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TAXONOMIC DESCRIPTION

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Bdellovibrio reynosensis sp. nov., from a Mexico soil sample

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Abstract

A novel predatory bacterium, strain LBG001^T, has been isolated from Reynosa, Mexico. The 16S rRNA shares approximately 97% sequence identity with many reported strains in the genus *Bdellovibrio* including the type strain *Bdellovibrio bacteriovorus* HD100^T. Phylogenetic trees based on the 16S rRNA gene and on 30 concatenated housekeeping genes or core genes showed that LBG001^T is on a separate branch from the *B. bacteriovorus* group. LBG0001^T has a genome size of 3582323 bp with a G+C content of 43.1 mol%. The average nucleotide identity, average amino acid identity and digital DNA–DNA hybridization values with other members of the genus *Bdellovibrio* (<79, <72 and <17%, respectively) qualifies the strain to represent a new species in the genus. Strain LBG001^T formed visible plaques on all 10 tested Gram-negative bacterial species. The phenotypic characteristics, phylogenetic analysis and genomic taxonomic studies support the classification of the strain as representing a new species for which the name *Bdellovibrio reynosensis* sp. nov. is proposed. The type strain is LBG001^T(=ATCC TSD-288^T=CM-CNRG 0932^T).

INTRODUCTION

Bdellovibrio species are obligate predators of Gram-negative bacteria. They are small, motile and comma-shaped with a single polar flagellum. They belong to the class Oligoflexia. This class contains other obligate predatory bacteria such as *Bacteriovorax*, *Halobacteriovorax* and *Peredibacter*, as well as the non-predatory bacteria *Silvanigrella*, *Fluviispira* and *Oligoflexus* [1–5]. While *Halobacteriovorax* is salt-tolerant and mostly isolated from marine environments, *Bdellovibrio*, *Bacteriovorax* and *Peredibacter* are isolated from soil and freshwater environments [4]. Of the predatory bacteria in the Oligoflexia group, *Bdellovibrio* is the most studied. The *Bdellovibrio* predation strategy can be periplasmic or epibiotic [6, 7]. *Bdellovibrio bacteriovorus* HD100^T is the type strain for periplasmic predators and *Bdellovibrio exovorus* JSS^T is the type strain for epibiotic predators, which was recently separated from *Bdellovibrio* as a new genus *Pseudobdellovibrio* [8]. Isolation of *Bdellovibrio* species can be challenging due to low abundance and the need for a correct choice of prey and culture conditions. Most studies in the *Bdellovibrio* make use of the type strain *B. bacteriovorus* HD100^T or 109J as they have a wide prey range and their genomic, phenotypic and life-cycle have been well studied.

Bdellovibrio species are increasingly being explored as alternatives to antibiotics and probiotics in agriculture, food and medicine. There is a need to isolate and characterize more *Bdellovibrio* species as their prey preference and predation efficiency differ. In our attempt to obtain *Bdellovibrio* for potential use in food preservation, we isolated a strain and herein confirm it to represent a new species in the genus *Bdellovibrio*. This study presents the phenotypic and genomic characteristics of the novel strain LBG001^T.

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Keywords: *Bdellovibrio reynosensis*; genome comparison; genome sequence; new species; predatory bacteria.

Abbreviations: AAI, genomic average amino acid identity; ANI, average nucleotide identity; BPGA, bacterial pan genome analysis; dDDH, digital DNA–DNA hybridization; DNB, diluted nutrient broth; FastANI, fast alignment-free computation of whole-genome ANI.

The complete genome sequence was deposited at GenBank of NCBI with the accession number CP093442. The accession number of 16S rRNA gene of LBG001^T in GenBank is ON152670.

Two supplementary figures and two supplementary tables are available with the online version of this article.

