Phylo-taxonomogenomics of 182 strains of genus *Leuconostoc* elucidates its robust taxonomy and biotechnological importance

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Abstract

Genus *Leuconostoc* is a group of a diverse range of lactic acid bacteria (LAB) majorly found in dairy, food and environmental ecology. These microbes are commercially important for several industries due to their intrinsic genomic attributes such as bacteriocins, carbohydrate-active enzymes, plasmids etc. Even though the species of *Leuconostoc* are commercially significant, their taxonomy is largely based on old, low resolution traditional methods. There have been several taxonomic reclassifications in the past which are inadequate for microbiologist and food industry professionals to truly demarcate any new strain of genus *Leuconostoc*. The current taxonomy of the genus is largely based on classical approaches, which are in utmost need of reinvestigation by whole genome-based approaches. In the present study, the taxono-phylogenomic analysis clearly depicted sixteen species including three novel genomospecies in addition to several reshufflings across the species namely, *L. mesenteroides*, *L. pseudomesenteroides*, *L. gelidum* and *L. lactis*. The presence of a wide range of carbohydrate-active enzymes, type III polyketide synthase and vector plasmids suggested the biotechnological potential of

constituent strains of the genera. Further, the absence of antibiotic gene clusters reaffirms their utility in industries such as food and dairy. Such large-scale in-depth genome-based study can shed light on the nature of the genome dynamics of the species and help to obtain a more robust taxonomic classification.

Keywords: *Leuconostoc*, reclassification, taxonogenomic, phylogenomics, genomospecies, CAZymes, type III PKS.

Abbreviations

GH: Glycoside Hydrolase; CE: Carbohydrate Esterase; PL: Polysaccharide Lyase; GT: Glycosyltransferase; AA: Auxiliary Activities; CBM: Carbohydrate-Binding Module; ANI: Average Nucleotide Identity; dDDH: digital DNA-DNA hybridization; LAB: Lactic Acid Bacteria; Type III PKS: Type III polyketide synthase

Introduction

The genus *Leuconostoc* [1] belongs to the family *Leuconostocaceae* [2] which is one among the widely used group of lactic acid bacteria (LAB). *Leuconostoc* was first isolated by Cienkowski from a slime outbreak in a sugar factory in 1878 [3]. The isolate was named *Ascococcus mesenteroides* which produces dextran slime in sucrose solution [3, 4]. In 1911, an aroma bacteria "X" was isolated from a creamery starter which was later named *Leuconostoc* in 1930 [3, 5]. Historically, the taxonomy of *Leuconostoc* is a long tug of war across the several families of LAB. *Leuconostoc* sp. often occurs in similar habitats as *Lactobacillus* and *Lactococcus*, and was considered as an intermediate between *Streptococcus* and *Lactobacillus*. Genome based investigation of *Lactobacillaceae* and *Leuconostocaceae* suggests union of these two families [6]. In accordance with the latest standing in nomenclature of *Leuconostoc* (<https://lpsn.dsmz.de/genus/leuconostoc>), there are 16 valid species and along with 11 synonyms. Species of genus *Leuconostoc* are facultatively anaerobic, Gram-positive, nonmotile, catalase-negative, asporogenous, psychrotolerant or psychrotrophic bacteria with optimum growth temperature of 25-30 °C with an average GC content of 37.5% [2]. These are primarily associated with plant matter, fermenting vegetables, industries such as dairy, food and pharma etc. [4, 7-10]. Few reports of their presence in chilled stored meats and human blood are a matter of concern [11, 12]. *Leuconostoc* have been known as a component of starter cultures in dairy since the 1920s, but its factual information about dairy is not very well documented [13]. These microbes are especially, known for their probiotic properties and ability to catalyse the production of several biotechnologically important products [14, 15]. *L. mesenteroides* is the type species of genus *Leuconostoc* [1] which is explored quite extensively in industries. *L. mesenteroides* species are used as a probiotic candidates which enables them to survive and grow under various stress conditions present in the gastrointestinal tract [16]. Species of *Leuconostoc* is an ideal fermenter of simple carbohydrates and have the capacity

to metabolize a wide range of carbohydrates, sugar alcohols and gluconate [17, 18]. Although the *Leuconostoc* sp. has been identified for safe use in the food industry and accorded "generally recognized as safe" (GRAS) status, there are several reports of its disease-causing nature [19, 20]. Interestingly, the strains of *L. mesenteroides* follow dual lifestyles [16] causing disease in plants and humans [21-24].

Even though the species of the genus *Leuconostoc* are widely used for several purposes, the taxonomy is largely unexplored. All the earlier attempts to improve the taxonomy of genus *Leuconostoc* were based on limited phenotypic based methods or lower resolution phylogenetic approaches including housekeeping genes such as 16S rRNA, *rpoB*, *recA* gene etc. [25-28]. As these are based on very limited information, such methods do not provide a robust classification [29]. These studies largely lack a whole genome-based approach to obtain a robust taxonomic, identification of the key functional attributes across the several species of genus *Leuconostoc*. Although, there are some genome based study such as species of *Leuconostoc gasicomitatum* [30] was emended to *Leuconostoc gelidum* subsp. *gasicomitatum* [31]. Later *Leuconostoc mesenteroides* subsp. *suionicum* [32] was emended to *Leuconostoc suionicum* [33]. Most recently genome-based identification of *L. falkenbergense* sp. nov. [34] using whole genome-based sequence information from previously reported strains of *L. pseudomesenteroides*. Another recent study suggests the reclassification of *L. mesenteroides* MTCC 10508 as a strain of *L. suionicum* [35]. All the studies Are focusing on limited strains from some species of *Leuconostoc* and not considering the whole genus *Leuconostoc*.

To obtain robust taxonomy of *Leuconostoc* sp., we reinvestigated and re-evaluated the phylogeny, genetic relatedness, and genomic determinants of the species within the present genus *Leuconostoc* (<https://lpsn.dsmz.de/genus/leuconostoc>). Implementation of these methods resulted in a robust taxonomic framework. We have identified three novel genomospecies namely, GS1 GS2 and GS3. We observed several large reclassifications across the strains of species *L. gelidum* subsp. *gasicomitatum*, *L. pseudomesenteroides*, *L. lactis* and *L. mesenteroides*. We have also identified species-specific unique genes in the pangenome of the genus *Leuconostoc*. We identified the presence of type III polyketide synthase system in all representative strains *Leuconostoc*, which signifies the antimicrobial ability against pathogenic bacteria. The abundance of the carbohydrate-active enzyme was also identified which includes majorly glycoside hydrolase and glycosyltransferase responsible for degradation, modification, and creation of glycosidic bonds. Furthermore, we believe such a large whole genome-based investigation can help in the estimation and evaluation of new potential strains or species belonging to the genus *Leuconostoc*. In recent days, the whole genome-based taxonomic evaluation became one of the most robust approaches [6]. Our investigation is an attempt to understand the genus *Leuconostoc* whose industrial importance is widely known but have underexplored taxonomic classification.

Methods

Genome dataset procurement, initial QC and annotation

All the genomes affiliated to genus *Leuconostoc* available in the public repository as of 31 March 2021 were procured from NCBI (<https://www.ncbi.nlm.nih.gov/genome/?term=leuconostoc>) and EzBioCloud (<https://www.ezbiocloud.net/taxonomy>). Procured genomes were quality assessed using checkM v1.1.0 [36] with completeness and contamination bar of 95% and less than 3% respectively. There were altogether 183 including an outgroup genome resources were taken in the study (Table 1). Genome sequences for the type strains of the species *L. lactis* [25], *L. miyukkimchii* [37], *L. palmae* [38], were not included in the analyses due to the absence or poor-quality data in public databases. Also, synonym species/subspecies were strains of the *L. amelibiosum*, *L. argentinum*, *L. durionis*, *L. ficulneum*, *L. fructosum*, *L. oeni*, *L. paramesenteroides*, *P. pseudoficulneum* were not included due to their unavailability in the public repository. All the genomes were annotated using prokka v1.12 [39].

Phylogenetic and Phylogenomic analysis

16S rRNA gene predicted using barnap v0.8 (<https://github.com/tseemann/barnap>) was used to fetch 16S rRNA gene sequences from all 183 genomes. Multiple sequence alignment of 16S rRNA was performed using clustalw [40]. A phylogenetic tree based on maximum likelihood (ML) was constructed using mega 7 [41] with a bootstrap replication of 1000. *Weissella viridescens* DSM 20410 was used as an outgroup. Whole genome-based phylogeny was implemented using PhyloPhlAn v3.0 [42] which used more than 400 most conserved genes across the strains under investigation. PhyloPhlAn uses usearch [43] for searching the gene cluster, muscle [44] for performing multiple sequence alignment and fasttree [45] for phylogenetic tree generation. A core genome-based tree was also generated using roary v3.1.2 [46] with 70% (inter-species similarity) cut off from the core genome alignment obtained with mafft [47]. All the phylogenetic tree generated was annotated using iTOL (<https://itol.embl.de/>) [48] for more lucid representation.

Genome similarity assessment

Genome similarity assessment was performed using several methods. Average nucleotide identity (ANI) was calculated using orthoANI v1.2 [49, 50] which uses usearch v8.1 [43] to find the orthologous cluster across the genomes for similarity comparison. A genome similarity assessment cut-off of 96% for orthoANI was used. Another tool fastANI v1.32 [51] (<https://github.com/ParBLiSS/FastANI>) was implemented to calculate nucleotide identity. fastANI uses a novel algorithm, which utilizes Mashmap with an intra and inter-species demarcation of >96% and <83% [52]. Digital DNA-DNA hybridization (dDDH) [53] was implemented using an online web portal of genome-to-genome distance calculator 2.1 (GGDC) (<http://ggdc.dsmz.de/ggdc.php#>). Heatmap of the genome similarity assessment was generated using GENE-E (<https://software.broadinstitute.org/GENE-E/>).

Pangenome and core genome assessment

Pangenome analysis was implemented using roary v3.1.2 [46] with gff files obtained from prokka with blastp percentage identity of 85%. The flower plot indicates the core gene, unique gene and species specific to genes (Figure 3A). fasttree v2.1.10 [45] was implemented on the core gene alignment to obtain the core gene phylogeny. Core genome obtained was annotated with eggNOG-mapper [54] (<http://eggno-mapper.embl.de/>).

Plasmid identification, antibiotic resistance and unique functional genomic attributes

To obtain the presence of plasmid in the strains of genus *Leuconostoc*, abricate v1.0.1 (<https://github.com/tseemann/abricate>) was implemented using plasmidFinder v2.1 database [55]. Antibiotic resistance genes were also checked using the card module v3.08 [56], ResFinder v4.1 [57] and ARG-ANNOT [58] of abricate. Genomic attributes for the prediction of biosynthetic gene clusters were identified using antiSMASH v6 [59]. All the type strains and the novel genomospecies were checked for the presence of a biosynthetic gene cluster.

Carbohydrate active enzyme analysis

Carbohydrate-active enzymes (CAZy enzymes) (<http://www.cazy.org/>) among all the type strains and the novel genomospecies obtained from genome similarity analysis were identified using dbCAN2 [60]. dbCAN2 scans the genome using Hidden Markov model (HMM) profile which uses HMMdb v7 [61] (e-value of $< 1e-15$, coverage > 0.35), DIAMOND [62] (e-value $< 1e-102$) and Hotpep [63] (frequency > 2.6 , hits > 6) to improve the prediction. The genes were annotated by at least two of the methods were taken for further analysis. The detailed carbohydrate-active enzyme family information was obtained on the CAZyme (<http://www.cazy.org/>). Identified CAZymes were broadly classified as glycoside hydrolase (GHs), glycosyltransferases (GTs), carbohydrate esterases (CEs), carbohydrate-binding enzymes (CBM), auxiliary active enzymes (AAs), and polysaccharide lyases (PLs).

