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A taxonomic note on the genus *Lactobacillus*: Description of 23 novel genera, emended description of the genus *Lactobacillus* Beijerinck 1901, and union of *Lactobacillaceae* and *Leuconostocaceae*

Jinshui Zheng[1, $], Stijn Wittouck[2, $], Elisa Salvetti[3, $], Charles M.A.P. Franz[4], Hugh M.B. Harris[5], Paola Mattarelli[6], Paul W. O'Toole[5], Bruno Pot[7], Peter Vandamme[8], Jens Walter[9, 10], Koichi Watanabe[11, 12], Sander Wuyts[2], Giovanna E. Felis[3, #*], Michael G. Gänzle[9, 13#*], Sarah Lebeer[2 #]

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[1]Huazhong Agricultural University, State Key Laboratory of Agricultural Microbiology, Hubei Key Laboratory of Agricultural Bioinformatics, Wuhan, Hubei, P.R. China.
[2]Research Group Environmental Ecology and Applied Microbiology, Department of Bioscience Engineering, University of Antwerp, Antwerp, Belgium
[3] Dept. of Biotechnology, University of Verona, Verona, Italy
[4] Max Rubner-Institut, Department of Microbiology and Biotechnology, Kiel, Germany
[5] School of Microbiology & APC Microbiome Ireland, University College Cork, Co. Cork, Ireland
[6] University of Bologna, Dept. of Agricultural and Food Sciences, Bologna, Italy
[7] Research Group of Industrial Microbiology and Food Biotechnology (IMDO), Vrije Universiteit Brussel, Brussels, Belgium
[8] Laboratory of Microbiology, Department of Biochemistry and Microbiology, Ghent University, Ghent, Belgium
[9] Department of Agricultural, Food & Nutritional Science, University of Alberta, Edmonton, Canada
[10] Department of Biological Sciences, University of Alberta, Edmonton, Canada
[11] National Taiwan University, Dept. of Animal Science and Technology, Taipei, Taiwan R.O.C.;
[12] Food Industry Research and Development Institute, Bioresource Collection and Research Center, Hsinchu, Taiwan R.O.C.
[13] Hubei University of Technology, College of Bioengineering and Food Science, Wuhan, Hubei, P.R. China.

[$] indicates shared first authorship;

# indicates shared last authorship

*corresponding authors;

Giovanna E. Felis, University of Verona, Dept. of Biotechnology, Strada le Grazie 15, 37134 Verona, tel: +39 045 6835627; email: giovanna.felis@univr.it;

Michael G. Gänzle, University of Alberta, Dept. of AFNS, 4-10 Ag/For Centre, Edmonton, AB, Canada, T6G 2P5, tel: + 1 780 492 0774; mail: mgaenzle@ualberta.ca

ABSTRACT

The genus *Lactobacillus* comprises 262 species (March 2020) that are extremely diverse at phenotypic, ecological, and genotypic levels. This study evaluated the taxonomy of *Lactobacillaceae* and *Leuconostocaceae* on the basis of whole genome sequences. Parameters that were evaluated included core genome phylogeny, (conserved) pairwise average amino acid identity, clade-specific signature genes, physiological criteria and the ecology of the organisms. Based on this polyphasic approach, we propose reclassification of the genus *Lactobacillus* into 25 genera including the emended genus *Lactobacillus,* which includes host-adapted organisms that have been referred to as the *L. delbrueckii* group, *Paralactobacillus* and 23 novel genera for which the names *Holzapfelia*, *Amylolactobacillus*, *Bombilactobacillus*, *Companilactobacillus, Lapidilactobacillus, Agrilactobacillus, Schleiferilactobacillus, Loigolactobacilus, Lacticaseibacillus, Latilactobacillus, Dellaglioa, Liquorilactobacillus, Ligilactobacillus, Lactiplantibacillus, Furfurilactobacillus, Paucilactobacillus, Limosilactobacillus, Fructilactobacillus, Acetilactobacillus, Apilactobacillus, Levilactobacillus, Secundilactobacillus,* and *Lentilactobacillus* are proposed. We also propose to emend the description of the family *Lactobacillaceae* to include all genera that were previously included in families *Lactobacillaceae* and *Leuconostocaceae*. The generic germ “lactobacilli” will remain useful to designate all organisms that were classified as *Lactobacillaceae* until 2020. This reclassification reflects the phylogenetic position of the micro-organisms, and groups lactobacilli into robust clades with shared ecological and metabolic properties, as exemplified for the emended genus *Lactobacillus* encompassing species adapted to vertebrates (such as *L. delbrueckii, L. iners, L. crispatus, L. jensensii L. johnsonii,* and *L. acidophilus*) or invertebrates (such as *L. apis* and *L. bombicola)*.

INTRODUCTION

The genus *Lactobacillus* was proposed by Beijerinck in 1901 and includes Gram-positive, fermentative, facultatively anaerobic and non-sporeforming microorganisms. The genus is classified in the phylum *Firmicutes*, class *Bacilli*, order *Lactobacillales*, family *Lactobacillaceae*, which contains the genera *Lactobacillus, Paralactobacillus* and *Pediococcus*. The *Leuconostocaceae,* including the genera *Convivina*, *Fructobacillus, Leuconostoc*, *Oenococcus* and *Weissella,* are the closest relative at the family level [1].

The early taxonomy of lactobacilli was based on phenotypic traits including optimal growth temperature, sugar utilization, and spectrum of metabolites produced [2]. Later in the 20th century, genotypic and chemotaxonomic criteria including DNA-DNA hybridisation, the mol% GC content and the chemical structure of the peptidoglycan were used for delineation of new bacterial species. Since 1983, the similarity of 16S rRNA genes has been used in bacterial taxonomy to provide phylogenetic schemes as backbones for classification and nomenclature [3]. Within the last 15 years, the sequencing of whole bacterial genomes became widely available and average nucleotide identity (ANI) values of genes shared between two bacterial genomes was introduced as the gold standard for delineation of new bacterial species [4, 5]. Although proposals have been made to apply a method-free species concept that is based on cohesive evolutionary forces [6], an ANI value of 95% (94 – 96%) has been almost consistently used in recent years to describe new bacterial species [7, 8] and was suggested to reflect biological significance of the prokaryotic species concept [9]. Published species of *Lactobacillaceae* and *Leuconostocaceae* were recently evaluated based on single-copy core genes and a fixed genome-genome similarity cutoff; the species were exclusive and discontinuous [10].

The introduction of genotypic methods such as 16S rRNA-based phylogeny already revealed the extensive diversity of the genus *Lactobacillus*, which includes the genus *Pediococcus* as an integral part [11–13]. Phylogenetic trees on the basis of single genes including the 16S rRNA gene allow grouping of species to phylogenetic clades, however, they do not have sufficient resolution to inform on the phylogenetic relationships of different clades [13, 14]. Phylogenetic studies of lactobacilli and pediococci on the basis of core genome phylogeny confirmed this phylogenetic heterogeneity; in addition the greater resolution of core genome phylogeny established the presence of consistent clades or phylogroups that are characterized by common phenotypic and ecological traits [12–17]. Physiological and phylogenetic considerations, and genomic analyses also replaced the earlier differentiation between “obligate homofermentative”, “facultative heterofermentative” and “obligate heterofermentative” lactic acid bacteria with a simpler differentiation of homofermentative lactic acid bacteria that metabolize hexoses via the Embden-Meyerhoff pathway to pyruvate as the key metabolic intermediate, and heterofermentative lactic acid bacteria, that metabolize hexoses via the phosphoketolase pathway to pyruvate and acetyl-phosphate as key intermediates [14, 18]. Within the genus *Lactobacillus*, homofermentative and heterofermentative lactobacilli form distinct phylogenetic clades [14, 16], while homolactic or heterolactic metabolism is conserved in other lactic acid bacteria at the family level. Pentose metabolism, however, is variable at the species or strain level [14].

It has been increasingly recognized that the genus *Lactobacillus* as currently defined displays a level of genetic diversity that by far exceeds what is generally found in bacterial genera and even bacterial families. The different phylogroups within the genus, however, are composed of species with a phylogenetic and physiological diversity that match the diversity of other bacterial genera [14]. Since 2015, several large-scale phylogenetic analyses based on core genome phylogeny of a comprehensive representation of species of the genera *Lactobacillus* and *Pediococcus* have revealed the discrepancy between the taxonomy of these genera and other bacterial genera [14, 16, 17]. The continuous species descriptions in the last years - 81 since 2015 - has brought the number of validly named species of *Lactobacillus* and *Pediococcus* to 273 (Figure 1 and Table S1), thus further increasing the diversity that is associated with the genus *Lactobacillus.* The current taxonomy, although widely accepted by medical community, food and health-related industries, by lay-persons, and used in national and international regulations, impedes research aimed at understanding the ecology, physiology, evolution and applications of this important group of organisms. This is because micro-organisms that are genetically very distinct and metabolically, ecologically, and functionally very diverse are grouped within the same genus. The lack of refined taxonomic structure, moreover, encourages the addition of new species to a genus that has already been shown to be overly heterogeneous and prevents the detection and description of functional properties or other communalities shared between members of the subgroups. However, a proposal for a formal re-evaluation of the taxonomy of the genera *Lactobacillus* and *Pediococcus* has not been made so far.

Here we re-evaluate the genetic relatedness and phylogeny of the species within the present genus *Lactobacillus* and its sister taxa in the *Lactobacillaceae* and *Leuconostocaceae* through a polyphasic approach [19]. For this, we considered Average Nucleotide Identity (ANI), Average Amino Acid Identity (AAI) and core-gene Average Amino Acid Identity (cAAI), core genome phylogeny, signature genes, and metabolic or ecological criteria. Within the *Lactobacillaceae*, 26 lineages were identified that are reliably separated and are characterised by conserved phenotypes and clade-specific signature genes. Twenty-three of these clades are described here as new genera, the description of the genera *Lactobacillus* and *Paralactobacillus* is emended while the description of the genus *Pediococcus* remains unchanged. Furthermore, data of the present study demonstrate that the family *Leuconostocaceae* Schleifer 2010 should be considered a later synonym of the family *Lactobacillaceae* Winslow et al. 1917 (Approved Lists 1980).

METHODS

Phylogenomic re-evaluation with RAxML and genome sequences of type strains

Genome sequences for type stains of all species in the families *Lactobacillaceae* and *Leuconostocaceae* which were available on August 19th, 2019 were obtained from Genbank (Genome set 1; Table S1). A listing of all species in the *Lactobacillaceae* is also available on https://site.unibo.it/subcommittee-lactobacillus-bifidobacterium/en and http://lactobacillus.ualberta.ca; the file hosted on the websites will be periodically updated by adding new species that have been validly published. All genomes were reannotated by Prokka [20], which uses Prodigal [21] for gene prediction. Protein sequences for each genome were extracted for gene clustering. FastOrtho was used to generate gene families based on protein sequences. First, an all-against-all alignment was performed by Blastp [22] with an E-value cutoff of 10^{-10}. Then, ortholog groups were created with the MCL algorithm with an inflation value of 2. The clustering results were filtered by a local Perl script as previously described [14] to reduce the influence of the fragmented protein sequences. All of the 114 single-copy core gene families of *Lactobacillaceae* and *Leuconostocaceae* were used for phylogenetic analysis. Protein sequences of each family were aligned by Muscle [23]. All the 114 alignments were trimmed with TrimAl [24] and were concatenated into a new alignment through a local Perl script. RAxML [25] was used for phylogenetic analysis based on the core gene alignment with PROTGAMMAILGF (LG+I+G+F) as the substitution model and 500 bootstrap samplings. The phylogenetic tree was visualized with iTOL [26].

Phylogenomic re-evaluation with iqtree and best quality genomes

A second tree of *Lactobacillaceae* and *Leuconostocaceae* species was calculated by using one representative genome per species (Genome set 2) as described earlier [10]. Of the 2459 high-quality genomes analysed, 16 genomes could not be assigned to a known species owing to low whole-genome similarity or low 16S rRNA gene similarity to type strains; we labeled these species as "unassigned species". In addition, multiple outgroups were added. To select outgroups, we used the Genome Taxonomy Database [27] to filter for the best quality genome for each of the 50 genera belonging to the order *Lactobacillales* (excluding species of *Lactobacillaceae* and *Leuconostocaceae)*, as evaluated by CheckM completeness values. Potential outgroups with more than 5% estimated contamination were excluded. The list of genomes used in the analysis is shown in Table S2. Genes were predicted for ingroup and outgroup genomes with Prodigal version 2.6.3 [21]. Single-copy core genes were extracted using progenomics version 0.1.0 [28] with the following options: 30 seed genomes, minimum presence in 25 seed genomes, and required single-copy presence in 99% of all genomes. Core genes were aligned using mafft version v7.407 [29]. The aligned core genes were then concatenated into a protein supermatrix, and columns with more than 10% gaps were removed using trimal version 1.4.rev15 [24]. A phylogeny was inferred on the supermatrix with iqtree version 1.6.11 [30], using the LG+G+F protein substitution model. Branch support was calculated using 1000 bootstrap trees with the UFBoot2 algorithm [31]. Finally, the full tree was rooted using the clade (*Listeria*, *Listeria_A*, *Brochothrix*) as outgroup. The tree was visualized using ggtree version 1.16.0 [32].

Calculation of average amino acid identity (AAI) and average amino acid identity of core proteins (cAAI)

AAI was calculated between each pair of type strain genome sequences (Genome set 1) using CompareM [33]. cAAI values were additionally calculated to minimize the impact of horizontal gene transfer on pairwise AAI values. Acquisition of genes by lateral gene transfer substantially contributes to genetic diversity in bacteria [34]. The extent of gene acquisition by lateral gene transfer depends on the lifestyle of the micro-organism [35]. Lateral gene transfer distorts the molecular clock of bacterial evolution and the inferred phylogenetic relationship between different species [36], particularly for micro-organisms that share a habitat and evolve by acquisition of similar genes. To minimize the impact of lateral gene transfer, we defined the cAAI based on the protein sequences of core gene families. We used soft core gene families that are shared by more than 90% of the genomes studied. Protein sequences belonging to the soft-core gene families of each genome were used to caculate cAAI by CompareM. Differences between cAAI and AAI indicate divergent or convergent evolution through acquisition of diverse or common genes, respectively. In addition, habitat adaptation by specific phylogenetic clades was assessed by analysis of clade-specific genes as described below.

Identification of genes that are exclusive to specific phylogenetic clades (signature genes)

The complete pangenome of all best-quality genomes (Genome set 2) was inferred using OrthoFinder 2.3.3 [37] with MMseqs2 version d36de [38] as sequence search program. For the analysis of gene family presence/absence and signature genes, the outgroup genomes were removed from the tree and the pangenome dataset. The gene family presence/absence plot was created by grouping together gene families with the same presence/absence pattern across species, leaving out two types of trivial patterns: gene family presence in a single species and gene family presence in all species. The patterns with a frequency (number of gene families) of four or more were then visualized in descending order of frequency. Signature genes were defined as gene families present in all genomes of a clade (subtree) and absent in all other genomes. Phylogroups were defined by their type species; species were assigned to the phylogroup of the type species they shared the most recent common ancestor with.

For all analysis involving the core genome phylogenetic tree and the gene family presence/absence patterns, R version 3.6.1 (https://www.R-project.org) was used for data processing and visualization. R packages that were crucial included the tidyverse version 1.2.1 (https://CRAN.R-project.org/package=tidyverse) and tidygenomes version 0.1.2 [39]. The code used for these analyses is deposited in two repositories on GitHub [40].

RESULTS

Phylogenomic evaluation of *Lactobacillaceae*

A core genome phylogenetic tree of all *Lactobacillaceae* type strains for which genome sequence data was available in August 2019 is shown in Figure 2. The *Lactobacillaceae* consistently form 26 phylogenetic groups that match all prior core-genome phylogenetic analyses of the family although more than 60 genomes were added since 2015 [13, 14, 16, 17] and are supported with 100% bootstrap values, indicating they have been shaped by cohesive evolutionary forces. Below, we propose genus status for each of these 26 phylogenetic groups, which include an emended genus *Lactobacillus* (for the phylogenetic group that includes *L. delbrueckii,* the type species of *Lactobacillus*), *Paralactobacillus*, *Pediococcus* and 23 new genera consisting of species previously assigned to the genus *Lactobacillus*.

The *L. delbrueckii* group that contains the type strain of the genus forms a monophyletic clade with *L. floricola* and *L. amylophilus*. Heterofermentative lactobacilli together with pediococci and the *L. plantarum* group also form a monophyletic clade; the remaining homofermentative lactobacilli, however, are not monophyletic (Figure 2). Virtually all of the *Lactobacillus* species that were described over the past 2 years cluster within one of the phylogenetic groups identified in 2017 (Figure 2)[17]. Of the recently described species, only the candidate species *Lactobacillus jinshani* [41] can not be assigned to one of the established phylogenetic groups and forms a separate lineage that is currently represented by only this candidate species.

We have previously shown that the lifestyle of species within groups, as inferred from isolation source, genomic, functional, ecological, and physiological information, is remarkably conserved within these groups and can be assigned to insect or flower-associated habitats, vertebrate hosts, to a free-living lifestyle, or to a nomadic lifestyle that transitions between different habitats [17]. For example, the *L. mali* group that predominantly includes micro-organisms with a free-living lifestyle clusters separately from the *L. salivarius* group, which predominantly includes micro-organisms with a vertebrate host-adapted lifestyle [17, 27](Figure 2). New species that were described since 2017 all conform to the lifestyle that was assigned to other species in the same phylogenetic tree (Figure 2)[17].

Evaluation on basis of cAAI and AAI values.

To validate the assumption that each of these 26 phylogenetic groups in the *Lactobacillaceae* encompass a phylogenetic diversity that is commonly assigned to a bacterial genus, all 38,364 pairwise cAAI and AAI values for the *Leuconostocaceae* and *Lactobacillaceae* species for which genome sequences of the type strains were available were calculated (Table S3 and Table S4). The intra-family cAAI and AAI values for *Lactobacillaceae*, which are largely shaped by intra-genus cAAI values of *Lactobacillus* species, overlap with the inter-family cAAI and AAI values for *Lactobacillaceae* and *Leuconostocaceae*, confirming the phylogenetic heterogeneity of *Lactobacillus* as well as the lack of a clear speration between *Lactobacillaceae* and *Leuconostocaceae* (Figure 3 and Figure S1). If intra-group cAAI and AAI values are calculated for the 26 phylogenetic groups of *Lactobacillaceae* excluding *Pediococcus* species, the distribution of intra-group cAAI and AAI values matched the intra-genus distribution observed in *Pediococcus*, *Weissella*, and *Leuconostoc* (Figure 4 and Figure S2). Inter-genus cAAI values of more than 70% are observed for the *L. brevis* and *L. collinoides* groups. Despite these relatively high cAAI values, the assignment of the *L. brevis* group and the *L. collinoides* group is justified on the basis of the consistent clustering in phylogenetic trees (Figure 2) and the distinct metabolism and ecology of species in the *L. brevis* and *L. collinoides* groups. Likewise, the description of the genus

Convivina despite high AAI values to *Fructobacillus* was based on ecological and metabolic criteria *Fructobacillus* [42].

The intra-group distribution of cAAI and AAI values is shown in Figure 5 and Figure S3. With the exception of the *L. brevis, L. collinoides, L. reuteri* and *L. salivarius* groups, all groups are exclusive, i.e. the lowest intra-group cAAI values are higher than the highest inter-group cAAI values for any species in the group (indicated in red in Figure 5; data provided in Table S3). The *L. delbrueckii* group, the *L. casei* group and the *L. salivarius* group are among the most diverse groups. The diversity within the *L. casei* and the *L. salivarius* groups relative to other groups is higher on the basis of AAI values (Figure S3) than when assessed on the basis of cAAI values (Figure 5). This implies that the diversification of the species in these groups is mediated by horizontal gene transfer and acquisition of lifestyle-associated genes (see below). This observation matches the diverse lifestyles in the *L. salivarius* group, which contains free-living species or species with unknown lifestyle in addition to host-adapted species. Information on the ecology of the divergent *L. pantheris / L. sharpeae* clade within the *L. casei* group is currently too limited to conclude on the lifestyle of these organisms.

Identification of genes that are exclusive to specific phylogenetic clades (signature genes)

To determine whether the 26 phylogenetic groups can be characterized by clade-specific genes, we analyzed the presence/absence of gene families within all species of the families *Lactobacillaceae* and *Leuconostocaceae* [43]. Gene families that are present in all best-quality genomes of a certain clade but are absent in all other genomes were termed signature genes. Signature genes reflect a common evolutionary history of a phylogenetic clade or result from horizontal gene transfer and relate to common lifestyles, ecologies, and physiological properties. Signature genes therefore allow inferences about the evolutionary forces that likely shaped the cluster.

Most of the proposed new genera are supported by signature genes. This is especially the case for the *L. delbrueckii*, *L. alimentarius*, *L. mellifer, L. concavus*, *L. perolens*, *L. sakei, L. coryniformis, L. casei*, *L. plantarum*, *L. rossiae*, *L. vaccinostercus*, *L. kunkeei*, *L. fructivorans* and *L. brevis* groups. Each of these phylogroups contain at least four signature genes (Figure 6, Table S5). The genera *Leuconostoc*, *Fructobacillus*, *Oenococcus*, *Weissella* and *Pediococcus* also show a relatively large number of signature genes. Of the remaining groups, signature genes can be identified if the most distant member(s) of the group is (are) omitted (Figure 2). The *L. buchneri* group contains signature genes if *L. senioris* is omitted and the *L. collinoides* group contains signature genes if the *L. malefermentans / L. oryzae* outgroup is omitted. The *L. reuteri*, *L. salivarius*, and *L. mali* groups do not contain signature genes and can also not be divided into sub-clades that contain signature genes (Fig. 6). Of note, the *L. reuteri* group and the *L. salivarius* group were also identified as non-exclusive on the basis of cAAI values (Fig. 5). The remaining six phylogroups contain only one genome, making it impossible to assess their harbouring of signature genes. Although phylogroups with a smaller number of species obviously show larger numbers of signature genes, the impact of phylogroup sample size is limited. Even large phylogroups such as the *L. delbrueckii* and *L. alimentarius* groups show a relatively large number of signature genes. The identification of signature genes thus conforms to the phylogenetic analyses (Fig. 2) and cAAI values (Fig. 5), likely reflecting a common evolutionary history of phylogroups/genera, and is therefore suitable to provide additional information on the delineation of bacterial genera. The current signature genes analysis supports most of the new genera proposed in this work, particularly the separation of the *L. brevis* and *L. collinoides* groups, which were combined in earlier studies [16, 27], and the separation of the *L. salivarius* and *L. mali* groups, which were also assigned to a single phylogenetic group in the past [11, 13, 14].

Phylogenomic evaluation of *Lactobacillaceae* and *Leuconostocaceae*

We further used the phylogenetic trees and cAAI values to explore the relationships of *Lactobacillaceae* and *Leuconostocaceae*. To identify clades and nodes that are consistently identified by different approaches, we deliberately used two different datasets, type strain genomes and best-quality genomes, and different bioinformatics pipelines. The overall topology of the phylogenetic trees was remarkably consistent. However, the core genome phylogenetic tree generated using the type strains of the 26 phylogenetic groups of the *Lactobacillaceae*, 31 type strains of other genera in the *Lactobacillales,* and 8 type strains from *Bacillales* as outgroup placed the *Leuconostocaceae* as a monophyletic cluster within the *Lactobacillaceae* that shares the root with heterofermentative lactobacilli, the genus *Pediococcus*, and the *L. plantarum* group (Figure 7A). The core genome tree based on the genome set used for the signature gene analysis (best-quality genomes) placed the *Leuconostocaceae* as a monophyletic cluster within the heterofermentative lactobacilli, sharing the root with the *L. rossiae*, *L. reuteri* and *L. vaccinostercus* groups (Figure 7B and Figure S4). This means that the family *Lactobacillaceae* is not monophyletic unless *Leuconostocaceae* are included. The close relationship of *Leuconostocaceae* and *Lactobacillaceae* is also supported by the cAAI values (Figure 8 and Table S3). Inter-family cAAI and AAI values between *Leuconostocaceae* and *Lactobacillaceae* overlap with the intra-family cAAI values. Moreover, the cAAI values between *Leuconostocaceae* and heterofermentative lactobacilli (Table S3) range from 53 to 60% and are thus in the same range as the cAAI values between heterofermentative lactobacilli and the *L. delbrueckii* group (54% to 58%). These findings do not support a taxonomic separation of the two families.

DISCUSSION

Family-level considerations. The genus *Pediococcus* has consistently been recognized as an integral part of the genus *Lactobacillus*. Some studies also suggested that the family *Leuconostocaceae*, which was described in in 2010 on the basis of 16S rRNA sequence similarities [1, 44], are, on the contrary, an integral part of the lactobacilli [15, 16]. The phylogenetic and comparative genomic analyses conducted here confirmed that *Leuconostocaceae* and *Lactobacillaceae* are closely related and intertwined. Moreover, two different datasets and bio-informatic approaches placed the *Leuconostocaceae* as a monophyletic cluster within the *Lactobacillaceae.* This result is also in line with the Genome Taxonomy Database (https://gtdb.ecogenomic.org/, 24), in which the members of the *Leuconostocaceae* were considered as members of the *Lactobacillaceae.*

The current analyses also indicate that heterofermentative lactobacilli are more closely related to *Leuconostoc* and *Weissella* than they are to the *L. delbrueckii* group (Figure 8, Table S2 and S3). This confirms that the two fermentation types, homofermentative and heterofermentative, are closely linked to the phylogeny of lactobacilli. The genetic relatedness between heterofermentative lactobacilli and *Leuconostocaceae* as assessed on the basis of cAAI values is closer than the relationship between heterofermentative lactobacilli and the *L. delbrueckii* group. Exceptions are *Oenococcus* species, which share less than 54.5% cAAI to any current member of the *Lactobacillaceae*. Despite the overall congruent topology, the phylogenetic trees generated in this study are inconsistent with respect to the position of *Leuconostocaceae* within the *Lactobacillaceae*. Depending on the dataset used for calculation of the tree, the root of *Leuconostocaceae* is shared with all heterofermentative lactobacilli, *Pediococcus* and the *L. plantarum* group (Figure 7A), or shared with the *L. reuteri*, *L. vaccinostercus* and the *L. rossiae* group only (Figure 8 and Figures S4 and S5) [16]. All of these trees support the observation that *L. iners* and *Oenococcus* species are the most distantly related members of *Lactobacillaceae* and *Leuconostocaceae*, respectively, with respect to their cAAI values (50.58%). The uncertainty with respect to the last common ancestor of *Leuconostocaceae* and *Lactobacillaceae* has no implications for their taxonomic assignment into a single family. As each node separating homofermentative from heterofermentative lactic acid bacteria represents a switch of a micro-organism from homofermentation to heterofermentation, however, it relates to the molecular and ecological evolution of lactic acid bacteria and may thus be of interest for future studies.

Within *Lactobacillaceae,* the *L. delbrueckii* group forms a robust monophyletic clade with the *L. floricola* group and the *L. amylophilus* group. Species in this clade also differ from other lactobacilli with regards to physiological criteria, e.g. vancomycin sensitivity related to the inter-peptide of the peptidoglycan, the absence of pyruvate formate lyase, and the absence of the pentose-phosphate pathway enabling homofermentative pentose metabolism [14, 45]. The *L. mellifer* group and the *L. alimentarius* group represent the link between the *L. delbrueckii* group and other lactobacilli with respect to phylogeny and phenotypes; *Pediococcus* and the *L. plantarum* group represent the evolutionary link between homofermentative and heterofermentative lactic acid bacteria. Although pediococci and the *L. plantarum* group obviously share major metabolic features with homofermentative lactobacilli [18], they are phylogenetically related to heterofermentative lactobacilli and *Leuconostocaceae* (this study).

Criteria for delineation of new genera. Considerations of the different forces that shape bacterial evolution led to the proposal of a methods-free concept in bacterial taxonomy that considers ecological divergence rather than numerical thresholds [6]. For species level taxonomy, the ANI between two genomes has been consistently used to delineate new taxa, however, the phylogenetic signal of ANI values is lost for ANI values below 70%, i.e. ANI is not a useful metrics for genus level taxonomy. This was particularly noted for the taxonomy of genus *Lactobacillus* [14, 16]. The pairwise average amino acid identity (AAI) and the conserved proteins (POCP) have been proposed for classification at the genus level [5, 46]; of these two, the AAI is the more powerful metrics because it is based on the proteins sequences and does not only account for the presence or absence of protein. Although formal thresholds for genus-level AAI values have not been established, the vast majority bacterial intra-genus AAI values is higher than 68 % [5]. Moreover, AAI values can be calculated on the basis of core proteins to exclude proteins that were acquired by lateral gene transfer (this study), an approach that was also employed for comparison on the basis of nucleotide identities [10]. Threshold values for the delineation of new bacterial genera on the basis of AAI or cAAI values have not been consistently used [43] but the transition zones for intra-genus and inter-genus AAI and cAAI values can be derived by comparison with other bacterial genera, or alternative taxonomic approaches [27]. A framework for taxonomy of isolates with unknown ecology including uncultured organisms was previously established on the basis of the relative evolutionary distance of bacteria as determined by core genome phylogeny [27]. This Genome Taxonomy Database classified species of the genus *Lactobacillus* into 18 phylogenetic clades equivalent to genera which overlap with the 24 phylogenetic clades that were proposed on the basis of ecological and phylogenetic considerations [14, 17]. An approach focusing on ecology and evolution has also been applied to lactobacilli [17] and demonstrated a remarkable overlap of their phylogeny and ecology. A methods-free approach, however, relies on information on the ecology of a multiple isolates of a specific bacterial taxon. Currently, ecology and evolution are well-studied for only a small subset of species in the genus *Lactobacillus,* while the ecology of a large number of species and several phylogenetic groups remains unclear because of the lack of data or the low number of species in the group [17]. Building on previous studies on the taxonomy, ecology and phylogeny of *Lactobacillus*, we based the delineation of novel genera on the following criteria, listed in decreasing order of priority: (i) the novel genera represent monophyletic phylogenetic groups; (ii) intra-genus AAI and cAAI values are higher than inter-genus AAI and cAAI values, and these show limited overlap; (iii) species in the proposed genera have common characteristics with regard to ecology and physiology that differentiate the proposed genus from other genera, and this distinction is generally supported by the presence signature genes [17, 43]; and (iv) the proposed genera are largely consistent with the previously established phylogenetic groups [13, 14, 17] and with the classification based on relative evolutionary distance [27].

Classification of the *Lactobacillaceae* species into 26 genera comprising an emended genus *Lactobacillus* (i.e. one confined to the *L. delbrueckii* group), *Pediococcus, Paralactobacillus*, and 23 new genera that correspond to the phylogenetic groups shown in Fig. 2 fits these four criteria best. The proposed genera *Lacticaseibacillus* (the *L. casei* group) and *Ligilactobacillus* (the *L. salivarius* group) remain relatively heterogeneous, particularly with respect to their AAI values, indicating that specific subgroups in these genera currently adapt to different ecological habitats. This was proposed for the *L. casei* group with respect to oxidative stress tolerance [47] and for the *L. salivarius* group where megaplasmids and specific exopolysaccharide clusters may relate to human host adaptation [48]. Conversely, the proposed genus *Secundilactobacillus* (the *L. collinoides* group) and the proposed genus *Levilactobacillus* (the *L. brevis* group) are relatively homogeneous with respect to their cAAI values, but they are separated by phylogenetic analysis, their metabolism, and their ecology. The *L. collinoides* group is differentiated from *L. brevis* by adaptation to hexose-depleted habitats, which is reflected by lack of mannitol-dehydratase, diol-dehydratase activity, and a metabolic focus on pentoses. These metabolic and ecological differences are also supported by the more divergent AAI values and the identification of signature genes.

Overall, the available evidence is highly consistent in its support with the proposed taxonomic classification. Moreover, 16S rRNA sequence identities and AAI values readily allow new species to be assigned to one of the 26 genera of *Lactobacillaceae*. Species that exhibit a 16S rRNA gene identity that is greater than 94.5% to the type species of a genus [49] and cluster integral to that genus when using 16S rRNA phylogeny are generally assigned correctly even in the absence of further analyses (Fig. S6). However, 16S rRNA gene identity and 16S rRNA phylogeny should be complemented with core genome phylogeny in combination with whole-genome similarity metrics to validate the taxonomy at the genus level [4]. We compared the performance of several whole-genome metrics, i.e. ANI, CNI, AAI and cAAI. Of these four, ANI and AAI can easily be computed using publicly available tools. Novel species of *Lactobacillaceae* can be classified on the genus level using an AAI threshold of 68% to the type strain of the most closely related genus [5] (Fig. S3 and S7). Values below that level require a more detailed analysis that also includes core genome phylogeny and cAAI values, and may justify the description of novel genera when phylogenetic placement and AAI and cAAI values are supported by metabolic and ecological criteria. We believe that this proposed taxonomy will facilitate further research and discovery. The diversity of lactobacilli – the generic term remains useful to designate organisms in all 25 genera that are currently classified as *Lactobacillus* species - is likely much greater than currently known as a majority of strains were isolated from humans, domesticated animals, and food. Sampling of more diverse plant or environmental sources, and of wild animals will likely extend our perspective on the phylogenetic and metabolic diversity of *Lactobacillaceae.*

Species-level considerations.

TAXONOMIC IMPLICATIONS OF THE STUDY.

Principle 8 of the International Code of Nomenclature of Prokaryotes states that each order or taxon of a lower rank with a given circumscription, position, and rank can bear only one correct name, i.e. the earliest that is in accordance with the Rules of this Code. Based on the data discussed above, we consider the family *Leuconostocaceae* Schleifer 2010, which was circumscribed on the basis of phylogenetic analyses of 16S rRNA sequences a later synonym of the family *Lactobacillaceae* Winslow et al. 1917 (Approved Lists 1980). Below we propose an emended description of the *Lactobacillaceae* family.

We further propose that the 23 phylogenetic groups and single lines of descent (Figure 2) represent novel genera. The new taxa are described below and an emended description of the genera *Lactobacillus* and *Paralactobacillus* are proposed. The new genera are described in an order that reflects their phylogenetic relationships and recognizes the distinct phylogenetic position of homofermentative and heterofermentative lactobacilli (Figures 2, 5, 6, 7 and 8).

The genome based analyses confirmed that the only strain of *P. lolii* that has been described, *P. lolii* DSM 19927^T, is a strain of *P. acidilactici*, with cAAI and AAI values to the *P. acidilactici* type strain of 99.4% and 98.1%, respectively [50] (Tables S3 and S4). *P. lolii* is thus a later synonym of *P. acidilactici*.

The genome-based analyses also suggested that the two previously described subspecies of *L. aviarius* should be elevated to species level. *Lactobacillus aviarius* was isolated from the intestine of chickens in 1984 and two subspecies were recognised based on different sugar fermentation profiles: *L. aviarius* subsp. *aviarius* does not ferment trehalose and cellobiose (while *L. aviarius* subsp. *araffinosus* does) but metabolises galactose, lactose, melibiose and raffinose (while *L. aviarius* subsp. *araffinosus* does not) [51]. The availability of the genome sequences of the type strains of both subspecies revealed that they are only distantly related, which support that these two subspecies should be recognised as different species.