ISOLATION AND ECOLOGY

Strain LBG001^T was isolated from soil using *Klebsiella oxytocoa* as the prey. The soil sample was collected at 26.0698623° N, −98.3135799° W, Reynosa, Tamaulipas, Mexico on 16 September, 2019. It was collected from the rhizosphere of an *Agave* plant in a dark agricultural soil. The samples were taken to the lab and 50 g soil was moved into 100 ml sterile HEPES buffer. The mixture was placed in a shaker at 150 r.p.m. for 2 h at 30 °C. Then it was filtered using a 0.45 µm sterile filter. The filtrate was used for co-culture with *K. oxytoca* to allow for the enrichment of predatory bacteria. The co-culture was set up in a shaker at 30 °C at 150 r.p.m. for 48 h. The culture was centrifuged at 1308 *g* for 30 min at 4 °C and the supernatant was collected for the use of the double-layer agar plate technique [9]. A 100 µl serially diluted coculture supernatant was mixed with a 300 µl suspension of prepared *K. oxytoca* in 5 ml 55°C-molten diluted nutrient broth (DNB) top agar. The mixtures were immediately vortexed and plated on top of DNB bottom agar plates. Plates were incubated at 30 °C for 10 days. Plates were monitored daily for the presence of plaques. Plaques that appeared after 48 h were considered probable *Bdellovibrio*. Well-separated plaques were observed on plates at a dilution factor of 4. The plaques were then observed for differences in morphological characteristics. The plaques appeared small, circular and transparent. Therefore, a single representative plaque was chosen and purified for three more times to obtain a pure culture. The isolate was identified by PCR using the 16S rRNA gene-specific primers for *Bdellovibrio* [10]. The purified *Bdellovibrio* strain was cryopreserved at −80 °C in 20% glycerol.

PHYLOGENY

The *Bdellovibrio* strain was revived from the cryopreserved stock vial by predation on *K. oxytoca* as described previously [11]. The coculture was centrifuged at 1308 g for 30 min at 4 °C to remove residual prey cells. The supernatant was filtered through a 0.45 µm filter. The filtrate was confirmed to be prey-free by streaking on a lysogeny broth agar plate, which was then incubated at 37 °C. The *Bdellovibrio* were collected by centrifugation at 36, 286 g at 4°C for 30 min. DNA was extracted from the concentrated cells using the WizardGenomic DNA Purification kit (Promega) following the manufacturer's instructions. Whole-genome sequencing was done by combining short-read and long-read data. The short-read data was generated using the Nextera XT DNA Library Prep kit (Illumina) and the NextSeq 550 sequencing instrument (Illumina). The long-read data was generated using the Native Barcoding Kit (Nanopore) and MinION instrument (Nanopore). A *de novo* assembly of reads was carried out on the PATRIC platform and the online Medusa web server [12, 13]. The assembled genome was comprised of a single circular chromosome. This genome sequence is deposited on the GenBank with accession number CP093442.

We made use of the 16S rRNA gene, housekeeping genes and whole-genome sequences in our phylogenetic analysis. LBG001^T encodes two identical 16 S rRNA genes separated by 804827 bp. The 16S rRNA nucleotide sequences were first aligned with MUSCLE and a neighbour-joining phylogenetic tree was reconstructed on MEGA X using default parameters at the bootstrap value of 1000 replicates. *Bacteriovorax stolpii* DSM 12778^T was one of the outgroup members (See Table S1, available in the online version of this article for details). We further did a similar analysis based on concatenated sequences of 30 housekeeping genes on MEGA X (supplementary materials, Text 1) as well as that based on the concatenated sequences of orthologous core genes, which were obtained using the BPGA pipeline.

BLAST analysis of the 16S rRNA gene sequence on the EzBioCloud database (www.ezbiocloud.net/identify) identified the organism to be a member of the genus *Bdellovibrio*. The result reported its top match as *B. bacteriovorus* strain R0, the third being HD100^T with a percentage identity of 97.63 and 97.14 respectively. The 16S rRNA gene sequence comparison was performed on the EMBL-EBI server. The percentage identity of ≤97% across the tested members of this genus (Tables S1 and S2) suggests that the newly isolated strain LBG001^T is a member of a new species in the genus *Bdellovibrio* [14, 15].

The 16S rRNA neighbour-joining phylogenetic tree showed LBG001^T, *B. bacteriovorus* W and *B. bacteriovorus* R0 branching out far away from the *B. bacteriovorus* HD100^T, supporting the proposal for the re-designation of *B. bacteriovorus* R0 and *B. bacteriovorus* W as *Bdellovibrio* sp. R0 and *Bdellovibrio* sp. W, respectively (Fig. 1). The redesignation of these strains is further confirmed by the concatenated 30 housekeeping genes (Fig. 2). The phylogenetic tree based on concatenated core genes showed that LBG001^T does not belong to any known species of *Bdellovibrio* strains as it formed a distinct branch on the tree (Fig. 3). R0 did not occur in Fig. 3 due to its incomplete genome sequence.

The digital DNA–DNA hybridization (DDH) values of LBG001^T against the 10 most closely related species were calculated using the Genome-to-Genome Distance Calculator [16]. The genomic average nucleotide identity (ANI) and FastANI and genomic average amino acid identity (AAI) were also calculated for further investigation of species delineation [17, 18].