Result and Discussion

Genomic features of the genus *Leuconostoc*

A total of 182 genomes of the genus *Leuconostoc* were used for the present study. Their average genome size ranged from 1 mb to 2.5 mb with an average GC content of 37%. The genomic attributes including #tRNA, #rRNA, #CDS etc. are summarized in table 1.

Phylogenomics of the genus *Leuconostoc* reveals major phylogroups

Due to high similarity 16S rRNA based phylogeny could not resolve the constituent species of the genus *Leuconostoc*. For instance, *L. inhae* and *L. gelidum* subsp. *gasicomitatum*; *L. rapi* and *L. kimchii*; *L. falkenbergense* and few strains of *L. pseudomesenteroides*; *L. mesenteroides*, *L. suionicum*, *L. litchi* and

L. fallax could not form distinct clade (Supplementary Figure 1). To get more accurate phylogeny, we obtained core genome-based phylogeny using roary and PhyloPhlAn (Figure 1, Supplementary Figure 2). Both of these approaches resulted in major reshuffling across the *Leuconostoc* sp. Strains of major species of genus *Leuconostoc* namely, *L. mesenteroides*, *L. pseudomesenteroides*, *L. gelidum* and *L. lactis* were not forming species-specific clades. Rather, each of these four species were splitting into two distinct phylogroups.

Out of 76 strains of *L. mesenteroides* 74 formed a distinct phylogroup along with the *L. mesenteroides* subsp. *mesenteroides* ATCC8293^T [1] confirming their species status. However, two of the remaining isolates namely, *L. mesenteroides* subsp. *mesenteroides* CBA3607 and *L. mesenteroides* CBA3628 formed a distinct phylogroup. Similarly, out of 29 strains of *L. pseudomesenteroides* 4 strains including *L. pseudomesenteroides* LMG11482^T [26] could be distinguished from the remaining 25 strains. Interestingly, these 25 strains of *L. pseudomesenteroides* formed a phylogroup with *L. falkenbergense* LMG10779^T [34]. Further, out of 12 strains of *L. gelidum* only one strain *L. gelidum* subsp. *gelidum* JB7 was forming phylogroup with *L. gelidum* subsp. *gelidum* KCTC3527^T [64]. Whereas, remaining 10 strains (*L. gelidum* subsp. *gasicomitatum*) were forming a phylogroup with the *L. inhae* KCTC3774^T [65]. Similarly, 13 strains of *L. lactis* were also forming two distinct phylogroups comprising of 10 and 3 strains respectively. However, due to the poor genome quality of the *L. lactis* type strain, we could not include in the present analysis. Overall, we could deduce 16 distinct phylogroups including 4 distinct unary strains which are representatives of previously described species namely, *L. fallax* ATCC700006^T [66], *L. rapi* DSM27776^T [27], *L. holzapfelii* CCUG54536^T [67], *L. litchii* MB7^T [67]

Taxonogenomic assessment led to the identification of the novel genomospecies and reassignment of strains

Earlier taxonomic classification of species of *Leuconostoc* was mostly based on the classical taxonomy [1]. Description of the major species of genus *Leuconostoc* such as *L. mesenteroides* [1], *L. citreum* [26], *L. carnosum* [64], *L. inhae* [65] etc. was devoid of the whole genome-based approach such as ANI, dDDH and AAI etc., due to which, the current taxonomic classification of the *Leuconostoc* suggests them as a valid species (<https://lpsn.dsmz.de/genus/leuconostoc>). Robust phylogenomics of the genus *Leuconostoc* revealed several major reshufflings which need to be further confirmed by taxonogenomics.

Our whole genome-based taxonomic evidence using ANI (OrthoANI and fastANI) and dDDH correlated with the phylogenomics. For instance, three phylogroups consisting of earlier defined *L. lactis* and *L. mesenteroides* strains were found to be forming three novel genomospecies (GS1, GS2 and GS3) (Figure 2, Supplementary Figure 3). In addition to novel genomospecies, some of the previously defined strains of *L. pseudomesenteroides* and *L. gelidum* were identified as *L. falkenbergense* and *L. inhae*

respectively. The remaining species stands valid in accordance with the standing in nomenclature (<https://lpsn.dsmz.de/genus/leuconostoc>) (LPSN link, table 2).

Pan genome-based identification of core genome and species-specific genes

Pan-genome analysis using roary resulted in a comparatively small core genome (270 genes) and a large pan genome (22906 genes) which reveals a wide diversity of gene content within genus *Leuconostoc*. Here, we could get unique genes specific to the 16 species identified using taxonogenomics and phylogenomics (Figure 3A). *L. mesenteroides* (3822 genes) and *L. citreum* (2497 genes) largely contributed to the diversity of the pangenome. While, GS3 (134 genes), *L. suionicum* (148 genes) and *L. gelidum* (165 genes) had the least species-specific genes. Interestingly, amongst the unary species members, *L. fallax* showed the highest diversity with 1309 genes. The gene clusters obtained suggested a high number of accessory genes (shell and cloud) of 22,559 depicting a high degree of diversity across the species of genus *Leuconostoc*. Pan-genome matrix as well depicted the presence of species-specific genes (Figure 3C). Functional classification of the core genes suggested the majority of the information storage and processing (44%) and metabolism (32%) related genes (Figure 3B).

Unique genomic attributes across spp. of *Leuconostoc*.

High diversity in the genus *Leuconostoc* is evident from the gene content analysis. On the contrary, they were found to harbour pLCK4 (12183 bp) and LkipL4719 (21924 bp) plasmids in 97 and 86 genomes respectively. Plasmid pLCK4 was originally derived from *L. citreum* KM20 [68], which is one among the four high copy number plasmids of *L. citreum* KM 20 [68]. Plasmid pLCK4 which is considered to be a part of pMBLT00 [69], is considered to be a shuttle vector for inducing overproduction of D-lactate in *Leuconostoc* and *Lactococcus lactis* strains [69]. LkipL4719 is first reported in the *Leuconostoc kimchii* IMSNU 11154 [70] which harbours several metal transport gene families, suggesting its intrinsic nature across the species of *Leuconostoc* [70]. Additionally, 8 different plasmids namely pKLC4 (36602) in 11 genomes, pIGMS32 (or ColRNAI_1) (9294 bp) in 6 genome, pJB01 (2235 bp) in genome and pLFE1 (4031 bp) in 2 genomes. Whereas plasmid pYSI8 (4973 bp), pMG828-1 (Col(MG828)_1) (1902 bp), pJE1 (5149 bp) and pBI143 (2747 bp) are present in one genome each (Figure 1). In addition to low diversity in the plasmid, antibiotic resistance genes were also present but only in 4 genomes out of 182 *Leuconostoc* strains analysed using CARD, resfinder and arg-annot database integrated in abricate (supplementary table 2). However, genomic analysis of the *Leuconostoc* human pathogens is limited due to a lack of genomic resources.

Whereas, we found Type III polyketide synthase (PKSs) in all the type strains of 16 species identified (Figure 4 A). Type III polyketide synthase (PKSs) are homodimers of ketosynthase which catalyze the condensation of one or several molecules of extender substrate onto a starter substrate through an iterative decarboxylative Claisen condensation reactions [71, 72]. Microbial type III PKSs seem to use an acyl–acyl carrier protein (ACP) as a starter substrate, [73], and in some cases, type III PKS genes

form a cluster with ACP or fatty acid biosynthetic genes [74, 75]. Future studies on type III PKSs will provide important insights into the properties of these enzymes and their role in the biosynthesis of natural products. Moreover, strains of genus *Leuconostoc* is reported to harbour several bacteriocins belonging to class IIa bacteriocins, leucocin H, mesentericin etc. [76-79] imparting antimicrobial activity against foodborne pathogens [80]. In-depth genomic investigation of bacteriocins and antimicrobial peptides are the need of the hour to explore the potential of the species of genus *Leuconostoc*.

Carbohydrate-Active Enzyme (CAZymes)

Among type strains of 16 phylogroups identified using genome similarity and phylogenomic assessment reveals the presence of CAZyme groups of GH, GT, CR, AA, CBM and PL using dbCAB2. These CAZymes groups are the enzymes involved in the degradation, modification, and creation of glycosidic bonds. Altogether 1344 protein-coding genes were detected by one of three methods namely hotpep, Diamond and HMMER (Figure 4 B). We found all the major CAZyme groups distributed across the strains represented with a heatmap (Figure 4 B) reveals the differential presence of all the classes of CAZyme in the strains of *Leuconostoc*. Most of the identified gene clusters were distributed across GH (52%), GT (40%), CE (4.75%), CMB (2.2) and PL (1%) families. (Summarized in supplementary table 1). We found diverse GHs namely GH13 (7.07%), GH70 (5.49%), GH73 (5.38%), GH1 (5.12%), GH32 (4.85%), GH25 (4.54%), GH65 (2.95%) across *Leuconostoc* sp. GHs catalyse the cleavage of O-glycosidic bonds linking the carbohydrate moieties or carbohydrate and non-carbohydrate moieties. GH13 family of CAZymes reveals the presence of amylases, beta-glucosidases, beta-xylosidases, beta-galactosidase gene cluster across the species of *Leuconostoc*. Similarly, the GH70 family includes transglucosylases which catalyse the intra- or intermolecular replacement of glycoside molecules at the anomeric position, giving rise to new glycoside molecules, such as oligosaccharides [81]. GH73 family includes N-acetylmuramidase which cleaves the β -1,4-glycosidic bond between the N-acetylglucosaminyl (GlcNAc) and N-acetylmuramyl (MurNAc) moieties in bacterial peptidoglycan [82]. Glycosyl transferases are primarily involved in the formation of glycosidic bonds by transfer of sugar moiety from the activated sugar donor to the acceptor molecule. We identified three major GTs namely GT4 (13.5%), GT2 (12.6%) and GT51 (4.3%). GT4 a glycosyltransferase family 4 protein is responsible for accessory Sec system glycosyltransferase GtfA. GT2 glycosyltransferase family 2 protein is responsible for undecaprenyl-diphospho-muramoyl pentapeptide and beta-N-acetylglucosaminyltransferase and putative glycosyltransferase, exosortase G system-associated. GT51 is responsible for PBP1A family penicillin-binding protein and murein polymerases. These are majorly involved in the synthesis of the peptidoglycan cell wall and play crucial roles in maintaining the integrity of the cell wall [83]. Likewise, CAZymes present under CE, CBM and PL categories are CE9 (2.11%), CE1 (2.1%), CBM50 (1.79%) and PL1 (1%).