Emended description of the family *Lactobacillaceae*

The emended family *Lactobacillaceae* is circumscribed on the basis of phylogenomic analyses reported in the present paper, and includes all the genera previously included in families *Lactobacillaceae* Winslow et al. 1917 (Approved Lists 1980) and *Leuconostocaceae* Schleifer 2010, i.e. *Convivina*, *Fructobacillus, Lactobacillus, Leuconostoc*, *Oenococcus, Paralactobacillus, Pediococcus* and *Weissella*.

Cells are Gram-positive, non-sporeforming facultative or strict anaerobic bacteria. Cells are coccoid or rod-shaped, which may form chains, pairs or tetrads (genus *Pediococcus*). Main product of the fermentative metabolism is lactate, and other products may be acetate, ethanol, CO2, formate, or succinate. Complex nutritional requirements for amino acids, peptides, nucleic acid derivatives, vitamins, salts, fatty acids or fatty acid esters, and fermentable carbohydrates. *Lactobacillaceae* are the only family in the *Lactobacillales* that includes homofermentative and heterofermentative micro-organisms.

Type genus: *Lactobacillus* Beijerinck 1901 212 (Approved Lists).

HOMOFERMENTATIVE LACTOBACILLACEAE

EMENDED DESCRIPTION OF *LACTOBACILLUS*

Lactobacillus species are Gram-positive, homofermentative, thermophilic and non-sporeforming rods. Most *Lactobacillus* species do not ferment pentoses and none of the organisms encode genes for the pentose phosphate pathway or pyruvate formate lyase. The emended description of the genus includes all organisms that were previously assigned to the *L. delbrueckii* group [17]. *Lactobacillus* species are host-adapted; the *Lactobacillus melliventris* clade (previously termed the Firm-5 clade) is adapted to social bees [52] while all other *Lactobacillus* species are adapted to vertebrate hosts. *Lactobacillus* species ferment a relatively broad spectrum of carbohydrates and have the strain-specific ability to ferment extracellular fructans, starch, or glycogen [53, 54]. The *L. melliventris* clade species also ferment a wider range of carbohydrates when compared to insect-adapted species in the genera *Apilactobacillus* and *Bombilactobacillus*. In intestinal habitats, *Lactobacillus* species are generally associated with heterofermentative lactobacilli. For specific examples, it was shown that cohabitation of *Lactobacillus* species with heterofermentative lactobacilli is based on long-term evolutionary relationships in biofilms [55] and a complementary preference for carbon sources [18, 56]. Many *Lactobacillus* spp. are able to ferment mannitol, which also reflects co-habitation with heterofermenters. The metabolic focus of *L. delbrueckii* on lactose [57] explains its dominance in yoghurt and cheese fermentations but also relates to its presence in the intestine of suckling piglets [54]. The genus *Lactobacillus* remains a relatively heterogenous genus with *L. iners* as the most distant member. *L. iners* has the smallest genome size among all *Lactobacillaceae*, which reflects its strict adaptation to the human vagina.

In addition to their relevance in intestinal and vaginal ecosystems, *Lactobacillus* species frequently occur in dairy and cereal fermentations and are widely used as starter cultures for production of fermented dairy products [58, 59].

A phylogenetic tree of all species in the genus *Lactobacillus* is provided in Figure S6A.

The type species of the genus *Lactobacillus* is *L. delbrueckii*. Although the nomenclature of species in the emended genus *Lactobacillus* remains unchanged, a list of species and a list of their properties is provided below.

Lactobacillus delbrueckii

Lactobacillus delbrueckii (*Bacillus delbrücki*) (del.brueck'i.i. N.L. gen. n. *delbrueckii*, of Delbrück, named for M. Delbrück, a German bacteriologist).

Type species of the genus *Lactobacillus*. Because of the high phenotypic and genotypic similarities between *L. delbrueckii, L. leichmannii, L. lactis* and *L. bulgaricus*, only *L. delbrueckii* is retained as a separate species. Both *L. lactis* and *L. leichmannii* are treated as *L. delbrueckii* subsp. *lactis* and *L. bulgaricus* as *L. delbrueckii* subsp. *bulgaricus* [60]. All strains produce D(-)- lactic acid.

Lactobacillus delbrueckii subsp. *bulgaricus*

Lactobacillus delbrueckii subsp. *bulgaricus* (bul.ga'ri.cus. N.L. masc. adj. *bulgaricus*, Bulgarian).

Strains of this subspecies were previously referred to as *L. bulgaricus*. *L. delbrueckii* subsp. *bulgaricus* ferment glucose to D(-)- lactic acid and also metabolise fructose, mannose and lactose, but not sucrose [60, 61]. *L. delbrueckii* subsp. *bulgaricus* undergoes genome reduction which particularly relates to loss or silencing of genes coding for metabolism of carbohydrates [57]. The genome size is 1.76 Mbp and the mol% GC content of DNA is 49.9.

Isolated from yoghurt and cheese and an important starter cultures in the production of these foods [58, 59] but also detected by culture-independent methodology in the intestinal microbiota of suckling piglets [54].

The type strain is ATCC 11842^T = CCUG 41390^T = CIP 101027^T = DSM 20081^T = IFO (now NBRC) 13953^T = JCM 1002^T = LMG 6901^T = LMG 13551^T = NCTC 12712^T = VKM B-1923^T.

Genome sequence accession number: JQAV00000000.

16S rRNA gene accession number: CR954253.

Lactobacillus delbrueckii subsp. *delbrueckii*

Lactobacillus delbrueckii (del.bruec'ki.i. N.L. gen. n. *delbrueckii,* of Delbrück, named after M. Delbrück, a German bacteriologist).

L. delbrueckii subsp. *delbrueckii* ferment glucose to D(-)-lactic acid and also metabolise sucrose, fructose and mannose, but not lactose. Characteristics of the species/subspecies are provided by [61–65]. The genome size is 1.75 Mbp and the mol% GC content of DNA is 49.9.

Isolated from vegetable source, sour grain mash and fermented grains.

The type strain is ATCC 9649^T = CCUG 34222^T = CIP 57.8^T = DSM 20074^T = IFO (now NBRC) 3202^T = JCM 1012^T = LMG 6412^T = NCIMB 8130^T (formerly NCDO 213) = NRRL B-763^T = VKM B-1596^T.

Genome sequence accession number: AZCR00000000.

16S rRNA gene accession number: AY773949.

Lactobacillus delbrueckii **subsp.** ***indicus***

Lactobacillus delbrueckii subsp. *indicus* (in'di.cus. L. masc. adj. *indicus*, of India, Indian, referring to the geographical origin of the strains).

Lactobacillus delbrueckii subsp. *indicus* metabolise sucrose, fructose, lactose and mannose, but is unable to ferment maltose and trehalose [66]. The genome size is 1.88 Mbp and the mol% GC content of DNA is 49.5.

Isolated from a fermented dairy product dahi from India.

The type strain is NCC725^T = CCUG 51390^T = DSM 15996^T = JCM 15610^T = LMG 22083^T.

Genome sequence accession number: AZFL00000000.

16S rRNA gene accession number: AY421720.

Lactobacillus delbrueckii **subsp.** ***jakobsenii***

Lactobacillus delbrueckii subsp. *jakobsenii* (ja.kob.se'ni.i. N.L. gen. n. *jakobsenii*, of Jakobsen, named after Mogens Jakobsen for his significant contributions in the field of food microbiology including biodiversity, production and safety of African fermented foods and beverages).

Lactobacillus delbrueckii subsp. *jakobsenii* metabolise sucrose, maltose and trehalose but is unable to ferment lactose [67]. The genome size is 1.75 Mbp and the mol% GC content of DNA is 50.3.

Isolated from dolo wort used in the production of the fermented African beverge dolo in Burkina Faso.

The type strain is ZN7a-9^T=DSM 26046^T = LMG 27067^T.

Genome sequence accession number: JQCG00000000.

16S rRNA gene accession number: ALPY00000000.

Lactobacillus delbrueckii **subsp.** ***lactis***

Lactobacillus delbrueckii subsp. *lactis* (lac'tis. L. gen. n. *lactis*, of milk).

L. delbrueckii subsp. *lactis* includes strains previously designated as *L. lactis* and *L. leichmannii*; *L. delbrueckii* subsp. *lactis* ferment glucose to D(-)-lactic acid and also metabolises sucrose, fructose and mannose, maltose and trehalose [60]. The genome size is 1.87 Mbp and the mol% GC content of DNA is 49.9.

Isolated from milk, cheese, compressed yeasts and grain mash.

The type strain is L 110^T = ATCC 12315^T = CCUG 31454^T = CIP 101028^T = DSM 20072^T = JCM 1248^T = LMG 7942^T = NBRC 102622^T = NRRL B-4525^T.

Genome sequence accession number: AZDE00000000.

16S rRNA gene accession number: AY050173.

Lactobacillus delbrueckii **subsp.** ***sunkii***

Lactobacillus delbrueckii subsp*. sunkii* (sun’ki.i. N.L. gen. n. *sunkii*, of sunki, the name of the non-salted, traditional, Japanese pickle from which the type strain was isolated).

L. delbrueckii subsp. *sunkii* ferment glucose to D(-)- lactic acid and also metabolise sucrose, fructose and mannose, maltose but not lactose [68]. The genome size is 2.0 Mbp and the mol% GC content of DNA is 50.1.

Isolated from a traditionally fermented Japanese red turnip.

The type strain is YIT 11221^T = DSM 24966^T = JCM 17838^T.

Genome sequence accession number: CP018217.

16S rRNA gene accession number: AB641833.

Lactobacillus acetotolerans

Lactobacillus acetotolerans (a.ce.to.to’le.rans. L. neut. n. *acetum* vinegar; L. pres. part. *tolerans* tolerating, enduring; N.L. part. adj. *acetotolerans* vinegar tolerating).

Lactobacillus acetotolerans produces DL-lactic acid from glucose, mannose, fructose and trehalose but not from arabinose, sucrose, lactose, melibiose and raffinose [69]. The genome size is 1.59 Mbp and the mol% GC content of DNA is 36.3.

The species is part of the core microbiome of mash fermentations for production of grain liquor and vinegar in China and Japan [58]; it was also isolated from other plant fermentations, silage, and from the intestine of swine, ducks, and cattle.

The type strain is ATCC 43578^T = CCUG 32229^T = CIP 103180^T = DSM 20749^T = JCM 3825^T = LMG 10751^T = NBI 3014^T.

Genome sequence accession number: AYZC00000000.

16S rRNA gene accession number: M58801.

Lactobacillus acidophilus

Lactobacillus acidophilus (a.ci.do’phi.lus. N.L. neut. n. *acidum* acid; Gr. masc. adj. *philos* loving; N.L. masc. adj. *acidophilus* acid-loving).

Lactobacillus acidophilus produces DL-lactic acid from cellobiose, galactose, lactose, maltose, mannose, sucrose and trehalose, but not from mannitol [70–72]. Specific strains have been used as probiotics. The genome size of the type strain is 1.95 Mbp and the mol% GC content of DNA is 34.6.

Isolated from the intestinal tract of humans and animals, human mouth, human vagina, sourdough and wine.

The type strain is ATCC 4356^T = CCUG 5917^T = CIP 76.13^T = DSM 20079^T = IFO (now NBRC) 13951^T = JCM 1132^T = LMG 9433^T = LMG 13550^T = NCTC 12980^T = NRRL B-4495^T = VKM B-1660^T.

Genome sequence accession number: AZCS00000000.

16S rRNA gene accession number: AY773947.

Lactobacillus amylolyticus

Lactobacillus amylolyticus (a.my.lo.ly'ti.cus. Gr. neut. n. *amylon* starch; N.L. masc. adj. *lyticus* (from Gr. masc. adj. *lytikos*) able to loosen; N.L. masc. adj. *amylolyticus* starch-digesting).

Lactobacillus amylolyticus an grow up to 52°C with an optimum growth temperature between 45 °C and 48°C. No growth occurs at 20°C. These bacteria produce DL-lactic acid from glucose, fructose, galactose, glucose, maltose, mannose, sucrose raffinose and melibiose. Neither acid nor gas are produced from arabinose, cellobiose, lactose, mannitol, rhamnose, ribose and trehalose [73]. The genome size is 1.54 Mbp and the mol% GC content of DNA is 38.2.

Isolated from malt, mash, and unhopped wort in breweries but was also identified in sourdough and tofu whey.

The type strain is LA 5^T = CCUG 39901^T = DSM 11664^T = JCM 12529^T = LMG 18796^T.

Genome sequence accession number: AZEP00000000.

16S rRNA gene accession number: FR683095.

Lactobacillus amylovorus

Lactobacillus amylovorus (a.my.lo.vo'rus. Gr. neut. n. *amylon* starch, L. v. *vorare* to devour, N.L. masc. adj. *amylovorus* starch-devouring). The species includes strains that were previously designated as *Lactobacillus sobrius* [74].

Lactobacillus amylovorus produces both D(-) and L(+) lactic acid and acid is produced from cellobiose, fructose, galactose, glucose, maltose, mannose, sucrose, starch, and trehalose. Arabinose, melezitose, melibiose, raffinose, rhamnose and ribose are not fermented. The ability to ferment starch and the presence of an extracellular amylolytic enzyme are distinguishing characteristics [75]. Growth maximum is 45 to 48°C. The genome size of the type strain is 2.02 Mbp and the mol% GC content of DNA is 37.8.

The microorganism is a characteristic representative of swine intestinal microbiota [54, 76]; also isolated from sourdough and cattle waste-corn fermentation.

The type strain is ATCC 33620^T = CCUG 27201^T = CIP 102989^T = DSM 20531^T = JCM 1126^T = LMG 9496^T = NCAIM B.01458^T = NRRL B-4540^T.

Genome sequence accession number: AZCM00000000.

16S rRNA gene accession number: AY944408.

Lactobacillus apis

Lactobacillus apis (a'pis. L. gen. n. *apis* of/from a honey bee, the genus name of the true honey bee *Apis mellifera* L., referring to the insect host of the first strains).

Lactobacillus apis cells produce L-lactic acid from glucose. Growth is found under strictly anaerobic and microaerophilic conditions. Produces acid from glucose, fructose, mannose and salicin, but not from galactose, maltose, raffinose, cellobiose, sucrose and lactose [77]. The genome size is 1.70 Mbp and the mol% GC content of DNA is 36.9.

Isolated from the stomach contents of honeybees (*Apis mellifera* L.).

The type strain is R4B^T = CCM 8403^T = LMG 26964^T.

Genome sequence accession number: PDKP00000000.

16S rRNA gene accession number: KF386017.

Lactobacillus bombicola

Lactobacillus bombicola [bom.bi'co.la. L. masc. n. *bombus* a boom, a deep hollow noise, buzzing, also the zoological genus name of the bumble bee; L. suf. *–cola* (derived from L. masc. or fem. n. incola *incola*, inhabitant) dwelling, occurring in; N.L. masc. n. *bombicol*a occurring in *Bombus*].

Lactobacillus bombicola produces only D(-)-lactic acid from glucose. It is capable of utilizing cellobiose, ribose, glucose, fructose, mannose, and trehalose for growth an acid production, but not arabinose, maltose, lactose, melibiose, and sucrose [42]. The genome size is 1.64 Mbp and the mol% GC content of DNA is 34.6.

Isolated from the gut of a *Bombus lapidarius* bumble bee.

The type strain is H70-3^T = LMG 28288^T = DSM 28793^T.

Genome sequence accession number: NPNG00000000.

16S rRNA gene accession number: LK054485.

Lactobacillus colini

Lactobacillus colini (co.li'ni. N.L. gen. n. *colini* of *Colinus*, scientific name of bobwhites).

L. colini ferments a broad range of hexoses and disaccharides but pentoses are not fermented. Optimum growth is observed at 37°C and between pH 5.0 and 5.5 [78]. The mol% GC content of DNA is 35.6.

Isolated from bobwhites, a ground-dwelling bird [78].

The type strain is 111144 L1^T = DSM 101872^T = KCTC 21086^T.

Genome accession number: not available at time of publication.

16S rRNA gene accession number: KU161105.

Lactobacillus crispatus

Lactobacillus crispatus (cris.pa'tus. L. part. adj. *crispatus* curled, crisped, referring to morphology observed original in broth media).

Lactobacillus crispatus is synonymous with *Lactobacillus acidophilus* group A2 of Johnson et al. [72]. It produces DL-lactic acid from glucose, cellobiose, fructose, galactose, lactose, maltose, mannose, and sucrose [79–81]. Arabinose, mannitol, melezitose or rhamnose are not fermented. Grows equally well at 37 and 45°C. The genome size is 2.06 Mbp and the mol% GC content of DNA is 36.6.

One of the predominant species found in the human female lower genital tract. Isolated from human feces, vagina, and buccal cavities, from crops and caeca of chicken and from patients with purulent pleurisy, leucorrhea and urinary tract infections. Also isolated from type II sourdoughs.

The type strai is VPI 3199^T = ATCC 33820^T = CCUG 30722^T = CIP 102990^T = CIPP II^T = DSM 20584^T = JCM 1185^T = LMG 9479^T.

Genome sequence accession number: AZCW00000000.

16S rRNA gene accession number: AF257097.

Lactobacillus equicursoris

Lactobacillus equicursoris (e.qui.cur'so.ris. L. masc. n. *equus* a horse; L. gen. n. *cursoris* of a runner or racer; N.L. gen. n. *equicursoris* of a racing horse, referring to the isolation of the type strain from faeces of a thoroughbred racehorse).

L. equicursoris produces D(-)- lactic acid from glucose. It utilises glucose, fructose, galactose, mannose, cellobiose, lactose and mannitol for growth and acid production [82]. The genome size is 2.05 Mbp and the mol% GC content of DNA is 47.7.

Isolated from a thoroughbred racehorse.

The type strain is DI70^{T} = DSM 19284^{T} = JCM 14600^{T}.

Genome sequence accession number: AZDU00000000.

16S rRNA gene accession number: AB290830.

Lactobacillus fornicalis

Lactobacillus fornicalis (for.ni.cá lis. N.L. masc. adj. *fornicalis,* of the posterior fornix).

L. fornicalis produces DL- lactic acid from glucose. Acid is produced from ribose, fructose, galactose, glucose, mannose, maltose, cellobiose, sucrose, trehalose, melezitose, mannitol and sorbitol [83]. The mol% GC content of DNA is 37.

Isolated from the human posterior vaginal fornix.

The type strain is TV 1018^{T} = DSM 13171^{T} = ATCC 700934^{T}.

Genome sequence accession number: not available at the time of publication.

16S rRNA gene accession number: Y18654.

Lactobacillus gallinarum

Lactobacillus gallinarum (gal.li.na'rum. L. gen. pl. n. *gallinarum* of hens).

Lactobacillus gallinarum produce DL-lactic acid. Acid is produced from glucose, mannose, galactose, sucrose, fructose, cellobiose, melibiose, and raffinose. No acid formation from arabinose, rhamnose, ribose, trehalose, and mannitol. Synonymous with *Lactobacillus acidophilus* group A4 of Johnson et al. [72]. Strains are tolerant to 4.0% NaCl. [72, 84]. The genome size of the type strain is 1.94 Mbp and the mol% GC content of DNA is 36.5.

Isolated from the chicken intestine.

The type strain is L917, Scav^{T} = ATCC 33199^{T}= CCUG 30724^{T} = CIP 103611^{T} = DSM 10532^{T} = JCM 2011^{T} = LMG 9435^{T} = VPI 1294^{T}.

Genome sequence accession number: AZEL00000000.

16S rRNA gene accession number: AJ417737.

Lactobacillus gasseri

Lactobacillus gasseri (gas'se.ri. N.L. gen. n. *gasseri*, of Gasser, named for F. Gasser, a French bacteriologist).

Lactobacillus gasseri strains are all positive for glucose, mannose, galactose, maltose, sucrose and fructose fermentation and produce DL-lactic acid. Strains do not ferment ribose, mannitol and raffinose. Further characteristics are provided by [84–86]. The genome size is 1.89 Mbp and the mol% GC content of DNA is 35.3.

One of the predominant species in the human female lower genital tract. Also isolated from the human mouth, intestinal tract, and from the intestine of animals. Also found in wounds, urine, blood, carious dentine, and pus of patients suffering from septic infections. .

The type strain is 63 AM^{T} of Gasser = ATCC 33323^{T} = CCUG 31451^{T} = CIP 102991^{T} = DSM 20243^{T} = JCM 1131^{T} = LMG 9203^{T} = NRRL B-14168^{T} = NRRL B-4240^{T}.

Genome sequence accession number: NC_008530.

16S rRNA gene accession number: AF519171.

Lactobacillus gigeriorum

Lactobacillus gigeriorum (gi.ge.ri.o‘rum. L. gen. pl. n. *gigeriorum* of or from the entrails or gizzards of poultry).

Lactobacillus gigeriorum produces mainly D-lactic acid from glucose, fructose, mannose, maltose, sucrose, galactose and cellobiose. Ribose, mannitol, lactose and raffinose are not fermented [87]. The genome size is 1.91 Mbp and the mol% GC content of DNA is 36.9.

Isolated from a crop of a chicken.

The type strain is 202^T = LEM 202^T = CRBIP 24.85^T = DSM 23908^T.

Genome sequence accession number: AYZO00000000.

16S rRNA gene accession number: FR681899.

Lactobacillus hamsteri

Lactobacillus hamsteri (ham’ste.ri. N.L. gen. n. *hamster* of the hamster from which the isolate was derived).

Lactobacillus hamsteri produces DL-lactic acid from glucose, cellobiose, sucrose, mannitol, raffinose and ribose. No acid produced from melizitose [88]. The genome size is 1.84 Mbp and the mol% GC content of DNA is 35.1.

Isolated from the intestine of a hamster.

The type strain is Ha5F1^T = ATCC 43851^T= CCUG 30726^T = CIP 103365^T = DSM 5661^T = JCM 6256^T= LMG 10754^T.

Genome sequence accession number: AZGI00000000.

16S rRNA gene accession number: AJ306298.

Lactobacillus helsingborgensis

Lactobacillus helsingborgensis (hel.sing.bor.gen’sis. N.L. masc. adj. *helsingborgensis* pertaining to Helsingborg, the site of Lund University, Campus Helsingborg, Sweden, where the type strain was characterized).

Lactobacillus helsingborgensis growth occurs at 15 to 50 °C and D(-)-lactic acid is produced as the end product from hexose fermentation. Acid is produced during fermentation of glucose, mannose, sorbose, sorbitol and sucrose, but not from maltose or lactose [89]. The genome size is 2.02 Mbp and the mol% GC content of DNA is 36.4.

Isolated from the honey stomach of the honeybee *A. mellifera mellifera,* and from alfalfa silage.

The type strain is Bma5N^T = DSM 26265^T = CCUG 63301^T.

Genome sequence accession number: JXJR00000000.

16S rRNA gene accession number: JX099553.

Lactobacillus helveticus

Lactobacillus helveticus (hel.ve’ti.cus. L. masc. adj. *helveticus* Swiss, referring to the isolation of the type strain from Emmental [Swiss] cheese).

Lactobacillus helveticus produces DL-lactic acid from glucose galactose, lactose, mannose, and trehalose but not from cellobiose, mannitol, raffinose, and sucrose. *L. helveticus* [2, 90] is an earlier heterotypic synonym of *Lactobacillus suntoryeus* [91]. The genome size of the type strain is 1.83 Mbp and the mol% GC content of DNA is 36.8.

Part of the core microbiome of chicken [92] but was also isolated from sour milk, cheese starter cultures and cheese, particularly Emmental and Gruyère cheeses, and in tomato pomace and silage.

The type strain is 12, Lh12^T = ATCC 15009^T = CCUG 30139^T = CIP 103146^T = DSM 20075^T = IFO (now NBRC) 15019^T = JCM 1120^T = LMG 6413^T = LMG 13555^T = NRRL B-4526^T.

Genome sequence accession number: AZEK00000000.

16S rRNA gene accession number: AM113779.

Lactobacillus hominis

Lactobacillus hominis (ho'mi.nis. L. gen. n. *hominis* of a human being).

Lactobacillus hominis produces acid from galactose, glucose, fructose, mannose, cellobiose, maltose, lactose, sucrose, trehalose and raffinose. Mainly D-lactic acid (about 90 %) is produced from glucose [93]. The genome size is 1.93 Mbp and the mol% GC content of DNA is 35.2.

Isolated from the human intestine.

The type strain is 61D^T = CRBIP 24.179^T = DSM 23910^T.

Genome sequence accession number: AYZP00000000.

16S rRNA gene accession number: FR681902.

Lactobacillus iners

Lactobacillus iners (in'ers. L. masc. adj. *iners*, inactive, lazy).

Lactobacillus iners grows on blood agar but not on MRS or Rogosa agar, reflecting a strict adaptation to the human vagina. L(+)-Lactic acid is produced from glucose, some strains produce acid from maltose but acid is not produced from lactose, mannitol, raffinose, ribose, and sucrose [94]. The genome size is 1.27 Mbp and the mol% GC content of DNA is 32.5.

One of the predominant species found in the human female lower genital tract; also occurs on human skin [95]

The type strain is CCUG 28746^T = CIP 105923^T = DSM 13335^T = JCM 12513^T = LMG 18914^T.

Genome sequence accession number: AZET00000000.

16S rRNA gene accession number: Y16329.

Lactobacillus intestinalis

Lactobacillus intestinalis (in.tes.tina'lis. N.L. masc. adj. *intestinalis*, pertaining to the intestine). *Lactobacillus intestinalis* produce DL-lactic acid from glucose, mannose, fructose, galactose, sucrose and mannitol, but not from arabinose, xylose, rhamnose, and trehalose [96]. The genome size is 2.01 Mbp and the mol% GC content of DNA is 35.4.

Isolated from the intestines of rats, mice, and pigs.

The type strain is Th4^T = ATCC 49335^T= CCUG 30727^T = CIP 104793^T = DSM 6629^T = JCM 7548^T = LMG 14196^T.

Genome sequence accession number: AZGN00000000.

16S rRNA gene accession number: AJ306299.

Lactobacillus jensenii

Lactobacillus jensenii (jen.se'ni.i. N.L. gen. n. *jensenii*, of Jensen, named for S. Orla-Jensen, a Danish microbiologist).

Lactobacillus jensenii produces only the D(-) lactic enantiomer. Cellobiose, sucrose and maltose fermented; lactose, mannitol and arabinose not fermented [97]. The genome size is 1.61 Mbp and the mol% GC content of DNA is 34.33.

One of the predominant species in the human female lower genital tract.

The type strain is 62G^T = ATCC 25258^T = CCUG 21961^T = CCUG 35572^T = CIP 69.17^T = DSM 20557^T = JCM 1146^T = JCM 15953^T = LMG 6414^T = NRRL B-4550^T.

Genome sequence accession number: AYYU00000000.

16S rRNA gene accession number: AF243176.

Lactobacillus johnsonii

Lactobacillus johnsonii (john.so'ni.i. N.L. gen. n. *johnsonii* of Johnson; named for J. L. Johnson, an American microbiologist). Synonymous with *L. acidophilus* group B2 of Johnson et al. [72].

Lactobacillus johnsonii strains all ferment glucose, mannose, galactose, maltose, sucrose and fructose and produce DL-lactic acid.*L. johnsonii* does not ferment mannitol or ribose [84]. The genome size is 1.77 Mbp and the mol% GC content of DNA is 34.4.

Isolated from humans (gut, vagina) and the feces of birds, rodents, calves and pigs, and from type II sourdoughs.

The type strain is ATCC 33200^T = CCUG 30725^T = CIP 103620^T = DSM 10533^T = JCM 2012^T = VPI 7960^T.

Genome sequence accession number: AZCY00000000.

16S rRNA gene accession number: AJ002515.

Lactobacillus kalixensis

Lactobacillus kalixensis (ka.lix.en'sis. N.L. masc. adj. *kalixensis* pertaining to Kalix, a town in northern Sweden, where the gastric biopsies were sampled).

Lactobacillus kalixensis produces both D(-)- and L(+)-lactate from galactose, glucose, fructose, mannose, cellobiose, maltose, lactose, sucrose, trehalose and raffinose. Acid is not produced arabinose, ribose, xylose, rhamnose and mannitol [98]. The genome size is 2.08 Mbp and the mol% GC content of DNA is 36.1.

Isolated from a biopsy of the healthy human gastric mucosa.

The type strain is Kx127A2^T = CCUG 48459^T = DSM 16043^T = JCM 15954^T = LMG 22115^T.

Genome sequence accession number: AZFM00000000.

16S rRNA gene accession number: AY253657.

Lactobacillus kefiranofaciens

Lactobacillus kefiranofaciens (ke.fi.ra.no.fa'ci.ens. N.L. neut. n. *kefiranum*, a polysaccharide of kefir grain, kefiran; L. v. *facio*, produce; N.L. part. adj. *kefiranofaciens*, kefiran producing).

Lactobacillus kefiranofaciens produces DL-lactic acid with an excess of D(-)-lactic acid from glucose, fructose, galactose, sucrose, maltose, lactose, and raffinose, but not from arabinose, ribose, cellobiose or trehalose [99].

Two subspecies are recognised.

Lactobacillus kefiranofaciens **subsp.** ***kefiranofaciens***

Lactobacillus kefiranofaciens subsp. *kefiranofaciens* (ke.fi.rano. fa'ci.ens. L. n. *kefiran*, a polysaccharide of kefir grain, kefiran; L. v. *facio*, produce; N.L. part. adj. *kefiranofaciens*, kefiran producing).

The genome size of the type strain is 2.26 Mbp and the mol% GC content of DNA is 37.2.

Part of the microbiota of kefir grains [99, 100] but also isolated from other fermented dairy products.

The type strain is WT-2B^T = ATCC 43761^T= CCUG 32248^T = CIP 103307^T = DSM 5016^T = JCM 6985^T = LMG 19149^T.

Genome sequence accession number: AZGG00000000.

16S rRNA gene accession number: AM113781.

Lactobacillus kefiranofaciens **subsp.** ***kefirgranum***

Lactobacillus kefiranofaciens subsp. *kefirgranum* (ke.fir.gra'num. Turkish n. kefir, Caucasian sour milk; L. n. *granum* grain; N.L. neut. n. *kefirgranum* kefir grain).

The genome size of the type strain is 2.10 Mbp and the mol% GC content of DNA is 37.5.

Part of the core microbiome of kefir grains [100, 101].

The type strain is GCL 1701^T = ATCC 51647^T = CCUG 39467^T = CIP 104241^T = DSM 10550^T = JCM 8572^T = LMG 15132^T.

Genome sequence accession number: AZEM00000000.

16S rRNA gene accession number: AM113782.

Lactobacillus kimbladii

Lactobacillus kimbladii (kim.bla'di.i. N.L. gen. n. *kimbladii* named after beekeeper Tage Kimblad, for his significant contributions to the discovery of the LAB microbiota in the honey stomach of honeybees).

Lactobacillus kimbladii grows at 15 to 50°C and D(-)-lactate from glucose, fructose, mannose and tagatose, but not from ribose, sorbitol, cellobiose and lactose [89]. The genome size is 2.19 Mbp and the mol% GC content of DNA is 36.0.

Isolated from the honey stomach of the honeybee *A. mellifera.*

The type strain is Hma2N^T=DSM 26263^T=CCUG 63633^T.

Genome sequence accession number: JXLH00000000.

16S rRNA gene accession number: JX099549.

Lactobacillus kitasatonis

Lactobacillus kitasatonis (ki.ta.sa.to'nis. L. gen. n. *kitasatonis* referring to Shibasaburo Kitasato, the founder of Kitasato Institute, the father of Japanese bacteriology).

Lactobacillus kitasatonis produces DL-lactic acid from mannose, maltose, galactose, sucrose and fructose while acid is not produced from arabinose, xylose, ribose, trehalose, melibiose and raffinose [102]. The genome size of the type strain is 1.91 Mbp and the mol% GC content of DNA is 37.5.

Isolated from the intestine of animals including chicken and swine.

The type strain is T. Mitsuoka Ch-J-2-1^T =JCM 1039^T = KCTC 3155^T.

Genome sequence accession number: AZFU00000000.

16S rRNA gene accession number: AB107638.

Lactobacillus kullabergensis

Lactobacillus kullabergensis (kul.la.ber.gen'sis. N.L. masc. adj. *kullabergensis* of or belonging to the nature reserve Kullaberg, where the discovery of these strains was made in 2005).

Lactobacillus kullabergensis grows at 15–50°C; D(-)-lactate is produced as the end product from hexose fermentation. Acid is produced from glucose, fructose, trehalose and gentiobiose, but not from ribose, galactose, mannose, maltose, lactose and sucrose [89]. The genome size is 2.12 Mbp and the mol% GC content of DNA is 35.8.

Isolated from the honey stomach of the honeybee *A. mellifera mellifera*.

The type strain is Biut2N^T=DSM 26262^T=CCUG 63631^T.

Genome sequence accession number: JXBY00000000.

16S rRNA gene accession number: JX099550.

Lactobacillus melliventris

Lactobacillus melliventris (mel.li.ven'tris. L. neut. n. *mel*, *mellis* honey; L. masc. n. *venter*, *-tris* belly, stomach; N.L. gen. n. *melliventris* of the honey stomach, referring to the isolation of the first strains from the honey stomach of honeybees).

Lactobacillus melliventris grows from 15 to 50°C. Produce acid from glucose, fructose, mannose and gentiobiose, but not from galactose, ribose, sucrose, maltose and lactose [89]. The genome size is 2.12 Mbp and the mol% GC content of DNA is 35.9.

Isolated from the homey stomach of honeybees.

The type strain is Hma8N^T = DSM 26256^T = CCUG 63629^T.

Genome sequence accession number: JXLI00000000.

16S rRNA gene accession number: JX099551.

Lactobacillus mulieris

Lactobacillus mulieris (mu.li'.e.ris. L. gen. n. *mulieris* of a woman, from where the bacterium was isolated).

Lactobacillus mulieris grows in the pH range of 5.0 - 8.5 and from 30 to 45°C; optimum growth is observed at 37°C [103]. Lactic acid is produced from glucose, fructose, mannose, N-acetylglucosamine, several disaccharides and starch but not from pentoses [103]. The genome size is 1.66 Mbp and the mol% GC content of DNA is 34.2.

Isolated from the urine of a woman; several strains previously classified as *L. jensenii* should be classified as *L. mulieris* [103].

The type strain is c10Ua161M^T = CECT 9755^T = DSM 108704^T.

Genome sequence accession number: SDGL00000000.

16S rRNA gene accession number: MK775269.

Lactobacillus panisapium

Lactobacillus panisapium (pa.nis.a'pi.um. L. masc. n. *panis* bread; L. fem. n *apis* bee; N.L. gen. n. *panisapium* of bee bread).

Lactobacillus panisapium is facultatively anaerobic but optimal growth is observed under anaerobic conditions. Growth occurs from 15 up to 55°C (optimum 37°C) and it produces acid from cellobiose, fructose, galactose, glucose, melibiose, ribose, sucrose, mannose and raffinose [104]. The genome size is 1.83 Mbp and the mol% GC content of DNA is 37.4.