Based on microbial genome taxonomy, strains of the same species are expected to share a >95% ANI, >95% AAI and >70% DDH [19]. The results of LBG001^T with the other *Bdellovibrio* genomes are presented in Table 1 and Table 2. Our result (ANI, ≤79%; FastANI, ≤80%; AAI, ≤72%; DDH, 17%) confirms that LBG001^T does not belong to the *B. bacteriovorus* and any other known species. Thus, strain LBG001^T represents a novel species within the genus for which the name *Bdellovibrio reynosensis* sp. nov. is proposed.

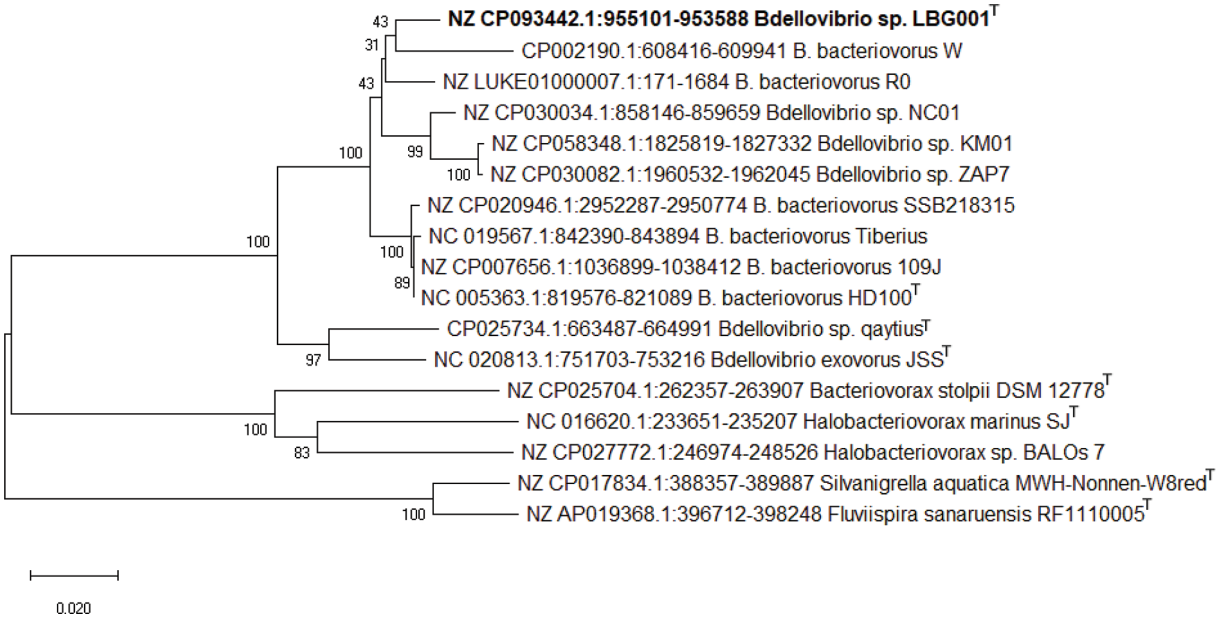

Fig. 1. Neighbour-joining tree reconstructed using 16S rRNA gene sequences.

GENOME FEATURES

Genome features of LBG001^T were analysed on PATRIC [13], prophage analysis on PHASTER [20], genome island on islandviewer4 [21] and metabolic reconstruction on BlastKOALA KEGG [22]. LBG001^T has a single circular chromosome with a size of 3582323 bp and a G+C content of 43.12 mol%. Comparative analysis of the genome features of LBG001^T with other representative obligate periplasmic and epibiotic predatory bacteria *B. bacteriovorus* HD100^T, *Bdellovibrio* sp. W, *Bdellovibrio* sp. NC01 and *Pseudobdellovibrio exovorus* are presented in Table 3. The LBG001^T genome size is bigger than that of the epibiotic predator *P. exovorus*. But smaller than that of all periplasmic *Bdellovibrio* strains with a complete genome sequence except for W, which has a genome size of 3.01 Mb, while its G+C (mol%) content is the lowest among the periplasmic *Bdellovibrio* strains, similar to W genome (43.3 mol%). The LBG001^T genome was predicted to contain one incomplete prophage (Fig. S1), with a region length of 29.4 kb. Five smaller genomic islands were identified (Fig. S2), of which the largest with a size of 25936 bp contains ribosomal proteins (50S ribosomal protein L24, 50S ribosomal protein L28 and 30S ribosomal protein S18), hypothetical proteins and other enzymes. But this incomplete prophage is not located at the islands, indicating that this prophage could be ancient event by phage attack. The ribosomal genes found in the genetic islands of LBG 001^T were further analysed. Of the four ribosomal proteins associated with the genome islands, three were found to be part of the LBG001^T core genome. The presence of the ribosomal proteins, sigma-54 dependent transcriptional regulator, DNA replication and repair protein RecF and DNA gyrase subunit A in the genome islands and being part of the LBG001^T core genome suggest ancient gene transfer. Ancient lateral transfer of prey genes into *Bdellovibrio* genome have previously being established [23]. The core genome and pan-genome analysis of the most closely related strains with periplasmic predatory lifestyles are presented in Table 4. It is noticeable that LBG001^T contains a high number of genome-specific genes (911).