Conclusion

Several taxonomic reclassifications were found by the present study inferring the true phylogenetic positioning of the strains of genus *Leuconostoc* (Table 2). True phylogeny will help future research to better identify and reclassify the strains of the genus belonging to biotechnologically important genera. In-depth genomic investigations of the strains suggest the presence of several determinants such as plasmid and type III PKS system etc. and the absence of antibiotic gene cluster also approves GRAS status. However, minor reports of *Leuconostoc* strains as human pathogens have raised concerns about their biotechnological implications. The present phylo-taxonogenomic study provides a robust taxonomic framework of the genus which will be valuable in the identification of these clinically relevant strains. Such future genomic investigations of strains from diverse niches including nosocomial, environment, food and industry will shed light on their niche-specific attributes. This will be critical in surveillance to demarcate safe to use strains for food and industry from their pathogenic counterparts. Thus, our work is expected to promote research on the biotechnological important genus which is long overlooked and to better understand the intrinsic property of these important microbes.

Figure and table legends

Figure 1: Whole genome-based core genome phylogenomic tree obtained using roary: Phylogenetic tree was obtained using fasttree on the core gene alignment using mafft in roary run. For circular representation iTOL was used and labelled in accordance to the species group. Bootstrap values are represented with blue dots. *Weissella viridescens* DSM 20410 was used as an outgroup. Genomospecies 1, genomospecies 2 and genomospecies 3 represent the novel group of bacteria within the genus *Leuconostoc*. The plasmid was labelled in the genome with coloured dots at the circumference.

Figure 2: Whole genome-based similarity assessment using OrthoANI and dDDH. A). All is to all ANI similarity heatmap showing separate groups obtained by using a cut-off of 96%. B). Heatmap of digital DNA-DNA hybridization all across the type strains with the cut-off of 70% genome similarity.

Figure 3: Pan-genome analysis: A). Pan-genome representation of all the gene clusters obtained from roary (22906). Core gene (270), and species-specific genes (unique gene) along with the number of strains in the group is marked in each group of genera *Leuconostoc*. B) Distribution of COG-based functional categories of core genes of the *Leuconostoc* genus. Here, the x-axis represents the number of genes and y-axis represents the functional categories. The count of gene cluster is indicated across classes in the box plot. C). Pan-genome plot representing the gene presence-absence across the strains. Core genome phylogroups are represented in the left isolates.

Figure 4: Type III PKS and CAZymes: A). The presence of type III PKS gene cluster was present in all the type strains in the study. The presence of the core biosynthetic gene in almost all the type strains was identified. Other genes such as additional biosynthetic genes, transporter genes etc. were also

identified. B). Heatmap showing all the different classes of the carbohydrate-active enzyme classified under GH: Glycoside Hydrolase; CE: Carbohydrate Esterase; PL: Polysaccharide Lyase; GT: Glycosyltransferase; AA: Auxiliary Activities; CBM: Carbohydrate-Binding Module. Venn diagram revealing carbohydrate-active enzyme identified by three different approaches of HMMER, diamond and hotpep. Heatmap was generated based on the presence of the carbohydrate-active enzyme by at least two approaches.

Supplementary Figure 1: 16S rRNA tree: A phylogenetic tree based on ML-based obtained by 16S rRNA gene sequences of all the strains under study. Bootstrap values are represented by blue dots. Strain name of some of the complete genome which resulted in multiple copies of 16S rRNA were appended with 1, 2, 3 etc.

Supplementary Figure 2: Phylogenetic tree obtained using PhyloPhlAn: A phylogenetic tree based on more than 400 conserved genes. Bootstrap values are marked with blue dots.

Supplementary Figure 3: fastANI: Heatmap obtained using genome similarity matrix obtained using fastANI.

Table 1: Metadata of the strains used in the study. A detailed description of all the strains used in the study along with the assembly statistics such as assembly size, %GC content, number of CDS, etc. general identification of the strains such as strain Id, NCBI accession number and source etc. are also summarized.

Table:2: A descriptive list of the earlier classification and robust reclassification of the strain based on this study.

Supplementary Table 1: A descriptive list of antibiotic resistance genes predicted using several databases such as using CARD, resfinder and arg-annot.

Supplementary Table 2: A descriptive list of CAZyme identified using dbCAN2.

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Table 1: Metadata of the strains used in the study. A detailed description of all the strains used in the study along with the assembly statistics such as assembly size, %GC content, number of CDS, etc. general identification of the strains such as strain Id, NCBI accession number and source etc. are also summarized.

Strains ID	Accession	BioSample	BioProject	Assembly Level	Genome Size(Mb)	GC%	#CDS	#Contigs	#rRNA	#tRNA	#tmRNA	completeness/contamination	Source
L. carnosum CBA3620	GCA_007954525.1	SAMN11843679	PRJNA544551	Complete	1.70133	37.3348	1618	3	12	67	1	99.48/1.05	kimchi
L. carnosum DSM5576 T	GCA_014207505.1	SAMN14908560	PRJNA632261	Scaffold	1.82066	37	1740	16	3	49	1	99.48/1.05	chill-stored meats
L. carnosum JB16	GCA_000300135.1	SAMN02603179	PRJNA174298	Complete	1.77347	37.091	1655	5	12	67	1	99.48/1.05	Kimchi, Korean traditional fermented food
L. carnosum MFPA29A1405	GCA_900322425.1	SAMEA104699785	PRJEB25279	Contig	1.66684	37.2698	1598	22	4	48	1	99.48/1.05	Beef carpaccio
L. carnosum MFPC16A2803	GCA_900322415.1	SAMEA104699786	PRJEB25280	Scaffold	1.81202	36.9587	1770	50	3	34	1	99.48/1.05	Beef carpaccio
L. carnosum WC0318	GCA_008690985.1	SAMN11618753	PRJNA542256	Scaffold	1.74508	37.2	1655	11	5	51	1	99.48/1.05	Cooked ham
L. carnosum WC0319	GCA_008690925.1	SAMN11618754	PRJNA542256	Scaffold	1.69968	37.1	1610	8	5	49	1	99.48/1.05	Cooked ham
L. carnosum WC0320	GCA_008690965.1	SAMN11618755	PRJNA542256	Contig	1.81154	37.1	1752	14	5	51	1	99.48/1.05	Cooked ham
L. carnosum WC0321	GCA_008690875.1	SAMN11618756	PRJNA542256	Scaffold	1.80189	37.1	1735	24	5	52	1	99.48/1.05	Cooked ham
L. carnosum WC0322	GCA_008690865.1	SAMN11618757	PRJNA542256	Scaffold	1.85285	37	1806	13	5	50	1	99.48/1.05	Cooked ham
L. carnosum WC0323	GCA_008690845.1	SAMN11618758	PRJNA542256	Scaffold	1.77288	37.2	1700	17	5	52	1	99.48/1.05	Cooked ham
L. carnosum WC0324	GCA_008690825.1	SAMN11618759	PRJNA542256	Contig	1.76563	37.1	1699	12	5	49	1	99.48/1.05	Cooked ham
L. carnosum WC0325	GCA_008690785.1	SAMN11618761	PRJNA542256	Scaffold	1.8298	37.2	1773	24	5	52	1	99.48/1.05	Cooked ham
L. carnosum WC0326	GCA_008689765.1	SAMN11618763	PRJNA542256	Contig	1.76965	37.2	1679	19	5	49	1	99.48/1.05	Sausage
L. carnosum WC0327	GCA_008689755.1	SAMN11618764	PRJNA542256	Contig	1.76938	37.2	1678	18	5	49	1	99.48/1.05	Sausage
L. carnosum WC0328	GCA_008689695.1	SAMN11618767	PRJNA542256	Scaffold	1.81458	37.1	1745	27	5	51	1	98.95/1.05	Sausage
L. carnosum WC0329	GCA_008689675.1	SAMN11618768	PRJNA542256	Scaffold	1.65083	37.2	1562	13	5	52	1	99.48/1.05	Cooked ham
L. citreum 1301 LGAS	GCA_001077275.1	SAMN03197274	PRJNA267549	Scaffold	1.82335	39	1715	37	9	60	1	99.89/0.19	Host: Homo sapiens
L. citreum CBA3621	GCA_007954785.1	SAMN11843662	PRJNA544551	Complete	1.90325	38.9138	1826	2	12	69	1	99.89/0.56	kimchi
L. citreum CBA3623	GCA_007954705.1	SAMN11843666	PRJNA544551	Complete	1.96941	38.9123	1848	6	12	69	1	99.33/0	kimchi
L. citreum CBA3624	GCA_007954565.1	SAMN11843677	PRJNA544551	Complete	1.89477	38.9513	1778	5	12	69	1	99.89/0.56	kimchi
L. citreum CBA3627	GCA_008033195.1	SAMN11843672	PRJNA544551	Complete	1.90325	38.9138	1824	2	12	69	1	99.89/0.56	kimchi
L. citreum CW28	GCA_002591805.1	SAMN06343424	PRJNA375706	Contig	1.98292	38.7	1873	9	12	69	1	99.33/0	corn fermented beverage
L. citreum DmW 111	GCA_002115685.1	SAMN06767174	PRJNA383560	Contig	1.82988	38.8	1768	19	7	53	1	99.33/0.75	from a built environment(Host: Drosophila)

L. citreum EFEL 2700	GCA_002804045.1	SAMN08014125	PRJNA418065	Chromosome	1.92383	38.964	1808	5	12	69	1	99.33/0	(host:Brassica rapa subsp. pekinensis)
L. citreum F192-5	GCA_008326505.1	SAMD00166981	PRJDB8200	Scaffold	2.06178	38.4	1989	42	3	47	1	99.89/0	
L. citreum G4	GCA_006381855.1	SAMN09099490	PRJNA470672	Contig	1.83552	38.8	1770	4	7	52	1	99.89/0	sourdough
L. citreum KM20	GCA_000026405.1	SAMN02603482	PRJNA16062	Complete	1.89661	38.8804	1777	5	12	69	1	99.89/0	
L. citreum LBAE C10	GCA_000239895.2	SAMEA2272656	PRJEA78993	Contig	1.93443	38.8	1850	76	3	49	1	99.89/0.08	
L. citreum LBAE C11	GCA_000239915.2	SAMEA2272136	PRJEA78995	Contig	1.96996	38.7	1848	83	3	49	1	99.89/0	
L. citreum LBAE E16	GCA_000239935.2	SAMEA2272523	PRJEA78997	Contig	1.8016	38.9	1737	45	3	49	1	99.89/0	
L. citreum NBRC102476	GCA_007989545.1	SAMD00166019	PRJDB6146	Contig	1.78757	38.9	1703	25	3	29	1	99.89/0	
L. citreum NRIC1776 T	GCA_008326545.1	SAMD00166982	PRJDB8200	Scaffold	1.80678	38.9	1737	8	3	47	1	99.89/0	Honey dew of rye ear
L. citreum NRRL B-1299	GCA_000820985.2	SAMEA2668124	PRJEB5537	Scaffold	1.75381	39	1769	1	9	53	1	99.33/0	
L. citreum NRRL B-742	GCA_000820965.2	SAMEA2668125	PRJEB5535	Scaffold	1.7181	39.2	1720	1	9	67	1	99.25/0	
L. citreum TMW21194	GCA_009792915.1	SAMN07739528	PRJNA401313	Contig	1.73532	38.9	1639	8	5	51	1	99.89/0	food
L. citreum TR116	GCA_004359915.1	SAMN07629511	PRJNA404070	Contig	1.83094	38.8	1764	31	5	51	1	99.89/0	yellow pea flour sourdough
L. citreum TR153	GCA_006406175.1	SAMN09099486	PRJNA470672	Contig	1.89839	38.7	1844	39	5	51	1	99.89/0	sourdough
L. citreum WiKim0101	GCA_009707745.1	SAMN13267039	PRJNA588925	Chromosome	2.01927	38.9102	1861	6	12	69	1	99.16/0.19	kimchi
L. falkenbergense LMG10779 T	GCA_014634805.1	SAMD00244137	PRJDB7793	Contig	1.96383	39.1	1876	94	3	50	1	100/0.18	fermentating string beans and traditional yogurt
L. fallax ATCC700006 T	GCA_004354645.1	SAMN08555278	PRJNA434383	Scaffold	1.66052	37.7	1589	16	15	86	1	99.3/0.52	sauerkraut
L. gelidum subsp gasicomitatum C120c	GCA_900009505.1	SAMEA3718674	PRJEB12226	Scaffold	1.99276	36.5	1889	31	3	42	1	99.44/0	vegetable salad
L. gelidum subsp gasicomitatum C122c	GCA_900016145.1	SAMEA3718675	PRJEB12227	Scaffold	2.00836	36.6	1914	22	3	43	1	98.88/0.19	vegetable salad
L. gelidum subsp gasicomitatum KG16-1	GCA_001536305.1	SAMEA3608619	PRJEB11303	Complete	2.05073	36.8506	1963	4	12	67	1	100/0.11	
L. gelidum subsp gasicomitatum KSL4-2	GCA_900016165.1	SAMEA3718676	PRJEB12228	Scaffold	2.08949	36.6	1993	23	3	44	1	99.33/0.11	Acetic acid preserved herring with carrots
L. gelidum subsp gasicomitatum LMG18811 T	GCA_000196855.1	SAMEA2272393	PRJEA48123	Complete	1.95408	36.7	1862	1	12	68	1	99.44/0	modified-atmosphere packaged, tomato-marinated broiler meat strips
L. gelidum subsp gasicomitatum MFPA44A1401	GCA_900218135.1	SAMEA104233143	PRJEB21908	Contig	1.89091	36.8	1798	50	2	48	1	100/0	beef carpaccio
L. gelidum subsp gasicomitatum PB1a	GCA_900016185.1	SAMEA3718677	PRJEB12229	Scaffold	2.08363	36.6	1987	29	3	48	1	99.44/0.56	carrot