Isolated from bee bread of *Apis cerana*.

The type strain is Bb 2-3^T = DSM 102188^T = ACCC 19955^T.

Genome sequence accession number: NPNH01000000.

16S rRNA gene accession number: KX447147.

Lactobacillus paragasseri

Lactobacillus paragasseri (pa.ra.gas'se.ri. Gr. prep. *para*, resembling; N.L. gen. n. *gasseri*, a species epithet; N.L. gen. n. *paragasseri*, resembling *Lactobacillus gasseri*).

Lactobacillus paragasseri produces both D(-)- and L(+)-lactic acid as end products of glucose fermentation (75:25 ratio). Also ferments maltose, lactose, sucrose and trehalose, but not ribose and raffinose [105]. The genome size is 1.94 Mbp and the mol% GC content of DNA is 34.9.

Occurs in the human gastrointestinal tract.

The type strain is M. Rogosa 208XR^T = JCM 5343^T = ATCC 4963^T = LMG 11478^T = NCFB 1375^T = KCTC 3172^T = NCIMB 8931^T = VPI 0334^T.

Genome sequence accession number: AP018549.

16S rRNA gene accession number: LC374363.

Lactobacillus pasteurii

Lactobacillus pasteurii (pas.teu'ri.i. N.L. gen. masc. n. *pasteurii* of Pasteur).

Lactobacillus pasteurii produces mainly D(-)-lactic acid from glucose; acid is also produced from ribose, fructose, mannose, cellobiose, maltose, lactose and sucrose [93]. The genome size is 1.87 Mbp and the mol% GC content of DNA is 38.5.

Isolated from the human intestine.

The type strain is 1517^T = CRBIP 24.76^T = DSM 23907^T.

Genome sequence accession number: AYZN00000000.

16S rRNA gene accession number: FR681901.

Lactobacillus porci

Lactobacillus porci (por'ci. L. gen. n. *porci* of a pig, referring to the isolation of the type strain from small intestine of a pig).

Lactobacillus porci grows between 15 and 50 °C and produces D(-)-lactic acid from glucose; acid is also produced from mannose, cellobiose, maltose, lactose, trehalose, raffinose and sucrose [106]. The mol% GC content of DNA is 51.5.

Isolated from the swine intestine.

The type strain is SG816^T = KCTC 21090^T = NBRC 112917^T.

Genome sequence accession number: not available at the time of publication.

16S rRNA gene accession number: MF346092

Lactobacillus psittaci

Lactobacillus psittaci (psit.ta'ci. L. gen. masc. n. *psittaci* of the parrot, from which the organism was first isolated).

Lactobacillus psittaci produces acid from glucose, raffinose and sucrose, but not from lactose, mannitol and trehalose [107]. The genome size is 1.54 Mbp and the mol% GC content of DNA is 35.6.

Isolated from a hyacinth macaw.

The type strain is B 1491/99^T = CCUG 42378^T = CIP 106492^T = DSM 15354^T = JCM 11552^T.

Genome sequence accession number: AZFB00000000.

16S rRNA gene accession number: AJ272391.

Lactobacillus rodentium

Lactobacillus rodentium (ro.den'ti.um. L. gen. pl. n. *rodentium* of gnawers, referring to the fact that the microorganism was isolated from wild rodents).

Lactobacillus rodentium utilizes glucose, fructose, maltose, melibiose and sucrose, but not ribose, mannitol or trehalose [108]. The genome size is 1.52 Mbp and the mol% GC content of DNA is 34.0.

Isolated from the colon of wild mice (*Mus musculus*) and other rodent species [55, 108].

The type strain is MYMRS/TLU1^T = DSM 24759^T = CCM 7945^T.

Genome sequence accession number: BFBY00000000.

16S rRNA gene accession number: HQ851022.

Lactobacillus taiwanensis

Lactobacillus taiwanensis (tai.wa.nen'sis. N.L. masc. adj. *taiwanensis* of Taiwan, referring to the origin of the type strain).

L. taiwanensis produces both D and L lactic acid enantiomers from glucose fermentation. Fructose, mannose, maltose, lactose, sucrose and trehalose are also fermented. No acid is produced from raffinose or ribose [109]. The genome size is 1.88 Mbp and the mol% GC content of DNA is 34.0.

Occurs in the mouse gastrointestinal tract [55] but also isolated from silage cattle feed.

The type strain is FIRDI 006^T = BCRC 17755^T = DSM 21401^T.

Genome sequence accession number: AYZG00000000.

16S rRNA gene accession number: EU487512.

Lactobacillus ultunensis

Lactobacillus ultunensis (ul.tun.en'sis. N.L. masc. adj. *ultunensis* pertaining to Ultuna, the site of Swedish University of Agricultural Sciences in Uppsala, Sweden).

Lactobacillus ultunensis produces both D- and L-lactate from glucose. Acid is produced from galactose, fructose, mannose, cellobiose, maltose, lactose, sucrose, and trehalose. Acid is not produced from arabinose, ribose, rhamnose and melezitose. Growth occurs at 42 but not at 45°C [98]. The genome size of the type strain is 2.16 Mbp and the mol% GC content of DNA is 36.0.

Isolated from a biopsy of a healthy human gastric mucosa.

The type strain is Kx146C1^T = CCUG 48460^T = DSM 16047^T = JCM 16177^T = LMG 22117^T.

Genome sequence accession number: AZFO00000000.

16S rRNA gene accession number: AY253660.

Lactobacillus xujianguonis

*Lactobacillus xujianguonis (*xu.jian.guo'nis. N.L. gen. masc. n. *xujianguonis* of Xu Jianguo, recognized for contributions to medical microbiology).

Lactobacillus xujianguonis grows optimally at 37 – 40°C and at neutral pH [110]. DL-lactic acid is produced from pentoses, hexoses, disaccharides, sorbitol and mannitol. The genome size of the type strain is 2.22 Mbp and the mol% GC content of DNA is 38.8.

Isolated from a Himalayan marmot (*Marmota himalayana*).

The type strain is HT111-2^T = CGMCC 1.13855^T = KCTC 15803^T.

Genome sequence accession number: RXIA00000000.

16S rRNA gene accession number: MK294239.

DESCRIPTION OF *AMYLOLACTOBACILLUS* GEN. NOV.

Amylolactobacillus (A.my.lo.lac.to.ba.cil'lus Gr. neut. n. *amylon* starch; N.L. masc. n. *Lactobacillus* a bacterial genus); N.L. masc. n. *Amylolactobacillus*, a lactobacillus that ferments starch.

Strains of *Amylolactobacillus* are thin rods, (0.5–0.9 µm wide and 1.2–3 µm long) occurring singly and in short chains, non-motile, Gram-positive, catalase- negative, oxidase-negative, non-spore-forming. *Amylolactobacillus* species are homofermentative and display extracellular amylolytic enzyme activity. The mol% GC content is between 43.6 and 43.6.

The type species is *Amylolactobacillus amylophilus*; *Amylolactobacillus* was previously referred to as *L. amylophilus* group.

Description of *Amylolactobacillus amylophilus* comb. nov.

Amylolactobacillus amylophilus (a.my.lo'phi.lus. Gr. neut. n. *amylon* starch; Gr. masc. adj. *philos* loving; N.L. masc. adj. *amylophilus* starch-loving).

Basonym: *Lactobacillus amylophilus* Nakamura and Crowell 1981, 216^{VP} (Effective publication: Nakamura and Crowell 1979, 539).

A. amylophilus strains ferment starch to L(+)-lactic acid, they also metabolise fructose, galactose, glucose, mannose and maltose [111]. The genome size is 1.56 Mbp. The mol% GC content of DNA is 43.6 [111].

Isolated from swine waste-corn fermentation, corn-starch processing industrial wastes and kocho (*Ensete ventricosum*) bread.

The type strain is ATCC 49845^T = LMG 6900^T = DSM 20533^T = CCUG 30137^T = CIP 102988^T = IFO (now NBRC) 15881^T = JCM 1125^T = NCAIM B.01457^T = NRRL B-4437^T = NRRL B-4476^T.

Genome sequence accession number: AYYS00000000.

16S rRNA gene accession number: M58806.

Description of *Amylolactobacillus amylotrophicus* comb. nov.

Amylolactobacillus amylotrophicus (a.my.lo.tro'phi.cus. Gr. neut. n. *amylon* starch; N.L. masc. adj. *trophicus* from Gr. masc. adj. *trophikos* nursing, tending; N.L. masc. adj. *amylotrophicus* growing on starch, pertaining to the ability to ferment starch).

Basonym: *Lactobacillus amylotrophicus* Naser et al. 2006, 2526^{VP}. The classification of *A. amylotrophicus* as separate species was disputed as the first published genome sequence of the type strain of *A. amylotrophicus* was virtually identical to the sequence of *A. amylophilus* [14, 16]. The 16S rRNA, *pheS* and *rpoA* sequences provided with the new description, however, clearly differentiate *A. amylotrophicus* from *A. amylophilus*.

Phenotypic properties that differentiate *A. amylotrophicus* from *A. amylophilus* include the production of acid from D-cellobiose and salicin [112]. The mol% GC content of DNA is 43.6.

Isolated from corn silage.

The type strain is LMG 11400^T = DSM 20534^T = JCM 1124^T = NRRL B-4436^T.

Genome sequence accession number: not available at the time of publication.

16S rRNA gene accession number: AM236149.

DESCRIPTION OF *HOLZAPFELIA* GEN. NOV.

Holzapfelia (Holz.ap.fe'li.a. N.L. fem. n. *Holzapfelia*, named after Wilhelm Holzapfel, a microbiologist and taxonomist who made significant contributions to the understanding of the physiology and applications of lactic acid bacteria).

Strains of *Holzapfelia* are Gram positive, rod-shaped, catalase negative, homofermentative, and aerotolerant. The type strain of the single species in the genus was isolated from mountain flowers, other strains were identified in bee larvae. *H. floricola* grows at 15 but not at 37°C; glucose and fructose are the only carbohydrates that are fermented. The sources of isolation as well as genomic and physiological properties of the organism indicate an insect- and flower associated lifestyle of the genus.

The type species of *Holzapfelia* is *H. floricola*.

Description of *Holzapfelia floricola* comb. nov.

Holzapfelia floricola (flo.ri'co.la. L. fem. n. *flos* flower, blossom; L. suff. –*cola* from L. masc. or fem. n. *incola* dweller; N.L. fem. n. *floricola* flower-dweller).

Basonym: *Lactobacillus floricola* Kawasaki et al. 2011, 1358^{VP}.

The description of the species is identical of that of the genus (19). The genome size is 1.29 Mbp, the mol% GC content is 34.5.

Isolated from flowers.

The type strain is Ryu1-2^T = DSM 23037^T = JCM 16512^T = NRIC 0774^T.

Genome sequence accession number: AYZL00000000**.**

16S rRNA gene accession number: AB523780.

DESCRIPTION OF *BOMBILACTOBACILLUS* GEN. NOV.

Bombilactobacillus (Bom.bi.lac.to.ba.cil'lus. L. masc. n. *bombus*, buzzing of bees and bumblebees, N.L. masc. n. *Lactobacillus* a bacterial genus; N.L. masc. n. *Bombilactobacillus,* a lactobacillus from bees and bumble bees.

Bombilactobacillus species have been isolated from the stomach and the hindgut of honey bees (*Apis mellifera*) and bumble bees where they are associated with the heterofermentative sister genus *Apilactobacillus*. *Bombilactobacillus* species have genome sizes which range from 1.81 to 1.84 Mbp and a mol% GC content ranging from 34.7 to 39.5. They are homofermentative and thermophilic; comparable to other insect-associated lactobacilli, bombilactobacilli ferment only a narrow spectrum of carbohydrates.

A phylogenetic tree on the basis of 16S rRNA genes of all species in the genus *Bombilactobacillus* is provided in Figure S6B.

The type species is *Bombilactobacillus mellifer* comb. nov; *Bombilactobacillus* was previously referred to as *L. mellifer* group.

Description of *Bombilactobacillus mellifer* comb. nov.

Bombilactobacillus mellifer (mel'li.fer. L. masc. adj. *mellifer*, honey-producing, referring to the origin from the stomach and digestive tract of honey bees *Apis mellifera*).

Basonym: *Lactobacillus mellifer* Olofsson et al. 2014, 3113^{VP}

Description provided by [89]. *B. mellifer* grows over a wide temperature range (15 – 50°C) and pH values (pH 3 – 12) but ferments only few hexoses, sucrose, and raffinose [89]. The genome size is 1.82 Mbp. The mol% GC content of DNA is 39.5.

Isolated from isolated from the honey stomach of the honeybee *Apis mellifera.*

The type strain is Bin4N^T = DSM 26254^T = CCUG 63291^T.

Genome sequence accession number: JXJQ00000000.

16 rRNA gene sequence accession number: JX099543.

Description of *Bombilactobacillus bombi* comb. nov.

Bombilactobacillus bombi (bom'bi. L. masc. n. *bombus*, buzzing of bees and *Bombus*, N.L. gen. n. *bombi* of *Bombus*, of a bumblebee).

Basonym: *Lactobacillus bombi* Killer et al. 2014, 2615^{VP}

Description provided by [113]; compared to other bombilactobacilli, *B. bombi* ferments a wider range of carbohydrates.

The genome size is 1.84 Mbp. The mol% GC content of DNA is 34.7.

Isolated from the digestive tract of laboratory-reared bumblebee queens (*Bombus terrestris*).

The type strain is BTLCH M1/2^T = DSM 26517^T = CCM 8440^T.

Genome sequence accession number: CP031513 (strain BI-2.5; the genome sequence for the type strain is not available).

16 rRNA gene sequence accession number: KJ078643.

Description of *Bombilactobacillus mellis* comb. nov.

Bombilactobacillus mellis (mel'lis. L. gen. n. *mellis*, of honey, referring to the isolation from the digestive tract of *A. mellifera*)

Basonym: *Lactobacillus mellis* Olofsson et al. 2014, 3115^{VP}

The characteristics as provided by [89] are comparable to *B. mellifer*. The genome size is 1.81 Mbp. The mol% GC content of DNA is 36.4.

Isolated from the honey stomach of the honeybee *Apis mellifera*.

The type strain is Hon2N^{T} = DSM 26255^{T} = CCUG 63289^{T}.

Genome sequence accession number: JXBZ00000000.

16 rRNA gene sequence accession number: JX099545.

DESCRIPTION OF *COMPANILACTOBACILLUS* GEN. NOV

Companilactobacillus (Com.pani.lac.to.ba.cil'lus. M. L. n. *companio* friend, partner; N.L. masc. n. *Lactobacillus* a bacterial genus; N.L. masc. n.; *Companilactobacillus,* Companion-lactobacillus, the name refers to the association of *Companilactobacillus* species with other lactobacilli, particularly heterofermentative organisms, in cereal and vegetable fermentations [114]).

Companilactobacillus spp. are Gram-positive, homofermentative and non-sporeforming rods. Strains of *Companilactobacillus* were isolated from fermented vegetables, particularly fermented mustard or onion greens, and fruits (17 type strains; 5 of these from mustard or onion fermentations), sourdough or related cereal fermentations (7 type strains), sausages or meat (7 type strains) or other plant sources; one isolates was obtained from a fermented dairy product. *Companilactobacillus* appears not to be dominant in any of these fermentations but occurs consistently (type I sourdoughs and fermented mustard or onion greens) or occasionally (meat, salami). *Companilactobacillus metriopterae* was isolated from a grasshopper and forms and outgroup that differs with respect to genome size (*C. metriopterae* 1.50 Mbp; other species range from 2.17 to 2.9 Mbp); mol% GC content of DNA (*C. metriopterae* 32.8; other species range from 34.1 to 38.6) and physiological properties. The temperature requirements for growth are inconsistent; all strains grow between 25 and 30°C, most but not all species grow at 15°C and some species grow at 45°C. The fermentation of pentoses by *Companilactobacillus* is species- or strain-specific. Information on the ecology or lifestyle of companilactobacilli is scarce.

A phylogenetic tree on the basis of 16S rRNA genes of all species in the genus *Companilactobacillus* is provided in Figure S6C.

The type species is *Companilactobacillus alimentarius* comb. nov; *Companilactobacillus* was previously referred to as *L. alimentarius* group*.*

Description of *Companilactobacillus alimentarius* comb. nov.

Companilactobacillus alimentarius (a.li.men.ta'ri.us. L. masc. adj. *alimentarius* related to food).

Basonym: *Lactobacillus alimentarius* (ex Reuter 1970) Reuter 1983a*,* 672^{VP}

Growth is observed between 15 and 37°C and with pentoses, hexoses, and disaccharides as carbon source [115]. The genome size is 2.34 Mbp. The mol% GC content of DNA is 35.4.

Isolated as spoilage organisms from marinated fish products, as fermentation organisms in fermented sausages, as spoilage organism in ready-to-eat meats. A strain of the species had been used as biopreservatives culture [116]. It occurs in association with *Fructilactobacillus sanfranciscensis* in type I sourdoughs [114] and was isolated in other plant fermentations.

The type strain is R13^T = ATCC 29643^T= CCUG 30672^T = CIP 102986^T= DSM 20249^T = JCM 1095^T = LMG 9187^T.

Genome sequence accession number: AZDQ00000000.

16S RNA gene sequence accession number: M58804.

Description of *Companilactobacillus allii* comb. nov.

Companilactobacillus allii (al'li.i. L. gen. n. *allii* of Egyptian onions (*Allium proliferum*), the source of fermented onions, pa-kimchi, from which the type strain was isolated).

Basonym: *Lactobacillus allii* Jung et al. 2017, 4939^{VP}

Growth is observed at 25 and 37°C; hexoses and disaccharides but not pentoses are fermented [117]. The genome size is 2.51 Mbp. The mol% GC content of DNA is 35.3.

Isolated from scallion kimchi.

The type strain is WiKim39^T=KCTC 21077^T=JCM 31938^T.

Genome sequence accession numbers: CP019323 (chromosome) and CP019324 (plasmid).

16S RNA gene sequence accession number: NR_159082.

Description of *Companilactobacillus baiquanensis* comb. nov.

Companilactobacillus baiquanensis (bai.quan.en´sis. N.L. masc. adj. *baiquanensis*, pertaining to Baiquan, a county in the Heilongjiang province of China).

Basonym: *Lactobacillus baiquanensis* Wei and Gu 2019, 3192^{VP}

The type strain grows at 15 and 37 but not at 45°C; DL-lactic acid is produced from ribose, hexoses, and maltose [118]. The genome size is 2.24 Mbp; the mol% G+C content is 34.4.

Isolated from fermented from Chinese cabbage.

The type strain is 184-8^T = LMG 31050^T = NCIMB 15152^T = CCM 8895^T = KCTC 21131^T.

Genome sequence accession number: RHOQ00000000.

16S RNA gene sequence accession number: MK110828.

Description of *Companilactobacillus bobalius* comb. nov.

Companilactobacillus bobalius (bo.ba'li.us. N.L. masc. adj. *bobalius* pertaining to the grape variety Bobal).

Basonym: *Lactobacillus bobalius* Mañes-Lázaro et al. 2008, 2702^{VP}; the validity of the species was questioned but re-established on the basis of ANI values [119].

Growth occurs in the range of 15 to 40°C and with pentoses, hexoses, and disaccharides as carbon sources [120]. The genome size is 2.88 Mbp. The mol% GC content of DNA is 35.3.

Isolated from grape must and forage.

The type strain is 203^{T} = CECT 7310^{T} = DSM 19674^{T} = JCM 16180^{T}.

Genome sequence accession number: AZDY00000000.

16S RNA gene sequence accession number: AY681134.

Description of *Companilactobacillus crustorum* comb. nov.

Companilactobacillus crustorum (crus.tor'um. L. gen. pl. n. *crustorum*, of baked goods or cakes).

Basonym: *Lactobacillus crustorum* Scheirlinck et al. 2007, 1466^{VP}

Growth is observed at 15 and at 45°C; pentoses are not fermented; disaccharide fermentation is strain dependent [121]. The genome size is 2.22 Mbp. The mol% GC content of DNA is 35.

Isolated from sourdough, dairy products and forages. Some strains degrade saponins by β-glucuronidase activity [122].

The type strain is CCUG 53174^{T} = JCM 15951^{T} = LMG 23699^{T}.

Genome sequence accession number: AZDB00000000.

16S RNA gene sequence accession number: AM285450.

Description of *Companilactobacillus farciminis* comb. nov.

Companilactobacillus farciminis (far.ci'mi.nis. L. gen. n. *farciminis* of sausage).

Basonym: *Lactobacillus farciminis* Reuter 1983, 672^{VP}

Growth is observed between 15 and 42°C and with hexoses and disaccharides but not with pentoses as carbon source [115]. The genome size is 2.48 Mbp. The mol% GC content of DNA is 36.4.

Isolated from meat products, sourdough, fermentend fish, cold-smoked salmon, soy sauce mash, dairy products, table olives and fermented vegetables and corn silage.

The type strain is Rv4 na^{T} = ATCC 29644^{T}= DSM 20184^{T} = JCM 1097^{T}= LMG 9200^{T} = NRRL B-4566^{T}.

Genome sequence accession number: AZDR00000000.

16S RNA gene sequence accession number: M58817.

Description of *Companilactobacillus formosensis* comb. nov.

Companilactobacillus formosensis (for.mo.sen'sis. N.L. masc. adj. *formosensis* of or pertaining to Formosa [Taiwan] where the type strain was isolated).

Basonym: *Lactobacillus formosensis* Chang et al. 2015, 105^{VP}

Growth is observed between 25 and 45°C but not at 10°C; hexoses and disaccharides are fermented; pentoses are not fermented [123]. The genome size is 2.47 Mbp. The mol% GC content of DNA is 35.5.

Isolated from fermented soybean meal for use as poultry feed; it has been used experimentally as silage inoculant.

The type strain is S215^{T}=NBRC 109509^{T}=BCRC 80582^{T}.

Genome sequence accession number: QWDI00000000.

16S RNA gene sequence accession number: AB794060.

Description of *Companilactobacillus furfuricola* comb. nov.

Companilactobacillus furfuricola (fur.fu.ri'co.la. L. masc. n. *furfur* rice bran; L. suff. –*cola* from L. masc. or fem. n. *incola* inhabitant; N.L. masc. n. *furfuricola* rice bran-inhabitant).

Basonym: *Lactobacillus furfuricola* Irisawa et al. 2014, 2904^{VP}

Growth is observed between 20 and 37°C [124]. The genome size is 2.64 Mbp. The mol% GC content of DNA is 38.6.

Isolated from rice bran paste for Japanese pickles.

The type strain is Nu 27^{T}=JCM 18764^{T}=NRIC 0900^{T}=DSM 27174^{T}.

Genome sequence accession number: RHNT00000000.

16S RNA gene sequence accession number: AB910349.

Description of *Companilactobacillus futsaii* comb. nov.

Companilactobacillus futsaii (fut.sai'i. N.L. gen. n. of *futsai*, the Taiwanese fermented mustard product from which the type strain was isolated).

Basonym: *Lactobacillus futsaii* Chao et al. 2012, 489^{VP}. Two subspecies of *C. futsaii,* "*C. futsaii* ssp. *futsaii*" and "*C. futsaii* ssp. *chongqingii*" were described [125] but have not yet been included on the Validation Lists. The two subspecies are highly similar with respect to DNA-DNA hybridization values, 16rRNA and *recA* gene sequence similarity and were established on the basis of a divergent *pheS* sequence, requiring further confirmation.

Growth is observed between 15 and 30°C; hexoses and disaccharides but not pentoses support acid formation [126]. The genome size is 2.53 Mbp. The mol% GC content of DNA is 35.6.

Isolated from traditional fermented mustard products, fu-tsai and suan-tsai; it has been used experimentally for fermentation of shrimp waste [127].

The type strain is YM 0097^{T} = BCRC 80278^{T} = JCM 17355^{T}.

Genome sequence accession number: AZDO00000000

16S RNA gene sequence accession number: HQ322270.S

Description of *Companilactobacillus ginsenosidimutans* sp. nov.

Companilactobacillus ginsenosidimutans (gin.se.no.si.di.mu'tans N.L. neut. n. *ginsenosidium*, ginsenoside, L. pres. part. *mutans* transforming, N.L. part. adj. *ginsenosidimutans*, ginsenoside converting).

Effective publication Jung et al. 2013 as *Lactobacillus ginsenosidimutans. C. ginsenosidimutans* is a kimchi isolate that converts ginsenosides by β-glucosidase activity [128]. The genome size is 2.59 Mbp. The mol% GC content of DNA is 36.7.

Isolated from kimchi.

The type strain is EMML 3041^{T} = KACC 15420^{T} = LMG 31607^{T} = DSM 24154^{T}.

Genome sequence accession number: CP012034.

16S RNA gene sequence accession number: HQ389549.

Description of *Companilactobacillus halodurans* sp. nov.

Companilactobacillus halodurans (ha.lo.du'rans. Gr. n. *hals, halos* salt; L. pres. part. *durans* enduring; N.L. part. adj. *halodurans* salt-enduring, resisting).

Effective publication Schuster et al., 2019, as *Lactobacillus halodurans. C. halodurans* grows between 10 and 37°C and between pH 4.0 and 8.0, and at NaCl concentrations of up to 14% [129]. Acid is produced from ribose, hexoses, and some disaccharides. The genome size is 2.84 Mbp. The mol% GC content of DNA is 35.8.

Isolated from spoiled fermented sausage.

The type strain is TMW1.2172^{T} = DSM 109452^{T} = LMG31402^{T}.

Genome sequence accession number: VDFP00000000.

16S RNA gene sequence accession number MK968448.

Description of *Companilactobacillus heilongjiangensis* comb. nov.

Companilactobacillus heilongjiangensis (hei.long.ji.ang.en'sis. N.L. masc. adj. *heilongjiangensis* pertaining to Heilongjiang*,* a river flowing through the province of China where the bacterium was isolated).

Basonym: *Lactobacillus heilongjiangensis* Gu et al. 2013, 4098^{VP}

Hexoses and disaccharides but not pentoses are fermented [130]. The genome size is 2.79 Mbp. The mol% GC content of DNA is 37.5.

Isolated from fermented vegetables and type I sourdough.

The type strain is S4-3^{T} = LMG 26166^{T} = DSM 28069^{T} = NCIMB 14701^{T}.

Genome sequence accession number: CP012559.

16S RNA gene sequence accession number: JF411966.

Description of *Companilactobacillus huachuanensis* comb. nov.

Companilactobacillus huachuanensis (hua.chuan.en´sis. N.L. masc. adj. *huachuanensis* pertaining to Huachuan County, a county in the Heilongjiang province of China).

Basonym: *Lactobacillus huachuanensis* Fu and Gu 2019, 2812^{VP}

The physiological properties of *C. huachuanensis* are comparable to *C. heilongjiangensis* [131]. The genome size is 3.02 Mbp. The mol% GC content of DNA is 36.4.

Isolated from fermented Chinese cabbage.

The type strain is 395-6.2^{T} = CCM 8927^{T} = NCIMB15188^{T} = LMG31179^{T}.

Genome sequence accession number: BJDF00000000.

16S RNA gene sequence accession number: LC438522.

Description of *Companilactobacillus hulinensis* comb. nov.

Companilactobacillus hulinensis (hu.lin.en´sis. N.L. masc. adj. *hulinensis*, pertaining to Hulin, a county in the Heilongjiang province of China).

Basonym: *Lactobacillus hulinensis* Wei and Gu, 2019, 10^{VP}

Growth is observed at 15 and 37 but not at 45°C; DL-lactic acid is produced from hexoses and pentoses [118]. The genome size is 2.35 Mbp, the mol% G+C is 36.7.

Isolated from fermented Chinese cabbage.

The type strain is 8-1(1)^T = LMG 31047^T = NCIMB 15156^T = CCM 8898^T = KCTC 21115^T.

Genome sequence accession number: RHOO00000000.

16S RNA gene sequence accession number: MK110830.

Description of *Companilactobacillus insicii* comb. nov.

Companilactobacillus insicii (in.si’ci.i. L. gen. n. *insicii* from minced meat).

Basonym: *Lactobacillus insicii* Ehrmann et al. 2016, 241^{VP}

Growth is observed in the range of 8 – 45°C [132]; the genome size is 2.54 Mbp. The mol% GC content of DNA is 34.9.

Isolated from pork salami.

The type strain is TMW 1.2011^T = CECT 8802^T = DSM 29801^T.

Genome sequence accession number: RHNU00000000.

16S RNA gene sequence accession number: KP677494.

Description of *Companilactobacillus jidongensis* comb. nov.

Companilactobacillus jidongensis (ji.dong.en´sis. N.L. masc. adj. *jidongensis*, pertaining to Jidong, a county in the Heilongjiang province of China).

Basonym: *Lactobacillus jidongensis* Wei and Gu 2019, 3192^{VP}

Growth is observed at 10 but not at 37°C; DL-lactic acid is produced from hexoses but not from pentoses [118]. The genome size is 2.71 Mbp. The mol% GC content of DNA is 36.5.

Isolated from fermented Chinese cabbage.

The type strain is 204-8^T = LMG31054^T = NCIMB15159^T = CCM8900^T = KCTC21133^T = LMG31054^T.

Genome sequence accession number: RHOP00000000.

16S RNA gene sequence accession number: MK110829.

Description of *Companilactobacillus kedongensis* comb. nov.

Companilactobacillus kedongensis (ke.dong.en´sis. N.L. masc. adj. *kedongensis,* pertaining to Kedong, a county in the Heilongjiang province of China).

Basonym: *Lactobacillus kedongensis* Wei and Gu 2019, 3191^{VP}

Characteristics of *C. kedongensis* are generally similar to *C. jidongensis* [118]. The genome size is 2.27 Mbp, the mol% G+C content is 36.2.

Isolated from fermented Chinese cabbage.

The type strain is 116-2^T = LMG31051^T = NCIMB 15158^T = CCM 8899^T = KCTC 21124^T.

Genome sequence accession number: RHOR00000000.

16S RNA gene sequence accession number: MK110817.

Description of *Companilactobacillus keshanensis* comb. nov.

Companilactobacillus keshanensis (ke.shan.en´sis. N.L. masc. adj. *keshanensis*, pertaining to a county in the Heilongjiang province of China).

Basonym: *Lactobacillus keshanensis* Wei and Gu 2019, 3191^{VP}

Characteristics of *C. keshanensis* are similar to *C. jidongensis* [118]. The genome size is 2.30 Mbp. The mol% GC content of DNA is 35.6.

Isolated from fermented Chinese cabbage.

The type strain is 33-7^{T} = LMG 31166^{T} = NCIMB 15153^{T} = CCM 8936^{T} = KCTC 21118^{T} = LMG 31166^{T}.

Genome sequence accession number: RHOS00000000.

16S RNA gene sequence accession number: MK110816.

Description of *Companilactobacillus kimchiensis* comb. nov.

Companilactobacillus kimchiensis (kim.chi.en'sis. N.L. gen. n. *kimchiensis* from kimchi, a Korean fermented-vegetable food).

Basonym: *Lactobacillus kimchiensis* Kim et al. 2013, 1358^{VP}.

Hexoses and disaccharides but not pentoses are fermented; growth is observed at 15 – 37°C [133]. The genome size is 2.70 Mbp. The mol% GC content of DNA is 35.5.

Isolated from kimchi.

The type strain is L133^{T} = DSM 24716^{T} = JCM 17702^{T} = KACC 15533^{T}.

Genome sequence accession number: JQCF00000000.

16S RNA gene sequence accession number: HQ906500.

Description of *Companilactobacillus kimchii* comb. nov.

Companilactobacillus kimchii (kim'chi.i. N.L. gen. n. *kimchii* from kimchi, a Korean fermented-vegetable food).

Basonym: *Lactobacillus kimchii* Yoon et al. 2000, 1794^{VP}; the classification of this taxon as a separate species has been questioned but was confirmed on the basis of ANI values [119].

Growth occurs in the range of 10 to 40°C and with pentoses, hexoses, and disaccharides as carbon sources [134]. The genome size is 2.74 Mbp. The mol% GC content of DNA is 35.1.

Isolated from kimchi.

The type strain is MT-1077^{T} = ATCC BAA-131^{T} = DSM 13961^{T} = JCM 10707^{T} = KCTC 8903P^{T}.

Genome sequence accession number: AZDH00000000.

16S RNA gene sequence accession number: AF183558.

Description of *Companilactobacillus metriopterae* comb. nov.

Companilactobacillus metriopterae (me.tri.o.pte'rae. N.L. fem. gen. n. *metriopterae* of *Metrioptera*, the genus of grasshoppers from which the type strain was isolated).

Basonym: *Lactobacillus metriopterae* Chiba et al. 2018, 1486^{VP}; the species includes strains previously described as *Lactobacillus terrae* Kim et al. 2018 [135, 136]

C. metriopterae forms an outgroup of *Companilactobacillus* and has the smallest genome size (1.50 Mbp) and mol% GC content (32.8); it seems to transition to an insect associated lifestyle. *C. metriopterae* is pigmented and ferments fewer carbohydrates than other companilactobacilli.

Isolated from the gut of grasshopper *Metrioptera engelhardti*, other isolates were obtained from soil.

The type strain is Hime 5-1^T=JCM 31635^T=DSM 103730^T.

Genome sequence accession number: RSTD00000000.

16S RNA gene sequence accession number: LC190736.

Description of *Companilactobacillus mindensis* comb. nov.

Companilactobacillus mindensis (min.den'sis. N.L. adj. *mindensis* from Minden, Germany, where the type strain was isolated).

Basonym: *Lactobacillus mindensis* Ehrmann et al. 2003, 11^{VP}

Growth is observed between 15 and 30°C. Pentoses are not fermented [137]. The genome size is 2.34 Mbp. The mol% GC content of DNA is 38.2.

Isolated from a type I sourdough.

The type strain is TMW 1.80^T = CCUG 48642^T = DSM 14500^T = JCM 12532^T = LMG 21508^T.

Genome sequence accession number: AZEZ00000000.

16S RNA gene sequence accession number: AJ313530.

Description of *Companilactobacillus mishanensis* comb. nov.

Companilactobacillus mishanensis (mi.shan.en´sis. N.L. masc. adj. *mishanensis,* pertaining to Mishan, a county in the Heilongjiang province of China).

Basonym: *Lactobacillus mishanensis* Wei and Gu 2019, 3193^{VP}

Characteristics are similar to *C. hulinensis* [118]. The genome size is 2.47 Mbp, the mol% G+C is 36.6.

Isolated fermented from Chinese cabbage.

The type strain is 256-3^T = LMG 31048^T = NCIMB 15160^T = CCM 8901^T = LMG 31048^T.

Genome sequence accession number: RHON00000000.

16S RNA gene sequence accession number: MK110831.

Description of *Companilactobacillus musae* comb. nov.

Companilactobacillus musae (mu'sae. N.L. gen. n. *musae* of *Musa*; pertaining to banana fruit from *Musa paradisiaca* var. *sapientum*).

