums of C₁₆:1ω6c and/or C₁₆:1ω7c or C₁₈:1ω6c and/or C₁₈:1ω7c. The predominant quinone system is ubiquinone-8. Growth is observed in Nutrient Broth at 10–45°C and pH 4.5–10.0, with optimal growth at 20°C and pH 5.0. Growth occurs in the presence of 0–6% (w/v) NaCl as well as ampicillin. Strain CCA6 is positive for lysine decarboxylase. No growth occurs on d-sucrose, d-melibiose, d-tagatose, inositol, or methyl-a-d-glucopyranoside. Strain CCA6 is clearly separated from the related *Enterobacter* type strains by MLSA based on partial sequences of the *atpD*, *gyrB*, *infB*, and *rpoB* gene. The genome size of the type strain is 4,476,585 bp, which has a G+C content of 54.3%.

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CONFLICT OF INTERESTS

None declared.

AUTHOR CONTRIBUTIONS

HA an ZK designed, carried out the experiments, and wrote the manuscript. AM revised the manuscript.

ETHICS STATEMENT

None required.

DATA ACCESSIBILITY

The 16S rRNA gene sequence of strain CCA6 is available in the GenBank/EMBL/DDBJ databases under accession number LC368255. The complete genome sequence of strain CCA6 has been deposited in the DDBJ/EMBL/GenBank under accession number AP019007. The type strain is CCA6T and was deposited in two international strain collection institutes with the following accession numbers: HUT 8142T = KCTC 62525T.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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FIGURE A1 Growth rates at 30°C of strain CCA6 and E. coli MG1655. The results for strain CCA6 and E. coli MG1655 are shown as filled and open symbols, respectively. The media are indicated as follows: circles, Nutrient Broth (pH 7.0) and squares, LB media (pH 7.0). The OD_{600} was measured using a Bio Microplate Reader HITS (Scinics, Tokyo, Japan). Experiments were performed in triplicate
FIGURE A2 Effects of culture conditions on growth of strain CCA6. (a) Effects of culture temperature. Cells were cultured in Nutrient Broth (pH 7.0). (b) Effects of culture pH. Cells were cultured in Nutrient Broth at 30°C. (c) Effect of NaCl concentration. Cells were cultured in Nutrient Broth (pH 7.0) at 30°C. Error bars indicate SE (n = 3).

TABLE A1 Genome properties of type strains of Enterobacter, Klebsiella, Kosakonia, Lelliottia, Pluralibacter, Pseudescherichia, Pseudomonas, and Raoultella species used in this study