Metabolic reconstruction of the LBG001^T genome supports a predatory lifestyle. The genome LBG001^T has complete glycolysis, tricarboxylic acid and pentose phosphate pathway cycles as well as the complete pathways for histidine, cysteine and methionine metabolism, while its fatty acid elongation and fatty acid biosynthesis are incomplete. The LBG001^T genome contains genes characterized as genetic signatures of predatory bacteria [24]. For example, it uses the mevalonate pathway for isoprenoid biosynthesis, unlike the non-predatory bacteria

Though *Bdellovibrio* is generally an obligate predatory bacterium, mutation at a region known as the host interaction locus (*hit*) has resulted in mutant strains that are facultative [25]. Such facultative mutants can be isolated and grow on complex media [9, 26]. The *hit* locus was first identified to be the switch from host-dependent to a host-independent *Bdellovibrio* [25] or to be the species *B. bacteriovorus* [27, 28]. The *hit* locus comprises *bd0108* and the 3′ one-third of *bd0109* in the *Bdellovibrio* genome HD100^T [29]. Pairwise sequence alignment of *bd0109* and phylogenetic analysis confirmed that this gene is well conserved in all *Bdellovibrio*, *Bacteriovorax* and *Halobacteriovorax* strains, suggesting *bd0109* could be necessary for their predatory lifestyle.

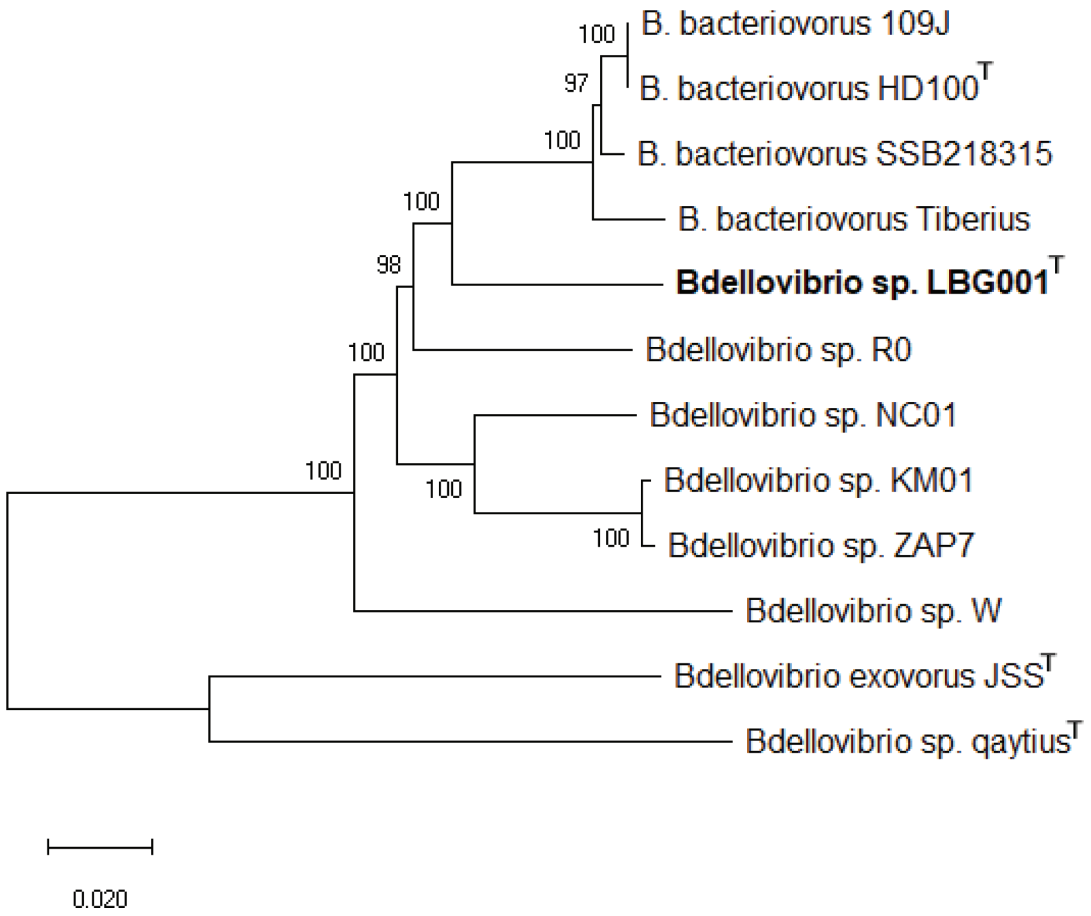

Fig. 2. Concatenated phylogenetic tree of 30 housekeeping genes showing the relatedness of *Bdellovibrio reynosensis* sp. nov. to the type strain *B. bacteriovorus* HD100^T.