Basonym: *Lactobacillus musae* Chen et al. 2017, 5148^{VP}

Growth is observed between 25 and 37°C and with hexoses and disaccharides but not with pentoses as carbon sources [138]. The genome size is 2.35 Mbp. The mol% GC content of DNA is 34.6.

Isolated from banana fruits.

The type strain is 313^T=NBRC 112868^T = BCRC 81020^T.

Genome sequence accession number: BIFW00000000.

16S RNA gene sequence accession number: LC184607.

Description of *Companilactobacillus nantensis* comb. nov.

Companilactobacillus nantensis (nan.ten'sis. N.L. masc. adj. *nantensis* pertaining to Nantes, from where the first stain of this species was isolated).

Basonym: *Lactobacillus nantensis* Valcheva et al. 2006*,* 589^{VP}

Growth occurs at 15 but not at 45°C; a wide range of carbohydrates including ribose, hexoses, and disaccharides are fermented [139]. The genome size is 2.91 Mbp. The mol% GC content of DNA 36.2.

Isolated from a type I sourdough.

The type strain is LP33^{T} = TMW 1.1265^{T} = CIP 108546^{T} = DSM 16982^{T} = JCM 16171^{T}.

Genome sequence accession number: AZFV00000000.

16S RNA gene sequence accession number: AY690834.

Description of *Companilactobacillus nodensis* comb. nov.

Companilactobacillus nodensis (no.den'sis. N.L. masc. adj. *nodensis* referring to Noda, the Japanese city in which the type strain was isolated).

Basonym: *Lactobacillus nodensis* Kashiwagi et al. 2009, 64^{VP}

Growth is observed between 15 and 37 °C and with pentoses and hexoses but not disaccharides as carbon source [140]. The genome size is 2.68 Mbp. The mol% GC content of DNA is 37.6.

Isolated from fermented rice bran paste and has been used experimentally as adjunct culture in cheese [141].

The type strain is iz4b-1^{T} = DSM 19682^{T} = JCM 14932^{T}.

Genome sequence accession number: AZDZ00000000.

16S RNA gene sequence accession number: AB332024.

Description of *Companilactobacillus nuruki* comb. nov.

Companilactobacillus nuruki (nu.ru'ki. N.L. gen. n. *nuruki* of Nuruk, a Korean traditional rice fermentation starter).

Basonym: *Lactobacillus nuruki* Heo et al. 2018, 3277^{VP}

Growth is observed between 4 and 40°C; a wide spectrum of carbohydrates including pentoses, hexoses, and disaccharides is fermented [142].

The genome size is 2.58 Mbp. The mol% GC content of DNA is 34.2.

Isolated from Nuruk, a rice bran fermentation starter.

The type strain is SYF10-1a^{T} = KACC 18726^{T} = NBRC 112011^{T}.

Genome sequence accession number: NIPR00000000.

16S RNA gene sequence accession number: MG786754.

Description of *Companilactobacillus paralimentarius* comb. nov.

Companilactobacillus paralimentarius (par.a.li.men.ta'ri.us. Gr. pref. *para* beside; L. masc. adj. *alimentarius,* a species epithet*;* N.L. masc. adj. *paralimentarius* beside *C. alimentarius*, referring to the close relationship with this organism).

Basonym: *Lactobacillus paralimentarius* Cai et al. 1999, 1455^{VP}

The physiological properties of *C. paralimentarius* as described [143] are similar to *C. alimentarius*. The genome size is 2.55 Mbp. The mol% GC content of DNA is 35.1.

Isolated from sourdough, other cereal fermentations, and from poultry meat.

The type strain is TB 1^T = CCUG 43349^T = CIP 106794^T = DSM 13238^T = JCM 10415^T = LMG 19152^T.

Genome sequence accession number: AZES00000000.

16S RNA gene sequence accession number: AB018528.

Description of *Companilactobacillus salsicarnum* sp. nov.

Companilactobacillus salsicarnum (sal.si.carn´um. L. adj. *salsus*, salted; L. gen.n. *carnis* of meat; N.L. gen. n. *salsicarnum* of salted meat, referring to salami as the source of isolation).

Effective publication Schuster et al., 2019 as *Lactobacillus salsicarnum. C. salsicarnum* grows between 10 and 37°C and between pH 4.5 and 8.5, and at NaCl concentrations of up to 8% [129]. Acid is produced from ribose and arabinose, hexoses, and maltose and trehalose. The genome size is 2.43 Mbp. The mol% GC content of DNA is 36.6.

Isolated from spoiled fermented sausage.

The type strain is TMW 1.2098^T = DSM 109451^T = LMG 31401^T.

Genome sequence accession number: VDFN00000000.

16S RNA gene sequence accession number MK968446.

Description of *Companilactobacillus suantsaicola* comb. nov.

Companilactobacillus suantsaicola (suan.tsai'co.la. N.L. neut. n. *suantsaium*, from suan-tsai, fermented mustard greens; L. suff. *–cola* from L. masc. or fem. n. *incola* inhabitant; N.L. masc. n. *suantsaicola* occurring in suan-tsai.)

Basonym: *Lactobacillus suantsaicola* Lin et al. 2019, 8^{VP}

Growth is observed between 20 and 37°C and at pH 4.0 to 10.0 [144]. The genome size is 2.60 Mbp. The mol% GC content of DNA is 36.9.

Isolated from suan-tsai, a traditional fermented mustard green product of Taiwan.

The type strain is $R7^T$ = BCRC 81127^T = NBRC 113530^T.

Genome sequence accession number: RKLY00000000.

16S RNA gene sequence accession number: MH810311.

Description of *Companilactobacillus tucceti* comb. nov.

Companilactobacillus tucceti (tuc.ce'ti. L. gen. n. *tucceti*, from a sausage, referring to the origin of the type strain).

Basonym: *Lactobacillus tucceti* Chenoll et al. 2009, 925^{VL}

The type strain grows at 15 and 37 but not at 45°C [145]. The genome size is 2.17 Mbp. The mol% GC content of DNA is 34.1.

Isolated from sausage.

The type strain is R $19c^T$ = CECT 5920^T = DSM 20183^T = JCM 18037^T.

Genome sequence accession number: AZDG00000000.

16S RNA gene sequence accession number: AJ576006.

Description of *Companilactobacillus versmoldensis* comb. nov.

Companilactobacillus versmoldensis (vers.mold.en'sis. N.L. masc. adj. *versmoldensis* is pertaining to Versmold, the town in Germany where the strains were isolated).

Basonym: *Lactobacillus versmoldensis* Kröckel et al. 2003, 516^{VP}

Description is provided by [146]. The genome size is 2.37 Mbp. The mol% GC content of DNA is 38.3.

Isolated from poultry salami.

The type strain is KU-3^T = ATCC BAA-478^T = DSM 14857^T = JCM 16174^T = NCCB 100034^T.

Genome sequence accession number: AZFA00000000.

16S RNA gene sequence accession number: AJ496791.

Description of *Companilactobacillus zhachilii* comb. nov.

Companilactobacillus zhachilii (zha.chi'li.i. N.L. gen. n. *zhachilii* of zha-chili, a Chinese fermented mustard green product).

Basonym: *Lactobacillus zhachilii* Zhang et al., 2019, 2199^{VP}

Growth is observed between 15 and 45°C and with a wide range of hexoses and disaccharides but not with pentoses [147]. The genome size is 2.71 Mbp. The mol% GC content of DNA is 36.3.

Isolated from Zha-Chili, a traditional fermented product from mustard greens.

The type strain is $HBUAS52074^T$ = $GDMCC1.1417^T$ = $KCTC21106^T$.

Genome sequence accession number: CP031933.

16S RNA gene sequence accession number: MH392835.

Description of *Companilactobacillus zhongbaensis* comb. nov.

Companilactobacillus zhongbaensis (zhong.ba.en´sis. N.L. masc. adj. *zhongbaensis* from Zhongba*,* a county in Tibet, China, where the type strain was isolated).

Basonym: *Lactobacillus zhongbaensis* Wei and Gu 2019, 3193^{VP}

Growth is observed at 15 and 37 but not at 45°C; DL-lactic acid is produced from a broad range of pentoses, hexoses, and disaccharides [118]. The genome size is 3.04 Mbp, the mol% G+C is 39.4.

Isolated from a fermented dairy product.

The type strain is $M1575^T$ = LMG 31045^T = NCIMB 15149^T = CCM 8892^T.

Genome sequence accession number: RHOM00000000.

16S RNA gene sequence accession number: MK110832.

DESCRIPTION OF *LAPIDILACTOBACILLUS* GEN. NOV.

Lapidilactobacillus (La.pi.di.lac.to.ba.cil'lus L. masc. n. *lapis*, stone, referring to the isolation source of the type species *Lapidilactobacillus concavus*; N.L. masc. n. *Lactobacillus* a bacterial genus; N.L. masc. n. *Lapidilactobacillus*, a lactobacillus isolated from stone [walls]).

The cells are Gram-positive rods or cocci, homofermentative, non motile, non-spore-forming, facultatively anaerobes, and catalase-negative. The pH-range for growth and pentose utilization is strain dependent, the optimum pH is between 6.0 and 7.0. They are homofermentative and mainly produce L-lactic acid. The optimum temperature for growth is 30–37 °C. No ammonia is produced from arginine. The mol% GC content of DNA is between 38.1 and 49.0.

A phylogenetic tree on the basis of 16S rRNA genes of all species in the genus *Lapidiactobacillus* is provided in Figure S6D.

The type species is *Lapidilactobacillus concavus* comb. nov.; *Lapidilactobacillus* was previously referred to as *L. concavus / dextrinicus* group.

Description of *Lapidilactobacillus concavus* comb. nov.

Lapidilactobacillus concavus (con.ca'vus. L. masc. adj. *concavus*, curved, referring to the curved shape of the cells).

Basonym: *Lactobacillus concavus* Tong and Dong 2005, 2201^{VP}

Cells of *L. concavus* are non-motile curved rods; the optimum pH for growth is 6.0-6.4; they can also grow at 8% (v/v) ethanol but not in 6.5% (w/v) NaCl [148]. The genome size of the type strain is 1.90 Mbp. The mol% GC content of DNA is 43.3.

Isolated from the walls of a distilled-spirit-fermenting cellar in China.

The type strain is C-5-1^T = DSM 17758^T = AS 1.5017^T = JCM 14153^T = LMG 22739^T.

Genome sequence accession number: AZFX00000000.

16S rRNA gene accession number: AY683322.

Description of *Lapidilactobacillus bayanensis* comb. nov.

Lapidilactobacillus bayanensis (ba.yan.en´sis. N.L. masc. adj. *bayanensis* pertaining to Bayan, a county in the Heilongjiang province of China).

Basonym: *Lactobacillus bayanensis* Wei and Gu 2019, 3191^{VP}

Cells grow at 15 but not at 37°C. L(+)-lactic acid and D(-)-lactic acid are produced from glucose, fructose, mannose, and maltose; pentoses or other disaccharides are not fermented [118]. The genome size of the type strain is 2.43 Mbp. The mol% GC content of DNA is 40.1.

Isolated from fermented Chinese cabbage.

The type strain 54-5^T = LMG 31166^T = NCIMB 15153^T = CCM 8936^T = KCTC 21118T.

Genome sequence accession number: RHOX00000000.

16S rRNA gene accession number: MK110807.

Description of *Lapidilactobacillus dextrinicus* comb. nov.

Lapidilactobacillus dextrinicus (dex.tri'ni.cus. N.L. neut. n. *dextrinum*, dextrin; L. suff. -*icus*, suffix used with the sense of belonging to; N.L. masc. adj. *dextrinicus*, related to dextrin).

Basonym: *Lactobacillus dextrinicus* (Coster and White 1964) Haakensen *et al*. 2009, 620^{VP}.

Strains of *L. dextrinicus* were previously classified as *Pediococcus dextrinicus* (Coster and White 1964) Back 1978 (Approved Lists 1980) or *Pediococcus cerevisiae* subsp. *dextrinicus*. Cells are spherical, and may occur singly, in pairs or clusters and rarely in chains. Clusters of four may be observed, but they do not divide in two perpendicular directions at right angles. Only L(+)-lactic acid is produced from maltose, dextrin and starch [149]. The genome size of the type strain is 1.81 Mbp. The mol% GC content of DNA is 38.1.

Isolated from silage, fermenting vegetables, beer and sliced vacuum-packed cooked sausage.

The type strain is ATCC 33087^T = CCUG 18834^T = CIP 103407^T = DSM 20335^T = JCM 5887^T = LMG 11485^T = NCIMB 701561^T = VKM B-1603^T.

Genome sequence accession number: AYYK00000000.

16S rRNA gene accession number: D87679.

DESCRIPTION OF *AGRILACTOBACILLUS* GEN. NOV.

Agrilactobacillus (A.gri.lac.to.ba.cil'lus. L. adj.masc. n. *ager,* a field; N.L. masc. n. *Lactobacillus,* a bacterial genus; *Agrilactobacillus,* a lactobacillus from fields or soil).

Gram positive, rod-shaped, catalase negative, homofermentative, and aerotolerant. The genome size ranges from 2.33 to 3.47 Mbp; the mol% GC content of DNA ranges from 42.1 - 44.0. Origin, physiological properties and genome characteristics suggest a free-living lifestyle of the genus. Isolated from compost that included shochu mash, and from vegetables (mustard) in Indonesia and China.

The type species of the genus is *A. composti*.

Description of *Agrilactobacillus composti* comb. nov.

Agrilactobacillus composti (com.pos'ti. N.L. gen. n. *composti* of compost, the source of the type strain).

Basonym: *Lactobacillus composti* Endo and Okada 2007, 872^{VP}

The type strain grows over a relatively wide pH range and in the range of 10 to 37°C but not at 45°C [150]. The genome size is 3.47 Mbp and the mol% GC content of DNA is 44.0.

Isolated from compost from shochu mash solids and from pulque, a Mexican alcoholic beverage [151].

The type strain is NRIC 0689^T = DSM 18527^T = JCM 14202^T.

Genome sequence accession number: AZGA00000000.

16S rRNA gene accession number: AB268118.

Description of *Agrilactobacillus yilanensis* comb. nov.

Agrilactobacillus yilanensis (yi.lan.en´sis. N.L. masc. adj. *yilanensis* pertaining to Yilan, a county in the Heilongjiang province of China).

Basonym: *Lactobacillus yilanensis* Wei and Gu 2019, 3189^{VP}

The type strain grows at 15 but not at 45°C and ferments a wide range of pentoses, hexoses, and disaccharides [118]. The genome size is 2.33 Mbp and the mol% GC content of DNA is 41.7.

Isolated from a Chinese cabbage fermentation.

The type strain is 54-2^T = LMG 31058^T = NCIMB 15154^T=CCM 8896^T=KCTC 21120^T.

Genome sequence accession number: RHOY00000000.

16S rRNA gene accession number: MK110806.

DESCRIPTION OF *SCHLEIFERILACTOBACILLUS* GEN. NOV.

Schleiferilactobacillus (Schlei.fer.i.lac.to.ba.cil'lus. L. masc. noun *Schleiferi*, of (Karl-Heinz) Schleifer, a German microbiologist and taxonomist who made seminal contributions to bacterial taxonomy.

N.L.masc. n. *Lactobacillus* a bacterial genus; N.L. masc. n. *Schleiferilactobacillus*, a lactobacillus named after Karl-Heinz Schleifer).

Gram positive, rod-shaped, catalase negative, homofermentative, and aerotolerant. Strain of the genus were isolated from spoiled beverages including beer and fermented dairy beverages, fermented vegetables, and fermented cereals. Growth is observed in the range of 15 – 42°C; a wide range of carbohydrates including pentoses, hexoses and oligosaccharides are fermented. The genome size ranges from 3.14 - 3.32 Mbp; the mol% GC content of DNA ranges from 49.1 to 56.3.

A phylogenetic tree on the basis of 16S rRNA genes of all species in the genus *Schleiferilactobacillus* is provided in Figure S6E.

The type species of the genus is *S. perolens* comb. nov.; *Schleiferilactobacillus* was previously referred to as *L. perolens* group.

Description of *Schleiferilactobacillus perolens* comb. nov.

Schleiferilactobacillus perolens (per.o'lens, Latin preposition *per* through, penetrating; L. pres. part. *olens* having an odor; N.L. part. adj. *perolens* smelling, referring to the copious diacetyl production by strains of the species).

Basonym: *Lactobacillus perolens* Back et al. 2000*,* 3^{VP}

Description of the species is as provided by [152]. Spoilage was attributed to copious amounts of diacetyl produced by *S. perolens*. The genome size is 3.31 Mbp and the mol% GC content of DNA is 49.1.

Isolated from spoiled soft drinks and brewery environments.

The type strain is L 533^T = DSM 12744^T = JCM 12534^T = LMG 18936^T.

Genome sequence accession number: AZEC00000000.

16S rRNA gene accession number: Y19167.

Description of *Schleiferilactobacillus harbinensis* comb. nov.

Schleiferilactobacillus harbinensis (har.bi.nen'sis. N.L. masc. adj. *harbinensis* pertaining to Harbin, a city in northeastern China where the type strain was isolated).

Basonym: *Lactobacillus harbinensis* Miyamoto et al. 2006, 2^{VL}

Description of the species is as provided by [153]. The genome size is 3.14 Mbp and the mol% GC content of DNA is 53.8.

Isolated from fermented vegetables "Suan Cai", the brewery environment, fermented cereals and tomato pomace, and spoiled soft drinks.

The type strain is AHU 1762^T = DSM 16991^T = JCM 16178^T = NBRC 100982^T = SBT 10908^T.

Genome sequence accession number: AZFW00000000.

16S rRNA gene accession number: AB196123.

Description of *Schleiferilactobacillus shenzhenensis* comb. nov.

Schleiferilactobacillus shenzhenensis (shen.zhen.en'sis. N.L. masc. adj. *shenzhenensis* of Shenzhen, the city in the South of China where the type strain was isolated).

Basonym: *Lactobacillus shenzhenensis* Zou et al. 2013, 1821^{VP}

Growth is observed at 15 and 45 °C [154]. The genome size is 3.27 Mbp and the mol% GC content of DNA is 56.3.

Isolated from a fermented dairy beverage.

The type strain is LY-73^T = CCTCC M 2011481^T = KACC 16878^T.

Genome sequence accession number: AVAA00000000.

16S rRNA gene accession number: JX523627.

DESCRIPTION OF *LACTICASEIBACILLUS* GEN. NOV.

Lacticaseibacillus (Lac.ti.ca.se.i.ba.cil'lus. L. neut. n. *lac* milk; L. n. *caseus* cheese, referring to the casei-group lactobacilli; L. masc. n. *bacillus* a rod; N.L. masc. n. *Lacticaseibacillus* a milk derived rodlet from the [*Lactobacillus*] *casei* group).

Strains of *Lacticaseibacillus* are homofermentative; some but not all species metabolize pentoses via the phosphoketolase pathway. The mol % GC content of DNA is between 46 and 58.0. The genome size ranges from 1.93 to 3.14 Mbp. Strains are non-motile, oxidase negative, often producing D(-)- and L(+)-lactic acid from glucose. The temperature range for growth is variable, but never below 10°C and never above 45°C. One subspecies survives 70°C for 40 seconds. Lys-D-Asp is the most common type of the peptidoglycan. The genus has considerable economic importance as it harbors several species that are used as starter cultures in dairy fermentations and as probiotics [58, 59].

A phylogenetic tree on the basis of 16S rRNA genes of all species in the genus *Lacticaseibacillus* is provided in Figure S6F.

The type species is *Lacticaseibacillus casei* comb. nov.; *Lacticaseibacillus* was previously referred to as *L. casei* group.

Description of *Lacticaseibacillus casei* comb. nov.

Lacticaseibacillus casei (ca'se.i. L. gen. n. *casei* of cheese).

Basonym: *Lactobacillus casei* (Orla Jensen 1916, Hansen and Lessel 1971, 71 (Approved Lists) (*Streptobacterium casei* Orla-Jensen 1919, 166).

The species includes strains previously classified as *Lactobacillus zeae* [155]. Original characteristics of *L. casei* strains are provided by [2, 156, 157]. *L. casei* is differentiated from most other lactobacilli by catalase activity [47]. The genome size of the type strain is 2.83 Mbp. The mol% GC content of DNA is 46.5.

Isolates were obtained from diverse sources including chinese traditional pickle, infant feces, corn liquor, oat silage, commercial dietery supplements sputum, nasopharynx [47]. Information on the lifestyle of *L. casei* is counded by the unclear taxonomy over the past decades; most genomes of designated as *L. casei* in the NCBI database should be classified as *L. paracasei* instead [10, 47].

The type strain is 03 [7, IAM 12473, Orland L-323, R.P. Tittsler 303]^T = ATCC 393^T = BCRC 10697^T = CCUG 21451^T = CECT 475^T = CIP 103137^T = DSM 20011^T = IAM 12473^T = NBRC 15883^T = JCM 1134^T = KCTC 3109^T = LMG 6904^T = NCIMB 11970^T = NCIMB 11970^T = NRRL B-1922^T.

Genome sequence accession number: BALS00000000.

16S rRNA gene accession number: AF469172.

Description of *Lacticaseibacillus baoqingensis* comb. nov.

Lacticaseibacillus baoqingensis (boa.qing.en'sis. N.L. masc. adj. *boaqingensis* of Boaqing, from where the type strain was isolated).

Basonym: *Lactobacillus baoqingensis* Long and Gu 2019, 2347^{VP}

Original characteristics of *L. baoqingensis* strains are as provided by Long and Gu [158].

The genome size of the type strain is 2.86 Mbp. The mol% GC content of DNA is 50.9.

Isolated from a vegetable fermentation.

The type strain is 47-3^{T} = NCIMB 15165^{T} = CCM 8903^{T} = LMG 31064^{T}.

Genome sequence accession number: RHOI00000000.

16S rRNA gene accession number: MK110840.

Description of *Lacticaseibacillus brantae* comb. nov.

Lacticaseibacillus brantae (bran'tae. N.L. gen. n. *brantae*, of *Branta*, isolated from *Branta canadensis,* Canada goose).

Basonym: *Lactobacillus brantae* Volokhov et al. 2012, 2068^{VP}

Original characteristics of *L. brantae* strains are provided by [159]. The genome size of the type strain is 1.93 Mbp. The mol% GC content of DNA is 47.5.

Isolated from the faeces of wild Canada goose (*Branta canadensis*) and from experimental sourdoughs.

The type strain is SL1108^{T} = ATCC BAA-2142^{T} = DSM 23927^{T} = LMG 26001^{T}.

Genome sequence accession number: AYZQ00000000.

16S rRNA gene accession number: HQ022861.

Description of *Lacticaseibacillus camelliae* comb. nov.

Lacticaseibacillus camelliae (ca.mel'li.ae. N.L. gen. n. *camelliae*, of *Camellia sinensis* fermented tea leaves).

Basonym: *Lactobacillus camelliae* Tanasupawat et al. 2007, 1371^{VL} [160]

Original characteristics of *L. camelliae* strains are as provided by [161] .The genome size of the type strain is 2.57 Mbp. The mol% GC content of DNA is 55.4.

Isolated from fermented tea (*Camellia sinensis*) leaves and fermented tomato pomace.

The type strain is MCH3-1^{T} = BCC 21233^{T} = DSM 22697^{T} = JCM 13995^{T} = NRIC 0672^{T}.

Genome sequence accession number: AYZJ00000000.

16S rRNA gene accession number: AB257864.

Description of *Lacticaseibacillus chiayiensis* comb. nov.

Lacticaseibacillus chiayiensis (chia.yi.en'sis. N.L. masc. adj. *chiayiensis* of Chiayi, from where the type strain was isolated).

Basonym: *Lactobacillus chiayiensis* effective publication Huang et al. 2018, 3382 (Approved Lists)

Original characteristics of *L. chiayiensis* strains are provided by [162, 163]. The genome size of the type strain is 2.87 Mbp. The mol% GC content of DNA is 47.1.

Isolated from cow manure.

The type strain is NCYUAS^{T} = BCRC 81062^{T} = NBRC 112906^{T}.

Genome sequence accession number: MSSM00000000.

16S rRNA gene accession number: MF446960.

Description of *Lacticaseibacillus hulanensis* comb. nov.

Lacticaseibacillus hulanensis (hu.lan.en'sis. N.L. masc. adj. *hulanensis* pertaining to Hulan, a district of Harbin city in China).

Basonym: *Lactobacillus hulanensis* Zhao and Gu et al. 2019, 5^{VP}

Original characteristics of *L. hulanensis* strains are provided [164]**.** The genome size of the type strain is 2.36 Mbp. The mol% GC content of DNA is 52.7.

Isolated from suancai, fermented Chinese cabbage

The type strain is ZW163^{T} = NCIMB15193^{T} = CCM8926^{T} = CCTCC AB 2019015^{T}.

Genome sequence accession number: RRYD00000000.

16S rRNA gene accession number: LC436604.

Description of *Lacticaseibacillus jixianensis* comb. nov.

Lacticaseibacillus jixianensis (ji.xian.en'sis. N.L. masc. adj. *jixianensis* pertaining to Jixian, a county in the Heilongjiang province of China).

Basonym: *Lactobacillus jixianensis* Long and Gu, 2019, 2346^{VP}

Original characteristics of *L. jixianensis* strains are provided by [158]. The genome size of the type strain is 2.47 Mbp. The mol% GC content of DNA is 58.3.

Isolated from fermented Chinese cabbage.

The type strain is 159-4^{T} = CCM 8911^{T} = NCIMB 15175^{T}.

Genome sequence accession number: RHOJ00000000.

16S rRNA gene accession number: MK110836.

Description of *Lacticaseibacillus manihotivorans* comb. nov.

Lacticaseibacillus manihotivorans (ma.ni.ho.ti.vo'rans. N.L. neut. n. *manihotum* cassava; L. v. *vorare* to devour; N.L. part. adj. *manihotivorans* cassava-devouring).

Basonym: *Lactobacillus manihotivorans* Morlon-Guyot et al. 1998, 1107^{VP}

Strains of *L. manihotivorans* express extracellular amylases [165]. The genome size of the type strain is 3.14 Mbp. The mol% GC content of DNA is 47.7.

Isolated from sour cassava starch fermentation and from tomato pomace silage.

The type strain is OND 32^{T} = CCUG 42894^{T} = CIP 105851^{T} = DSM 13343^{T} = JCM 12514^{T} = LMG 18010^{T}.

Genome sequence accession number: AZEU00000000.

16S rRNA gene accession number: AF000162.

Description of *Lacticaseibacillus nasuensis* comb. nov.

Lacticaseibacillus nasuensis (na.su.en'sis. N.L. masc. adj. *nasuensis*, named after Nasu-shiobara City, where strains were first isolated).

Basonym: *Lactobacillus nasuensis* Cai et al. 2012, 1143^{VP}

Original characteristics of *L. nasuensis* strains are provided [166]. The genome size of the type strain is 2.28 Mbp. The mol% GC content of DNA is 57.0.

Isolated from a Sudan grass [*Sorghum sudanense* (Piper) Stapf.] silage.

The type strain is SU 18^T = JCM 17158^T = CGMCC 1.10801^T.

Genome sequence accession number: AZDJ00000000.

16S rRNA gene accession number: AB608051.

Description of *Lacticaseibacillus pantheris* comb. nov.

Lacticaseibacillus pantheris (pan'ther.is. N.L. gen. n. *pantheris* of the panther, referring to the isolation of the strains from jaguar feces).

Basonym: *Lactobacillus pantheris* Liu and Dong 2002, 1747^{VP}

Characteristics of the species are described in [167]. *L. pantheris* together with *L. thailandensis, L. sharpie, L. songhuajiangensis* and *L. hulanensis* forms a monophyletic outgroup to *Lacticaseibacillus*; however, physiological characteristics and their ecology, as far as data are available, are similar to other *Lacticaseibacillus* spp. The genome size of the type strain is 2.55 Mbp. The mol% GC content of DNA is 52.9.

Isolated from the faeces of a jaguar in Beijing Zoo and from fermented vegetables.

The type strain is A24-2-1^T = DSM 15945^T = AS 1.2826^T = JCM 12539^T = LMG 21017^T.

Genome sequence accession number: AZFJ00000000.

16S rRNA gene accession number: AF413523.

Description of *Lacticaseibacillus paracasei* comb. nov.

Lacticaseibacillus paracasei (pa.ra.ca'se.i. Gr. prep. *para* resembling; N.L. gen. n. *casei* a species epithet; N.L. gen. n. *paracasei* resembling *Lactobacillus casei*).

Basonym: *Lactobacillus paracasei* Collins et al. 1989, 107^{VP}

Strains of this species including strains previously referred to as *L. casei* subsp. *alactosus, L. casei* subsp. *pseudoplantarum* and *L. casei* subsp. *tolerans* were transferred from *L. casei* [168]. Original characteristics of *L. paracasei* strains are described in [168]. Cells have superoxide dismutase activity [47], are rods (0.8–1.0 × 2.0–4.0 µm), often with square ends, occurring singly or in chains. Growth is observed between 10 and 40°C. Some strains grow at 5 and 45°C. Two subspecies are validly published. The genome size of the type strain is 2.88 Mbp. The mol% GC content of DNA is 46.5.

Strains of this species have a nomadic lifestyle and were isolated from a variety of courses including the human oral cavity [169], fermented cereals, vegetables, meats, dairy products, and in invertebrate hosts.

The type strain is DSM 5622^T = ATCC 25302^T = AS 1.2826^T = JCM 8130^T = LMG 13087^T.

Genome sequence accession number: AZGH00000000.

16S rRNA gene accession number of the type strain: D79212.

Two subspecies are recognized: *Lacticaseibacillus paracasei* subsp. *paracasei* and *Lacticaseibacillus paracasei* subsp. *tolerans.*

Description of *Lacticaseibacillus paracasei* subsp. *paracasei* comb. nov.

Lacticaseibacillus paracasei subsp. *paracasei* (pa.ra.ca'se.i. Gr. prep. *para* resembling; N.L. gen. n. *casei* a species epithet; N.L. gen. n. *paracasei* resembling *Lactobacillus casei*).

Basonym *Lactobacillus paracasei* subsp. *paracasei* Collins et al. 1989, 107^{VP}

The genome size of the type strain is 2.88 Mbp. The mol% GC content of DNA is 46.5.

Isolated from dairy products, sewage, silage, humans and clinical sources.

The type strain is DSM 5622^{T} = ATCC 25302^{T} = AS 1.2826^{T} = JCM 8130$^{T\ T}$ = LMG 13087^{T}.

Genome sequence accession number: AZGH00000000.

16S rRNA gene accession number: D79212.

Description of *Lacticaseibacillus paracasei* subsp. *tolerans* comb. nov.

Lacticaseibacillus paracasei subsp. *tolerans* (to.le'rans. L. masc. part. *tolerans* tolerating, enduring; means survival during the pasteurization of milk).

Basonym *Lactobacillus paracasei* subsp. *tolerans* Abo-Elnaga and Kandler 1965, Collins et al. 1989, 108^{VP}

Some strains of the subspecies were initially described as *L. casei* subsp. *tolerans* [168]. Original characteristics of *L. paracasei* subsp. *tolerans* strains are described in [170]. The genome size of the type strain is 2.38 Mbp. The mol% GC content of DNA is 46.4.

Isolated from dairy products and tomato pomace silage.

The type strain is 7/74^{T} = ATCC 25599^{T} = CCUG 34829^{T} = CIP 102994^{T} = CIP 103024^{T} = DSM 20258^{T} = NBRC 15906^{T} = JCM 1171^{T} = LMG 9191^{T} = NCIMB 9709^{T}.

Genome sequence accession number: AYYJ00000000.

16S rRNA gene accession number of the type strain: AB181950.

Description of *Lacticaseibacillus porcinae* comb. nov.

Lacticaseibacillus porcinae (por.ci'nae. L. gen. n. *porcinae* of pork).

Basonym *Lactobacillus porcinae* Nguyen et al. 2013, 1758^{VP}

Original characteristics of *L. porcinae* strains are described in [171]. The genome size of the type strain is 2.84 Mbp. The mol% GC content of DNA is 47.2.

Isolate from nem chua (fermented beef) in northern Vietnam.

The type strain is R-42633^{T} = CCUG 62266^{T} = LMG 26767^{T}.

Genome sequence accession number: RHNS00000000.

16S rRNA gene accession number: HE616585.

Description of *Lacticaseibacillus rhamnosus* comb. nov.

Lacticaseibacillus rhamnosus (rham.no'sus. N.L. masc. adj. *rhamnosus* pertaining to rhamnose).

Basonym *Lactobacillus rhamnosus* (Hansen 1968, Collins et al. 1989, 108^{VP} (*Lactobacillus casei* subsp. *rhamnosus* Hansen 1968, 76.)

Original characteristics of *L. rhamnosus* strains are described in by [172]. The genome size of the type strain is 2.95 Mbp. The mol% GC content of DNA is 46.7.

The species has a nomadic lifestyle and was isolated from a broad range of habitats including dairy products, fermented meat, fish, vegetables and cereals, sewage, humans (oral, vaginal and intestinal), invertebrate hosts and clinical sources [17, 169].

The type strain is ATCC 7469^T = CCUG 21452^T = CIP A157^T = DSM 20021^T = NBRC 3425^T = JCM 1136^T = LMG 6400^T = NCAIM B.01147^T = NCCB 46033^T = NCIMB 6375^T = NCTC 12953^T = NRRL B-442^T = VKM B-574^T.

Genome sequence accession number: AZCQ00000000.

16S rRNA gene accession number: D16552.

Description of *Lacticaseibacillus saniviri* comb. nov.

Lactobacillus saniviri (sa.ni.vi'ri. L. masc. adj. *sanus* healthy; L. gen. n. *viri*, of a man; N.L. gen. n. *saniviri*, of a healthy man).

Basonym *Lactobacillus saniviri* Oki et al. 2012, 605^{VP}

Original characteristics of *L. saniviri* strains are described in [173]. The genome size of the type strain is 2.44 Mbp. The mol% GC content of DNA is 47.7.

Isolated from the faeces of a healthy man and from fermented rice and fish.

The type strain is YIT 12363^T = JCM 17471^T = DSM 24301^T.

Genome sequence accession number: JQCE00000000.

16S rRNA gene accession number: AB602569.

Description of *Lacticaseibacillus sharpeae* comb. nov.

Lacticaseibacillus sharpeae (shar'pe.ae. N.L. gen. n. *sharpeae* of Sharpe; named for M. Elisabeth Sharpe, an English bacteriologist).

Basonym *Lactobacillus sharpeae* Weiss et al. 1981, 266^{VP}

Original characteristics of *L. sharpeae* strains are described in [174, 175]. The genome size of the type strain is 2.45 Mbp. The mol% GC content of DNA is 53.4.

Isolated from municipal sewage and spoiled meat.

The type strain is 71^T = ATCC 49974^T = CIP 101266^T = DSM 20505^T = JCM 1186^T = LMG 9214^T = NRRL B-14855^T.

Genome sequence accession number: AYYO00000000.

16S rRNA gene accession number: M58831.

Description of *Lacticaseibacillus songhuajiangensis* comb. nov.