L. gelidum subsp gasicomitatum PB1e	GCA_900016175.1	SAMEA3718678	PRJEB12230	Scaffold	2.08518	36.5	2014	22	3	43	1	99.44/0	carrot
L. gelidum subsp gasicomitatum PL111	GCA_900016205.1	SAMEA3718679	PRJEB12231	Scaffold	2.0581	36.5	1960	29	3	50	1	99.44/0	carrot
L. gelidum subsp gasicomitatum TMW 2.1619	GCA_009296125.1	SAMN05756392	PRJNA342276	Complete	1.92438	36.8534	1814	4	12	58	1	99.64/0.56	meat
L. gelidum subsp gelidum JB7	GCA_000298875.1	SAMN02603178	PRJNA174297	Complete	1.8935	36.7	1768	1	12	67	1	99.44/0.19	kimchi, Korean traditional fermented food
L. gelidum subsp gelidum KCTC3527 T	GCA_000166715.2	SAMN02470198	PRJNA60229	Contig	1.95728	36.6	1845	43	3	47	1	99.44/0.19	vacuum-packed meats
L. holzapfelii CCUG54536 T	GCA_012396485.1	SAMN14517846	PRJNA622446	Contig	1.75843	44	1668	18	5	50	1	99.37/0.28	coffee fermentation
L. inhae KCTC3774 T	GCA_000166735.2	SAMN02472184	PRJNA60231	Contig	2.29809	36.4	1622	893	3	48	1	95.81/6.07	kimchi
L. kimchii C2	GCA_000219785.1	SAMN02603135	PRJNA67911	Complete	1.87727	37.9	1792	1	12	68	1	100/0	kimchi
L. kimchii IMSNU11154 T	GCA_000092505.1	SAMN02603394	PRJNA40837	Complete	2.10179	37.9101	2025	6	12	68	1	100/0	kimchi, a traditional Korean food
L. kimchii NKJ218	GCA_004551615.1	SAMN10887832	PRJNA521423	Complete	1.99344	37.7797	1892	4	12	68	1	100/0	kimchi
L. lactis 1300 LCIT	GCA_001062635.1	SAMN03197273	PRJNA267549	Scaffold	1.80711	43.1	1687	58	9	63	1	99.44/0.26	Host: Homo sapiens
L. lactis aa 0143	GCA_004167235.1	SAMN10239554	PRJNA496358	Contig	1.73814	43.2	1637	38	3	46	1	99.44/0	stool(host:Homo sapiens)
L. lactis BIOML-A1	GCA_009678855.1	SAMN11946164	PRJNA544527	Contig	1.748	43.1	1632	30	4	46	1	99.44/0	(host:Homo sapiens)
L. lactis CBA3625	GCA_007954605.1	SAMN11843673	PRJNA544551	Complete	1.79161	43.3467	1714	2	12	68	1	99.44/0.56	kimchi
L. lactis CBA3626	GCA_007954665.1	SAMN11843668	PRJNA544551	Complete	1.83981	43.1491	1742	2	12	70	1	99.44/1.12	kimchi
L. lactis CCK940	GCA_002287365.1	SAMN07482638	PRJNA397634	Contig	1.74151	43.3	1657	2	12	69	1	100/0	kimchi
L. lactis KACC91922	GCA_000709265.1	SAMN02730106	PRJNA244961	Contig	1.68817	43.4	1619	35	3	50	1	99.44/0.67	Kimchi
L. lactis KCTC3773	GCA_000179875.1	SAMN02470199	PRJNA52539	Contig	1.72068	42.9	1663	98	3	48	1	99.44/0	
L. lactis KFRI01	GCA_001998805.1	SAMN05219201	PRJNA325075	Complete	1.71519	43.3281	1613	3	12	69	1	99.44/0	kimchi
L. lactis LN19	GCA_002092595.1	SAMN05981500	PRJNA352459	Contig	1.72439	42.9	1633	47	6	51	1	99.44/0.14	dairy
L. lactis LN24	GCA_002092695.1	SAMN05981502	PRJNA352459	Contig	1.72466	42.9	1641	48	6	52	1	99.44/0.14	dairy
L. lactis NBRC 12455	GCA_006539105.1	SAMD00097163	PRJDB6024	Contig	1.64349	43.5	1531	49	3	39		99.44/0	
L. lactis WiKim40	GCA_001698145.1	SAMN05300424	PRJNA327015	Complete	1.78807	43.1131	1654	4	12	68	1	100/0.56	Kimchi
L. litichii MB7 T	GCA_008107645.1	SAMN10786216	PRJNA516297	Scaffold	1.86586	35.8	1789	13	3	48	1	100/0	Litchi chinensis
L. mesenteroides CBA3628	GCA_007954745.1	SAMN11843664	PRJNA544551	Complete	1.86456	36.9975	1757	4	12	71	1	100/0	kimchi
L. mesenteroides subsp cremoris ATCC19254 T	GCA_000160595.1	SAMN00139187	PRJNA34629	Scaffold	1.73507	38.5	1511	29	3	49	1	100/0	Hansen's dried starter powder

L. mesenteroides subsp cremoris LMGCF01	GCA_002092045.1	SAMN05981463	PRJNA352459	Contig	1.64067	38	1449	115	5	51	1	99.82/0	dairy
L. mesenteroides subsp cremoris LMGCF02	GCA_002092135.1	SAMN05981464	PRJNA352459	Contig	1.72228	37.9	1570	112	5	53	1	100/0	dairy
L. mesenteroides subsp cremoris LMGCF03	GCA_002092145.1	SAMN05981465	PRJNA352459	Contig	1.66544	38	1494	116	5	53	1	100/0	dairy
L. mesenteroides subsp cremoris LMGCF04	GCA_002092155.1	SAMN05981466	PRJNA352459	Contig	1.64019	38	1446	124	5	52	1	100/0	dairy
L. mesenteroides subsp cremoris LMGCF05	GCA_002092085.1	SAMN05981467	PRJNA352459	Contig	1.63731	38	1452	118	5	53	1	100/0	dairy
L. mesenteroides subsp cremoris LMGCF07	GCA_002092215.1	SAMN05981469	PRJNA352459	Scaffold	1.63929	38.1	1431	109	5	53	1	100/0	dairy
L. mesenteroides subsp cremoris LMGCF09	GCA_002092105.1	SAMN05981471	PRJNA352459	Contig	1.62909	38.1	1468	105	5	53	1	100/0	dairy
L. mesenteroides subsp cremoris LMGCF10	GCA_002092245.1	SAMN05981472	PRJNA352459	Contig	1.61642	38	1452	109	5	51	1	100/0	dairy
L. mesenteroides subsp cremoris LMGCF11	GCA_002092315.1	SAMN05981473	PRJNA352459	Contig	1.67437	38.2	1488	86	5	53	1	99.87/0	dairy
L. mesenteroides subsp cremoris LMGCF12	GCA_002092385.1	SAMN05981474	PRJNA352459	Contig	1.66343	38.1	1474	113	4	54	1	100/0.53	dairy
L. mesenteroides subsp cremoris LMGCF13	GCA_002092465.1	SAMN05981475	PRJNA352459	Contig	1.63644	38.3	1451	219	4	50	1	100/1.06	dairy
L. mesenteroides subsp cremoris LMGCF14	GCA_002092335.1	SAMN05981476	PRJNA352459	Contig	1.62752	38	1462	105	5	52	1	100/0	dairy
L. mesenteroides subsp cremoris LMGCF16	GCA_002092515.1	SAMN05981478	PRJNA352459	Contig	1.61323	38	1448	124	5	52	1	100/0	dairy
L. mesenteroides subsp cremoris LMGCF17	GCA_002092425.1	SAMN05981479	PRJNA352459	Contig	1.62949	38	1457	101	5	52	1	100/0	dairy
L. mesenteroides subsp cremoris LMGCF18	GCA_002092495.1	SAMN05981480	PRJNA352459	Contig	1.62399	38	1456	105	5	52	1	100/0	dairy