However, the sequences of the *bd0108* protein are not well conserved and have high diversity in different species, although the homologues of *bd0109* are in the same operon. This small protein in LBG001^T showed 43% identity with *bd0108* of HD100^T, much lower than the comparison of *bd0109* homologue between these two strains (87% identity). There were no conserved regions of this small protein in *Halobacteriovorax*, *Bacteriovorax* and the epibiotic strain in *Pseudobdellovibrio*, while some regions are conserved in the periplasmic predation strains of *Bdellovibrio*. This small protein in LBG001^T showed the highest identity (62%) with a protein from a metagenomic sample strain. It also shares 52% identity with that in strain NC01, but the conserved region only occurred in the first 42 amino acids. A sequence multi-alignment of the small protein in LBG001^T with those in periplasmic predation members of *B. bacteriovorus* revealed a conserved region located at residues 34–42. The first 20 amino acids of all homologues are signal peptides although their signal sequences are completely different. Thus, all the members of this group contain these two genes but in a very different evolutionary manner: *bd0109* homologues are conserved and can be considered an essential gene while *bd0108* evolved much faster.

We could not conclude if LBG001^T exists as host-independant mutants, as such strains have not been successfully isolated so far.

GENETIC BASIS OF PREDATION

Orthologous genes related to predation in the LBG001^T genome were identified by comparison with other previously identified *Bdellovibrio* essential predatory genes. Duncan and colleagues used transposon mutagenesis to identify 104 genes that are of importance in 109J predation of planktonic *E. coli* cells [30], of which 100 genes are present in LBG001 and 64 genes occur in the core genome of *Bdellovibrio* periplasmic predation strains. If all *Bdellovibrio* shares a similar mechanism of predation, the presence or absence of some predation genes might be the basis of different prey ranges or predation efficiency observed among *Bdellovibrio* strains. The genetic basis underlying the *Bdellovibrio* predation strategy remains incomplete, making the study of different species of interest.