Lacticaseibacillus songhuajiangensis (song.hua.ji.ang.en'sis. N.L. masc. adj. *songhuajiangensis* pertaining to the Songhuajiang River, a river flowing through Heilongjiang Province of China).

Basonym *Lactobacillus songhuajiangensis* Gu et al. 2013, 4698^{VP}.

Original characteristics of *L. songhuajiangensis* strains are described in [176]. The genome size of the type strain is 2.61 Mbp. The mol% GC content of DNA is 52.7.

Isolated from traditional sourdough.

The type strain is 7-19^T = LMG 27191^T = NCIMB 14832^T = CCUG 62990^T.

Genome sequence accession number: RHNR00000000.

16S rRNA gene accession number: HF679038.

Description of *Lacticaseibacillus thailandensis* comb. nov.

Lacticaseibacillus thailandensis (thai.lan.den'sis. N.L. masc. adj. *thailandensis*, pertaining to Thailand, where the type strain was isolated).

Basonym *Lactobacillus thailandensis* Tanasupawat et al. 2007, 1371^{VL}

Original characteristics of *L. thailandensis* strains are described in [161]. The genome size of the type strain is 2.06 Mbp. The mol% GC content of DNA is 53.5.

Isolated from fermented fish (pla-ra) in Thailand.

The type strain is MCH5-2^T = BCC 21235^T = DSM 22698^T = JCM 13996^T = NRIC 0671^T.

Genome sequence accession number: AYZK00000000.

16S rRNA gene accession number: AB257863.

EMENDED DESCRIPTION OF *PARALACTOBACILLUS*

Paralactobacillus (Pa.ra.lac.to.ba.cil'lus. Gr. prep. *para* resembling; N.L. masc. n. *Lactobacillus* a bacterial genus; *Paralactobacillus* resembling the genus *Lactobacillus*).

Cell are Gram-positive, homofermentative, non-motile, non-spore-forming rods, usually occurring singly or as pairs. They produce both D(-)- and L(+)- lactic acid from glucose. They produce acid from mannose and salicin but not from lactose, melibiose, raffinose, ribose or xylose. They grow at 15°C but not at 45°C and with 6.5 % NaCl.

The type species *P. selangorensis* was isolated from a Malaysian food ingredient, chili bo [177] and later transferred to the genus *Lactobacillus*, proposing *Lactobacillus selangorensis* comb. nov. [178]. Given the data presented in the present study we adopt the proposal of Leisner et al. [177].

Description of *Paralactobacillus selangorensis* comb. nov.

Paralactobacillus selangoresis (se.lan.gor.en'sis. N.L. masc. adj. *selangorensis*, belonging to the province of Selangor, Malaysia); Leisner et al. 2000, Haakensen *et al*. 2011, 2982^{VP}

Cells are able to grow on acetate agar and can lower the pH to below 4.15 in La-broth [179]. No growth occurs with 6.5% NaCl [177]. The genome size of the type strain is 2.09 Mbp; the mol % GC content of DNA is 46.

The species was isolated from a Malaysian food ingredient called chili bo.

The type strain is ATCC BAA-66^T = CCUG 43347^T = CIP 106482^T = DSM 13344^T = LMG 17710^T.

Genome sequence accession number: JQAZ00000000.

16S rRNA gene accession number: AF049745.

DESCRIPTION OF *LATILACTOBACILLUS* GEN. NOV.

Latilactobacillus (La.ti.lac.to.ba.cil'lus. L. masc. adj. *latus* wide, broad; N.L. masc. n. *Lactobacillus* a bacterial genus name; N.L. masc. n. *Latilactobacillus* a widespread lactobacillus).

Species of *Latilactobacillus* are homofermentative, their mol% GC content is between 40 and 42 and the genome size ranges from 1.82 to 2.12 Mbp; they produce both D(–)- and L-(+)-lactic acid with the exception of *L. fuchuensis*, which produces only the L(+)- isomer. Strains in the species lead a free-living lifestyle and are mesophilic; many strains are psychrotrophic and grow below 8°C. *L. sakei* and *L. curvatus* have commercial importance as meat starter cultures [58, 59].

A phylogenetic tree on the basis of 16S rRNA genes of all species in the genus *Latilactobacillus* is provided in Figure S6G.

The type species is *Latilactobacillus sakei* comb. nov.; *Latilactobacillus* was previously referred to as *L. sakei* group.

Description of *Latilactobacillus sakei* comb. nov.

Latilactobacillus sakei (sa'ke.i. N.L. gen. n. *sakei* of sake).

Basonym: *Lactobacillus sakei* corrig. Katagiri, Kitahara and Fukami 1934, 157 (Approved Lists); emend. Klein et al. 1996

L. sakei strains are frequently slightly curved and irregular cells, especially during stationary growth phase. Many of the strains grow also at 2–4°C, the majority of them produce L(+)-lactic acid in MRS broth [180].

Isolated from sauerkraut, fermented plant material, fermented seafood, cold smoked salmon, fermented or refrigerated meat products, spontaneous sourdoughs, and prepacked finished dough [181]. It is used commercially as starter culture for fermented meats [58, 59].

Two subspecies are recognised: *Latilactobacillus sakei* subsp. *carnosus* and *Latilactobacillus sakei* subsp. *sakei.*

Description of *Latilactobacillus sakei* subsp. *carnosus* comb. nov.

Latilactobacillus sakei subsp. *carnosus* (car.no'sus. L. masc. adj. *carnosus* pertaining to meat).

Basonym: *Lactobacillus sakei* subsp. *carnosus* Torriani et al. 1996, 1162^{VP}

L. sakei subsp. *carnosus* was formerly also referred to as *Lactobacillus curvatus* subsp. *melibiosus* [182]. Characteristics of the species are described in [183]. The genome size of the type strain is 1.99 Mbp. The mol% GC content of DNA is 41.0.

Isolated from fermented meat products, vacuum-packaged meat, sauerkraut, and other fermented plant material.

The type strain is R 14b/a^T = LMG 17302^T = DSM 15831^T = CCUG 31331^T = CIP 105422^T = JCM 11031^T.

Genome sequence accession number: AZFG00000000.

16S rRNA gene accession number: AY204892.

Description of *Latilactobacillus sakei* subsp. *sakei* comb. nov.

Latilactobacillus sakei subsp. *sakei* (sa'ke.i. N.L. gen. n. *sakei* of sake).

Basonym: *Lactobacillus sakei* subsp. *sakei* corrig. Katagiri, Kitahara and Fukami 1934, 157 (Approved Lists); emend. Klein et al., 1996

L. sakei subsp. *sakei* strains produce ammonia from arginine and acetoin from glucose and they grow in the presence of 10% NaCl. The genome size of the type strain is 1.91 Mbp. The mol% GC content of DNA is 41.1.

Isolated from sake starter, fermented meat products, vacuum-packaged meat, sauerkraut and other fermented plant material, and human faeces [183].

The type strain is T.S [K. Kitahara 37]^{T} = ATCC 15521^{T}= LMG 9468^{T} = DSM 20017^{T} = CCUG 30501^{T} = CIP 103139^{T} = IFO (now NBRC) 15893^{T} = JCM 1157^{T}.

Genome sequence accession number: AZDN00000000.

16S rRNA gene accession number: AM113784.

Description of *Latilactobacillus curvatus* comb. nov.

Latilactobacillus curvatus (cur.va'tus. L. masc. adj. *curvatus* curved).

Basonym: *Lactobacillus curvatus* (*Bacterium curvatum* Troili-Petersson 1903, 137) Abo-Elnaga and Kandler 1965; Troili-Petersson 1980 (Approved Lists); emend. Klein et al. 1996

Some *L. curvatus* strains are motile [184]; they occur in pairs, short chains, and frequently in horseshoe forms. Characteristics of the species are provided by [170, 180, 185]. The genome size of the type strain is 1.82 Mbp. The mol% GC content of DNA is 42.0.

Isolated from cow dung, fermented and vacuum-packaged refrigerated meat and fish products, dairy products such as milk and cheese, fermented plant products like sauerkraut, sourdough (including prepacked finished dough and pressed yeast), radish, pickles and kimchi, other plant-derived materials like honey and from the environmental fermentation process of corn or grass silage [186].

The type strain is 1^{T} = LMG 9198^{T} = DSM 20019^{T} = LMG 13553^{T} = ATCC 25601^{T}= CCUG 30669^{T} = CIP 102992^{T} = IFO (now NBRC) 15884^{T} = JCM 1096^{T} = NRRL B-4562^{T}.

Genome sequence accession number: AZDL00000000.

16S rRNA gene accession number: AM113777.

Description of *Latilactobacillus fuchuensis* comb. nov.

Latilactobacillus fuchuensis (fu.chu.en'sis. N.L. masc. adj. *fuchuensis* of Fuchu, the city where this bacterium was originally isolated).

Basonym: *Lactobacillus fuchuensis* Sakala et al. 2002, 1153^{VP}

Original characteristics of *L. fuchuensis* strains are described in [187]. The genome size of the type strain is 2.12 Mbp. The mol% GC content of DNA is 41.8.

Isolated from vacuum-packaged refrigerated beef, common carp intestine and other seafood products.

The type strain is B5M10^{T} = DSM 14340^{T} = CCUG 47133^{T} = JCM 11249^{T}.

Genome sequence accession number: AZEX00000000.

16S rRNA gene accession number: AB370875.

Description of *Latilactobacillus graminis* comb. nov.

Latilactobacillus graminis (gra'mi.nis. L. gen. n. *graminis* of grass).

Basonym: *Lactobacillus graminis* Beck et al. 1989, 93^{VP} (Effective publication: Beck et al. 1988, 282)

Strains of this species show a flocculant sediment after three days of growth in MRS broth [188]. The genome size of the type strain is 1.84 Mbp. The mol% GC content of DNA is 40.3.

Isolated from grass silage, meat products, sourdough, gut of snail *Cornum aspersum* and grapes.

The type strain is G90(1)^T = LMG 9825^T = DSM 20719^T = ATCC 51150^T= CCUG 32238^T = CIP 105164^T = JCM 9503^T = NRRL B-14857^T.

Genome sequence accession number: AYZB00000000.

16S rRNA gene accession number: AM113778.

DESCRIPTION OF *LOIGOLACTOBACILLUS* GEN. NOV.

Loigolactobacillus (Loi.go.lac.to.ba.cil'lus. Gr. masc. n. *loigos* destruction, ruin, havoc; N.L. masc. n *Lactobacillus* a bacterial genus; *Loigolactobacillus,* a lactobacillus with spoilage potential).

Cells are are non-motile, non-spore-forming, Gram-positive, catalase negative rods, found singly and in pairs. They are homofermentative and produce both D-(−)- and L-(+)- lactic acid isomers. Pentose fermentation is species specific; most of species produce acid from D-mannose and D-mannitol. The mol% GC content is between 40.6 and 44.3.

A phylogenetic tree on the basis of 16S rRNA genes of all species in the genus *Loigolactobacillus* is provided in Figure S6H.

The type species of the genus is *L. coryniformis* comb. nov.; *Loigolactobacillus* was previously referred to as *L. coryniformis* group.

Description of *Loigolactobacillus coryniformis* comb. nov.

Loigolactobacillus coryniformis (co.ry.ni.for'mis. Gr. fem. n. *coryne* a club; L. fem. n. *forma* shape; N.L. masc. adj. *coryniformis* club-shaped).

Basonym: *Lactobacillus coryniformis* Abo-Elnaga and Kandler 1965, 18 (Approved Lists)

L. coryniformis cells are short, coccoid rods, frequently pear-shaped. Pantothenic acid, niacin, riboflavin, biotin, and p-aminobenzoic acid are essential for the growth of all or the majority of the strains tested [170].

Two subspecies are recognized: *Loigolactobacillus coryniformis* subsp. *coryniformis* and *Loigolactobacillus coryniformis* subsp. *torquens*.

Description of *Loigolactobacillus coryniformis* subsp. *coryniformis* comb. nov.

Loigolactobacillus coryniformis subsp. *coryniformis* (co.ry'ni.for'mis. Gr. n. *coryne* a club; L. adj. *formis* shaped; N.L. adj. *coryniformis* club-shaped).

Basonym: *Lactobacillus coryniformis* subsp. *coryniformis* Abo-Elnaga and Kandler 1965, 18 (Approved Lists)

L. coryniformis subsp. *coryniformis* strains produce L-(+) isomer of the lactis acid at amounts of 15-20% of total lactic acid [170]. The genome size of the type strain is 2.71 Mbp. The mol% GC content of DNA is 42.9.

Isolated from silage, cow dung, dairy barn air and sewage, and from table olives, wheat, pickled vegetable, cheese and ting, a fermented sorghum porridge.

The type strain is ATCC 25602^T = CIP 103133^T = DSM 20001^T = CCUG 30666^T = JCM 1164^T = LMG 9196^T = NRRL B-4391^T.

Genome sequence accession number: AZCN00000000.

16S rRNA gene accession number: M58813.

Description of *Loigolactobacillus coryniformis* subsp. *torquens* comb. nov.

Loigolactobacillus coryniformis subsp. *torquens* (tor'quens. L. part. adj. *torquens*, twisting).

Basonym: *Lactobacillus coryniformis* subsp. *torquens* Abo-Elnaga and Kandler 1965, 18 (Approved Lists)

L. coryniformis subsp. *torquens* strains exclusively produce D(-)-lactic acid [170]. The genome size of the type strain is 2.78 Mbp. The mol% GC content of DNA is 42.9.

Isolated from cheese, yaks' milk cheese, silage and tomato pomace silage.

The type strain is CECT 4129 = ATCC 25600^T = CCUG 30667^T = CIP 103134^T = DSM 20004^T = JCM 1166^T = LMG 9197^T = NRRL B-4390^T.

Genome sequence accession number: AZDC00000000.

16S rRNA gene accession number: AJ575741.

Description of *Loigolactobacillus backii* comb. nov.

Loigolactobacillus backii (back'i.i. N.L. gen. n. *backii*, named in recognition of Werner Back, a German microbiologist who contributed to the microbiological and technological development of brewing).

Basonym: *Lactobacillus backii* Tohno et al. 2013, 3858^{VP}

L. backii strains are rod-shaped and occur singly, in pairs and in chains; they show leucin aminopeptidase, valine aminopeptidase, cystine aminopeptidase, acid phosphatase, naphthol-AS-BI-phosphohydrolase, β-galactosidase, β -glucosidase and N-acetyl- β -glucosaminidase activities [189]. The genome size of the type strain is 2.78 Mbp. The mol% GC content of DNA is 40.7.

Isolated from a spoiled lager beer.

The type strain is L-1062 = JCM 18665^T = LMG 23555^T = DSM 18080^T = L1062^T.

Genome sequence accession number: ASM166367v1. For bioinformatics analysis, the closed genome of strain TMW1.1989 was used: CP014873 (chromosome), CP014874 (plasmid) and CP014875 (second plasmid).

16S rRNA gene accession number: AB779648.

Description of *Loigolactobacillus bifermentans* comb. nov.

Loigolactobacillus bifermentans (bi.fer.men'tans. L. pref. *bi* twice; L. pres. part. *fermentans* leavening; N.L. part. adj. *bifermentans* doubly fermenting).

Basonym: *Lactobacillus bifermentans* (ex Pette and van Beynum 1943) Kandler et al. 1983, 896^{VP}

L. bifermentans strains are non-motile irregular rods with rounded or often tapered ends; clumps are often observed. Lactic acid is fermented to acetic acid, ethanol, traces of propionic acid, carbon dioxide and free H_2 [190]. The genome size of the type strain is 3.14 Mbp. The mol% GC content of DNA is 44.3.

Isolated from spoiled Edam and Gouda cheeses where it forms undesired small cracks [191], from fermented masau fruits and from Himalayan fermented milk products.

The type strain is N2^{T} = ATCC 35409^{T} = CCUG 32234^{T} = CIP 102811^{T} = DSM 20003^{T} = JCM 1094^{T} = LMG 9845^{T}.

Genome sequence accession number: AZDA00000000.

16S rRNA gene accession number: JN175330.

Description of *Loigolactobacillus iwatensis* comb. nov.

Loigolactobacillus iwatensis (i.wa.ten'sis. N.L. masc. adj. *iwatensis* of or belonging to Mount Iwate, where the first strains were isolated).

Basonym: *Lactobacillus iwatensis* Tohno et al. 2013, 3856^{VP}

L. iwatensis strains are facultatively anaerobic, non-spore-forming and non-motile rods. They are homofermentative; they are positive for C4 esterase, leucine aminopeptidase, valine aminopeptidase and acid phosphatase [189]. The genome size of the type strain is 2.62 Mbp. The mol% GC content of DNA is 40.6.

Isolated from orchardgrass silage.

The type strain is IWT246^{T} = JCM 18838^{T} = DSM 26942^{T}.

Genome sequence accession number: RHNP00000000.

16S rRNA gene accession number: AB773428.

Description of *Loigolactobacillus jiayinensis* comb. nov.

Loigolactobacillus jiayinensis (jia.yin.en'sis. N.L. masc. adj. *jiayinensis*, pertaining to Jiayin, a county in the Heilongjiang province of China).

Basonym: *Lactobacillus jiayinensis* Long and Gu 2019, 2348^{VP}

Cells are non-motile, rod-shaped, singly or in pairs [158]. The genome size of the type strain is 3.04 Mbp. The mol% GC content of DNA is 42.6.

Isolated from a fermentation Chinese cabbage.

The type strain is 257-1^{T} = NCIMB 15166^{T} = CCM 8904^{T} = LMG 31065^{T}.

Genome sequence accession number: RHOF00000000.

16S rRNA gene accession number: MK110846.

Description of *Loigolactobacillus rennini* comb. nov.

Loigolactobacillus rennini (ren.ni'ni. N.L. gen. n. *rennini*, of rennet).

Basonym: *Lactobacillus rennini* Chenoll et al. 2006, 451^{VP}

L. rennini strains are non-motile rods, found singly and in pairs. They grow at pH 3.7, 4.5 and 8.0, and in medium with 5 and 10% (w/v) NaCl [192]. The genome size of the type strain is 2.27 Mbp. The mol% GC content of DNA is 40.7.

Isolated from rennet and are associated with cheese spoilage.

The type strain is 1-7^{T} = CECT 5922^{T} = DSM 20253^{T} = JCM 14279^{T}.

Genome sequence accession number: AYYI00000000.

16S rRNA gene accession number: LC258150.

Description of *Loigolactobacillus zhaoyuanensis* comb. nov.

Loigolactobacillus zhaoyuanensis (zhao.yuan.en'sis. N.L. masc. adj. *zhaoyuanensis*, pertaining to Zhaoyuan, a county in the Heilongjiang province of China).

Basonym: *Lactobacillus zhaoyuanensis* Long and Gu, 2019, 2348^{VP}

Cells are non-motile rods, usually singly or in pairs. They grow at 15–33°C and pH 5–10. Both isomers of lactic acid are produced (93 % D(-)-lactate and 7 % L(+)-lactate) [158]. The genome size of the type strain is 2.70 Mbp. The mol% GC content of DNA is 42.7.

Isolated from fermented Chinese cabbage.

The type strain is 187-3^T = NCIMB 15172^T = CCM 8910^T.

Genome sequence accession number: RHOE00000000.

16S rRNA gene accession number: MK110851.

DESCRIPTION OF *DELLAGLIOA* GEN. NOV.

Dellaglioa (Del.la.gli.o'a. N.L. fem. n. *Dellaglioa*, named after Franco Dellaglio, an Italian microbiologist, former chairman of the Subcommittee on taxonomy of *Bifidobacterium*, *Lactobacillus* and related organisms, known for his significant research contributions to the taxonomy of the lactic acid bacteria).

Strains of *Dellaglioa* are facultatively anaerobic, psychrophilic, nonmotile, homofermentative rod-shaped bacteria. Strains of the only species included in the genus are psychrotrophic and occur as meat spoilage organism.

The type species is *Dellaglioa algida.*

Description of *Dellaglioa algida* comb. nov.

Dellaglioa algida (al'gi.da. L. fem. adj. *algida* cold, referring to the ability to grow at low temperature).

Basonym: *Lactobacillus algidus* Kato et al. 2000, 1148^{VP}

Characteristics are described in [193]. The genome size of the type strain is 1,59 Mbp, the mol % GC content of DNA is 36.

Isolated as spoilage organisms from refrigerated beef and pork meat.

The type strain is M6A9^T = JCM 10491^T = LMG 19872^T = DSM 15638^T = CIP 106688^T.

Genome sequence accession number: AZDI00000000.

16S rRNA gene accession number: AB033209.

DESCRIPTION OF *LIQUORILACTOBACILLUS* GEN. NOV.

Liquorilactobacillus (Li.quo.ri.lac.to.ba.cil'lus L. masc. n. *liquor*, liquid; N.L. masc. n. *Lactobacillus* a bacterial genus; N.L. masc. n. *Liquorilactobacillus* a lactobacillus from liquids, referring to the isolation of most species from liquids including water, plant sap, and alcoholic beverages).

Homofermentative, their mol% GC content is between 33.9 and 40.0; most of the species are motile with the exception of *L. cacaonum*, *L. hordei*, *L. mali*. They contain meso-diaminopimelic acid. *Liquorilactobacillus* species were mostly isolated from fermented plant materials including alcoholic fermentations and water kefir. Many strains of *Liquorilactobacillus* produce dextran from sucrose [194].

A phylogenetic tree on the basis of 16S rRNA genes of all species in the genus *Liquorilactobacillus* is provided in Figure S6I.

The type species is *Liquorilactobacillus mali* comb. nov.; *Liquorilactobacillus* species were previously considered part of the *L. salivarius* group.

Description of *Liquorilactobacillus mali* comb. nov.

Liquorilactobacillus mali (ma'li. L. gen. n. *mali*, of an apple).

Basonym: *Lactobacillus mali* Carr and Davies 1970, 769 (Approved Lists); emend. Kaneuchi et al. 1988, 272

L. mali cells are non-motile or weakly motile with a few peritrichous flagella. Liquid cultures are turbid after few days, with subsequent clearing and sediment. They produce acetoin and dextran; malic acid is decomposed to lactic acid and CO_2. Most strains have a pseudocatalase activity when they grow on MRS agai with 0.1 % (w/v) glucose [195, 196]. The genome size of the type strain is 2.59. The mol% GC content of DNA is 36.1.

Isolated from wine must, fermenting cider, fermented molasses, water kefirs, cocoa bean fermentations and table olives.

The type strain is ATCC 27053^T = CCUG 30141^T = CCUG 32228^T = CIP 103142^T = DSM 20444^T = JCM 1116^T = LMG 6899^T = NBRC 102159^T = NCIB (now NCIMB) 10560^T = NRRL B-4563^T = VKM B-1600^T.

Genome sequence accession number: AYYH00000000.

16S rRNA gene accession number: M58824.

Description of *Liquorilactobacillus aquaticus* comb. nov.

Liquorilactobacillus aquaticus (a.qua'ti.cus. L. masc. adj. *aquaticus*, living, growing or found in water, or an aquatic environment).

Basonym: *Lactobacillus aquaticus* Mañes-Lázaro et al. 2009, 2217^{VP}

L. aquaticus cells are motile rods, which grow at pH 4.5-8.0 but not at pH 3.3. There is no growth in 5 or 10% NaCl.

The species is described in [197]. The genome size of the type strain is 2.41 Mbp. The mol% GC content of DNA is 37.4.

Isolated from a eutrophic freshwater pond.

The type strain is $IMCC1736^T$ = CECT 7355^T = DSM 21051^T = JCM 16869^T.

Genome sequence accession number: AYZD00000000.

16S rRNA gene accession number: DQ664203.

Description of *Liquorilactobacillus cacaonum* comb. nov.

Liquorilactobacillus cacaonum (ca.ca.o'num. N.L. gen. pl. n. *cacaonum*, of cacao beans).

Basonym: *Lactobacillus cacaonum* De Bruyne et al. 2009, 11^{VP}

L. cacaonum cells are non-motile small rods, they grow at 37C in MRS broth at pH 3.9; no growth is observed in MRS supplemented with NaCl [198]. The genome size of the type strain is 1.92 Mbp. The mol% GC content of DNA is 33.9.

Isolated from cocoa fermentation.

The type strain is R-34119^T = DSM 21116^T = LMG 24285^T.

Genome sequence accession number: AYZE00000000.

16S rRNA gene accession number: AM905389.

Description of *Liquorilactobacillus capillatus* comb. nov.

Liquorilactobacillus capillatus (ca.pil.la'tus. L. masc. adj. *capillatus*, hairy, referring to the characteristic of having long, hairy flagella).

Basonym: *Lactobacillus capillatus* Chao et al. 2008, 2557^{VP}

L. capillatus cells are motile by means of peritrichous flagella; they grow at pH 4.0 and pH 8.0 but they do not grow at 8% NaCl [199]. The genome size of the type strain is 2.24 Mbp. The mol% GC content of DNA is 37.6.

Isolated from fermented brine used for stinky tofu production.

The type strain is YIT 11306^{T} = BCRC 17811^{T} = DSM 19910^{T} = JCM 15044^{T}.

Genome sequence accession number: AZEF00000000.

16S rRNA gene accession number: AB365976.

Description of *Liquorilactobacillus ghanensis* comb. nov.

Liquorilactobacillus ghanensis (gha.nen'sis. N.L. masc. adj. *ghanensis*, pertaining to Ghana, where the species was first isolated).

Basonym: *Lactobacillus ghanensis* Nielsen et al. 2007, 1471^{VP}

L. ghanensis cells are motile with peritrichous flagella, and colonies have slightly uneven edges after 3-4 days of anaerobic growth. They do not grow at pH 8.0, nor at 6.5% NaCl [200]. The genome size of the type strain is 2.61 Mbp. The mol% GC content of DNA is 37.1.

Isolated from cocoa fermentations.

The type strain is $L489^{T}$ = CCUG 53453^{T} = DSM 18630^{T} = JCM 15611^{T}.

Genome sequence accession number: AZGB00000000.

16S rRNA gene accession number: DQ523489.

Description of *Liquorilactobacillus hordei* comb. nov.

Liquorilactobacillus hordei (hor'de.i. L. gen. n. *hordei*, from barley).

Basonym: *Lactobacillus hordei* Rouse et al. 2008, 2016^{VP}

L. hordei cells are non-motile rods, they grow at pH 4 and 8 but not at pH 3 and 9. They produce bacteriocins [201]. The genome size of the type strain is 2.30 Mbp. The mol% GC content of DNA is 34.8.

Isolated from malted barley, water kefirs and in Turkish traditional fermented gilaburu fruit juice.

The type strain is $UCC128^{T}$ = DSM 19519^{T} = JCM 16179^{T} = LMG 24241^{T}.

Genome sequence accession number: AZDX00000000.

16S rRNA gene accession number: EU074850.

Description of *Liquorilactobacillus nagelii* comb. nov.

Lacitilactobacillus nagelii (na.gel'i.i. N.L. gen. n. *nagelii*, of Nagel, after Charles W. Nagel, Washington State University, USA, for his contributions to the science of wines).

Basonym: *Lactobacillus nagelii* Edwards et al. 2000, 700^{VP}

L. nagelii cells are motile rods, they grow in MRS broth with 5%(w/v) NaCl (pH 4.5) at 25°C; both citrate and malate are utilized in the presence of glucose and dextran is formed from sucrose [202]. The genome size of the type strain is 2.50 Mbp. The mol% GC content of DNA is 36.7.

Isolated from partially fermented wine, spontaneous cocoa bean fermentations, water kefirs, fermented cassava food and silage fermentation of fruit residues.

The type strain is LuE$_{10}$^{T} = ATCC 700692^{T} = CCUG 43575^{T} = DSM 13675^{T} = JCM 12492^{T}.

Genome sequence accession number: AZEV00000000.

16S rRNA gene accession number: Y17500.

Description of *Liquorilactobacillus oeni* comb. nov.

Liquorilactobacillus oeni (oe'ni. Gr. masc. n. *oinos*, wine; N.L. gen. n. *oeni*, of wine).

Basonym: *Lactobacillus oeni* Mañes-Lázaro et al. 2009, 2013^{VP}

L. oeni cells are mostly motile and they grow at pH 4.5-8.0 but not at pH 3.3 and with 10% ethanol. L-Malic acid is transformed into L(+)-lactic acid. They produce exopolysaccharide from sucrose [203]. The genome size of the type strain is 2.12 Mbp. The mol% GC content of DNA is 37.3.

Isolated from Bobal wine.

The type strain is 59b^{T} = CECT 7334^{T} = DSM 19972^{T} = JCM 18036^{T}.

Genome sequence accession number: AZEH00000000.

16S rRNA gene accession number: AY681127.

Description of *Liquorilactobacillus satsumensis* comb. nov.

Liquorilactobacillus satsumensis (sat.su.men'sis. N.L. masc. adj. *satsumensis*, pertaining to Satsuma, old name for the southern part of Kyushu in Japan, from where the type strain was isolated).

Basonym: *Lactobacillus satsumensis* Endo and Okada 2005, 85^{VP}

L. satsumensis cells are motile rods with peritrichous flagella. Growth is observed in MRS broth at pH 3.5 containing 5% (w/v) NaCl but not with 10% (v/v) ethanol. Dextran is formed from sucrose [204]. The genome size of the type strain is 2.65 Mbp. The mol% GC content of DNA is 39.9.

Isolated from mashes of shochu, a traditional Japanese distilled spirit made from fermented rice and other starchy materials.

The type strain is DSM 16230^{T} = JCM 12392^{T} = NRIC 0604^{T}.

Genome sequence accession number: AZFQ00000000.

16S rRNA gene accession number: AB154519.

Description of *Liquorilactobacillus sicerae* comb. nov.

Liquorilactobacillus sicerae (si'ce.rae. L. gen. n. *sicerae* of cider).

Basonym: *Lactobacillus sicerae* Puertas et al. 2014, 2954^{VP}

L. sicerae cells are motile rods with polar flagella, they produce exopolysaccharides from sucrose and both malic and citric acids are utilized in the presence of glucose [205]. The genome size of the type strain is 2.49 Mbp. The mol% GC content of DNA is 37.5.

Isolated from spoiled apple cider.

The type strain is CUPV261^T = CECT 8227^T = KCTC 21012^T.

Genome sequence accession number: PRJEB5073.

16S rRNA gene accession number: HG794492.

Description of *Liquorilactobacillus sucicola* comb. nov.

Liquorilactobacillus sucicola (su.ci.co'la. L. n. *sucus*, juice, sap; L. suff. -*cola* (from L. masc. or fem. n. *incola*), inhabitant, dweller; N.L. masc. n. *sucicola*, a sap-dweller).

Basonym: *Lactobacillus sucicola* Irisawa and Okada 2009, 2664^{VP}

L. sucicola cells are motile rods by means of peritrichous flagella; they do not grow in GYP broth containing 5% (w/v) NaCl [206]. The genome size of the type strain is 2.46 Mbp. The mol% GC content of DNA is 38.5.

Isolated from the sap of an oak (*Quercus* sp.).

The type strain is NRIC 0736^T = DSM 21376^T = JCM 15457^T.

Genome sequence accession number: AYZF00000000.

16S rRNA gene accession number: AB433982.

Description of *Liquorilactobacillus uvarum* comb. nov.

Liquorilactobacillus uvarum (u.va'rum. L. gen. pl. n. *uvarum* of grapes).

Basonym: *Lactobacillus uvarum* Mañes-Lázaro et al. 2008, 2129^{VL}

L. uvarum cells are motile rods; they grow at pH 4.5 and 8 but not at pH 3.3. They produce exopolysaccharide from sucrose [207]. The genome size of the type strain is 2.69 Mbp. The mol% GC content of DNA is 36.9.

Isolated from from Bobal grape musts.

The type strain is 8^T = Lb8^T= CECT 7335^T = DSM 19971^T = JCM 16870^T.

Genome sequence accession number: AZEG00000000.

16S rRNA gene accession number: AY681126.

Description of *Liquorilactobacillus vini* comb. nov.

Liquorilactobacillus vini (vi'ni. L. gen. n. *vini* of wine).

Basonym: *Lactobacillus vini* Rodas et al. 2006, 516^{VP}

The cells are motile rods, they do not produce exopolysaccharide from sucrose, but they utilize citric and malic acids [208]. *L. vini* was the first organism for which metabolism of pentoses via the pentose phosphate pathway to lactate as sole end product was described [18]. The metabolism for homofermentative metabolism of pentoses was initially described for strains later classified as *L. vini* [18, 209]. The genome size of the type strain is 2.24 Mbp. The mol% GC content of DNA is 37.5.

Isolated from fermenting Spanish grape must and from bioethanol industrial processes in different distilleries of Brazil.

The type strain is Mont 4^T = CECT 5924^T = DSM 20605^T = JCM 14280^T.

Genome sequence accession number: AYYX00000000.

16S rRNA gene accession number: AJ576009.

DESCRIPTION OF *LIGILACTOBACILLUS* GEN. NOV.

Ligilactobacillus (Li.gi.lac.to.ba.cil'lus. L. v. *ligare* to tie, unite; N.L. masc. n. *Lactobacillus* a bacterial genus name; N.L. masc. n. *Ligilactobacillus* a lactobacillus with a host-associated life style).

Species of *Ligilactobacillus* are homofermentative, their mol% GC content is between 32.5 and 43.3. Several *Ligilactobacillus* species include strains that are motile. Most *Ligilactobacillus* species have been isolated from animals and humans and are adapted to vertebrate hosts. Several strains of *Ligilactobacillus* express urease, this enzyme is the most powerful bacterial tool to withstand gastric acidity; in lactobacilli, urease activity is associated with a vertebrate host adapted lifestyle [210, 211]. Several *Ligilactobacillus* species also commonly occur in fermented foods and are used commercially as starter cultures or probiotic cultures.

A phylogenetic tree on the basis of 16S rRNA genes of all species in the genus *Ligilactobacillus* is provided in Figure S6J.

The type species is *Ligilactobacillus salivarius* comb. nov.; *Ligilactobacillus* was previously referred to as *L. salivarius* group.

Description of *Ligilactobacillus salivarius* comb. nov.

Ligilactobacillus salivarius (sa.li.va'ri.us. L. masc. adj. *salivarius* salivary).

Basonym: *Lactobacillus salivarius* Rogosa et al. 1953, 691 (Approved Lists); emend. Li et al. 2006

L. salivarius strains require pteroylglutamic acid and niacin for good growth. Riboflavin is also markedly stimulatory. Good growth does not take place in media unless polyoxyethylene sorbitan monooleate (Tween 80) is added [61, 212]. The genome size of the type strains is 1.98 Mbp. The mol% GC content of DNA is 37.5.

Isolated from the mouth and intestinal tract of humans, cats, hamsters, chickens and swine, and from dairy products; the species shows no adaptation to specific hosts [213].

The type strain is H066^{T} = ATCC 11741^{T}= CCUG 31453^{T} = CIP 103140^{T} = DSM 20555^{T} = JCM 1231^{T} = LMG 9477^{T} = NRRL B-1949^{T}.

Genome accession number: AYYT00000000.

16S rRNA gene accession number: AF089108.

Description of *Ligilactobacillus acidipiscis* comb. nov.