L. mesenteroides subsp cremoris LMGCF19	GCA_002092415.1	SAMN05981481	PRJNA352459	Contig	1.64533	38	1517	113	5	53	1	100/0	dairy
L. mesenteroides subsp cremoris LMGCF20	GCA_002092455.1	SAMN05981482	PRJNA352459	Contig	1.63087	38	1474	109	5	53	1	99.74/0	dairy
L. mesenteroides subsp cremoris LN07	GCA_002092615.1	SAMN05981497	PRJNA352459	Contig	1.59621	38.1	1424	107	5	52	1	100/0	dairy
L. mesenteroides subsp cremoris T26	GCA_000686485.1	SAMN02767914	PRJNA205545	Scaffold	1.83247	38.4	1690	123	3	56	1	100/10.23	mesophilic cheese starter cultures
L. mesenteroides subsp cremoris TIFN8	GCA_000447945.1	SAMN02472108	PRJNA175676	Contig	1.71009	38.2	1452	173	7	61		99.21/0.26	propagated starter culture used in cheese manufacturing
L. mesenteroides subsp dextranicum DSM20484 T	GCA_001047695.1	SAMN03105774	PRJNA263697	Complete	1.85473	38.0389	1692	2	12	71	1	100/0.79	Cheese
L. mesenteroides subsp dextranicum FAM 18356	GCA_005864365.1	SAMN11653949	PRJNA543085	Contig	1.87153	37.8	1707	40	5	53	1	100/0	
L. mesenteroides subsp dextranicum FM06	GCA_002148235.1	SAMN06061940	PRJNA355067	Complete	1.94688	37.9649	1746	4	12	71	1	100/0	10 weeks old 45+ Samso cheese
L. mesenteroides subsp dextranicum LbT16	GCA_001184265.1	SAMN03463677	PRJNA280520	Contig	1.90636	37.8	1733	65	3	51	1	99.47/0	Taleggio cheese
L. mesenteroides subsp dextranicum LN05	GCA_002092565.1	SAMN05981496	PRJNA352459	Contig	2.00187	38	1835	250	16	57	1	98.53/2.95	dairy
L. mesenteroides subsp dextranicum LN08	GCA_002092625.1	SAMN05981498	PRJNA352459	Contig	1.96519	37.8	1866	106	5	54	1	100/0	dairy
L. mesenteroides subsp dextranicum LN32	GCA_002092705.1	SAMN05981505	PRJNA352459	Contig	1.84828	37.8	1696	68	5	54	1	100/0	dairy
L. mesenteroides subsp dextranicum LN34	GCA_002092775.1	SAMN05981506	PRJNA352459	Contig	1.87513	37.7	1719	110	5	53	1	100/0	dairy
L. mesenteroides subsp dextranicum NCTC10817	GCA_900452955.1	SAMEA4362418	PRJEB6403	Contig	1.97325	37.8	1860	3	12	71	1	100/0.53	
L. mesenteroides subsp dextranicum OG2	GCA_002276945.1	SAMN06718482	PRJNA375758	Contig	1.71628	37.9	1583	146	7	51	1	100/0	kefir
L. mesenteroides subsp dextranicum P45	GCA_000756355.1	SAMN03032191	PRJNA260860	Contig	1.87419	37.5	1726	6	9	52	1	100/0	fermented pulque

L. mesenteroides subsp dextranicum WC0331	GCA_008690745.1	SAMN11618762	PRJNA542256	Scaffold	2.01813	37.6	1923	10	5	53	1	100/0.53	Cooked ham
L. mesenteroides subsp jonggajibkimchii B5	GCA_004745755.1	SAMN10484942	PRJNA507123	Contig	2.12682	37.5	2037	26	5	53	1	100/0.18	Mike cake
L. mesenteroides subsp jonggajibkimchii BD3749	GCA_001583825.1	SAMN04508169	PRJNA312878	Complete	1.98657	37.8	1898	1	12	71	1	100/0	fermeted vegetable
L. mesenteroides subsp jonggajibkimchii CBA7131	GCA_003255835.1	SAMN07206913	PRJNA390217	Complete	2.08731	37.6375	1986	4	12	71	1	99.47/0	Korean adult feces
L. mesenteroides subsp jonggajibkimchii DRC1506 T	GCA_001886915.1	SAMN04198570	PRJNA299366	Complete	1.98392	37.6424	1787	4	12	71	1	99.89/0.53	Kimchi
L. mesenteroides subsp jonggajibkimchii KFRI- MG	GCA_000512955.1	SAMN02641526	PRJNA18679	Complete	1.89641	37.7	1796	1	12	69	1	100/0	
L. mesenteroides subsp jonggajibkimchii KIBGE-IB22	GCA_005049065.1	SAMN11431368	PRJNA532993	Scaffold	1.94823	37.5	1880	13	3	50	1	100/0.18	cabbage(host:Vegetables)
L. mesenteroides subsp jonggajibkimchii SRCM102735	GCA_009913935.1	SAMN08707610	PRJNA438180	Complete	2.05844	37.5883	1982	4	12	71	1	100/0	Soybean paste (Chonggugjang)
L. mesenteroides subsp jonggajibkimchii SRCM103356	GCA_004102585.1	SAMN10742283	PRJNA515114	Complete	2.03939	37.5826	1984	4	12	71	1	100/0.18	food
L. mesenteroides subsp jonggajibkimchii SRCM103453	GCA_004103675.1	SAMN10754493	PRJNA515383	Complete	2.1826	37.6453	2090	5	12	71	1	100/0	food
L. mesenteroides subsp jonggajibkimchii SRCM103460	GCA_004194375.1	SAMN10743321	PRJNA515149	Complete	2.08721	37.5882	1996	5	12	71	1	100/0	food
L. mesenteroides subsp jonggajibkimchii WC0333	GCA_008689685.1	SAMN11618766	PRJNA542256	Contig	2.08859	37.5	2031	35	5	53	1	100/0	Sausage

L. mesenteroides subsp jonggajibkimchii WiKim33	GCA_003433375.1	SAMN07156024	PRJNA387486	Complete	1.97006	37.6362	1883	4	12	71	1	100/0	Baechu-kimchi
L. mesenteroides subsp mesenteroides CBA3607	GCA_009676745.1	SAMN13258970	PRJNA544551	Complete	1.85432	37.008	1750	3	12	71	1	100/0	kimchi
L. mesenteroides subsp mesenteroides 213M0	GCA_001570665.1	SAMD00042708	PRJDB4328	Contig	2.03285	37.7	1946	58	3	49	1	99.93/0.53	
L. mesenteroides subsp mesenteroides 406	GCA_001515385.1	SAMD00042709	PRJDB4329	Contig	2.00431	37.7	1932	69	3	49	1	100/1.06	
L. mesenteroides subsp mesenteroides ATCC8293 T	GCA_000014445.1	SAMN02598482	PRJNA315	Complete	2.07576	37.6586	1967	2	12	71	1	100/0.53	fermenting olives
L. mesenteroides subsp mesenteroides AtHG50	GCA_004368765.1	SAMN08777814	PRJNA441539	Scaffold	2.03285	37.7	1960	60	3	52	1	100/0.53	
L. mesenteroides subsp mesenteroides BD1710	GCA_002117185.1	SAMN04530070	PRJNA314170	Complete	2.12404	37.6	2014	1	12	71	1	100/0.53	kefir
L. mesenteroides subsp mesenteroides CECT9217	GCA_900290445.1	SAMEA104569583	PRJEB24702	Contig	2.02219	37.7	1932	13	5	53	1	100/0	
L. mesenteroides subsp mesenteroides CECT9266	GCA_900312985.1	SAMEA104569776	PRJEB24710	Contig	2.10613	37.7	2032	44	5	53	1	99.82/0	
L. mesenteroides subsp mesenteroides CECT9268	GCA_900290155.1	SAMEA104569777	PRJEB24712	Contig	2.07557	37.7	2002	26	5	53	1	99.82/0	
L. mesenteroides subsp mesenteroides DE0394	GCA_007673005.1	SAMN11792554	PRJNA543692	Scaffold	1.93918	37.7	1816	358	3	48	1	100/1.6	environmental
L. mesenteroides subsp mesenteroides DRC0211	GCA_002009375.1	SAMN04198273	PRJNA299363	Complete	2.1241	37.5981	1962	5	12	71	1	100/0	Kimchi
L. mesenteroides subsp mesenteroides GL1	GCA_001541125.1	SAMN04231183	PRJNA300958	Scaffold	1.81597	38.1	1649	11	2	35	1	100/0.79	Dromedary milk
L. mesenteroides subsp mesenteroides J18	GCA_000234825.3	SAMN02603136	PRJNA75083	Complete	2.01726	37.6784	1883	5	12	71	1	100/0	
L. mesenteroides subsp mesenteroides KMB608	GCA_003346165.1	SAMN09398940	PRJNA474823	Contig	1.95951	37.7	1877	81	3	46	1	100/0	sheep milk

L. mesenteroides subsp mesenteroides KMB609	GCA_003346155.1	SAMN09398941	PRJNA474823	Contig	2.01223	37.7	1930	84	3	47	1	100/0.53	bryndza cheese
L. mesenteroides subsp mesenteroides KMB611	GCA_003346345.1	SAMN09398943	PRJNA474823	Contig	2.10341	37.5	2037	33	3	46	1	100/0.53	bryndza cheese
L. mesenteroides subsp mesenteroides LbE15	GCA_001184245.1	SAMN03463642	PRJNA280507	Contig	2.00792	37.6	1923	63	3	51	1	100/0	Taleggio cheese
L. mesenteroides subsp mesenteroides LbE16	GCA_001184255.1	SAMN03463665	PRJNA280516	Contig	2.03609	37.5	1964	85	3	51	1	100/0.53	Taleggio cheese
L. mesenteroides subsp mesenteroides LK-151	GCA_002370415.1	SAMD00065790	PRJDB5233	Complete	2.13737	37.7366	2017	4	9	68	1	100/0	
L. mesenteroides subsp mesenteroides LN25	GCA_002092735.1	SAMN05981503	PRJNA352459	Contig	2.2776	37.5	2180	70	6	54	1	100/1.06	dairy
L. mesenteroides subsp mesenteroides LN27	GCA_002092745.1	SAMN05981504	PRJNA352459	Contig	2.2246	37.5	2123	54	6	54	1	100/1.06	dairy
L. mesenteroides subsp mesenteroides M11	GCA_009497095.1	SAMN13018494	PRJNA577063	Scaffold	1.97939	37.8	1863	79	3	52	1	100/1.06	(host:Oreochromis niloticus)
L. mesenteroides subsp mesenteroides NBRC102481	GCA_007989505.1	SAMD00166021	PRJDB6187	Contig	1.69543	37.8	1630	109	3	45	1	98.41/0	
L. mesenteroides subsp mesenteroides NBRC3832	GCA_006538765.1	SAMD00093693	PRJDB6025	Contig	1.90981	37.6	1789	31	3	45	1	100/0.53	
L. mesenteroides subsp mesenteroides SRCM102733	GCA_009913915.1	SAMN08707608	PRJNA438180	Complete	2.05873	37.7211	1967	3	12	71	1	100/0	Gochujang
L. mesenteroides subsp mesenteroides TR154	GCA_006406185.1	SAMN09099487	PRJNA470672	Contig	1.85995	37.8	1756	43	5	53	1	100/0	sourdough
L. mesenteroides subsp mesenteroides WC0330	GCA_008690805.1	SAMN11618760	PRJNA542256	Scaffold	1.76569	37.9	1637	41	4	54	1	100/0.26	Cooked ham
L. mesenteroides subsp mesenteroides WC0332	GCA_008689715.1	SAMN11618765	PRJNA542256	Contig	1.8553	37.7	1744	39	5	54	1	100/0	Sausage
L. mesenteroides subsp mesenteroides Wikim17	GCA_000787735.1	SAMD00022975	PRJDB3305	Contig	1.85932	37.8	1748	41	4	53	1	100/0.26	