| Strains                      | Size (bp) | G+C (mol%) | Protein | Accession no. |
|------------------------------|-----------|------------|---------|---------------|
| *Enterobacter*               |           |            |         |               |
| *E. asburiae* ATCC 35953T    | 4,713,742 | 55.4       | 4,436   | CP011863      |
| *E. bugandensis* EB-247T     | 4,971,744 | 56.0       | 4,344   | FYBI00000000  |
| *E. cancerogenus* ATCC 33241T| 4,879,939 | 55.6       | 4,521   | FYBA00000000  |
| *E. chengduensis* WCHECI-C4T | 5,138,130 | 55.7       | 4,745   | MTSO00000000  |
| *E. cloaceae* subsp. cloaceae ATCC 13047T | 5,551,574 | 54.6       | 5,393   | JPPR00000000  |
| *E. hormaechei* subsp. hormaechei ATCC 49162T | 4,890,213 | 55.2       | 4,522   | MKEQ00000000  |
| *E. hormaechei* subsp. oharae DSM 16687T | 4,724,316 | 55.6       | 4,390   | CP017180      |
| *E. hormaechei* subsp. steigerwaltii DSM 16691T | 4,782,480 | 55.6       | 4,424   | CP017179      |
| *E. hormaechei* subsp. xiangfangensis LMG 27195T | 4,661,849 | 55.3       | 4,306   | CP017183      |
| *E. kobei* ATCC BAA-260T     | 4,700,329 | 55.5       | 4,424   | FTNJ00000000  |
| *E. ludwigi* EN-119T         | 4,952,770 | 54.6       | 4,459   | JTL00000000   |
| *E. mori* LMG 25706T         | 4,953,765 | 55.3       | 4,496   | AEXB00000000  |
| *E. mulleri* JM-458T         | 4,695,678 | 55.9       | 4,423   | FXLQ01000000  |
| *E. rogenkampii* DSM 16690T  | 4,748,414 | 56.0       | 4,451   | CP017184      |
| *E. sichuanensis* WCHECL1597T| 4,897,201 | 55.2       | 4,634   | POVL01000000  |
| *E. soli* ATCC BAA-2102T     | 4,960,767 | 53.8       | 4,571   | LXES00000000  |
| Strains | Size (bp) | G+C (mol%) | Protein | Accession no. |
|---------|-----------|------------|---------|---------------|
| *E. tabaci* CCUG 72520<sup>T</sup> | 4,927,887 | 55.5 | 4,627 | QZDQ00000000 |
| Klebsiella | | | | |
| *K. aerogenes* KCTC 2190<sup>T</sup> | 5,280,350 | 54.8 | 4,912 | CP002824 |
| *K. grimontii* 06D021<sup>T</sup> | 6,168,876 | 55.4 | 5,986 | FZTC00000000 |
| *K. michiganensis* DSM 25444<sup>T</sup> | 6,193,009 | 56.0 | 5,732 | PRDB00000000 |
| *K. pneumoniae* subsp. *oxaeae* ATCC 11296<sup>T</sup> | 4,925,250 | 57.2 | 4,458 | CDJH00000000 |
| *K. pneumoniae* subsp. *pneumoniae* ATCC 13883<sup>T</sup> | 5,544,684 | 57.0 | 5,205 | JOOW00000000 |
| *K. pneumoniae* subsp. *rhinoscleromatis* ATCC 13884<sup>T</sup> | 5,280,675 | 56.9 | 5,671 | ACZD00000000 |
| *K. quasipneumoniae* subsp. *quasipneumoniae* 01A030<sup>T</sup> | 5,465,736 | 58.0 | 5,287 | CCF00000000 |
| *K. quasipneumoniae* subsp. *similipneumoniae* 07A044<sup>T</sup> | 5,109,717 | 58.2 | 4,927 | CBZR00000000 |
| *K. variicola* DSM 15968<sup>T</sup> | 5,521,203 | 57.6 | 5,200 | CP010523 |
| Kosakonia | | | | |
| *K. arachidis* Ah-143<sup>T</sup> | 5,135,597 | 52.5 | 4,861 | FPDU00000000 |
| *K. oryzae* CGMCC 1.7012<sup>T</sup> | 5,380,462 | 54.0 | 4,980 | FOKO00000000 |
| *K. oryzenophytica* LMG 26432<sup>T</sup> | 4,878,776 | 53.7 | 4,459 | FYBE00000000 |
| *K. oryziphila* REICA_142<sup>T</sup> | 4,814,900 | 52.7 | 4,667 | FMBC00000000 |
| *K. pseudosacchari* JM-387<sup>T</sup> | 4,956,546 | 53.9 | 4,638 | FXWP00000000 |
| *K. radicincitans* DSM 16656<sup>T</sup> | 5,817,639 | 53.7 | 5,660 | AKYD00000000 |
| *K. sacchari* SP1<sup>T</sup> | 4,902,027 | 53.7 | 4,545 | CP007215 |
| Lelliottia | | | | |
| *L. amnigena* DSM 4486<sup>T</sup> | 4,370,208 | 52.9 | 4,070 | PDPA00000000 |
| *L. jeotgali* PFL01<sup>T</sup> | 4,603,334 | 54.2 | 4,243 | CP018628 |
| Pluralibacter | | | | |
| *P. gergoviae* NBRC 105706<sup>T</sup> | 5,662,775 | 58.6 | 5,176 | BCZ00000000 |
| Pseuderscherichia | | | | |
| *P. vulneris* NBRC 102420<sup>T</sup> | 4,374,581 | 56.4 | 4,196 | BBMZ00000000 |
| Raoultella | | | | |
| *R. ornithinolytica* NBRC 105727<sup>T</sup> | 5,533,930 | 55.7 | 5,099 | BCYR00000000 |
| *R. planticola* ATCC 33531<sup>T</sup> | 5,668,028 | 55.8 | 5,237 | JMP00000000 |
| Xenorhabdus | | | | |
| *X. nematophila* ATCC 19061<sup>T</sup> | 4,587,917 | 44.3 | 3,754 | FN667742 |

Note. Data are from the GenBank/EMBL/DDBJ databases.