Ligilactobacillus acidipiscis (a.ci.di.pis'cis. L. masc. adj. *acidus* sour; L. n. *piscis* fish; N.L. gen. n. *acidipiscis* of a sour fish, an isolation source of strains of this species).

Basonym: *Lactobacillus acidipiscis* Tanasupawat et al. 2000, 1481^{VP}. The species includes strains previously designated as *L. cypricasei* [214]

L. acidipiscis strains grow in 10% NaCl; some strains grow in the presence of 12% NaCl. They show no reaction in litmus milk and do not form slime from sucrose. Niacin and calcium pantothenate are required for growth [215]. The genome size of the type strain is 2.33 Mbp. The mol% GC content of DNA is 39.1.

Isolated from fermented fish (pla-ra and pla-chom) in Thailand but also found in dairy products, soy sauce mash, table olives, sake starter, tropical grasses, forage crops, bee pollen, and Chinese DaQu, a saccharification starter for production of vinegar and liquor from cereals.

The type strain is FS60-1^{T} = CCUG 46556^{T} = CIP 106750^{T} = DSM 15836^{T} = HSCC 1411^{T} = JCM 10692^{T} = NBRC 102163^{T} = NRIC 0300^{T} = PCU 207^{T} = TISTR 1386^{T}.

Genome sequence accession number: AZFI00000000.

16S rRNA gene accession number: AB023836.

Description of *Ligilactobacillus agilis* comb. nov.

Ligilactobacillus agilis (a'gi.lis. L. masc. adj. *agilis* agile, motile).

Basonym: *Lactobacillus agilis* Weiss et al. 1982, 266^{VP} (Effective publication: Weiss et al. 1981, 252)

L. agilis strains are motile with peritrichous flagella; motility is easily demonstrated in MRS broth [174]. The genome size of the type strain is 2.06 Mbp. The mol% GC content of DNA is 41.7.

Isolated from municipal sewage; *L. agilis* is the dominant species in the pigeon crops and it is also found in the gut and cecum of birds, human gut and vagina, porcine intestinal mucin and fermented food products such as masau fruits, Nigerian ogi, and cheese.

The type strain is CIP 101264^{T} = CCUG 31450^{T} = DSM 20509^{T} = JCM 1187^{T} = LMG 9186^{T} = NRRL B-14856^{T}.

Genome sequence accession number: AYYP00000000.

16S rRNA gene accession number: M58803.

Description of *Ligilactobacillus animalis* comb. nov.

Ligilactobacillus animalis (a.ni.ma'lis. L. gen. n. *animalis*, of an animal).

Basonym: *Lactobacillus animalis* Dent and Williams 1983, 439^{VP}; Effective publication: Dent and Williams 1982, 384

L. animalis strains grow at 45°C, cells in exponential growth phase occur singly or in pairs [216]. The genome size of the type strain is 1.89 Mbp. The mol% GC content of DNA is 41.1

Isolated from dental plaques and intestines of animals.

The type strain is 535^{T} = ATCC 35046^{T} = CCUG 33906^{T} = CIP 103152^{T} = DSM 20602^{T} = IFO (now NBRC) 15882^{T} = JCM 5670^{T} = LMG 9843^{T} = NCIMB 13278^{T} (formerly NCDO 2425^{T}) = NRRL B-14176^{T}.

Genome sequence accession number: AYYW00000000.

16S rRNA gene accession number: AB326350.

Description of *Ligilactobacillus apodemi* comb. nov.

Ligilactobacillus apodemi (a.po.de'mi. N.L. gen. n. *apodemi*, of *Apodemus speciosus*, the field mouse from which the organism was first isolated).

Basonym: *Lactobacillus apodemi* Osawa et al. 2006, 1695^{VP}

L. apodemi strains are non-motile, they are tannase-positive and they produce gallic acid from tannic acid but they do not convert gallic acid to pyrogallol [217]. The genome size of the type strain is 2.10 Mbp. The mol% GC content of DNA is 38.6.

Isolated from the faeces of a wild mouse faeces.

The type strain is ASB1^{T} = CIP 108913^{T} = DSM 16634^{T} = JCM 16172^{T}.

Genome sequence accession number: AZFT00000000.

16S rRNA gene accession number: AJ871178.

Description of *Ligilactobacillus araffinosus* sp. nov.

Ligilactobacillus araffinosus (a.raf.fi.no'sus. Gr. pref. *a* not; N.L. masc. adj. *raffinosus* of raffinose; N.L. masc. adj. *araffinosus*, not fermenting raffinose).

Basonym: *Lactobacillus aviarius* subsp. *araffinosus* Fujisawa et al. 1985, 223^{VP}; Fujisawa et al. 1986, (Effective publication: Fujisawa *et al*., 1984, 419). Placement of *L. araffinosus* in a separate species is supported by ANI values and digital DNA-DNA hybridization [10]. The availability of the genome sequences of the type strains of both subspecies revealed that they are only distantly related with an ANI value of 88.98%, substantially below the 95-96% threshold recognised for the species level. Furthermore, their core nucleotide identity (CNI) [10] is 91.1, which is below the 94% threshold at which two strains are allocated to the same species. Finally, their *in silico* DDH value is 37.80, which additionally supports that these two subspecies should be recognised as different species [10].

Cells are Gram- positive, non-motile, non-spore-forming rods with rounded ends, usually occurring singly or in short chains. *L. araffinosus* strains ferment trehalose and cellobiose, they do not produce acid from galactose, lactose, melibiose and raffinose [51]. The genome size of the type strain is 1.48 Mbp. The mol% GC content of DNA is 38.1.

Isolated from the intestine and faeces of birds.

The type strain is ML2^T = ATCC 43235^T= DSM 20653^T = CCUG 32231^T = CIP 103145^T = JCM 5667^T

Genome sequence accession number: AYYZ00000000.

16S rRNA gene accession number: AB289043.

Description of *Ligilactobacillus aviarius* comb. nov.

Ligilactobacillus aviarius (a.vi.a'ri.us. L. masc. adj. *aviarius*, pertaining to birds).

Basonym: *Lactobacillus aviarius* Fujisawa et al. 1985, 223^{VP}; Fujisawa et al. 1986; Effective publication: Fujisawa *et al*., 1984, 419

The cells are non-motile rods with rounded ends, occurring singly or in short chains. The final pH of glucose broth is 3.9 - 4.0. This species is strictly anaerobic [51]. The genome size of the type strain is 1.68 Mbp. The mol% GC content of DNA is 40.1.

Isolated from the intestine and faeces of birds.

The type strain is 75^T = ATCC 43234^T = DSM 20655^T = CCUG 32230^T = CIP 103144^T = JCM 5666^T = LMG 10753^T = NBRC 102162^T.

Genome sequence accession number: AYZA00000000.

16S rRNA gene accession number: M58808.

Description of *Ligilactobacillus ceti* comb. nov.

Ligilactobacillus ceti (ce'ti. L. gen. n. *ceti*, of a whale).

Basonym: *Lactobacillus ceti* Vela et al. 2008, 893^{VP}

Original characteristics of the species are described in [218]. The genome size of the type strain is 1.40 Mbp. The mol% GC content of DNA is 33.7.

Isolated from the lungs of a beaked whale.

The type strain is 142-2^T = CCUG 53626^T = DSM 22408^T = CECT 7185^T = JCM 15609^T.

Genome accession number: JQBZ00000000.

16S rRNA gene accession number: AM292799.

Description of *Ligilactobacillus equi* comb. nov.

Ligilactobacillus equi (e'qui. L. gen. n. *equi*, of the horse).

Basonym: *Lactobacillus equi* Morotomi et al. 2002, 214^{VP}

Strains of this species are non-motile rods and some of them contain filamentous cells [219]. The genome size of the type strain is 2.30 Mbp. The mol% GC content of DNA is 39.0.

Isolated from faeces of horses.

The type strain is YIT 0455^T = ATCC BAA-261^T = DSM 15833^T = CCUG 47129^T = JCM 10991^T.

Genome accession number: AZFH00000000.

16S rRNA gene accession number: AM292799.

Description of *Ligilactobacillus faecis* comb. nov.

Ligilactobacillus faecis (fae'cis. L. gen. n. *faecis* of faeces).

Basonym: *Lactobacillus faecis* Endo et al. 2013, 4505^{VP}.

Original characteristics of the species described in [220]. The mol% GC content of DNA is 41.1.

Isolated from faeces of a jackal (*Canis mesomelas*) and raccoons (*Procyron lotor*).

The type strain is AFL13-2^T = JCM 17300^T = DSM 23956^T.

Genome accession number: not available at time of publication

16S rRNA gene accession number: AB812750.

Description of *Ligilactobacillus hayakitensis* comb. nov.

Ligilactobacillus hayakitensis (ha.ya.ki.ten'sis. N.L. masc. adj. *hayakitensis*, of Hayakita, the name of the area where the bacterium was originally isolated).

Basonym: *Lactobacillus hayakitensis* Morita et al. 2007, 2838^{VP}

Original characteristics of the species are described in [221]. The genome size of the type strain is 1.70 Mbp. The mol% GC content of DNA is 34.1.

Isolated from the faeces of a thoroughbred as predominant species in the intestinal microbiota.

The type strain is $KBL13^T$ = DSM 18933^T = JCM 14209^T.

Genome accession number: AZGD00000000.

16S rRNA gene accession number: AB267406.

Description of *Ligilactobacillus murinus* comb. nov.

Ligilactobacillus murinus (mu.ri'nus. L. adj. *murinus* of mice).

Basonym: *Lactobacillus murinus* Hemme et al., 1982, 384^{VP}.

L. murinus strains are non-motile rods which slowly ferment ribose and arabinose. L-LDH is activated by FDP and Mn^{2+}. They do not hydrolyze urea and hippurate; they decarboxylate malate. Riboflavin is a required growth factor [222]. The genome size of the type strain is 2.20 Mbp. The mol% GC content of DNA is 40.1.

Isolated from the intestinal tract of mice and rats and from sourdough.

The type strain is 313^T = ATCC 35020^T = CCUG 33904^T = CIP 104818^T = CNRZ 220^T = DSM 20452^T = IFO (now NBRC) 14221^T = JCM 1717^T = LMG 14189^T.

Genome accession number: AYYN00000000.

16S rRNA gene accession number: AJ621554.

Description of *Ligilactobacillus pobuzihii* comb. nov.

Ligilactobacillus pobuzihii (po.bu.zi'hi.i. N.L. gen. n. *pobuzihii* referring to the isolation of the type strain from pobuzihi, fermented cummingcordia).

Basonym: *Lactobacillus pobuzihii* Chen et al. 2010, 1916^{VP}

Original characteristics of the species are described in [223]. The genome size of the type strain is 2.35 Mbp. The mol% GC content of DNA is 37.7.

Isolated from pobuzihi, fermented cummincordia, fermented fish, and traditional vinegar.

The type strain is E100301^T = RIFY 6501^T = JCM 18084^T = KCTC 13174^T = NBRC 103219^T.

Genome accession number: JQCN00000000.

16S rRNA gene accession number: AB326358.

Description of *Ligilactobacillus ruminis* comb. nov.

Ligilactobacillus ruminis (ru'mi.nis. N.L. gen. n. *ruminis* of rumen).

Basonym: *Lactobacillus ruminis* Sharpe et al. 1973, 47 (Approved Lists)

Strains of *L. ruminis* are motile by peritrichous flagella, anaerobic, and grow on surface only under reduced oxygen pressure; growth in liquid media is supported with the addition of cysteine-HCl. Strains isolated from sewage are nonmotile and do not grow at 45°C [224]. The genome size of the type strain is 2.01 Mbp. The mol% GC content of DNA is 43.4.

Isolated from rumen of cow and from sewage; also commonly found in the gut of humans, horses and pigs and bovine uterus. Genomic analyses indicated a differentiation of specific phylogenetic lineages of the species to specific vertebrate hosts [225].

The type strain is RFI^T = ATCC 27780^T = CCUG 39465^T = CIP 103153^T = DSM 20403^T = JCM 1152^T = LMG 10756^T = NBRC 102161^T = NRRL B-14853^T.

Genome accession number: AYYL00000000.

16S rRNA gene accession number: AB326354.

Description of *Ligilactobacillus saerimneri* comb. nov.

Ligilactobacillus saerimneri (sae.rim'ne.ri. N.L. gen. masc. n. *saerimneri* of Saerimner, a pig occurring in Nordic mythology, because the organism was isolated from pigs).

Basonym: *Lactobacillus saerimneri* Pedersen and Roos 2004, 1367^{VP}

Strains of this species grows aerobically in MRS agar but at a lower rate compared to anaerobic growth. They do not hydrolize esculine [226]. The genome size of the type strain is 1.69 Mbp. The mol% GC content of DNA is 42.6.

Isolated from pig faeces. The habitat of *L. saerimneri* is the intestines of pigs, the human gut and vagina and the cecum of chicken.

The type strain is GDA154^T = CCUG 48462^T = DSM 16049^T = JCM 15955^T = LMG 22087^T.

Genome accession number: AZFP00000000.

16S rRNA gene accession number: AY255802.

Description of *Ligilactobacillus salitolerans* comb nov.

Ligilactobacillus salitolerans (sa.li.to'le.rans. L. masc. n. *sal* salt; L. pres. part. *tolerans* tolerating; N.L. part. adj. *salitolerans* salt tolerating).

Basonym: *Lactobacillus salitolerans* Tohno et al. 2019, 967^{VP}

Characteristics of the species [227] are based on the description of one strain. The genome size of the type strain is 2.30 Mbp. The mol% GC content of DNA is 41.7.

Isolated from spent mushrooms substrates.

The type strain is YK43^T = JCM 31331^T = DSM 103433^T.

Genome accession number: BFFP01000000.

16S rRNA gene accession number: LC127508.

DESCRIPTION OF *LACTIPLANTIBACILLUS* GEN. NOV.

Lactiplantibacillus (Lac.ti.plan.ti.ba.cil'lus. L. neut. n. *lactis* milk; L. fem. n. *planta* plant, referring to the *plantarum*-group lactobacilli; L. masc. n. *bacillus* a rod; N.L. masc. n. *Lactiplantibacillus* a milk derived rodlet from the (*Lactobacillus*) *plantarum* group.

Lactiplantibacillus species are Gram-positive, non-spore-forming, homofermentative and non-motile rods. *Lactiplantibacillus* species ferment a wide range of carbohydrates; most species metabolise phenolic acids by esterase, decarboxylase and reductase activities. *Lactiplantibacillus plantarum* is atypical for its pseudocatalase activity and reduction of nitrate. For discrimination between the two subspecies of *L. plantarum,* sequencing of the *recA* and *cpn60* genes or AFLP profiling is necessary [228, 229]. The mol % GC content of DNA ranges between 42.9 and 48.7.

Lactiplantibacillus species are isolated from many different fermented foods including fermented vegetables, meats, dairy products, and fermented cereals [58, 59], but they are also found in insect-associated habitats or as temporary residents of vertebrate intestinal microbiota and are characterized by a nomadic behavior [230]. *L. plantarum* has been widely used as a model species for metabolic, ecological, and genetic studies in lactobacilli. *L. plantarum* is of commercial importance as starter culture for multiple food fermentations, and is applied as probiotic culture.

A phylogenetic tree on the basis of 16S rRNA genes of all species in the genus *Lactiplantibacillus* is provided in Figure S6K.

The type species is *Lactiplantibacillus plantarum* comb. nov.; *Lactiplantibacillus* was previously referred to as *L. plantarum* group.

Description of *Lactiplantibacillus plantarum* comb. nov.

Lactiplantibacillus plantarum (plan.ta'rum. L. gen. pl. n. *plantarum* of plants).

Basonym: *Lactobacillus plantarum* Bergey et al. 1923, 250 (Approved Lists)

Previously designated as *Streptobacterium plantarum* [2]. Cells are nonmotile rods occurring singly, in pairs, or in short chains. Some strains reduce nitrate in limited glucose concentration and pH 6.0 or higher. Some strains exhibit pseudocatalase activity, or true catalase when heme is present. They require calcium pantothenate and niacin to grow [2, 231].

The species has a nomadic lifestyle; it is a dominant member of the microbiota in spontaneous vegetable and olive fermentations and also occurs in sourdough, dairy fermentations, and fermented meats [58, 59]. *L. plantarum* contributes to spoilage of beer and wine. *L. plantarum* also is part of the microbiota of insects [232], and is isolated from the human intestinal tract, particularly the oral cavity.

Two subspecies are recognized: *Lactiplantibacillus plantarum* subsp. *plantarum* and *Lactiplantibacillus plantarum* subsp. *argentoratensis*.

Description of *Lactiplantibacillus plantarum* subsp. *plantarum*, comb. nov.

Lactiplantibacillus plantarum subsp. *plantarum* (plan.ta'rum. L. gen. pl. n. *plantarum* of plants).

Basonym: *Lactobacillus plantarum* subsp. *plantarum* Bringel et al. 2005, 1633^{VP}

The description is that of the species [2, 231]. The genome size of the type strain is 3.45 Mbp. The mol% GC content of DNA is 44.2.

Isolated from dairy products and dairy environments, silage, sauerkraut, pickled vegetables, sourdough, cow dung, the human mouth, intestinal tract and stools, and from sewage.

The type strain is ATCC 14917^{T} = CCUG 30503^{T} = CIP 103151^{T} = DSM 20174^{T} = IFO (now NBRC) 15891^{T} = JCM 1149^{T} = LMG 6907^{T} = NCIMB 11974^{T} = NRRL B-4496^{T}.

Genome sequence accession number: AZEJ00000000.

16S rRNA gene accession number: AJ965482.

Description of *Lactiplantibacillus plantarum* subsp. *argentoratensis*, comb. nov.

Lactiplantibacillus plantarum subsp. *argentoratensis* (ar.gen.to.ra.ten'sis. N.L. masc. adj. *argentoratensis*, of or pertaining to Argentoratus, the Roman name of the City of Strasbourg in Alsace, France).

Basonym: *Lactobacillus plantarum* subsp. *argentoratensis* Bringel et al. 2005, 1633^{VP}

Strains of this species differ from *L. plantarum* subsp. *plantarum* strains due to the absence of melezitose fermentation [229]. The genome size of the type strain is 3.20 Mbp. The mol% GC content of DNA is 45.

Isolated from starchy food, fermenting food of plant origin, timothy, orchardgrass and elephant grass silage, fermented Uttapam batter, fermented idli batter.

The type strain is DKO 22^{T} = CCUG 50787^{T} = CIP 108320^{T} = DSM 16365^{T} = JCM 16169^{T}.

Genome sequence accession number: AZFR00000000.

16S rRNA gene accession number: AJ640078.

Description of *Lactiplantibacillus daoliensis* comb. nov.

Lactiplantibacillus daoliensis (dao.li.en'sis. N.L. masc. adj. *daoliensis*, pertaining to Daoli, a district in Harbin city, China).

Basonym: *Lactobacillus daoliensis* Liu and Gu 2019, 3258^{VP}

Characteristics are similar to *L. pingfangensis* but the strain does not grow at 37°C [233]. The genome size of the type strain is 2.63 Mbp. The mol% GC content of DNA is 43.7.

Isolated from fermented Chinese cabbage.

The type strain is 116-1A^{T} = LMG 31171^{T} = NCIMB 15181^{T} = CCM 8934^{T}.

Genome sequence accession number: BJDH00000000.

16S rRNA gene accession number: LC438516.

Description of *Lactiplantibacillus daowaiensis* comb. nov.

Lactiplantibacillus daowaiensis (dao.wai.en'sis. N.L. masc. adj. *daowaiensis*, pertaining to Daowai, a district in Harbin city, China).

Basonym: *Lactobacillus daowaiensis* Liu and Gu 2019, 3258^{VP}

Characteristics are similar to *L. pingfangensis* but the strain does not grow at 37°C [233]. The genome size of the type strain is 2.85 Mbp. The mol% GC content of DNA is 44.0.

Isolated from fermented Chinese cabbage.

The type strain is 203-3^{T} =LMG 31172^{T} =NCIMB 15183^{T} = CCM 8933^{T}.

Genome sequence accession number: BJDJ00000000.

16S rRNA gene accession number: LC438517.

Description of *Lactiplantibacillus dongliensis* comb. nov.

Lactiplantibacillus dongliensis (dong.li.en'sis. N.L. masc. adj. *dongliensis* pertaining to a district in Harbin, China).

Basonym: *Lactobacillus dongliensis* Liu and Gu 2019, 3259^{VP}

Characteristics are similar to *L. pingfangensis* but the type strain of *L. dongliensis* also f.erments ribose [233]. The genome size of the type strain is 3.11 Mbp. The mol% GC content of DNA is 44.7.

Isolated from fermented Chinese cabbage.

The type strain is 218-3^{T} = LMG 31173^{T} = NCIMB 15184^{T} = CCM 8932^{T}.

Genome sequence accession number: BJDK00000000

16S rRNA gene accession number: LC438518.

Description of *Lactiplantibacillus fabifermentans* comb. nov.

Lactiplantibacillus fabifermentans (fa.bi.fer.men'tans. L. fem. n. *faba* a bean; L. pres. part. *fermentans* fermenting; N.L. part. adj. *fabifermentans* fermenting beans).

Basonym: *Lactobacillus fabifermentans* De Bruyne et al. 2009, 10^{VP}

Cells are non-motile long rods, usually singly, in pairs or in short chains. Colonies are circular with a convex elevation and an entire margin. They grow at 37°C, pH 3.9 and with 6% NaCl [198]. The genome size of the type strain is 3.28 Mbp. The mol% GC content of DNA is 45.0.

Isolated from cocoa bean heap fermentation, fermented grapes, and fermented cereals.

The type strain is R-34115^{T} = DSM 21115^{T} = LMG 24284^{T}.

Genome sequence accession number: AYGX00000000.

16S rRNA gene accession number: AM905388.

Description of *Lactiplantibacillus herbarum* comb. nov.

Lactiplantibacillus herbarum (her.ba'rum. L. gen. pl. n. *herbarum*, of herbs).

Basonym: *Lactobacillus herbarum* Mao et al. 2015, 4685^{VP}

Cells are non-motile rods, usually singly, in pairs or in short chains. The cell wall contains meso-diaminopimelic acid, alanine, glutamic acid, galactose and an unidentified sugar. They produce acetoin from pyruvate. *L. herbarum* can be distinguished from related species on the basis of sucrose fermentation (it does not ferment sucrose) and growth temperature (it cannot grow at 37°C) [234]. The genome size of the type strain is 2.90 Mbp. The mol% GC content of DNA is 43.5.

Isolated from fermented radish.

The type strain is TCF032-E4^{T} = CCTCC AB2015090^{T} = DSM 100358^{T}.

Genome sequence accession number: LFEE00000000.

16S rRNA gene accession number: NR_145899.

Description of *Lactiplantibacillus modestisalitolerans* comb. nov.

Lactiplantibacillus modestisalitolerans (mo.des.ti.sa.li.to'le.rans. L. masc. adj. *modestus* moderate; L. masc. n. *sal salis* salt; L. pres. part. *tolerans* tolerating; N.L. part. adj. *modestisalitolerans* moderately salt tolerating).

Basonym: *Lactobacillus modestisalitolerans* Miyashita et al. 2015, 2489^{VP}

Cells are non-motile, non-spore-forming, facultatively anaerobic rods. They grow at 15-40°C, pH 3.5-7.5, and 0-9% NaCl. They produce both lactic acid isomers. They hydrolyse aesculin, are tellurite and bile-aesculin tolerant and convert arginine to ornithine [235]. The genome size of the type strain is 2.75 Mbp. The mol% GC content of DNA is 48.6.

Isolated from Pla-som (fermented fish).

The type strain is NB446^{T} = NBRC 107235^{T} = BCC 38191^{T}.

Genome sequence accession number: BJEA00000000.

16S rRNA gene accession number: AB907192.

Description of *Lactiplantibacillus mudanjiangensis* comb. nov.

Lactiplantibacillus mudanjiangensis (mu.dan.ji.ang.en'sis. N.L. masc. adj. *mudanjiangensis* pertaining to the Mudanjiang River, a river flowing through the Heilongjiang province of China where the bacterium was isolated).

Basonym: *Lactobacillus mudanjiangensis* Gu et al. 2013, 4703^{VP}

Cells are facultatively anaerobic rods occurring singly. Growth is observed at 30 and 37°C and pH 4, they are resistant to 6% (w/v) NaCl [176]. The genome size of the type strain is 3.58 Mbp. The mol% GC content of DNA is 42.9.

Isolated from fermented Chinese cabbage [176] and fermented carrot juice [236] .

The type strain is 11050^{T} = LMG 27194^{T} = CCUG 62991^{T}

Genome sequence accession number: BJDY00000000.

16S rRNA gene accession number: HF679037.

Description of *Lactiplantibacillus nangangensis* comb. nov.

Lactiplantibacillus nangangensis (nan.gang.en'sis. N.L. masc. adj. *nangangensis*, pertaining to Nangang, a district in Harbin city, China).

Basonym: *Lactobacillus nangangensis* Liu and Gu 2019, 3258^{VP}

Characteristics are similar to *L. pingfangensis* but the strain does not grow at 37°C [233]. The genome size of the type strain is 2.90 Mbp. The mol% GC content of DNA is 44.3.

Isolated from fermented Chinese cabbage.

The type strain is $381\text{-}7^{T}$ = NCIMB 15186^{T} = CCM 8930^{T}.

Genome sequence accession number: BJDI00000000.

16S rRNA gene accession number: LC438520

Description of *Lactiplantibacillus paraplantarum* comb. nov.

Lactiplantibacillus paraplantarum (pa.ra.plan.tar'um. Gr. prep. *para* resembling; N.L. gen. n. *plantarum*, a species epithet; N.L. gen. pl. n. *paraplantarum*, resembling *L. plantarum*).

Basonym: *Lactobacillus paraplantarum* Curk et al. 1996, 598^{VP}

The cells are non-motile rods, usually singly, in pairs and sometimes in short chains. They grow at pH 5 and 7 and they tolerate NaCl up to a concentration of 8% [237]. The genome size of the type strain is 3.40 Mbp. The mol% GC content of DNA is 43.7.

Isolated as spoilage organisms from beer and from human faeces. They are also found in grape marmalade, dairy products, *jangajji* (a Korean fermented food), fermented vegetables, fermented fruits, fermented dates, rice bran pickles, silage, cocoa beans, fermented sourdough, fermented slurry, faecal microbiota of healthy dogs, traditional fura processing, wine and sow milk.

The type strain is CST 10961^{T} = ATCC 700211^{T} = CCUG 35983^{T} = CIP 104668^{T} = CNRZ 1885^{T} = CST 10961^{T} = DSM 10667^{T} = JCM 12533^{T} = LMG 16673^{T} = NRRL $B\text{-}23115^{T}$.

Genome sequence accession number: AZEO00000000.

16S rRNA gene accession number: AJ306297.

Description of *Lactiplantibacillus pentosus* comb. nov.

Lactiplantibacillus pentosus (pen.to'sus. N.L. masc. adj. *pentosus*, of pentose, pertaining to pentoses).

Basonym: *Lactobacillus pentosus* (ex Fred et al. 1921) Zanoni et al. 1987, 339^{VP}

The cells are non-motile straight rods and produce acid and clot in litmus milk [238]. The genome size of the type strain is 3.65 Mbp. The mol% GC content of DNA is 46.3.

Isolated from diverse sources including corn silage, fermenting olives, sewage, fermented mulberry leaf powders, fermented teas, glutinous rice dough, corn noodles, chili sauce, mustard pickles, stinky tofu, dairy products, mustard pickle, fermented idli batter, tempoyak, human vagina, human stools, and sourdoughs.

The type strain is $124\text{-}2^{T}$ = ATCC 8041^{T} = CCUG 33455^{T} = CIP 103156^{T} = DSM 20314^{T} = JCM 1558^{T} = LMG 10755^{T} = NCAIM $B.01727^{T}$ = NCCB 32014^{T} = NCIMB 8026^{T} (formerly NCDO 363) = NRRL $B\text{-}227^{T}$ = NRRL $B\text{-}473^{T}$.

Genome sequence accession number: AZCU00000000.

16S rRNA gene accession number: D79211.

Description of *Lactiplantibacillus pingfangensis* comb. nov.

Lactiplantibacillus pingfangensis (ping.fang.en'sis. N.L. masc. adj. *pingfangensis,* pertaining to a district in Harbin city, China).

Basonym: *Lactobacillus pingfangensis* Liu and Gu 2019, 7^{VP}

Growth is observed at 30 and 37 but not at 45°C; DL-lactic acid is produced from a wide range of hexoses and disaccharides but not from pentoses [233]. The genome size of the type strain is 2.90 Mbp; the mol% GC content of DNA is 44.2.

Isolated from fermented Chinese cabbage.

The type strain is 382-1^T = LMG 31176^T = NCIMB 15187^T = CCM 8935^T.

Genome sequence accession number: BJDG00000000.

16S rRNA gene accession number: LC438521.

Description of *Lactiplantibacillus plajomi* comb. nov.

Lactiplantibacillus plajomi (pla.jom'i. N.L. gen. n. *plajomi* of Pla-jom, referring to the isolation of the type strain from a traditional fermented fish product in Thailand).

Basonym: *Lactobacillus plajomi* Miyashita et al. 2015, 2488^{VP}

Cells are non-motile, facultatively anaerobic rods. They grow at 15-37°C, at pH 4.0-7.5 and with 0-8% NaCl. They are positive for Voges–Proskauer test, tellurite tolerance, bile-aesculin tolerance test and deamination of arginine [235]. The genome size of the type strain is 2.76 Mbp. The mol% GC content of DNA is 48.7

Isolated from Pla-jom (fermented fish) collected in Yasothon, Thailand.

The type strain is $NB53^T$ = NBRC 107333^T = BCC 38054^T.

Genome sequence accession number: BJDZ00000000.

16S rRNA gene accession number: AB907190.

Description of *Lactiplantibacillus songbeiensis* comb. nov.

Lactiplantibacillus songbeiensis (song.bei.en'sis. N.L. masc. adj. *songbeiensis* pertaining to Songbei, a district in Harbin city, China).

Basonym: *Lactobacillus songbeiensis* Liu and Gu 2019, 3259^{VP}

Characteristics are similar to *L. pingfangensis* but the type strain of *L. songbeiensis* also ferments ribose [233]. The genome size of the type strain is 3.03 Mbp. The mol% GC content of DNA is 44.4.

Isolated from fermented Chinese cabbage.

The type strain is 398-2^T = LMG 31174^T = NCIMB 15189^T = CCM 8931^T.

Genome sequence accession number: BJDL00000000.

16S rRNA gene accession number: LC438523.

Description of *Lactiplantibacillus xiangfangensis* comb. nov.

Lactiplantibacillus xiangfangensis (xi.ang.fang.en'sis. N.L. masc. adj. *xiangfangensis*, pertaining to Xiangfang, a district of Harbin city in China).

Basonym: *Lactobacillus xiangfangensis* Gu et al. 2012, 860^{VP}

Cells are non-spore-forming, facultatively anaerobic rods. They grow at 30 and 37°C [239]. The genome size of the type strain is 2.99 Mbp. The mol% GC content of DNA is 45.1.

Isolated from pickle and sourdough.

The type strain is 3.1.1^T = LMG 26013^T = NCIMB 14687^T.

Genome sequence accession number: JQCL00000000.

16S rRNA gene accession number: HM443954.

HETEROFERMENTATIVE *LACTOBACILLACEAE*

DESCRIPTION OF *FURFURILACTOBACILLUS* GEN. NOV.

Furfurilactobacillus (Fur.fu.ri.lac.to.ba.cil'lus. L. masc. n. *furfur* bran, relating to the origin of furfurilactobacilli from cereal fermentations; N.L. masc. n. *Lactobacillus* a bacterial genus name; N.L. masc. n. *Furfurilactobacillus* a lactobacillus from bran).

Heterofermentative and aerotolerant. Growth is observed at 15 and 37°C but not at 45°C. The two species in the genus with genome sequences available have a genome size of 2.9 – 3.0 Mbp and a mol% GC content of DNA of 43 – 44%. Species in the genus were isolated from sourdough or spoiled beer and have an exceptional capacity to metabolize phenolic compounds [240, 241]. The ecology of the genus remains largely unexplored but appears to be similar to the nomadic lifestyle of *L. plantarum*.

A phylogenetic tree on the basis of 16S rRNA genes of all species in the genus *Lactiplantibacillus* is provided in Figure S6L.

The type species of the genus is *Furfurilactobacillus rossiae* comb. nov.; *Furfurilactobacillus* was previously referred to as *L. rossiae* group.

Description of *Furfurilactobacillus rossiae* comb. nov.

Furfurilactobacillus rossiae (ros'si.ae. N.L. gen. n. *rossiae* of Rossi, named in recognition of Jone Rossi, a microbiologist working at the University of Perugia).

Basonym: *Lactobacillus rossiae* Corsetti et al. 2005, 39^{VP}. The species was initially named *"L. rossii"*

F. rossiae grows at 15°C but not at 45°C [242]. The genome size of the type strain is 2.87 Mbp. The mol% GC content of DNA is 43.3.

Isolated from wheat sourdough and from related cereal fermentations, beer, fruit, and fecal samples of children and swine. Owing to its capacity for metabolism of phenolic compounds and flavonoids, it was used experimentally as starter culture for cactus pear fermentation [243].

The type strain is CS1^T = ATCC BAA-822^T = DSM 15814^T = JCM 16176^T.

Genome sequence accession number: AZFF00000000.

16S rRNA gene accession number: AJ564009.

Description of *Furfurilactobacillus curtus* comb. nov.

Furfurilactobacillus curtus (cur'tus. L. masc. adj. *curtus* short, referring to the short cell morphology of the type strain).

Basonym: *Lactobacillus curtus* Asakawa et al. 2017, 3905^{VP}

It grows over a wide pH range (pH 3.5 – 8.5) and at 15°C but not at 45°C [244]. The mol% GC content of DNA is 43.

Isolated from spoiled beer.

The type strain is JCM 1149^T = ATCC 14917^T= DSM 20174 ^{T}= LMG 6907^T = NCIMB 11974^T = NRRL B-4496^T.

Genome sequence accession number: not available at the time of publication.

16S rRNA gene accession number: LC093898.

Description of *Furfurilactobacillus siliginis* comb. nov.

Furfurilactobacillus siliginis (si.li'gi.nis. L. gen. n. *siliginis*, of wheat flour, referring to the origin of the type strain in wheat sourdough).

Basonym: *Lactobacillus siliginis* Aslam et al. 2006, 2212^{VP}

This species has a narrow temperature range of growth (20 – 37°C) but a wide pH range (pH 4.0 – 8.0) [245]. The genome size of the type strain is 2.07 Mbp. The mol% GC content of DNA is 44.1.

Isolated from a wheat sourdough.

The type strain is M1-212^T = JCM 16155^T = DSM 22696^T = KCTC 3985^T = NBRC 101315^T.

Genome sequence accession number: JQCB00000000.

16S rRNA gene accession number: AB370882.

DESCRIPTION OF *PAUCILACTOBACILLUS* GEN. NOV.