L. mesenteroides subsp mesenteroides YL48	GCA_002886025.1	SAMN06298812	PRJNA371414	Contig	2.0584	37.6	1975	154	6	54	1	100/0	Root Surface(host:Carrot)
L. pseudomesenteroides 1159	GCA_000686465.1	SAMN02767913	PRJNA205546	Scaffold	2.03869	39	1969	100	3	49	1	100/0	mesophilic cheese starter cultures
L. pseudomesenteroides 4882	GCA_000297375.1	SAMEA3138421	PRJNA84285	Contig	2.00859	39.1	1936	106	5	59	1	93.12/0.18	
L. pseudomesenteroides AMBR10	GCA_901830415.1	SAMEA5665507	PRJEB32716	Contig	2.29673	39.2	2248	338	7	56	1	100/0.7	Human adenoid
L. pseudomesenteroides BM2	GCA_002092535.1	SAMN05981461	PRJNA352459	Contig	2.02255	39	1997	101	7	53	1	100/0	dairy
L. pseudomesenteroides CBA3630	GCA_008033175.1	SAMN11843675	PRJNA544551	Complete	2.31609	38.9999	2171	4	12	70	1	99.82/0.18	kimchi
L. pseudomesenteroides HPK01	GCA_002092075.1	SAMN05981330	PRJNA352459	Contig	1.95326	39.1	1853	92	5	51	1	100/0	dairy starter
L. pseudomesenteroides KMB610	GCA_003346375.1	SAMN09398942	PRJNA474823	Contig	1.9824	39	1919	57	3	43	1	100/0	bryndza cheese
L. pseudomesenteroides LMG11482 T	GCA_014634745.1	SAMD00239684	PRJDB7793	Contig	2.09581	38.9	1971	29	4	50	1	99.82/0	cane juice
L. pseudomesenteroides LMGCF06	GCA_002092035.1	SAMN05981468	PRJNA352459	Contig	1.95205	39.1	1848	83	5	51	1	100/0	dairy
L. pseudomesenteroides LMGCF08	GCA_002092165.1	SAMN05981470	PRJNA352459	Contig	2.19336	39.1	2069	267	5	53	1	100/11.2	dairy
L. pseudomesenteroides LMGCF15	GCA_002092375.1	SAMN05981477	PRJNA352459	Contig	1.92427	39.1	1833	78	5	51	1	100/0	dairy
L. pseudomesenteroides LMGH100	GCA_002072505.1	SAMN05981487	PRJNA352459	Contig	2.06006	39.1	1903	238	4	52	1	98.7/2.61	dairy
L. pseudomesenteroides LMGH278	GCA_002072495.1	SAMN05981488	PRJNA352459	Contig	1.9401	39.1	1852	106	5	51	1	100/0	dairy
L. pseudomesenteroides LMGH280	GCA_002072555.1	SAMN05981489	PRJNA352459	Contig	1.98015	39.1	1861	85	4	55	1	100/0.71	dairy

L. pseudomesenteroides LMGH284	GCA_002072575.1	SAMN05981490	PRJNA352459	Scaffold	2.07199	39	1952	222	4	52	1	99.21/2.03	dairy
L. pseudomesenteroides LMGH61	GCA_002072515.1	SAMN05981483	PRJNA352459	Scaffold	2.00878	39.1	1901	62	4	54	1	100/0	dairy
L. pseudomesenteroides LMGH83	GCA_002072475.1	SAMN05981484	PRJNA352459	Contig	2.05883	39.1	1885	201	4	53	1	98.4/1.41	dairy
L. pseudomesenteroides LMGH95	GCA_002072565.1	SAMN05981485	PRJNA352459	Contig	1.98982	39	1948	171	5	51	1	100/0.18	dairy
L. pseudomesenteroides LMGH97	GCA_002072585.1	SAMN05981486	PRJNA352459	Contig	1.98975	39	1946	132	5	50	1	100/0	dairy
L. pseudomesenteroides LMGTW1	GCA_002092235.1	SAMN05981491	PRJNA352459	Contig	1.9692	39	1924	125	5	52	1	100/0	dairy
L. pseudomesenteroides LMGTW3	GCA_002092355.1	SAMN05981492	PRJNA352459	Contig	1.89805	39.1	1834	87	5	52	1	100/0	dairy
L. pseudomesenteroides LMGTW6	GCA_002092255.1	SAMN05981493	PRJNA352459	Contig	1.88144	39.1	1821	90	5	52	1	100/0	dairy
L. pseudomesenteroides LMGTW8	GCA_002092295.1	SAMN05981494	PRJNA352459	Contig	1.98207	39	1936	118	5	52	1	100/0	dairy
L. pseudomesenteroides LN02	GCA_002092555.1	SAMN05981495	PRJNA352459	Contig	1.91243	39.1	1803	88	6	53	1	100/0	dairy
L. pseudomesenteroides LN12	GCA_002092635.1	SAMN05981499	PRJNA352459	Contig	1.86409	39.1	1762	85	6	52	1	100/0	dairy
L. pseudomesenteroides LN23	GCA_002092645.1	SAMN05981501	PRJNA352459	Contig	1.99273	39.1	1936	126	5	47	1	100/0.18	dairy
L. pseudomesenteroides MGYG-HGUT-00096	GCA_902363165.1	SAMEA5849597	PRJEB33885	Scaffold	2.29682			33	4	52	1	99.82/0	human gut
L. pseudomesenteroides PS12	GCA_000686505.1	SAMN02767912	PRJNA205547	Scaffold	1.93438	39.1	1863	91	3	48	1	100/0	undefined mesophilic cheese starter culture
L. pseudomesenteroides TR070	GCA_006382035.1	SAMN09099485	PRJNA470672	Contig	2.23055	38.8	2162	76	5	52	1	99.82/0	sourdough
L. rapi DSM27776 T	GCA_016908715.1	SAMN17619917	PRJNA695649	Contig	1.92491	38	1843	24	3	49	1	100/1.24	rutabaga

L. suionicum CECT 8486	GCA_900289255.1	SAMEA104569300	PRJEB24691	Contig	2.07002	37.3	1968	20	5	53	1	100/0.53	
L. suionicum CECT 9216	GCA_900290145.1	SAMEA104569335	PRJEB24693	Contig	2.06953	37.3	1972	18	5	53	1	100/0.53	
L. suionicum CECT8484	GCA_900289205.1	SAMEA104569299	PRJEB24690	Contig	2.06903	37.3	1974	18	5	53	1	100/0.53	
L. suionicum DSM20241 T	GCA_001891125.1	SAMN04811211	PRJNA318320	Complete	2.04883	37.5936	1923	2	12	71	1	100/0	Source unknown

522 **Table:2:** A descriptive list of the earlier classification and robust reclassification of the strain based on this study.

523

Strains ID	Earlier taxonomy	Taxonomy status	Proposed taxonomy
<i>L. carnosum</i> CBA3620	<i>L. carnosum</i>	Correct	<i>L. carnosum</i>
<i>L. carnosum</i> DSM5576 T	<i>L. carnosum</i>	Correct	<i>L. carnosum</i>
<i>L. carnosum</i> JB16	<i>L. carnosum</i>	Correct	<i>L. carnosum</i>
<i>L. carnosum</i> MFPA29A1405	<i>L. carnosum</i>	Correct	<i>L. carnosum</i>
<i>L. carnosum</i> MFPC16A2803	<i>L. carnosum</i>	Correct	<i>L. carnosum</i>
<i>L. carnosum</i> WC0318	<i>L. carnosum</i>	Correct	<i>L. carnosum</i>
<i>L. carnosum</i> WC0319	<i>L. carnosum</i>	Correct	<i>L. carnosum</i>
<i>L. carnosum</i> WC0320	<i>L. carnosum</i>	Correct	<i>L. carnosum</i>
<i>L. carnosum</i> WC0321	<i>L. carnosum</i>	Correct	<i>L. carnosum</i>
<i>L. carnosum</i> WC0322	<i>L. carnosum</i>	Correct	<i>L. carnosum</i>
<i>L. carnosum</i> WC0323	<i>L. carnosum</i>	Correct	<i>L. carnosum</i>
<i>L. carnosum</i> WC0324	<i>L. carnosum</i>	Correct	<i>L. carnosum</i>
<i>L. carnosum</i> WC0325	<i>L. carnosum</i>	Correct	<i>L. carnosum</i>
<i>L. carnosum</i> WC0326	<i>L. carnosum</i>	Correct	<i>L. carnosum</i>
<i>L. carnosum</i> WC0327	<i>L. carnosum</i>	Correct	<i>L. carnosum</i>
<i>L. carnosum</i> WC0328	<i>L. carnosum</i>	Correct	<i>L. carnosum</i>
<i>L. carnosum</i> WC0329	<i>L. carnosum</i>	Correct	<i>L. carnosum</i>
<i>L. citreum</i> 1301 LGAS	<i>L. citreum</i>	Correct	<i>L. citreum</i>
<i>L. citreum</i> CBA3621	<i>L. citreum</i>	Correct	<i>L. citreum</i>
<i>L. citreum</i> CBA3623	<i>L. citreum</i>	Correct	<i>L. citreum</i>
<i>L. citreum</i> CBA3624	<i>L. citreum</i>	Correct	<i>L. citreum</i>
<i>L. citreum</i> CBA3627	<i>L. citreum</i>	Correct	<i>L. citreum</i>
<i>L. citreum</i> CW28	<i>L. citreum</i>	Correct	<i>L. citreum</i>
<i>L. citreum</i> DmW 111	<i>L. citreum</i>	Correct	<i>L. citreum</i>
<i>L. citreum</i> EFEL 2700	<i>L. citreum</i>	Correct	<i>L. citreum</i>
<i>L. citreum</i> F192-5	<i>L. citreum</i>	Correct	<i>L. citreum</i>
<i>L. citreum</i> G4	<i>L. citreum</i>	Correct	<i>L. citreum</i>
<i>L. citreum</i> KM20	<i>L. citreum</i>	Correct	<i>L. citreum</i>
<i>L. citreum</i> LBAE C10	<i>L. citreum</i>	Correct	<i>L. citreum</i>