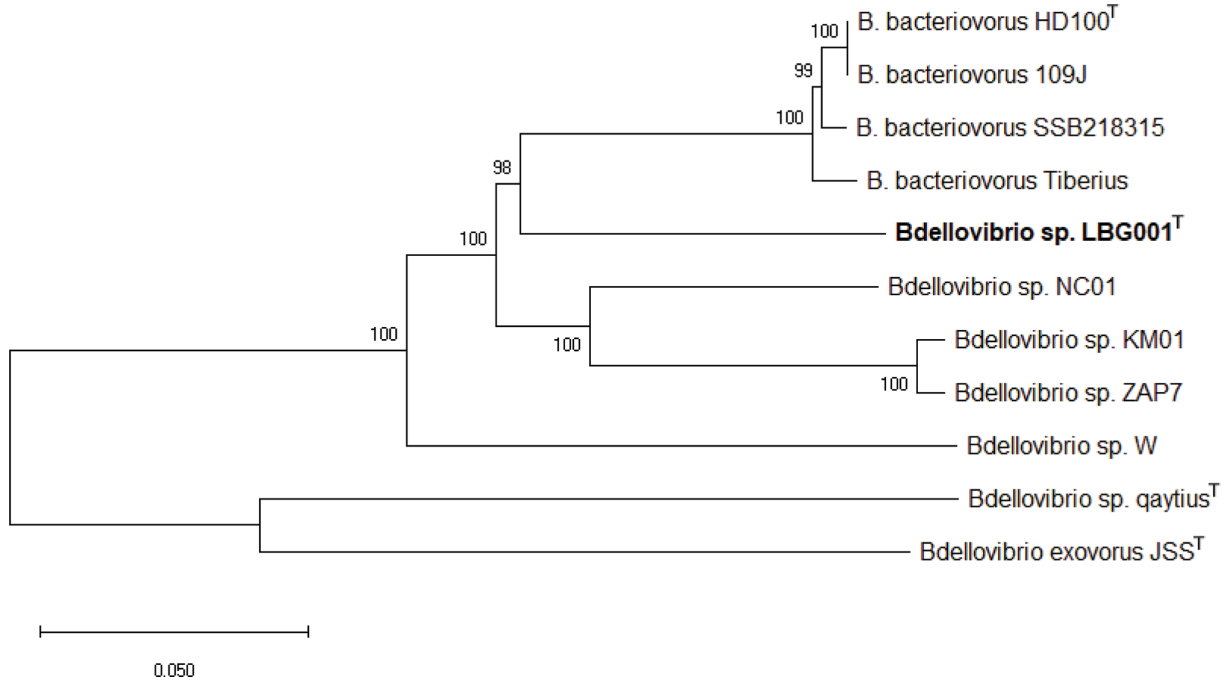

Fig. 3. The concatenated phylogenetic tree of core genes shared by 11 complete whole-genome sequenced *Bdellovibrio*. Concatenated core genes were recovered from the BPGA analysis. The tree was reconstructed on MEGA X using default parameters at 1000 bootstraps.

PHYSIOLOGY

We tested the LBG001^T prey range and the antibiotic susceptibility pattern. The double-layer plaque technique was used in investigating the prey range. The ability of the *Bdellovibrio* to form plaques on a prey lawn was considered positive for the prey bacteria under testing. The potential prey used in this study includes 10 Gram-negative bacteria *Pseudomonas aeruginosa* CDBB-B-1021 (ATCC 27853), *Acinetobacter baumanii* Jim01, *Klebsiella pneumonia subspecies pneumonia* B-969 (ATCC 13883), *Proteus vulgaris* ATCC 6380, *Vibrio parahaemolyticus*, *Serratia marcens* CDBB-B-1014 (ATCC 14756), *Enterobacter aerogenes* CDBB B-958 (ATCC 13048), *Salmonella enterica* subsp. *enterica* serovar Typhi CDBB-B-1101 (ATCC 7251), *Klebsiella oxytoca* B-968 (ATCC 13182), *Escherichia coli* DH5α and two Gram-positive bacteria: *Staphylococcus aureus* (ATCC25923), *Enterococcus*

Table 1. *In silico* DNA–DNA hybridization (% DDH), average nucleotide identity (% ANI) and average amino acid identity (AAI) values between *Bdellovibrio* sp. LBG 001^T and other *Bdellovibrio* strains

Strain	OrthoANI value (%)	OrthoAAI value (%)	In silico DDH (%)	
B. bacteriovorus HD100^T	77.65	71.15	16.6	
B. bacteriovorus 109J	77.53	71.21	16.7	
B. bacteriovorus SSB218315	77.10	71.20	16.5	
B. bacteriovorus Tiberius	77.41	71.16	16.7	Periplasmic predators
B. bacteriovorus W	77.30	66.51	14.6	
Bdellovibrio sp NC01	78.19	68.03	16.2	
Bdellovibrio ZAP7	77.61	66.30	15.3	
Bdellovibrio sp KM01	78.32	66.11	15.3	
Psuedobdellovibrio exovorus JSS^T	76.05	52.38	12.8	
Bdellovibrio sp. qaytius^T	75.37	50.93	12.7	Epibiotic predators

Table 2. FastANI genome comparison results of LBG001^{T}with other *Bdellovibrio* strains

Genome (A)	Genome (B)	% Identity	Genome (A)	Genome (B)	% Identity
LBG001^T	109J	78.802	109J	LBG001^T	78.8218
LBG001^T	Tiberius	78.8507	Tiberius	LBG001^T	78.9863
LBG001^T	HD100^T	79.002	HD100^T	LBG001^T	78.8588
LBG001^T	SSB	78.781	SSB	LBG001^T	78.8058
LBG001^T	NC01	79.5106	NC01	LBG001^T	79.1514
LBG001^T	KM01	78.8541	KM01	LBG001^T	79.0788
LBG001^T	ZAP7	78.8428	ZAP7	LBG001^T	79.1001
LBG001^T	W	78.3054	W	LBG001^T	78.239
LBG001^T	Exovorus^T	77.5308	Exovorus^T	LBG001^T	77.563
LBG001^T	Qaytius^T	77.1479	Qaytius^T	LBG001^T	77.0045

faecalis (ATCC 29212). Strain LBG001^T formed plaques on lawn prey plates of all 10 Gram-negative bacteria but not the two Gram-positive bacteria, suggesting LBG001^T has a wide Gram-negative prey range. LBG001^T can prey on *Proteus vulgaris* ATCC 6380, different from the type strain *B. bacteriovorus* HD100^T which has no ability to form plaques on *Proteus vulgaris* [5].