Paucilactobacillus (Pau.ci.lac.to.ba.cil'lus. L. masc. adj. *paucus* few; N.L. masc. n. *Lactobacillus* a bacterial genus name; N.L. masc. n. *Paucilactobacillus* a lactobacillus that ferments few carbohydrates).

Gram positive, rod-shaped, catalase negative, heterofermentative, and aerotolerant. Growth is observed at between 20 and 37 °C. Several species are psychrotrophic but *Paucilactobacillus suebicus* grows at 45°C. Strains in this genus were predominantly isolated from fermented plant material including silage, pickles, and fruit mashes. The adaptation to hexose depleted habitats is indicated by the lack of mannitol dehydrogenase in many strains of the genus; among heterofermentative lactobacilli, this property is shared only with *Secundilactobacillus* that is isolated from related habitats. *Paucilactobacillus* species preferentially metabolise pentoses and many strains do not ferment disaccharides. The mol% GC content of DNA ranges from 35.6 to 43.5; and the genome size ranges from 1.75 to 2.57 Mbp.

A phylogenetic tree on the basis of 16S rRNA genes of all species in the genus *Paucilactobacillus* is provided in Figure S6M.

The type species of the genus is *Paucilactobacillus vaccinostercus* comb. nov.; *Paucilactobacillus* was previously referred to as *L. vaccinostercus* group.

Description of *Paucilactobacillus vaccinostercus* comb. nov.

Paucilactobacillus vaccinostercus (vac.ci.no.ster'cus; L. masc. adj. *vaccinus*, from cows; L. neut. n. *stercus*, manure; N.L. masc. adj. *vaccinostercus*, from cow manure).

Basonym: *Lactobacillus vaccinostercus* Okada et al. 1979, 439^{VL}. Some strains of the species were previously designated as *Lactobacillus durianis* [246]

Growth occurs between 15 and 40°C, pH 4.4 and 7.5, and with pentoses, glucose and maltose as carbon source [247]. The genome size of the type strain is 2.57 Mbp. The mol% GC content of DNA is 43.9.

Isolated from cow dung and from fermented tea leaves and fermented cereals.

The type strain is X-94^T = TUA 055B^T = ATCC 33310^T = DSM 20634^T= LMG 9215^T.

Genome sequence accession number: AYYY00000000.

16S rRNA gene accession number: AJ621556.

Description of *Paucilactobacillus hokkaidonensis* comb. nov.

Paucilactobacillus hokkaidonensis (hok.kai.do.nen'sis. N.L. masc. adj. *hokkaidonensis* of Hokkaido in northern Japan from where the type strain was isolated).

Basonym: *Lactobacillus hokkaidonensis* Tohno et al. 2013, 2529^{VP}

Growth is observed in the range of 4°C to 37°C and in the pH range of 4.0 - 7.0; strains ferment pentoses, maltose and, variably, melibiose [248]. The genome size of the type strain is 2.33 Mbp. The mol% GC content of DNA is 38.1.

Isolated from grass silage.

The type strain is LOOC260^T = JCM 18461^T = DSM 26202^T.

Genome sequence accession number: JQCH00000000.

16S rRNA gene accession number: AB721549.

Description of *Paucilactobacillus kaifaensis* comb. nov.

Paucilactobacillus kaifaensis (kai.fa.en'sis. N.L. masc. adj. *kaifaensis*, pertaining to Kaifa, a district in Harbin city, China).

Basonym: *Lactobacillus kaifaensis* Liu and Gu 2019, 3259^{VP}

Growth is observed at 30 and 37 but not at 45°C. DL-Lactic acid is produced only from ribose, xylose, maltose, arabitol and gluconate [233]. The genome size of the type strain is 1.75 Mbp; the mol% GC content of DNA is 38.0.

Isolated from fermented Chinese cabbage.

The type strain is 778-3^T = LMG 31177^T = NCIMB 15191^T = CCM 8929^T.

Genome sequence accession number: BJDM00000000.

16S rRNA gene accession number: LC438525.

Description of *Paucilactobacillus nenjiangensis* comb. nov.

Paucilactobacillus nenjiangensis (nen.ji.ang.en'sis. N.L. masc. adj. *nenjiangensis*, pertaining to the Nenjiang River in the Chinese Heilongjiang province where the type strain was isolated).

Basonym *Lactobacillus nenjiangensis* Gu et al. 2013, 4704^{VP}

The type strain ferments several pentoses, hexoses, maltose, and sucrose. Growth is not observed at 45°C or below pH 4.0 [176]. The genome size of the type strain is 1.99 Mbp. The mol% GC content of DNA is 38.7.

Isolated from pickle.

The type strain is 11102^T=LMG 27192^T=NCIMB 14833^T.

Genome sequence accession number: BJEB00000000.

16S rRNA gene accession number: HF679039.

Description of *Paucilactobacillus oligofermentans* comb. nov.

Paucilactobacillus oligofermentans (o.li.go.fer.men'tans, Gr. masc. adj. oligos few; L. pres. part. fermentans, fermenting; N.L. part. adj. *oligofermentans*, fermenting few [carbohydrates]).

Basonym: *Lactobacillus oligofermentans* Koort et al. 2005, 2236^{VL}

Strains grow at 4 and 15°C but not at 37°C [249]. The genome size of the type strain is 1.83 Mbp. The mol% GC content of DNA is 35.6.

Isolated from marinated poultry meat at the end of its shelf life, and from fermented olives.

The type strain is $AMKR18^T$ = DSM 15707^T = JCM 16175^T = LMG 22743^T.

Genome sequence accession number: AZFE00000000.

16S rRNA gene accession number: AY733084.

Description of *Paucilactobacillus suebicus* comb. nov.

Paucilactobacillus suebicus (su.e'bi.cus. L. masc. adj. *suebicus*, from Swabia, a region in the South West of Germany where the type strain was isolated).

Basonym: *Lactobacillus suebicus* Kleynmans et al. 1989, 495^{VL}

The type strain exhibits high tolerance to acid and ethanol; growth is observed at pH 2.8 or at pH 3.3 and 14% ethanol. The type strain ferments pentoses, glucose, and maltose; growth is observed at 10°C and up to 45°C for some strains [250]. The genome size of the type strain is 2.65 Mbp. The mol% GC content of DNA is 39.0.

Isolated from fermented cherry mashes, from cider and silage.

The type strain is I, WC-t4-15^T = ATCC 49375^T= DSM 5007^T = JCM 9504^T = KCTC 3549^T = LMG 11408^T.

Genome sequence accession number: AZGF00000000.

16S rRNA gene accession number: AJ575744.

Description of *Paucilactobacillus wasatchensis* comb. nov.

Paucilactobacillus wasatchensis (wa.satch.en'sis. N.L. masc. adj. *wasatchensis* of the Wasatch mountains in Utah, U.S.A., the origin of the type strain).

Basonym: *Lactobacillus wasatchensis* Oberg et al. 2016, 163^{VP}

Growth is observed at 30 and 37°C but not at 45°C. In MRS, only ribose and galactose are fermented [251]. The genome size of the type strain is 1.90 Mbp. The mol% GC content of DNA is 39.8.

Isolated from spoiled cheddar cheese and from silage.

The type strain is $WDC04^T$ = DSM 29958^T = LMG 28678^T.

Genome sequence accession number: AWTT00000000.

16S rRNA gene accession number: NR_147709.

DESCRIPTION OF *LIMOSILACTOBACILLUS* GEN. NOV.

Limosilactobacillus (Li.mo.si.lac.to.ba.cil'lus. L. masc. adj. *limosus*, slimy, referring to the property of most strains in the genus to produce exopolysaccharides from sucrose; N.L. masc. n. *Lactobacillus* a bacterial genus name; N.L. masc. n. *Limosilactobacillus,* a slimy lactobacillus.

Gram positive, rod-or coccoid shaped, catalase negative, heterofermentative, and anaerobic or aerotolerant. Growth is observed at 37°C and, for most species, at 45°C but not at 15°C. Strains in the genus have very small genomes ranging from 1.6 Mbp for *L. equigenerosi* to 2.25 Mbp for *L. mucosae;* the mol % GC content as calculated from whole genome shotgun sequences ranges from 38.6.1 to 53.4. In comparison to other heterofermentative lactobacilli, *Limosilactobacillus* species ferment a relatively broad spectrum of carbohydrates, however, several species do not ferment glucose. Acid resistance is typically mediated by expression of urease, glutaminase, glutamate decarboxylase and / or arginine deiminase activities [252]. With the exception of *L. fermentum* and *L. secaliphilus*, strains in the genus were isolated from intestinal habitats, or were shown experimentally to have adapted to the intestine of vertebrate animals. *Limosilactobacillus reuteri* and other strains in the genus produce exopolysaccharides from sucrose to support biofilm formation on non-secretory epithelia in the upper intestinal tract [14, 253]. In their natural habitat, *Limosilactobacillus* spp. generally form stable associations with *Lactobacillus* spp.; the same association is observed in food fermentations with *Limosilactobacillus*. *Limosilactobacillus* spp., particularly *L. reuteri*, are produced commercially for use as starter culture and as probiotic culture.

A phylogenetic tree on the basis of 16S rRNA genes of all species in the genus *Limosilactobacillus* is provided in Figure S6N.

The type species of the genus is *Limosilactobacillus fermentum* comb. nov.; *Limosilactobacillus* was previously referred to as the *Lactobacillus reuteri* group.

Description of *Limosilactobacillus fermentum* comb. nov.

Limosilactobacillus fermentum (fer.men’tum. L. neut. n. *fermentum* which causes fermentation, leaven, ferment).

Basonym: *Lactobacillus fermentum* Beijerinck 1901, 233 (Approved Lists). The species includes strains previously classified as *Lactobacillus cellobiosus* [254]

L. fermentum is the only species in *Limosilactobacillus* that is not adapted to the intestine of vertebrates [17]. The genome size of the type strain is 1.90 Mbp. The mol% GC content of DNA is 52.4.

Occurs widely in spontaneously fermented cereals and other fermenting plant materials [58, 255], also in dairy products, manure and sewage, and the feces and vagina of humans.

The type strain is F (352)^{T} = ATCC 14931^{T} = DSM 20052^{T} = CIP 102980^{T} = JCM 1173^{T} = LMG 6902^{T}.

Genome sequence accession number: JQAU00000000.

16S rRNA gene accession number: JN175331.

Description of *Limosilactobacillus alvi* sp. nov.

Limosilactobacillus alvi (al’vi. L. gen. n. *alvi*, of the stomach, of the digestive organs).

The species was effectively but not validly published as *Lactobacillus alvi* Kim et al. 2011 [256]. Growth at 40°C is faster than at 37°C [256]. The mol% GC content of DNA is 42.7.

Isolated from the gizzard of hens.

The type strain is R54^{T} = KCCM 90099^{T} = LMG 31569^{T} = JCM 17644^{T}.

Genome sequence accession number: Not available at time of publication.

16S rRNA gene accession number: NR_118032.

Description of *Limosilactobacillus antri* comb. nov.

Limosilactobacillus antri (an'tri. L. gen. n. *antri* of a cave, referring to the antrum region of the stomach).

Basonym: *Lactobacillus antri* Roos et al 2005, 81^{VP}

The genome size of the type strain is 2.24 Mbp. The mol% GC content of DNA is 51.1.

Isolated from a biopsy of a healthy human gastric mucosa; strains of this species were also isolated from the intestine of other vertebrate animals [98].

The type strain is Kx146A4^{T} = LMG 22111^{T} = DSM 16041^{T}= CCUG 48456^{T}.

Genome sequence accession number: AZDK00000000.

16S rRNA gene accession number: AY253659.

Description of *Limosilactobacillus caviae* comb. nov.

Limosilactobacillus caviae (ca'vi.ae. N.L. gen. n. *caviae* of a cavia, of a guinea pig).

Basonym: *Lactobacillus caviae* Killer et al. 2017, 2908^{VP}

Description provided by [257]. The mol% GC content of DNA is 37.7.

Isolated from the oral cavity of a guinea pig.

The type strain is MOZM2^{T} = CCM 8609^{T} = DSM 100239^{T} = LMG 28780^{T}.

Genome sequence accession number: Not available at time of publication.

16S rRNA gene accession number: KT343143.

Description of *Limosilactobacillus coleohominis* comb. nov.

Limosilactobacillus coleohominis (co.le.o.ho'mi.nis. Gr. masc. n. *koleos* vagina; L. gen. n. *hominis* of humans; N.L. gen. n. *coleohominis* of the vagina of humans).

Basonym: *Lactobacillus coleohominis* Nikolaitchouk et al. 2001, 2084^{VP}.

The type strain was reported not to produce gas from glucose [258], however, the genome encodes for enzymes of the phosphoketolase pathway but lacks phosphofructokinase, the key enzyme of the Embden-Meyerhoff pathway [14]. The genome size of the type strain is 1.72 Mbp. The mol% GC content of DNA is 41.1.

Isolated from the human vagina; in addition, in human intestinal microbiota and from swine.

The type strain is DSM 14060^{T} = CCUG 44007^{T} = CIP 106820^{T}.

Genome sequence accession number: AZEW00000000.

16S rRNA gene accession number: AM113776.

Description of *Limosilactobacillus equigenerosi* comb. nov.

Limosilactobacillus equigenerosi (e.qui.ge.ne.ro'si. L. masc. n. *equus*, horse; L. masc. adj. *generosus*, of noble birth, well-bred; N.L. gen. n. *equigenerosi*, from a thoroughbred horse).

Basonym: *Lactobacillus equigenerosi* Endo et al. 2008, 917^{VP}

Acid tolerant and thermophilic organism; cells have a coccoid morphology [259]. The genome size of the type strain is 1.60 Mbp. The mol% GC content of DNA is 42.7.

Isolated from the intestinal tract of a thoroughbred horse.

The type strain is NRIC 0697^T = JCM 14505^T = DSM 18793^T.

Genome sequence accession number: AZGC00000000.

16S rRNA gene accession number: AB288050.

Description of *Limosilactobacillus frumenti* comb. nov.

Limosilactobacillus frumenti (fru.men'ti. L. gen. n. *frumenti* from cereal).

Basonym: *Lactobacillus frumenti* Müller et al. 2000, 2132^{VP}

Description provided in [260]. The genome size of the type strain is 1.73 Mbp. The mol% GC content of DNA is 42.6.

Isolated from an industrial rye bran fermentation but also identified in the intestine of poultry and swine, and in must and wine.

The type strain is TMW 1.666^T = DSM 13145^T = LMG 19473^T.

Genome sequence accession number: AZER00000000.

16S rRNA gene accession number: AJ250074.

Description of *Limosilactobacillus gastricus* comb. nov.

Limosilactobacillus gastricus (gas'tri.cus. N.L. masc. adj. *gastricus* from Gr. adj. *gastrikos* of the stomach).

Basonym: *Lactobacillus gastricus* Roos et al. 2005, 80^{VP}

Acid tolerant, anaerobic and thermophilic organisms [98]. The genome size of the type strain is 1.85 Mbp. The mol% GC content of DNA is 41.6.

Isolated from a biopsy of a human stomach, and from human milk.

The type strain is Kx156A7^T = LMG 22113^T = DSM 16045^T = CCUG 48454^T.

Genome sequence accession number: AZFN00000000.

16S rRNA gene accession number: AY253658.

Description of *Limosilactobacillus gorillae* comb. nov.

Limosilactobacillus gorillae gorillae (go.ril'lae. L. gen. n. *gorillae* of the western lowland gorilla).

Basonym: *Lactobacillus gorillae* Tsuchida et al. 2014, 4005^{VP}

Thermophilic organism [261]. The genome size of the type strain is 1.64 Mbp. The mol% GC content of DNA is 48.1.

Isolated from the faeces of a captive gorillas and from wild western lowland gorillas.

The type strain is KZ01^T = JCM 19575^T = DSM 28356^T.

Genome sequence accession number: BCAH00000000.

16S rRNA gene accession number: AB904716.

Description of *Limosilactobacillus ingluviei* comb. nov.

Limosilactobacillus ingluviei (in.glu'vi.ei. L. gen. n. *ingluviei* of a crop sac).

Basonym *Lactobacillus ingluviei* Baele et al. 2003, 135^{VP}. The species includes strains previously named as *L. thermotolerans* [262].

Thermophilic species with optimal growth at 42°C and poor growth at 30°C or below [263]. The genome size of the type strain is 2.16 Mbp. The mol% GC content of DNA is 49.9.

Isolated from the crop of a pigeon [263], birds (turkeys, chickens, geese) but also from cattle, carnivore faeces, and Korean rice wine (makgeolii).

The type strain is KR3^{T} = DSM 15946^{T} = LMG 20380^{T} = CCUG 45722^{T}.

Genome sequence accession number: AZFK00000000.

16S rRNA gene accession number: AF333975.

Description of *Limosilactobacillus mucosae* comb. nov.

Limosilactobacillus mucosae (mu.co'sae. N.L. gen. n. *mucosae* of mucosa).

Basonym: *Lactobacillus mucosae* Roos et al. 2000, 256^{VP}

Many strains of the species carry a mucus binding protein, a putative colonization factor of *L. mucosae*. The genome size of the type strain is 2.25 Mbp. The mol% GC content of DNA is 46.4.

Isolated from the intestine of a pig [264] but also found in the intestine of other vertebrates including humans, type II sourdough, and related cereal fermentations.

The type strain is S32^{T} = CCUG 43179^{T} = CIP 106485^{T} = DSM 13345^{T} = JCM 12515^{T}.

Genome sequence accession number: AZEQ00000000.

16S rRNA gene accession number: AF126738.

Description of *Limosilactobacillus oris* comb. nov.

Limosilactobacillus oris (or'is. L. gen. n. *oris*, of the mouth).

Basonym: *Lactobacillus oris* Farrow et al. 1988, 116^{VP}

The genome size of the type strain is 2.03 Mbp. The mol% GC content of DNA is 50.0.

Isolated from the human saliva [265], and, less frequently, from other human body sites including the vagina and mother's milk, and from foods such as corn dough and bran.

The type strain is 5A1^{T} = ATCC 49062^{T}= CCUG 37396^{T} = CIP 103255^{T} = CIP 105162^{T} = DSM 4864^{T} = JCM 7507^{T} = JCM 11028^{T} = LMG 9848^{T}.

Genome sequence accession number: AZGE00000000.

16S rRNA gene accession number: X94229.

Description of *Limosilactobacillus panis* comb. nov.

Limosilactobacillus panis (pa'nis. L. gen. n. *panis*, of bread).

Basonym: *Lactobacillus panis* Wiese et al. 1996, 452^{VP}

The genome size of the type strain is 2.01 Mbp. The mol% GC content of DNA is 48.1.

Isolated from a type II sourdough [266], other strains of the species occur in fermenting plant material, and in the intestine of birds.

The type strain is CCUG 37482^T = DSM 6035^T = JCM 11053^T.

Genome sequence accession number: AZGM00000000.

16S rRNA gene accession number: X94230.

Description of *Limosilactobacillus pontis* comb. nov.

Limosilactobacillus pontis (pon'tis. L. gen. n. *pontis*, of a bridge, referring to BRIDGE, which was the acronym of an EU funded research project).

Basonym: *Lactobacillus pontis* Vogel et al. 1994, 228^{VP}

Not all strains of *L. pontis* ferment glucose [267]; growth is observed at 15 and at 45°C. The genome size of the type strain is 1.67 Mbp. The mol% GC content of DNA is 43.5.

Isolated from type I and type II sourdough but also as typical representatives of the intestinal microbiota of swine [76]. Other sources of isolation include silage, dairy products, mezcal fermentation and wet wheat distillers' grain.

The type strain is LTH 2587^T = DSM 8475^T = LMG 14187^T.

Genome sequence accession number: AZGO00000000.

16S rRNA gene accession number: X76329.

Description of *Limosilactobacillus reuteri* comb. nov.

Limosilactobacillus reuteri (reu'te.ri. N.L. gen. n. *reuteri*, of Reuter; named for G. Reuter, a German bacteriologist).

Basonym: *Lactobacillus reuteri* Kandler et al. 1982, 266^{VL}

Prior to 1980, strains of the species were classified as *L. fermentum* Biotype II [268]. The species has been studied as model species to determine host-adaptation of intestinal lactobacilli, and co-adaptation of *Limosilactobacillus* and *Lactobacillus* spp. (e.g. *L. taiwanensis*) that coexist in biofilms in intestinal ecosystems and preferentially different substrates [55, 56, 269]. *L. reuteri* is divided in host-adapted lineages that are equivalent to the taxonomic rank of sub-species [269, 270] and differ in their ability to form biofilms in the mouse forestomach [271]. Few strains of *L. reuteri* produce the antimicrobial compound reutericyclin with a polyketide synthase, which is a unique ability among lactobacilli [272]. The genome size of the type strain is 1.94 Mbp. The mol% GC content of DNA is 38.6.

Isolated as dominant members of the intestinal microbiota of rodents, birds, swine, and in other intestinal ecosystems; also occurs in cereal fermentations, particularly type II sourdoughs [58]. Food isolates are of intestinal origin [273].

The type strain of the species is F 275^T = ATCC 23272^T = DSM 20016^T = JCM 1112^T = LMG 9213^T = LMG 13557^T.

Genome sequence accession number: AZDD00000000.

16S rRNA gene accession number: AP007281.

Description of *Limosilactobacillus secaliphilus* comb. nov.

Limosilactobacillus secaliphilus (se.ca.li.phi'lus. L. neut. n. *secale* rye; Gr. masc. adj. *philos* loving; N.L. masc. adj. secaliphilus rye-loving).

Basonym: *Lactobacillus secaliphilus* Ehrmann et al. 2007, 748^{VP}

The type strain does not ferment glucose [274]. The genome size of the type strain is 1.65 Mbp. The mol% GC content of DNA is 47.7.

Isolated from a type II sourdough; although other lactobacilli in type II sourdoughs are predominantly of intestinal origin [114], the habitat of *L. secaliphilus* remains unknown [274].

The type strain is TMW 1.1309^{T} = DSM 17896^{T} = CCUG 53218^{T}.

Genome sequence accession number: JQBW00000000.

16S rRNA gene accession number: AM279150.

Description of *Limosilactobacillus vaginalis* comb. nov.

Limosilactobacillus vaginalis (va.gi.na'lis. L. gen. n. *vaginalis*, of the vagina).

Basonym: *Lactobacillus vaginalis* Embley et al. 1989, 368^{VP}

Description provided in [275]. The genome size of the type strain is 1.79 Mbp. The mol% GC content of DNA is 30.5.

Frequently isolated as member of the microbiota of the human vagina.

The type strain of the species is Lac 19^{T} = ATCC 49540^{T} = CCUG 31452^{T} = CIP 105932^{T} = DSM 5837^{T} = JCM 9505^{T} = LMG 12891^{T}.

Genome sequence accession number: AZGL00000000.

16S rRNA gene accession number: AF243177.

Proposed species in the genus *Limosilactobacillus*:

The name "*Lactobacillus timonensis"* was effectively published for a species that clusters phylogenetically within the genus *Limosilactobacillus* [276]; however, its species description lacks essential information and a type strain was not deposited.

DESCRIPTION OF *SECUNDILACTOBACILLUS* GEN. NOV.

Secundilactobacillus (Se.cun.di.lac.to.ba.cil'lus. L. adj. *secundus*, second or next, following; N.L. masc. n. *Lactobacillus* a bacterial genus name; N.L. masc. n. *Secundilactobacillus* a lactobacillus that occurs in a secondary fermentation or as a spoilage organism after primary fermenters depleted hexoses and disaccharides).

Gram-positive, rod-shaped, catalase negative, heterofermentative. Most strains grow at 15°C and some also grow at 45°C, the pH range of growth is highly variable. The genome size ranges from 1.85 Mbp for *S. oryzae* to 3.62 Mbp for *S. collinoides*, the mol% GC content of DNA ranges from 41.03 – 47%. Strains in the genus lead a free-living lifestyle and were isolated as secondary fermentation or spoilage organisms from hexose-depleted habitats including silage, beer, liquor mashes and apple cider. Metabolic properties of *Secundilactobacillus* spp. match adaptation to hexose- depleted habitats. Many strains of the genus do not reduce fructose to mannitol, a trait which differentiates *Secundilactobacillus* from all other heterofermentative lactobacilli except *Paucilactobacillus*. Many strains in the genus metabolize diols via diol-hydratase and convert agmatine, a metabolite of arginine decarboxylation, via the agmatine deiminase pathway. Strains in the genus generally harbor genes coding for transaldolase / transketolase which mediate metabolism of pentoses to pyruvate.

A phylogenetic tree on the basis of 16S rRNA genes of all species in the genus *Secundilactobacillus* is provided in Figure S6O.

The type species of the genus is *Secundilactobacillus malefermentans* comb. nov.; *Secundilactobacillus* was previously referred to as the *Lactobacillus collinoides* group.

Description of *Secundilactobacillus malefermentans* comb. nov.

Secundilactobacillus malefermentans (ma.le.fer.men'tans. L. adv. *male*, bad; L. part. pres. *fermentans* fermenting; N.L. part. adj. *malefermentans* badly fermenting, referring to spoiled beer).

Basonym: *Lactobacillus malefermentans* (ex Russell and Walker 1953) Farrow et al. 1989, 371^{VL}. The species was initially described in 1953 [277]; the species name was later revived with a new type strain [278]

Strains of this species have a restricted carbohydrate fermentation pattern. Growth is observed between 10 and 37°C and between pH 4.1 and 8.0. The genome size of the type strain is 2.05 Mbp. The mol% GC content of DNA is 41.0.

Isolated from beer.

The type strain is D2 MF1^T = ATCC 49373^T= DSM 5705^T = JCM 12497^T= LMG 11455^T.

Genome sequence accession number: AZGJ00000000.

16S rRNA gene accession number: AM113783.

Description of *Secundilactobacillus collinoides* comb. nov.

Secundilactobacillus collinoides (col.lin.o.i'des. L. masc. adj. *collinus* hilly; Gr. suff. *eides* resembling, similar; N.L. masc. adj. *collinoides* hill-shaped, pertaining to colony form).

Basonym: *Lactobacillus collinoides* Carr and Davies 1972, 470 (Approved Lists). Prior to the species description, strains of *S. collinoides* were referred to as *L. brevis* var. *quinicus* or *L. pasteurianus* var. *quinicus*

Characteristics as described [279]; the genome size of the type strain is 3.62 Mbp. The mol% GC content of DNA is 46.1.

Isolated from compost, as spoilage organisms in apple cider, table olives, dairy products, fermented durian fruit, and wines.

The type strain is Cl3a^T = ATCC 27612^T = DSM 20515^T = JCM 1123^T = LMG 9194^T.

Genome sequence accession number: AYYR00000000.

16S rRNA gene accession number: AB005893.

Description of *Secundilactobacillus kimchicus* comb. nov.

Secundilactobacillus kimchicus (kim.chi'cus. N.L. neut. n. *kimchium*, kimchi; L. masc. suff. -icus pertaining to; N.L. masc. adj. *kimchicus* pertaining to or isolated from kimchi, a type of sauerkraut produced in Korea).

Basonym: *Lactobacillus kimchicus* Liang et al. 2011, 896^{VP}

Growth is observed at 15 and at 45°C and between pH 5.0 and 9.0 [280]. The genome size of the type strain is 2.59 Mbp. The mol% GC content of DNA is 46.6.

The species was isolated from kimchi.

The type strain is DCY51^T = JCM 15530 ^{T}= KCTC 12976^T.

Genome sequence accession number: AZCX00000000.

16S rRNA gene accession number: EU678893.

Description of *Secundilactobacillus mixtipabuli* comb. nov.

Secundilactobacillus mixtipabuli (mi.xti.pa'bu.li. L. masc. adj. *mixtus* mixed; L. neut. n. *pabulum* fodder; N.L. gen. n. *mixtipabuli* of mixed fodder, referring to the isolation of the type strain from silage).

Basonym: *Lactobacillus mixtipabuli* Tohno et al. 2015, 1983^{VP}

Characteristics as described by [281]. The genome size of the type strain is 2.52 Mbp. The mol% GC content of DNA is 43.7.

Isolated from silage.

The type strain is IWT30^{T} = JCM 19805^{T} = DSM 28580^{T}.

Genome sequence accession number: BCMF00000000.

16S rRNA gene accession number: AB894863.

Description of *Secundilactobacillus odoratitofui* comb. nov.

Secundilactobacillus odoratitofui (o.do.ra.ti.to'fu.i. L. part adj. *odoratus* smelly; N.L.N.L. gen. n. *tofui* of tofu; N.L. gen. n. *odoratitofui*, related to stinky tofy from which the type strain was isolated).

Basonym: *Lactobacillus odoratitofui* Chao et al. 2010, 2905^{VP}

Characteristics of the species are as described by [282]. The genome size of the type strain is 2.76 Mbp. The mol% GC content of DNA is 44.3.

Isolated from fermented brine used for stinky tofu production in Taipei County, Taiwan.

The type strain is YIT 11304^{T} = BCRC 17810^{T} = DSM 19909^{T} = JCM 15043^{T}.

Genome sequence accession number: AZEE00000000.

16S rRNA gene accession number: AB365975.

Description of *Secundilactobacillus oryzae* comb. nov.

Secundilactobacillus oryzae (o.ry'zae. L. gen. n. *oryzae* of rice).

Basonym: *Lactobacillus oryzae* Tohno et al. 2013, 2961^{VP}

Growth is observed between 4 and 45°C and between pH 5.0 and 8.0 [283]. The genome size of the type strain is 1.85 Mbp. The mol% GC content of DNA is 42.8.

Isolated from fermented rice grains in Tochigi, Japan.

The type strain is SG293^{T} = JCM18671^{T} = DSM 26518^{T}.

Genome sequence accession number: BBJM00000000.

16S rRNA gene accession number: AB731660.

Description of *Secundilactobacillus paracollinoides* comb. nov.

Secundilactobacillus paracollinoides (pa.ra.col.li.no'i.des. Gr. pref. *para* beside; N.L. masc. adj. *collinoides*, a species epithet; N.L. masc. adj. *paracollinoides* beside *S. collinoides*, referring to the close relationship with *S. collinoides*).

Basonym: *Lactobacillus paracollinoides* Suzuki et al. 2004, 116^{VP}. Strains of this species have been referred to as *L. pastorianus* prior to 2005 [284]

Growth is observed at 15 but not at 45°C [285]. The genome size of the type strain is 3.49 Mbp. The mol% GC content of DNA is 46.8.

Isolated as beer or cider spoilage organisms, and from fermented olives.

The type strain is LA2^{T} = DSM 15502^{T} = JCM 11969^{T}.

Genome sequence accession number: AZFD00000000.

16S rRNA gene accession number: AJ786665.

Description of *Secundilactobacillus pentosiphilus* comb. nov.

Secundilactobacillus pentosiphilus (pen.to.si'phi.lus. N.L. neut. n. *pentosum* pentose; Gr. masc. adj. philos, friend, loving; N.L. masc. adj. *pentosiphilus*, preferring pentoses).

Basonym: *Lactobacillus pentosiphilus* Tohno et al. 2017, 3643^{VP}

Strains of this species do not produce acid or gas from hexoses including glucose but ferment pentoses; growth is observed between 30 and 37°C [286]. The genome size of the type strain is 2.63 Mbp. The mol% GC content of DNA is 44.9.

Isolated from silage.

The type strain is IWT25^{T} = JCM 31145^{T} = DSM 102974^{T}.

Genome sequence accession number: BCMI00000000.

16S rRNA gene accession number: LC085284.

Description of *Secundilactobacillus silagei* comb. nov.

Secundilactobacillus silagei (si.la'ge.i. N.L. gen. n. *silagei* of silage, from which the type strain was isolated).

Basonym: *Lactobacillus silagei* Tohno et al. 2013, 4616^{VP}

Characteristics as described by [287]. The genome size of the type strain is 2.66 Mbp. The mol% GC content of DNA is 44.9.

Isolated from silage.

The type strain is IWT126^{T} = JCM 19001^{T} = DSM 27022^{T}.

Genome sequence accession number: BCMG00000000.

16S rRNA gene accession number: AB786910.

Description of *Secundilactobacillus silagincola* comb. nov.

Secundilactobacillus silagincola (si.lag.in'co.la. N.L. neut. n. *silagum*, silage; L. masc. n. *incola*, inhabitant; N.L. masc. n. *silagincola*, living in or isolated from silage).

Basonym: *Lactobacillus silangincola* Tohno et al. 2017, 3642^{VP}

Growth is observed between 10 and 37°C and between pH 4.0 and 7.5 [286]. The genome size of the type strain is 2.62 Mbp. The mol% GC content of DNA is 43.1.

Isolated from silage.

The type strain is IWT5^{T}=JCM 31144^{T}=DSM 102973^{T}.

Genome sequence accession number: BCMJ00000000.

16S rRNA gene accession number: LC085283.

Description of *Secundilactobacillus similis* comb.nov.

Secundilactobacillus similis (si'mi.lis. L. masc. adj. *similis*, similar, as the type strain is similar to closely related species).

Basonym: *Lactobacillus similis* Kitahara et al. 2010, 189^{VP}

S. similis grows at 15 but not at 45°C [288]. The genome size of the type strain is 3.49 Mbp. The mol% GC content of DNA is 47.0.

Isolated from fermented cane molasses at alcohol plants in Thailand, and from rice wine (makgeolii).

The type strain is M36^{T} = DSM 23365^{T} = JCM 2765^{T} = LMG 23904^{T}.

Genome sequence accession number: AYZM00000000.

16S rRNA gene accession number: AB282889.

DESCRIPTION OF *LEVILACTOBACILLUS* GEN. NOV.

Levilactobacillus (Le.vi.lac.to.ba.cil'lus. L. v. *levare* to lift up, release, relieve; N.L. masc. n. *Lactobacillus* a bacterial genus name; N.L. masc. n. *Levilactobacillus* a lactobacillus with leavening potential, referring to the occurrence of multiple species in the genus in type I sourdoughs that are used as sole leavening agent).

Gram-positive, rod-shaped, catalase negative, heterofermentative. Strains grow at 15°C but not at 45°C, are acid tolerant, growing generally in the pH range of 4.0 – 7.0 and produce DL-lactic acid. The genome size ranges from 1.97 Mbp for *Levilactobacillis bambusae* to 3.38 Mbp for *Levilactobacillis cerevisiae*, the mol% GC content ranges from 46.3 – 55.9%. Strains in the genus lead a free-living lifestyle and were isolated from sourdough or fermented vegetable products but also occur as spoilage organisms in alcoholic beverages. Strains in the genus generally harbor genes coding for transaldolase / transketolase which mediate metabolism of pentoses to pyruvate. *Levilactobacillus brevis* is used commercially as starter culture in food and feed applications.

A phylogenetic tree on the basis of 16S rRNA genes of all species in the genus *Levilactobacillus* is provided in Figure S6P.

The type species of the genus is *Levilactobacillus brevis* comb. nov.; *Levilactobacillus* was previously referred to as *L. brevis* group.

Description of *Levilactobacillus brevis* comb. nov.

Levilactobacillus brevis (bre'vis. L. adj. brevis short).