<i>L. citreum</i> LBAE C11	<i>L. citreum</i>	Correct	<i>L. citreum</i>
<i>L. citreum</i> LBAE E16	<i>L. citreum</i>	Correct	<i>L. citreum</i>
<i>L. citreum</i> NBRC102476	<i>L. citreum</i>	Correct	<i>L. citreum</i>
<i>L. citreum</i> NRIC1776 T	<i>L. citreum</i>	Correct	<i>L. citreum</i>
<i>L. citreum</i> NRRL B-1299	<i>L. citreum</i>	Correct	<i>L. citreum</i>
<i>L. citreum</i> NRRL B-742	<i>L. citreum</i>	Correct	<i>L. citreum</i>
<i>L. citreum</i> TMW21194	<i>L. citreum</i>	Correct	<i>L. citreum</i>
<i>L. citreum</i> TR116	<i>L. citreum</i>	Correct	<i>L. citreum</i>
<i>L. citreum</i> TR153	<i>L. citreum</i>	Correct	<i>L. citreum</i>
<i>L. citreum</i> WiKim0101	<i>L. citreum</i>	Correct	<i>L. citreum</i>
<i>L. falkenbergense</i> LMG10779 T	<i>L. falkenbergense</i>	Correct	<i>L. falkenbergense</i>
<i>L. fallax</i> ATCC700006 T	<i>L. fallax</i>	Correct	<i>L. fallax</i>
<i>L. gelidum</i> subsp <i>gasicomitatum</i> C120c	<i>L. gelidum</i> subsp <i>gasicomitatum</i>	Revisited	<i>L. inhae</i>
<i>L. gelidum</i> subsp <i>gasicomitatum</i> C122c	<i>L. gelidum</i> subsp <i>gasicomitatum</i>	Revisited	<i>L. inhae</i>
<i>L. gelidum</i> subsp <i>gasicomitatum</i> KG16-1	<i>L. gelidum</i> subsp <i>gasicomitatum</i>	Revisited	<i>L. inhae</i>
<i>L. gelidum</i> subsp <i>gasicomitatum</i> KSL4-2	<i>L. gelidum</i> subsp <i>gasicomitatum</i>	Revisited	<i>L. inhae</i>
<i>L. gelidum</i> subsp <i>gasicomitatum</i> LMG18811 T	<i>L. gelidum</i> subsp <i>gasicomitatum</i>	Revisited	<i>L. inhae</i>
<i>L. gelidum</i> subsp <i>gasicomitatum</i> MFPA44A1401	<i>L. gelidum</i> subsp <i>gasicomitatum</i>	Revisited	<i>L. inhae</i>
<i>L. gelidum</i> subsp <i>gasicomitatum</i> PB1a	<i>L. gelidum</i> subsp <i>gasicomitatum</i>	Revisited	<i>L. inhae</i>
<i>L. gelidum</i> subsp <i>gasicomitatum</i> PB1e	<i>L. gelidum</i> subsp <i>gasicomitatum</i>	Revisited	<i>L. inhae</i>
<i>L. gelidum</i> subsp <i>gasicomitatum</i> PL111	<i>L. gelidum</i> subsp <i>gasicomitatum</i>	Revisited	<i>L. inhae</i>
<i>L. gelidum</i> subsp <i>gasicomitatum</i> TMW 2.1619	<i>L. gelidum</i> subsp <i>gasicomitatum</i>	Revisited	<i>L. inhae</i>
<i>L. gelidum</i> subsp <i>gelidum</i> JB7	<i>L. gelidum</i> subsp <i>gelidum</i>	Correct	<i>L. gelidum</i>
<i>L. gelidum</i> subsp <i>gelidum</i> KCTC3527 T	<i>L. gelidum</i> subsp <i>gelidum</i>	Correct	<i>L. gelidum</i>
<i>L. holzapfelii</i> CCUG54536 T	<i>L. holzapfelii</i>	Correct	<i>L. holzapfelii</i>
<i>L. inhae</i> KCTC3774 T	<i>L. inhae</i>	Correct	<i>L. inhae</i>
<i>L. kimchii</i> C2	<i>L. kimchii</i>	Correct	<i>L. kimchii</i>
<i>L. kimchii</i> IMSNU11154 T	<i>L. kimchii</i>	Correct	<i>L. kimchii</i>
<i>L. kimchii</i> NKJ218	<i>L. kimchii</i>	Correct	<i>L. kimchii</i>
<i>L. lactis</i> 1300 LCIT	<i>L. lactis</i>	Revisited	GS2
<i>L. lactis</i> aa 0143	<i>L. lactis</i>	Revisited	GS2
<i>L. lactis</i> BIOML-A1	<i>L. lactis</i>	Revisited	GS2
<i>L. lactis</i> CBA3625	<i>L. lactis</i>	Revisited	GS2
<i>L. lactis</i> CBA3626	<i>L. lactis</i>	Revisited	GS2

<i>L. lactis</i> CCK940	<i>L. lactis</i>	Revisited	GS2
<i>L. lactis</i> KACC91922	<i>L. lactis</i>	Revisited	GS2
<i>L. lactis</i> KCTC3773	<i>L. lactis</i>	Revisited	GS1
<i>L. lactis</i> KFRI01	<i>L. lactis</i>	Revisited	GS2
<i>L. lactis</i> LN19	<i>L. lactis</i>	Revisited	GS1
<i>L. lactis</i> LN24	<i>L. lactis</i>	Revisited	GS1
<i>L. lactis</i> NBRC 12455	<i>L. lactis</i>	Revisited	GS2
<i>L. lactis</i> WiKim40	<i>L. lactis</i>	Revisited	GS2
<i>L. litchei</i> MB7 T	<i>L. litchei</i>	Correct	<i>L. litchei</i>
<i>L. mesenteroides</i> CBA3628	<i>L. mesenteroides</i>	Revisited	GS3
<i>L. mesenteroides</i> subsp <i>cremoris</i> ATCC19254 T	<i>L. mesenteroides</i>	Correct	<i>L. mesenteroides</i>
<i>L. mesenteroides</i> subsp <i>cremoris</i> LMGCF01	<i>L. mesenteroides</i>	Correct	<i>L. mesenteroides</i>
<i>L. mesenteroides</i> subsp <i>cremoris</i> LMGCF02	<i>L. mesenteroides</i>	Correct	<i>L. mesenteroides</i>
<i>L. mesenteroides</i> subsp <i>cremoris</i> LMGCF03	<i>L. mesenteroides</i>	Correct	<i>L. mesenteroides</i>
<i>L. mesenteroides</i> subsp <i>cremoris</i> LMGCF04	<i>L. mesenteroides</i>	Correct	<i>L. mesenteroides</i>
<i>L. mesenteroides</i> subsp <i>cremoris</i> LMGCF05	<i>L. mesenteroides</i>	Correct	<i>L. mesenteroides</i>
<i>L. mesenteroides</i> subsp <i>cremoris</i> LMGCF07	<i>L. mesenteroides</i>	Correct	<i>L. mesenteroides</i>
<i>L. mesenteroides</i> subsp <i>cremoris</i> LMGCF09	<i>L. mesenteroides</i>	Correct	<i>L. mesenteroides</i>
<i>L. mesenteroides</i> subsp <i>cremoris</i> LMGCF10	<i>L. mesenteroides</i>	Correct	<i>L. mesenteroides</i>
<i>L. mesenteroides</i> subsp <i>cremoris</i> LMGCF11	<i>L. mesenteroides</i>	Correct	<i>L. mesenteroides</i>
<i>L. mesenteroides</i> subsp <i>cremoris</i> LMGCF12	<i>L. mesenteroides</i>	Correct	<i>L. mesenteroides</i>
<i>L. mesenteroides</i> subsp <i>cremoris</i> LMGCF13	<i>L. mesenteroides</i>	Correct	<i>L. mesenteroides</i>
<i>L. mesenteroides</i> subsp <i>cremoris</i> LMGCF14	<i>L. mesenteroides</i>	Correct	<i>L. mesenteroides</i>
<i>L. mesenteroides</i> subsp <i>cremoris</i> LMGCF16	<i>L. mesenteroides</i>	Correct	<i>L. mesenteroides</i>
<i>L. mesenteroides</i> subsp <i>cremoris</i> LMGCF17	<i>L. mesenteroides</i>	Correct	<i>L. mesenteroides</i>
<i>L. mesenteroides</i> subsp <i>cremoris</i> LMGCF18	<i>L. mesenteroides</i>	Correct	<i>L. mesenteroides</i>
<i>L. mesenteroides</i> subsp <i>cremoris</i> LMGCF19	<i>L. mesenteroides</i>	Correct	<i>L. mesenteroides</i>
<i>L. mesenteroides</i> subsp <i>cremoris</i> LMGCF20	<i>L. mesenteroides</i>	Correct	<i>L. mesenteroides</i>
<i>L. mesenteroides</i> subsp <i>cremoris</i> LN07	<i>L. mesenteroides</i>	Correct	<i>L. mesenteroides</i>
<i>L. mesenteroides</i> subsp <i>cremoris</i> T26	<i>L. mesenteroides</i>	Correct	<i>L. mesenteroides</i>
<i>L. mesenteroides</i> subsp <i>cremoris</i> TIFN8	<i>L. mesenteroides</i>	Correct	<i>L. mesenteroides</i>
<i>L. mesenteroides</i> subsp <i>dextranicum</i> DSM20484 T	<i>L. mesenteroides</i>	Correct	<i>L. mesenteroides</i>
<i>L. mesenteroides</i> subsp <i>dextranicum</i> FAM 18356	<i>L. mesenteroides</i>	Correct	<i>L. mesenteroides</i>
<i>L. mesenteroides</i> subsp <i>dextranicum</i> FM06	<i>L. mesenteroides</i>	Correct	<i>L. mesenteroides</i>

<i>L. mesenteroides</i> subsp dextranicum LbT16	<i>L. mesenteroides</i>	Correct	<i>L. mesenteroides</i>
<i>L. mesenteroides</i> subsp dextranicum LN05	<i>L. mesenteroides</i>	Correct	<i>L. mesenteroides</i>
<i>L. mesenteroides</i> subsp dextranicum LN08	<i>L. mesenteroides</i>	Correct	<i>L. mesenteroides</i>
<i>L. mesenteroides</i> subsp dextranicum LN32	<i>L. mesenteroides</i>	Correct	<i>L. mesenteroides</i>
<i>L. mesenteroides</i> subsp dextranicum LN34	<i>L. mesenteroides</i>	Correct	<i>L. mesenteroides</i>
<i>L. mesenteroides</i> subsp dextranicum NCTC10817	<i>L. mesenteroides</i>	Correct	<i>L. mesenteroides</i>
<i>L. mesenteroides</i> subsp dextranicum OG2	<i>L. mesenteroides</i>	Correct	<i>L. mesenteroides</i>
<i>L. mesenteroides</i> subsp dextranicum P45	<i>L. mesenteroides</i>	Correct	<i>L. mesenteroides</i>
<i>L. mesenteroides</i> subsp dextranicum WC0331	<i>L. mesenteroides</i>	Correct	<i>L. mesenteroides</i>
<i>L. mesenteroides</i> subsp joggajibkimchii B5	<i>L. mesenteroides</i>	Correct	<i>L. mesenteroides</i>
<i>L. mesenteroides</i> subsp joggajibkimchii BD3749	<i>L. mesenteroides</i>	Correct	<i>L. mesenteroides</i>
<i>L. mesenteroides</i> subsp joggajibkimchii CBA7131	<i>L. mesenteroides</i>	Correct	<i>L. mesenteroides</i>
<i>L. mesenteroides</i> subsp joggajibkimchii DRC1506 T	<i>L. mesenteroides</i>	Correct	<i>L. mesenteroides</i>
<i>L. mesenteroides</i> subsp joggajibkimchii KFRI-MG	<i>L. mesenteroides</i>	Correct	<i>L. mesenteroides</i>
<i>L. mesenteroides</i> subsp joggajibkimchii KIBGE-IB22	<i>L. mesenteroides</i>	Correct	<i>L. mesenteroides</i>
<i>L. mesenteroides</i> subsp joggajibkimchii SRCM102735	<i>L. mesenteroides</i>	Correct	<i>L. mesenteroides</i>
<i>L. mesenteroides</i> subsp joggajibkimchii SRCM103356	<i>L. mesenteroides</i>	Correct	<i>L. mesenteroides</i>
<i>L. mesenteroides</i> subsp joggajibkimchii SRCM103453	<i>L. mesenteroides</i>	Correct	<i>L. mesenteroides</i>
<i>L. mesenteroides</i> subsp joggajibkimchii SRCM103460	<i>L. mesenteroides</i>	Correct	<i>L. mesenteroides</i>
<i>L. mesenteroides</i> subsp joggajibkimchii WC0333	<i>L. mesenteroides</i>	Correct	<i>L. mesenteroides</i>
<i>L. mesenteroides</i> subsp joggajibkimchii WiKim33	<i>L. mesenteroides</i>	Correct	<i>L. mesenteroides</i>
<i>L. mesenteroides</i> subsp mesenteroides CBA3607	<i>L. mesenteroides</i>	Revisited	GS3
<i>L. mesenteroides</i> subsp mesenteroides 213M0	<i>L. mesenteroides</i>	Correct	<i>L. mesenteroides</i>
<i>L. mesenteroides</i> subsp mesenteroides 406	<i>L. mesenteroides</i>	Correct	<i>L. mesenteroides</i>
<i>L. mesenteroides</i> subsp mesenteroides ATCC8293 T	<i>L. mesenteroides</i>	Correct	<i>L. mesenteroides</i>
<i>L. mesenteroides</i> subsp mesenteroides AtHG50	<i>L. mesenteroides</i>	Correct	<i>L. mesenteroides</i>
<i>L. mesenteroides</i> subsp mesenteroides BD1710	<i>L. mesenteroides</i>	Correct	<i>L. mesenteroides</i>
<i>L. mesenteroides</i> subsp mesenteroides CECT9217	<i>L. mesenteroides</i>	Correct	<i>L. mesenteroides</i>
<i>L. mesenteroides</i> subsp mesenteroides CECT9266	<i>L. mesenteroides</i>	Correct	<i>L. mesenteroides</i>
<i>L. mesenteroides</i> subsp mesenteroides CECT9268	<i>L. mesenteroides</i>	Correct	<i>L. mesenteroides</i>
<i>L. mesenteroides</i> subsp mesenteroides DE0394	<i>L. mesenteroides</i>	Correct	<i>L. mesenteroides</i>
<i>L. mesenteroides</i> subsp mesenteroides DRC0211	<i>L. mesenteroides</i>	Correct	<i>L. mesenteroides</i>
<i>L. mesenteroides</i> subsp mesenteroides GL1	<i>L. mesenteroides</i>	Correct	<i>L. mesenteroides</i>
<i>L. mesenteroides</i> subsp mesenteroides J18	<i>L. mesenteroides</i>	Correct	<i>L. mesenteroides</i>