The antibiotic susceptibility testing for strain LBG001^T on six antibiotics was carried out in liquid co-culture. Strain LBG001^T was resistant to kanamycin, gentamycin and ampicillin but sensitive to streptomycin, tetracycline and chloramphenicol. Its susceptibility to streptomycin supports a previous assessment of all wild *Bdellovibri*o strains being susceptible to streptomycin [5].

MICROSCOPY

Fluorescently labelled LBG001^T and *B. bacteriovorus* 109J were separately used to infect *Klebsiella pneumoniae* (ATCC 43816) for 10 and 80 min. The infected prey cells were examined on agarose pads on microscope slides by ×100 bright field and ×100 fluorescence microscopy using the FITC channel on a Revolve microscope (Echo Laboratories, RVL-100-B2). Details of the experimental protocol are in supplementary materials, Text 2. The results showed a prey-seeking LBG001^T at 10 mins (Fig. 4), where LBG001^T was attached to the prey, indicating the beginning of its attack. At 80 mins of infection, previously rod-shaped prey cells were seen as bdelloplasts, which are spherical prey cells that have been remodelled as the result of *Bdellovibrio* periplasmic

Table 3. A genome comparison of *Bdellovibrio* strains as indicaticated on the PATRIC database

Genomic features	LBG001^T	NC01	HD100^T	109J	Tiberius	SSB 218315	W	Qaytius^T	Exovorus^T
CDS	3395	3860	3592	3632	3737	3642	2872	3188	2649
tRNA	33	34	36	35	35	34	34	31	34
rRNA	4	4	4	3	6	3	6	2	3
Misc_RNA		4	2			5		4	
Repeat_region	9	6						4	0
Protein features									
Hypothetical proteins	1584	1875	1463	1532	1660	1554	1400	1780	1496
Proteins with functional assignments	1811	1985	2129	2100	2077	2088	1472	1408	1153
Proteins with GO assignments	494	536	617	613	620	510	541	473	501
Specialty genes									
Transporter	11	10	64	63	54		5		18
Drug target	1	1	1	1	1	1	1		
Antibiotic resistance	22	31	29	29	29	29	21	23	21

Table 4. Pan-genome analysis using complete Whole-genome sequenced periplasmic *Bdellovibrio*

Organism name	No. of core genes	No. of accessory genes	No. of unique genes	No. of exclusively absent genes
B. bacteriovorus 109J	1481	1944	122	5
B. bacteriovorus HD100^T	1481	1954	61	3
B. bacteriovorus SSB218315	1481	1890	97	11
B. bacteriovorus Tiberius	1481	1919	286	6
B. bacteriovorus W	1481	414	790	271
Bdellovibrio LBG001^T	1481	952	911	39
Bdellovibrio sp KM01	1481	2036	172	6
Bdellovibrio sp. NC01	1481	1111	1126	19
Bdellovibrio sp. ZAP7	1481	2066	297	2

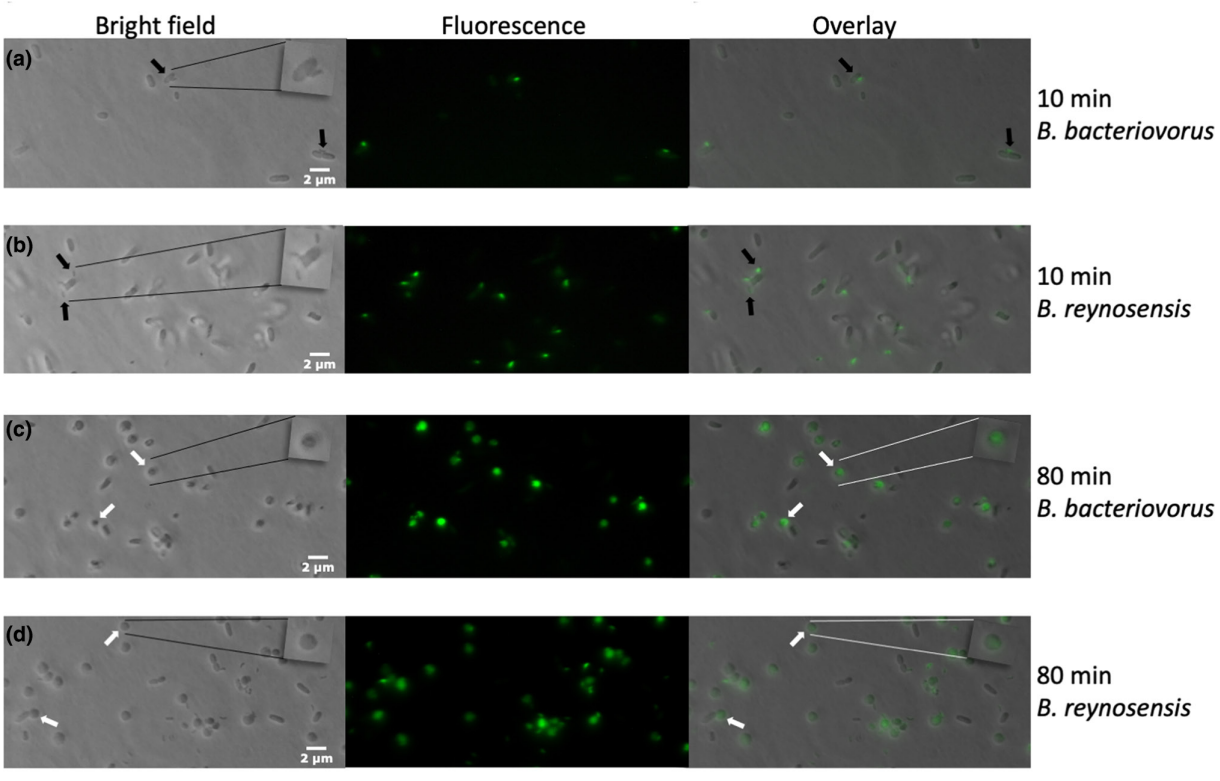

Fig. 4. *Bdellovibrio* predation of *Klebsiella pneumoniae*. *B.* bacteriovorus (a, c) and *B. reynosensis* sp. nov. (b, d) were fluorescently labelled, added to unlabeled *K. pneumoniae* resuspended in HEPES buffer, and incubated at 30 °C with aeration. After 10 and 80 min, cells were placed on agarose pads on slides and examined by bright field and fluorescence microscopy. Results were equivalent for both *Bdellovibrio* species. At 10 min, uninfected large, rod-shaped prey cells and small, extracellular but mostly attached fluorescent predator cells (filled arrows) are visible. At 80 min, prey cells have rounded into bdelloplasts with intracellular fluorescent predator (open arrows). Inset boxes in the upper right of some panels show enlarged images of example attached predator (a, b) and bdelloplasts (c, d).

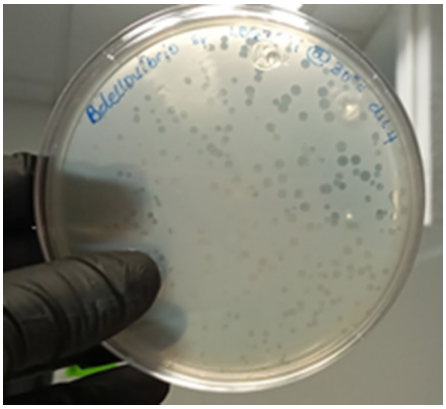

Fig. 5. Bdellovibrio *reynosensis* LBG001^T growing as plaques on a lawn plate of *Klebsiella oxytocoa*.

invasion. The results for LBG001^T were indistinguishable from predation by *B. bacteriovorus* 109J (Fig. 4), indicating that LBG001 is able to invade the prey cell in a periplasmic lifestyle.

DESCRIPTION OF *BDELLOVIBRIO REYNOSENSIS* SP. NOV.

*Bdellovibrio reynosens*is (rey.no.sen'sis. N.L. masc. adj. reynosensis, pertaining to Reynosa, the location where the type strain was isolated).

The isolated bacterium is a Gram-negative rod-like bacterium with fast darting motility. It forms a circular plaque on a lawn plate of *Klebsiella oxytoca* (Fig. 5) and other Gram-negative bacteria by endobiotic predation. Plaques appear after 48 h of incubation at 30 °C. Plaque diameters increase with incubation time. Strain LBG001^T grows in HEPES buffer in the presence of suitable prey, which can be set up at a temperature of 30 °C, pH 7, with or without agitation (with agitation is more suitable). LBG001^T is resistant to kanamycin, gentamycin and ampicillin but sensitive to streptomycin, tetracycline and chloramphenicol.

The type strain is LBG001^T (ATCC TSD-288^T=CM-CNRG 0932^T). It was isolated from a soil sample collected at Reynosa, Mexico. The complete whole-genome sequence has a size of 3.58 Mb and a DNA G+C content of 43.1 mol%.

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Author contribution
Y.O.A., strain isolation, experiments, writing the original draft; I.C.R.L., experiments; T.O.E., genomic data analysis; A.S.-V., experiments; D.V.C.E., project design and critical comments; A.C., genome sequencing and analysis, English editing; X.G., project design, data analysis and writing.

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

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