<i>L. mesenteroides</i> subsp <i>mesenteroides</i> KMB608	<i>L. mesenteroides</i>	Correct	<i>L. mesenteroides</i>
<i>L. mesenteroides</i> subsp <i>mesenteroides</i> KMB609	<i>L. mesenteroides</i>	Correct	<i>L. mesenteroides</i>
<i>L. mesenteroides</i> subsp <i>mesenteroides</i> KMB611	<i>L. mesenteroides</i>	Correct	<i>L. mesenteroides</i>
<i>L. mesenteroides</i> subsp <i>mesenteroides</i> LbE15	<i>L. mesenteroides</i>	Correct	<i>L. mesenteroides</i>
<i>L. mesenteroides</i> subsp <i>mesenteroides</i> LbE16	<i>L. mesenteroides</i>	Correct	<i>L. mesenteroides</i>
<i>L. mesenteroides</i> subsp <i>mesenteroides</i> LK-151	<i>L. mesenteroides</i>	Correct	<i>L. mesenteroides</i>
<i>L. mesenteroides</i> subsp <i>mesenteroides</i> LN25	<i>L. mesenteroides</i>	Correct	<i>L. mesenteroides</i>
<i>L. mesenteroides</i> subsp <i>mesenteroides</i> LN27	<i>L. mesenteroides</i>	Correct	<i>L. mesenteroides</i>
<i>L. mesenteroides</i> subsp <i>mesenteroides</i> M11	<i>L. mesenteroides</i>	Correct	<i>L. mesenteroides</i>
<i>L. mesenteroides</i> subsp <i>mesenteroides</i> NBRC102481	<i>L. mesenteroides</i>	Correct	<i>L. mesenteroides</i>
<i>L. mesenteroides</i> subsp <i>mesenteroides</i> NBRC3832	<i>L. mesenteroides</i>	Correct	<i>L. mesenteroides</i>
<i>L. mesenteroides</i> subsp <i>mesenteroides</i> SRCM102733	<i>L. mesenteroides</i>	Correct	<i>L. mesenteroides</i>
<i>L. mesenteroides</i> subsp <i>mesenteroides</i> TR154	<i>L. mesenteroides</i>	Correct	<i>L. mesenteroides</i>
<i>L. mesenteroides</i> subsp <i>mesenteroides</i> WC0330	<i>L. mesenteroides</i>	Correct	<i>L. mesenteroides</i>
<i>L. mesenteroides</i> subsp <i>mesenteroides</i> WC0332	<i>L. mesenteroides</i>	Correct	<i>L. mesenteroides</i>
<i>L. mesenteroides</i> subsp <i>mesenteroides</i> Wikim17	<i>L. mesenteroides</i>	Correct	<i>L. mesenteroides</i>
<i>L. mesenteroides</i> subsp <i>mesenteroides</i> YL48	<i>L. mesenteroides</i>	Correct	<i>L. mesenteroides</i>
<i>L. pseudomesenteroides</i>1159	<i>L. pseudomesenteroides</i>	Revisited	<i>L. falkenbergense</i>
<i>L. pseudomesenteroides</i> 4882	<i>L. pseudomesenteroides</i>	Revisited	<i>L. falkenbergense</i>
<i>L. pseudomesenteroides</i> AMBR10	<i>L. pseudomesenteroides</i>	Revisited	<i>L. falkenbergense</i>
<i>L. pseudomesenteroides</i> BM2	<i>L. pseudomesenteroides</i>	Revisited	<i>L. falkenbergense</i>
<i>L. pseudomesenteroides</i> CBA3630	<i>L. pseudomesenteroides</i>	Correct	<i>L. pseudomesenteroides</i>
<i>L. pseudomesenteroides</i> HPK01	<i>L. pseudomesenteroides</i>	Revisited	<i>L. falkenbergense</i>
<i>L. pseudomesenteroides</i> KMB610	<i>L. pseudomesenteroides</i>	Revisited	<i>L. falkenbergense</i>
<i>L. pseudomesenteroides</i> LMG11482 T	<i>L. pseudomesenteroides</i>	Correct	<i>L. pseudomesenteroides</i>
<i>L. pseudomesenteroides</i> LMGCF06	<i>L. pseudomesenteroides</i>	Revisited	<i>L. falkenbergense</i>
<i>L. pseudomesenteroides</i> LMGCF08	<i>L. pseudomesenteroides</i>	Revisited	<i>L. falkenbergense</i>
<i>L. pseudomesenteroides</i> LMGCF15	<i>L. pseudomesenteroides</i>	Revisited	<i>L. falkenbergense</i>
<i>L. pseudomesenteroides</i> LMGH100	<i>L. pseudomesenteroides</i>	Revisited	<i>L. falkenbergense</i>
<i>L. pseudomesenteroides</i> LMGH278	<i>L. pseudomesenteroides</i>	Revisited	<i>L. falkenbergense</i>
<i>L. pseudomesenteroides</i> LMGH280	<i>L. pseudomesenteroides</i>	Revisited	<i>L. falkenbergense</i>
<i>L. pseudomesenteroides</i> LMGH284	<i>L. pseudomesenteroides</i>	Revisited	<i>L. falkenbergense</i>
<i>L. pseudomesenteroides</i> LMGH61	<i>L. pseudomesenteroides</i>	Revisited	<i>L. falkenbergense</i>
<i>L. pseudomesenteroides</i> LMGH83	<i>L. pseudomesenteroides</i>	Revisited	<i>L. falkenbergense</i>

<i>L. pseudomesenteroides</i> LMGH95	<i>L. pseudomesenteroides</i>	Revisited	<i>L. falckenbergense</i>
<i>L. pseudomesenteroides</i> LMGH97	<i>L. pseudomesenteroides</i>	Revisited	<i>L. falckenbergense</i>
<i>L. pseudomesenteroides</i> LMGTW1	<i>L. pseudomesenteroides</i>	Revisited	<i>L. falckenbergense</i>
<i>L. pseudomesenteroides</i> LMGTW3	<i>L. pseudomesenteroides</i>	Revisited	<i>L. falckenbergense</i>
<i>L. pseudomesenteroides</i> LMGTW6	<i>L. pseudomesenteroides</i>	Revisited	<i>L. falckenbergense</i>
<i>L. pseudomesenteroides</i> LMGTW8	<i>L. pseudomesenteroides</i>	Revisited	<i>L. falckenbergense</i>
<i>L. pseudomesenteroides</i> LN02	<i>L. pseudomesenteroides</i>	Revisited	<i>L. falckenbergense</i>
<i>L. pseudomesenteroides</i> LN12	<i>L. pseudomesenteroides</i>	Revisited	<i>L. falckenbergense</i>
<i>L. pseudomesenteroides</i> LN23	<i>L. pseudomesenteroides</i>	Revisited	<i>L. falckenbergense</i>
<i>L. pseudomesenteroides</i> MGYG-HGUT-00096	<i>L. pseudomesenteroides</i>	Correct	<i>L. pseudomesenteroides</i>
<i>L. pseudomesenteroides</i> PS12	<i>L. pseudomesenteroides</i>	Revisited	<i>L. falckenbergense</i>
<i>L. pseudomesenteroides</i> TR070	<i>L. pseudomesenteroides</i>	Correct	<i>L. pseudomesenteroides</i>
<i>L. rapi</i> DSM27776 T	<i>L. rapi</i>	Correct	<i>L. rapi</i>
<i>L. suionicum</i> CECT 8486	<i>L. suionicum</i>	Correct	<i>L. suionicum</i>
<i>L. suionicum</i> CECT 9216	<i>L. suionicum</i>	Correct	<i>L. suionicum</i>
<i>L. suionicum</i> CECT8484	<i>L. suionicum</i>	Correct	<i>L. suionicum</i>
<i>L. suionicum</i> DSM20241 T	<i>L. suionicum</i>	Correct	<i>L. suionicum</i>

Phylogroups

L. carnosum

L. kimchii

L. gelidum

L. inhae

Genomospecies 1

Genomospecies 2

L. citreum

L. pseudomesenteroides

L. falkenbergense

Genomospecies 3

L. suionicum

L. mesenteroides

Plasmids

pLCK4

LkipL4719

pKLC4

pLGMS32

pLFE1

pYS18

pJB01

pMG828

pJE1

pBF143

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70 96 98.6 100

L. citreum

Genomospecies 1

Genomospecies 2

L. holzapfelii
L. kimchii
L. rapi

L. inhae

L. gelidum

L. carnosum

L. pseudomesenteroides

L. falckenbergense

Genomospecies 3

L. mensenteroides

L. suionicum
L. litchii
L. fallax

18.2 70 100

L. inhae

L. gelidum

L. carnosum

L. fallax

L. citreum

L. kimchii

L. rapi

L. falckenbergense

L. pseudomesenteroides

L. litchii
L. holzapfelii

Genomospecies 1

Genomospecies 2

Genomospecies 3

L. mensenteroides

L. suionicum

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(A)

(B)

(A)

Cell cycle control, cell division, chromosome partitioning (D)
 Cell wall/membrane/envelope biogenesis (M)
 Post-translational modification, protein turnover, and chaperones (O)
 Signal transduction mechanisms (T)
 Intracellular trafficking, secretion, and vesicular transport (U)
 Translation, ribosomal structure and biogenesis (J)
 Transcription (K)
 Replication, recombination and repair (L)
 Energy production and conversion (C)
 Amino acid transport and metabolism (E)
 Nucleotide transport and metabolism (F)
 Carbohydrate transport and metabolism (G)
 Coenzyme transport and metabolism (H)
 Lipid transport and metabolism (I)
 Inorganic ion transport and metabolism (P)
 Secondary metabolites biosynthesis, transport, and catabolism (Q)
 Function unknown (S)

(B)

(C)