Basonym: *Lactobacillus brevis* (*Betabacterium breve* Orla-Jensen 1919, 175) Bergey et al. 1934, 312 (Approved Lists)

The species was described in [2, 289]. Strains of *L. brevis* widely occur in vegetable and cereal fermentations and as beer-spoilage organisms and were also isolated from insects. Niche adaptation is mediated by acquisition of plasmids [290]. The genome size of the type strain is 2.47 Mbp. The mol% GC content of DNA is 46.0.

Isolated from milk, cheese, sauerkraut and rrelated vegetable fermentations, sourdough, silage, cow manure, faeces, and the mouth and intestinal tract of humans and rats.

The type strain is 14, Bb14^{T} = DSM 20054^{T} = ATCC 14869^{T} = JCM 1059^{T} = LMG 6906^{T} = LMG 7944^{T} = NRRL B-4527^{T}.

Genome sequence accession number: AZCP00000000.

16S rRNA gene accession number: M58810.

Description of *Levilactobacillus acidifarinae* comb. nov.

Levilactobacillus acidifarinae (a.ci.di.fa.ri'nae. L. masc. adj. *acidus* sour; L. fem. n. *farina;* N.L. gen. n. *acidifarinae* of sourdough).

Basonym: *Lactobacillus acidifarinae* Vancanneyt et al. 2005, 619^{VP}

Characteristics of the species are as described [291]. The genome size of the type strain is 2.92 Mbp. The mol% GC content of DNA is 51.5.

Isolated from type I wheat sourdough and fermented rice bran.

The type strain is R-19065^{T} = DSM 19394^{T} = CCM 7240^{T} = CCUG 50162^{T} = JCM 15949^{T} = LMG 2220^{T}.

Genome sequence accession number: AZDV00000000.

16S rRNA gene accession number: AJ632158.

Description of *Levilactobacillus bambusae* comb. nov

Levilactobacillus bambusae (bam.bu'sae. N.L. gen. n. *bambusae* of the plant genus *Bambusa* from which the type strain was isolated).

Basonym: *Lactobacillus bambusae* Guu et al. 2018, 2428^{VP}

Characteristics of the species are as described [292]; *L. bambusae* is more distantly related to other species in *Levilactobacillus* than any other species in the genus as documented by AAI, GC content and genome size. The genome size of the type strain is 1.97 Mbp. The mol% GC content of DNA is 46.3.

Isolated from traditional fermented bamboo shoots.

The type strain is BS-W1^{T} = BCRC 80970^{T} = NBRC 112377^{T}.

Genome sequence accession number: QCXQ00000000.

16S rRNA gene accession number: KX400838.

Description of *Levilactobacillus cerevisiae* comb. nov

Levilactobacillus cerevisiae (ce.re.vi'si.ae. L. gen. n. *cerevisiae*, of beer).

Basonym: *Lactobacillus cerevisiae* Koob et al. 2017, 3456^{VP}

Characteristics as described [293]. The genome size of the type strain is 3.38 Mbp. The mol% GC content of DNA is 49.6.

Isolated from spoiled beer.

The type strain is 2301^{T} = DSM 100836^{T} = LMG 29073^{T}.

Genome sequence accession number: RHNN00000000.

16S rRNA gene accession number: KT445896.

Description of *Levilactobacillus fujinensis* comb. nov.

Levilactobacillus fujinensis (fu.jin.en'sis. N.L. masc. adj. *fujinensis*, pertaining to Fujin, a county in the Heilongjiang province of China).

Basonym: *Lactobacillus fujinensis* Long and Gu 2019, 2351^{VP}

Characteristics of the species are as described [158]. The genome size of the type strain is 3 Mbp. The mol% GC content of DNA is 47.4.

Isolated from fermented Chinese cabbage.

The type strain is 218-6^T = CCM 8908^T = KCTC 21134^T = LMG 31067^T.

Genome sequence accession number: RHNX00000000.

16S rRNA gene accession number: MK110865.

Description of *Levilactobacillus fuyuanensis* comb. nov.

Levilactobacillus fuyuanensis (fu.yuan.en'sis. N.L. masc. adj. *fuyuanensis*, pertaining to Fuyuan, a county in the Heilongjiang province of China).

Basonym: *Lactobacillus fuyuanensis* Long and Gu 2019, 2351^{VP}

Characteristics of the species are as described [158]. The genome size of the type strain is 2.72 Mbp. The mol% GC content of DNA is 48.6.

Isolated from fermented Chinese cabbage.

The type strain is 244-4^T = CCM 8906^T = KCTC 21137^T=LMG 31052^T.

Genome sequence accession number: RHNZ00000000.

16S rRNA gene accession number: MK110862.

Description of *Levilactobacillus hammesii* comb. nov.

Levilactobacillus hammesii (ham.me'si.i. N.L. gen. n. *hammesii* of Hammes, in recognition of the scientist Walter P. Hammes, who contributed significantly to the taxonomy of lactic acid bacteria as well as the technology and microbial ecology of fermented foods).

Basonym: *Lactobacillus hammesii* Valcheva et al. 2005, 766^{VP}

Characteristics of the species are as described [294]. Strains produce antifungal fatty acids from linoleic acid [295]. The genome size of the type strain is 2.82 Mbp. The mol% GC content of DNA is 49.4.

Isolated from wheat and rye sourdoughs, ryegrass silages, and a municipal biogas plant.

The type strain is LP38^T = TMW 1.1236^T = DSM 16381^T = CCUG 51325^T = CIP 108387^T = JCM 16170^T.

Genome sequence accession number: AZFS00000000.

16S rRNA gene accession number: AJ632219.

Description of *Levilactobacillus huananensis* comb. nov.

Levilactobacillus huananensis (hua.nan.en'sis. N.L. masc. adj. *huananensis*, pertaining to Huanan, a county in the Heilongjiang province of China).

Basonym: *Lactobacillus huananensis* Long and Gu 2019, 2350^{VP}

Characteristics are described in [158]. The genome size of the type strain is 2.29 Mbp. The mol% GC content of DNA is 47.5.

Isolated from fermented Chinese cabbage.

The type strain is 151-2B^T = CCM 8913^T = KCTC 21129^T = LMG 31063^T.

Genome sequence accession number: RHOC00000000.

16S rRNA gene accession number: MK110857.

Description of *Levilactobacillus koreensis* comb. nov.

Levilactobacillus koreensis (ko.re.en'sis. N.L. masc. adj. *koreensis* of Korea, where the type strain was isolated).

Basonym: *Lactobacillus koreensis* Naam Bui et al. 2011, 774^{VP}

Characteristics of the species are as described [296]. The genome size of the type strain is 2.47 Mbp. The mol% GC content of DNA is 49.6.

Isolated from cabbage kimchi and from sourdough.

The type strain is DCY50^{T} = JCM 16448^{T} = KCTC 13530^{T}.

Genome sequence accession number: AZDP00000000.

16S rRNA gene accession number: FJ904277.

Description of *Levilactobacillus lindianensis* comb. nov.

Levilactobacillus lindianensis (lin.dian.en'sis. N.L. masc. adj. *lindianensis*, pertaining to Lindian, a county in the Heilongjiang province of China).

Basonym: *Lactobacillus lindianensis* Long and Gu, 2019, 2349^{VP}

Characteristics are described in [158]. The genome size of the type strain is 2.33 Mbp. The mol% GC content of DNA is 49.2.

Isolated from fermented Chinese cabbage.

The type strain is 220-4^{T} = NCIMB 15163^{T}=CCM 8902^{T}=KCTC 21136^{T}.

Genome sequence accession number: RHOD00000000.

16S rRNA gene accession number: MK110856.

Description of *Levilactobacillus mulengensis* comb. nov.

Levilactobacillus mulengensis (mu.leng.en'sis. N.L. masc. adj. *mulengensis*, pertaining to Muleng, a county in the Heilongjiang province of China).

Basonym: *Lactobacillus mulengensis* Long and Gu 2019, 2352^{VP}

Characteristics of the species are as described [158]. The genome size of the type strain is 3.11 Mbp. The mol% GC content of DNA is 50.3.

Isolated from fermented Chinese cabbage.

The type strain is 112-3^{T} = CCM 8909^{T} = KCTC 21123^{T} = LMG 31049^{T}.

Genome sequence accession number: RHNW00000000.

16S rRNA gene accession number: MK110866.

Description of *Levilactobacillus namurensis* comb. nov.

Levilactobacillus namurensis (na.mur.en'sis. N.L. masc. adj. *namurensis*, of the province of Namur, Belgium, the source of isolation of the type strain).

Basonym: *Lactobacillus namurensis* Scheirlinck et al. 2007, 226^{VP}

Characteristics of the species are as described [297]. The genome size of the type strain is 2.48 Mbp. The mol% GC content of DNA is 52.0.

Isolated from wheat sourdough and from vegetable fermentations.

The type strain is DSM 19117^T = CCUG 52843^T = JCM 15612^T = LMG 23583^T.

Genome sequence accession number: AZDT00000000.

16S rRNA gene accession number: AM259119.

Description of *Levilactobacillus parabrevis* comb. nov.

Levilactobacillus parabrevis (pa.ra.bre'vis. Gr. pref. *para* beside; L. masc. adj. *brevis*, a species epithet; N.L. masc. adj. *parabrevis* beside *L. brevis*, referring to the close relationship with *L. brevis*).

Basonym: *Lactobacillus parabrevis* Vancanneyt et al. 2006, 1556^{VP}

Characteristics of the species are as described [298]. The genome size of the type strain is 2.61 Mbp. The mol% GC content of DNA is 49.1.

The species is isolated from farmhouse red Cheshire cheese, wheat sourdough, fermented vegetables, and a municipal biogas plant.

The type strain is RODS-DW^T = SLB-MAS^T = ATCC 53295^T= LMG 11984^T.

Genome sequence accession number: AZCZ00000000.

16S rRNA gene accession number: AM158249.

Description of *Levilactobacillus paucivorans* comb. nov.

Levilactobacillus paucivorans (pau.ci.vo'rans. L. masc. adj. *paucus* few, low in number; L. part. pres. *vorans* devouring; N.L. part. adj. *paucivorans*, eating few [carbohydrates], referring to the few sugars that are fermented by the type strain).

Basonym: *Lactobacillus paucivorans* Ehrmann et al. 2010, 2356^{VP}

Characteristics of the species are as described [299]. The genome size of the type strain is 2.37 Mbp. The mol% GC content of DNA is 49.1.

Isolated from a storage tank of a brewery.

The type strain is TMW 1.1424^T = DSM 22467^T = JCM 18045^T = LMG 25291^T.

Genome sequence accession number: JQCA00000000.

16S rRNA gene accession number: FN185731.

Description of *Levilactobacillus senmaizukei* comb. nov.

Levilactobacillus senmaizukei (sen.mai.zu'ke.i. N.L. gen. n. *senmaizukei* of senmaizuke, a fermented pickle).

Basonym: *Lactobacillus senmaizukei* Hiraga et al. 2008, 1627^{VP}

Characteristics of the species are as described [300]. The genome size of the type strain is 2.22 Mbp. The mol% GC content of DNA is 48.6.

Isolated from senmaizuke, a fermented turnip product.

The type strain is L13^T = DSM 21775^T = NBRC 103853^T = TISTR 1847^T.

Genome sequence accession number: AYZH00000000.

16S rRNA gene accession number: AB297927.

Description of *Levilactobacillus spicheri* comb. nov.

Levilactobacillus spicheri (spi'.cher.i. N.L. gen. n. *spicheri* of Spicher. The name honours Gottfried Spicher, a German scientist who pioneered the microbiological and biochemical characterization of sourdough fermentation).

Basonym: *Lactobacillus spicheri* Meroth et al. 2004, 631^{VL}

Characteristics as described [301]. The genome size of the type strain is 2.75 Mbp. The mol% GC content of DNA is 55.9.

Isolated from wheat and rice sourdoughs, from fermented vegetables and a municipal biogas plant.

The type strain is LTH 5753^{T} = DSM 15429^{T} = JCM 15956^{T} = LMG 21871^{T}.

Genome sequence accession number: AZFC00000000.

16S rRNA gene accession number: AJ534844.

Description of *Levilactobacillus suantsaii* comb. nov.

Levilactobacillus suantsaii (suan.tsai'i. N.L. gen. n. *suantsaii* of suan-tsai, a fermented mustard product, from which the type strain was isolated).

Basonym: *Lactobacillus suantsaii* Liou et al. 2019, 1489^{VP}

Characteristics of the species are as described [302]. The genome size of the type strain is 2.43 Mbp. The mol% GC content of DNA is 51.1.

Isolated from suan-tsai, a traditional Taiwanese fermented mustard green.

The type strain is L88^{T} =BCRC 12945^{T}=NBRC 113535^{T}.

Genome sequence accession number: QXIL00000000.

16S rRNA gene accession number: MH730159.

Description of *Levilactobacillus suantsaiihabitans* comb. nov.

Levilactobacillus suantsaiihabitans (suan.tsai.i.ha'bi.tans. N.L. neut. n. s*uantsaium* suan-tsai, the name of a traditional fermented mustard green product of Taiwan; L. pres. part. *habitans*, inhabiting; N.L. part. adj. *suantsaiihabitans* inhabiting suan-tsai).

Basonym: *Lactobacillus suantsaiihabitans* Lin et al. 2019, 8^{VP}

Growth is observed in the range of 20 – 37°C but not at 15°C [144]. The genome size of the type strain is 2.87 Mbp. The mol% GC content of DNA is 51.8.

Isolated from a fermented mustard green product.

The type strain is R19^{T} = BCRC 81129^{T}= NBRC 113532^{T}.

Genome sequence accession number: RKLX00000000.

16S rRNA gene accession number: NH810313.

Description of *Levilactobacillus tangyuanensis* comb. nov.

Levilactobacillus tangyuanensis (tang.yuan.en'sis. N.L. masc. adj. *tangyuanensis*, pertaining to Tangyuan, a county in the Heilongjiang province of China).

Basonym: *Lactobacillus tangyuanensis* Long and Gu 2019, 2350^{VP}

Characteristics of the species are as described [158]. The genome size of the type strain is 2.19 Mbp. The mol% GC content of DNA is 49.8.

Isolated from fermented Chinese cabbage.

The type strain is 137-3^{T} = CCM 8907^{T} = KCTC 21125^{T} = LMG 31053^{T}.

Genome sequence accession number: RHOA00000000.

16S rRNA gene accession number: MK110859.

Description of *Levilactobacillus tongjiangensis* comb. nov.

Levilactobacillus tongjiangensis (tong.ji.ang.en'sis. N.L. masc. adj. *tongjiangensis*, pertaining to Tongjiang, a county in the Heilongjiang province of China).

Basonym: *Lactobacillus tongjianensis* Long and Gu 2019, 2351^{VP}

Characteristics of the species are as described [158]. The genome size of the type strain is 2.72 Mbp. The mol% GC content of DNA is 47.7.

Isolated from fermented Chinese cabbage.

The type strain is 218-10^{T} = CCM 8905^{T}=KCTC 21135^{T}=LMG 31055^{T}.

Genome sequence accession number: RHNY00000000.

16S rRNA gene accession number: MK110863.

Description of *Levilactobacillus yonginensis* comb. nov.

Levilactobacillus yonginensis (yong.in.en'sis. N.L. masc. adj. *yonginensis* of Yongin, the city in Korea where the organism was isolated).

Basonym: *Lactobacillus yonginensis* Yi et al. 2013, 3278^{VP}

Characteristics of the species are as described [303]; ginsenoside Rb1 is hydrolysed to Rd by β-glucosidase activity. The genome size of the type strain is 2.69 Mbp. The mol% GC content of DNA is 47.8.

Isolated from kimchi.

The type strain is THK-V8^{T} = KACC 16236^{T} = JCM 18023^{T} = ATCC 16236^{T}.

Genome sequence accession number: RHNO00000000.

16S rRNA gene accession number: JN128640.

Description of *Levilactobacillus zymae* comb. nov.

Levilactobacillus zymae (zy'mae. Gr. fem. n. *zyme* leaven, sourdough; N.L. gen. n. *zymae* of sourdough).

Basonym: *Lactobacillus zymae* Vancanneyt et al. 2005, 619^{VP}

Characteristics of the species are as described [291]. The genome size of the type strain is 2.71 Mbp. The mol% GC content of DNA is 53.6.

Isolated from a type I wheat sourdough, forages and fermented onions.

The type strain is R-18615^{T} = DSM 19395^{T} = CCM 7241^{T} = CCUG 50163^{T} = JCM 15957^{T} = LMG 22198^{T}.

Genome sequence accession number: AZDW00000000.

16S rRNA gene accession number: AJ632157.

DESCRIPTION OF *FRUCTILACTOBACILLUS* GEN. NOV.

Fructilactobacillus (Fruc.ti.lac.to.ba.cil'lus. L. masc. n. *fructus*, fruit; N.L. masc. n. *Lactobacillus* a bacterial genus name; N.L. masc. n. *Fructilactobacillus*, fruit-loving lactobacillus, referring to the preference for growth in presence of fructose as electron acceptor).

Gram positive, rod-shaped, catalase negative, heterofermentative, and aerotolerant. Growth is observed at 15°C but not at 37°C. Strains in the genus have very small genomes ranging from 1.23 Mbp for *Fructilactobacillus sanfranciscensis* to 1.44 Mbp for *Fructilactobacillus lindneri;* the mol% GC content of DNA as calculated from whole genome shotgun sequences ranges from 34.1 to 38.9. Comparable to other insect-associated lactobacilli, strains in the genus ferment only few carbohydrates; some strains ferment only maltose and sucrose. Most strains of the species are fructophilic and use fructose as electron acceptor rather than as carbon source. Several species in the genus are core member of insect intestinal microbiota, and were isolated from insects, flowers, and spoiled or fermented foods.

A phylogenetic tree on the basis of 16S rRNA genes of all species in the genus *Fructilactobacillus* is provided in Figure S6Q.

The type species of the genus is *Fructilactobacillus fructivorans* comb. nov.; *Fructilactobacillus* was previously referred to as *L. fructivorans* group.

Description of *Fructilactobacillus fructivorans* comb. nov.

Fructilactobacillus fructivorans (fruc.ti.vo'rans. L. masc. n. *fructus*, fruit; L. part. pres. *vorans*, eating, devouring; N.L. part. adj. *fructivorans*, fruit-eating, intended to mean fructose-devouring).

Basonym: *Lactobacillus fructivorans* Charlton et al. 1934, 1 (Approved Lists)

The type species of *Fructilactobacillus* was described as *Lactobacillus fructivorans* in 1934 [304] and includes strains that were previously described as *Lactobacillus heterohiochii, Lactobacillus trichodes* [305], and *L. homohiochii* [306]. *Lactobacillus homohiochii* was isolated from Saké mashes and described as homofermentative *Lactobacillus* species [307]. The heterofermentative *L. heterohiochii* (later classified as *F. fructivorans* comb. nov.) was isolated from the same mash. The type strain of *L. homohiochii*, which likely represents an organism related to *Lactobacillus acetotolerans*, has been lost [308]. *F. fructivorans* tolerates ethanol concentrations of up to 15%. The genome size of the type strain is 1.37 Mbp. The mol% GC content of DNA is 38.9.

F. fructivorans is stable member of the intestinal microbiota of fruit flies [309] as well as spoiled sake mashes [58]; it was also isolated from spoiled mayonnaise, salad dressings, sourdough, dessert wines and aperitifs.

The type strain is IFO (now NBRC) 13954^T = ATCC 8288^T = CCUG 32260^T = CIP 103042^T = DSM 20203^T = JCM 1117^T = LMG 9201^T = NRRL B-1841^T.

Genome sequence accession number: AZDS00000000.

16S rRNA gene accession number: NR_036789.

Description of *Fructilactobacillus florum* comb. nov.

Fructilactobacillus florum (flo'rum. L. gen. pl. n. *florum*, of flowers, from which the type strain was isolated).

Basonym: *Lactobacillus florum* Endo et al. 2010, 2481^{VP}

The species was described as composed by three fructophilic strains [310]. The genome size of the type strain is 1.35 Mbp. The mol% GC content of DNA is 41.1.

Iolated from peony and bietou flowers, and from grapes and wine.

The type strain is F9-1^T = DSM 22689^T = JCM 16035^T = NRIC 0771^T.

Genome sequence accession number: AYZI00000000.

16S rRNA gene accession number: AB498045.

Description of *Fructilactobacillus ixorae* comb. nov.

*Fructilactobacillus ixorae (*i.xo'rae. N.L. gen. n. *ixorae* of *Ixora coccinea*, West Indian Jasmine as source of isolation).

Basonym: *Lactobacillus ixorae* Techo et al. 2016, 5504^{VP}

The description is provided in [311]. The mol% GC content of DNA is 47.8.

Isolated from a flower (West-Indian jasmine).

The type strain is Ru20-1^T = LMG 29008^T = NBRC 111239^T = PCU 346^T = TISTR 2381^T.

Genome sequence accession number: not available at the time of publication.

16S rRNA gene accession number: LC094494.

Description of *Fructilactobacillus lindneri* comb. nov.

Fructilactobacillus lindneri (lind'ne.ri. N.L. gen. n. *lindneri* of Lindner, recognizing the German bacteriologist Lindner).

Basonym: *Lactobacillus lindneri* (Henneberg 1901); Back et al. 1997, 601^{VL} Earlier isolates were referred to as *Bacillus lindneri* or *Bacterium lindneri* [312]

The description is provided in [312]. The genome size of the type strain is 1.44 Mbp. The mol% GC content of DNA is 34.1.

Isolated from spoiled beer and from wine.

The type strain is KPA^T = CIP 102983^T = DSM 20690^T = JCM 11027^T = LMG 14528^T.

Genome sequence accession number: JQBT00000000.

16S rRNA gene accession number: X95421.

Description of *Fructilactobacillus sanfranciscensis* comb. nov.

Fructilactobacillus sanfranciscensis (san.fran.cis.cen'sis. N.L. masc. adj. *sanfranciscensis*, from San Francisco).

Basonym: *Lactobacillus sanfranciscensis* (ex Kline and Sugihara 1971) Weiss and Schillinger 1984, 503^{VL} The species was described as *Lactobacillus sanfrancisco* in 1971 [313] and re-named to *Lactobacillus sanfranciscensis* [314]. Isolates of *F. sanfranciscensis* described prior to 1978 were designated as *Lactobacillus brevis* subsp. *lindneri* [315]

Virtually all isolates of the species originate from traditional sourdoughs that are used as leavening agent [114]; one isolate was obtained from agave mash [151]. The extremely small genome size of 1.2 – 1.3 Mbp, the restricted carbohydrate fermentation pattern, which for includes only maltose for some strains, and the narrow pH range of growth (pH 3.9 – 6.6) [316, 317] document adaptation to a very narrow ecological niche. An insect origin of the species is suggested by culture-independent analysis of the microbiota of grain beetles [318]. The genome size of the type strain is 1.23 Mbp. The mol% GC content of DNA is 34.7.

The type strain is L-12^T = ATCC 27651^T= DSM 20451^T = LMG 16002^T.

Genome sequence accession number: AYYM00000000.

16S rRNA gene accession number: X76327.

Description of *Fructilactobacillus vespulae* comb. nov.

Fructilactobacillus vespulae (ves'pu.lae. N.L. gen. n. *vespulae* of the wasp *Vespula*).

Basonym: *Lactobacillus vespulae* Hoang et al. 2015, 3330^{VP}

The description is provided in [319]. The mol% GC content of DNA is 35.5.

Isolated from a queen wasp.

The type strain is DCY75^T = KCTC 21023^T = JCM 19742^T.

Genome sequence accession number: not available at the time of publication.

16S rRNA gene accession number: JX863367.

DESCRIPTION OF *ACETILACTOBACILLUS* GEN. NOV.

Acetilactobacillus, (A.ce.ti.lac.to.ba.cil'lus. L. neut. n. *acetum* vinegar, referring to the isolation of the sole representative of this genus from a grain vinegar mash; N.L. masc. n. *Lactobacillus* a bacterial genus name; N.L. masc. n. *Acetilactobacillus,* a lactobacillus from vinegar).

Gram-positive, rod-shaped, catalase negative, heterofermentative. Mesophilic, with a narrow temperature range of growth, and acid tolerant with an optimum pH of growth at 4.0. The spectrum of carbohydrates that support acid formation is unusual as it includes sugar alcohols and disaccharides but excludes most hexoses and all pentoses. The unusual substrate requirements and pH optimum for growth may reflect an ecological association with acetic acid bacteria. The sole representative of the genus was isolated from a grain vinegar mash (vinegar *pei*) and has a genome size of 2.33 Mbp with a mol% GC content of 41.7.

The type species of the genus is *Acetilactobacillus jinshanensis* sp. nov.

Description of *Acetilactobacillus jinshanensis* sp. nov.

Acetilactobacillus jinshanensis (jin.shan'en.sis. N.L. masc. adj. *jinshanensis*, referring to Jinshan, the site of isolation in Zhenjiang province, China).

The species was effectively but not validly published as *Lactobacillus jinshani* Yu et al. 2020 [41]. Growth is observed between 20 and 40°C with optimal growth at 35°C [41]. The optimum pH for growth is 4.0; growth occurs in the range of 3.0 – 5.0. The strain ferments several disaccharides and sugar alcohols but no pentoses. The genome size of the type strain is 2.33 Mbp. The mol% GC content of DNA is 41.7.

Isolated from a grain vinegar mash.

The type strain is HSLZ-75^T = CICC 6269^T = JCM 33270^T.

Genome sequence accession number: CP034726.

16S rRNA gene accession number: KT783533.

DESCRIPTION OF *APILACTOBACILLUS* GEN. NOV.

Apilactobacillus (A.pi.lac.to.ba.cil'lus. L. fem. n. *apis* bee; N.L. masc. n. *Lactobacillus* a bacterial genus name; N.L. masc. n. *Apilactobacillus* a lactobacillus from bees).

Gram positive, rod-shaped, heterofermentative. Growth is generally observed in the range of 15 – 37°C; many strains grow at acidic conditions below pH 3.0. Strains in the genus have small genomes ranging from 1.42 Mbp for *Apilactobacillus kosoi* to 1.58 Mbp for *Apilactobacillus quenuiae;* the mol% GC content of DNA ranges from 30.5 to 36.4. All strains in the genus convert fructose to mannitol; strains in the genus typically ferment very few carbohydrates including the pollen and bee-associated carbohydrates fructose, glucose, and sucrose but not maltose or pentoses. Comparable to *Fructilactobacillus*, *Apilactobacillus* has an insect-associated lifestyle and occurs on flowers, which serve as hub for dispersal of lactobacilli, and insects [320]. In contrast to *Fructilactobacillus*, *Apilactobacillus* has adapted to bees including honeybees (*A. apinorum, A. kunkeei*) and wild bees (*A. timberlakei, A. micheneri, A. quenuiae*). In the bee and bumblebee gut, *Apilactobacillus* is associated with its homofermentative sister genus *Bombilactobacillus*.

A phylogenetic tree on the basis of 16S rRNA genes of all species in the genus *Apilactobacillus* is provided in Figure S6R.

The type species of the genus is *Apilactobacillus kunkeei* comb. nov. *Apilactobacilus* was previously referred to as *L. kunkeei* group.

Description of *Apilactobacillus kunkeei* comb. nov.

Apilactobacillus kunkeei (kun’kee.i; N.L. gen.n. *kunkeei* of Kunkee, named in honor of the Californian microbiologist Ralph Kunkee).

Basonym: *Lactobacillus kunkeei* Edwards et al. 1998, 1083^{VL}

A facultative anaerobic organism [321]; the genome size of the type strain is 1.52 Mbp. The mol% GC content of DNA is 36.4.

Isolated form a sluggish grape wine fermentation but the species is typically associated with honey bees and flowers.

The type strain is YH-15^{T} = ATCC 700308^{T}= DSM 12361^{T} = JCM 16173^{T}.

Genome sequence accession number: AZCK00000000.

16S rRNA gene accession number: Y11374.

Description of *Apilactobacillus apinorum* comb. nov.

Apilactobacillus apinorum (a.pi.no’rum. N.L. gen. pl. n. *apinorum* of the *Apini*, referring to the isolation of this species from several species of honey bees).

Basonym: *Lactobacillus apinorum* Olofsson et al. 2014, 3113^{VP}

Growth is observed at anaerobic conditions in the range of 15 – 50°C and pH 3.0 - 12.0 [89]. The genome size of the type strain is 1.36 Mbp. The mol% GC content of DNA is 34.9.

Isolated from honey stomach of the honeybee.

The type strain is Fhon13N^{T} = DSM 26257^{T} = CCUG 63287^{T}.

Genome sequence accession number: JXCT00000000.

16S rRNA gene accession number: JX099541.

Description of *Apilactobacillus kosoi* comb. nov.

Apilactobacillus kosoi (ko'so.i. N.L. gen. n. kosoi, of kôso, a high sucrose fermented beverage in Japan, the origin of the type strain).

Basonym: *Lactobacillus kosoi* Chiou et al., 2018, 2707^{VL}

The species is described in [322, 323]. *A. kosoi* is most closely related to *A. micheneri*; major physiological properties are shared with *A. micheneri*, *A. timberlakei* and *A. quenuiae*. The genome size of the type strain is 1.42 Mbp. The mol% GC content of DNA is 30.5.

Isolated from koso, a Japanese sugar-vegetable fermented beverage.

The type strain is 10H^{T} = NBRC 113063^{T} = BCRC 81100^{T}.

Genome sequence accession number: BEXE01000000.

16S rRNA gene accession number: LC318484

Description of *Apilactobacillus micheneri* comb. nov.

Apilactobacillus micheneri (mi.che'ne.ri. N.L. gen. masc. n. *micheneri* named in honor of Charles D. Michener's contributions to the study of bees in natural habitats).

Basonym: *Lactobacillus micheneri* McFrederick et al. 2018, 1993^{VP}

Major physiological properties are shared with *A. timberlakei* and *A. quenuiae* [324]. The genome size of the type strain is 1.46 Mbp. The mol% GC content of DNA is 30.3.

Isolated from bees and flowers.

The type strain is Hlig3^{T} = DSM 104126^{T} = NRRL B-65473^{T}.

Genome sequence accession number: POSO00000000.

16S rRNA gene accession number: KT833121.

Description of *Apilactobacillus ozensis* comb. nov.

Apilactobacillus ozensis (o.zen'sis. N.L. masc. adj. *ozensis* of Oze, the Japanese National Park from where the type strain was isolated).

Basonym: *Lactobacillus ozensis* Kawasaki et al. 2011, 2437^{VP}

A. ozensis grows anaerobically but not aerobically; growth is inhibited by 1.5% NaCl [325]. The genome size of the type strain is 1.48 Mbp. The mol% GC content of DNA is 31.9.

Isolated from a chrysanthemum flower.

The type strain is Mizu2-1^{T} = DSM 23829^{T} = JCM 17196^{T}.

Genome sequence accession number: AYYQ00000000.

16S rRNA gene accession number: AB572588.

Description of *Apilactobacillus quenuiae* comb. nov.

Apilactobacillus quenuiae (que.nu'i.ae. N.L. gen. fem. n. *quenuiae*, named in recognition of Cécile Plateaux-Quénu's contributions to the biology of bees).

Basonym: *Lactobacillus quenuiae* Frederick et al. 2018, 1884^{VP}

A description of the speices is provided in [324]. The genome size of the type strain is 1.58 Mbp. The mol% GC content of DNA is 30.3.

Isolated as part of the core microbiome of wild bees and from flowers.

The type strain is HV_6^T = DSM 104127^T = NRRL B-65474^T.

Genome sequence accession number: POSN00000000.

16S rRNA gene accession number: KX656667.

Description of *Apilactobacillus timberlakei* comb. nov.

Apilactobacillus timberlakei (tim.ber.lake'i. N.L. gen. masc. n. *timberlakei* names in honor of Philip Timberlake's work on bee taxonomy).

Basonym: *Lactobacillus timberlakei* McFrederick et al. 2018, 1884^{VP}

Aerotolerant [324]; the genome size of the type strain is 1.54 Mbp. The mol% GC content of DNA is 30.5.

Isolated as part of the core microbiome of wild bees, and from flowers.

The type strain is HV_12^T = DSM 104128^T = NRRL B-65472^T.

Genome sequence accession number: POST00000000.

16S rRNA gene accession number: KX656650.

DESCRIPTION OF *LENTILACTOBACILLUS* GEN. NOV.

Lentilactobacillus (Len.ti.lac.to.ba.cil'lus. L. masc. adj. *lentus* slow, sluggish, referring to the slow growth of species in the genus with lactate or propanediol as carbon course; N.L. masc. n. *Lactobacillus* a bacterial genus name; N.L. masc. n. *Lentilactobacillus* a slow [growing] lactobacillus).

Gram-positive, rod-shaped, catalase negative, heterofermentative. Most strains grow at 15°C and some also grow at 45°C, the pH range of growth is highly variable but optimal growth is typically observed below pH 6.0. The genome size ranges from 1.57 Mbp for *Lentilactobacillus senioris* to 4.91 Mbp for *Lentilactobacillus parakefiri*, the mol% GC content of DNA ranges from 39.1 – 45.2%. Strains in the genus were isolated from silage, fermented vegetables, particularly as secondary fermentation or spoilage microbiota, (spoiled) wine and cereal mashes. Generally, strains in the species lead a free-living lifestyle; individual species of the genus, particularly *L. senioris*, appear to transition to a specialized, host adapted lifestyle. *Lentilactobacillus* species generally metabolize a broad spectrum of pentoses, hexoses, and disaccharides. Most species metabolize lactate to 1,2-propanediol and / or 1,2-propanediol to propanol and propionate; these pathways are virtually exclusive to heterofermentative lactobacilli and, among these, most common and most frequent in *Lentilactobacillus*. Most *Lentilactobacillus* species also convert agmatine, a product of bacterial decarboxylation of arginine, via the agmatine deiminase pathway [14, 326]; in lactobacilli, this pathway is associated with a free-living lifestyle. *Lentilactobacillus* species are used commercially as silage starter cultures, and in few dairy and cereal applications.

A phylogenetic tree on the basis of 16S rRNA genes of all species in the genus *Lentilactobacillus* is provided in Figure S6S.

The type species of the genus is *Lentilactobacillus buchneri* comb. nov.; *Lentilactobacillus* was previously referred to as *L. buchneri* group.

Description of *Lentilactobacillus buchneri* comb. nov.

Lentilactobacillus buchneri (buch'ne.ri. N.L. gen. n. *buchneri* of Buchner, referring to the German microbiologist Buchner).

Basonym: *Lactobacillus buchneri* (*Bacillus buchneri* [sic] Henneberg 1903, 163) Bergey et al. 1923, 251 (Approved Lists)

Biochemical characteristics of *L. buchneri* were described as being similar to *L. brevis* [11, 231] but *L. buchneri* differs with regards to the production of 1,2 propanediol from lactate. The genome size of the type strain is 2.45 Mbp. The mol% GC content of DNA is 44.4.

Isolated from pressed yeast, milk, cheese, fermenting plant material and the human mouth. *L. buchneri* is used commercially as silage inoculant.

The type strain is ATCC 4005^T = CCUG 21532^T = CIP 103023^T =DSM 20057^T = JCM 1115^T = LMG 6892^T = NCAIM B.01145^T = NRRL B-1837^T = VKM B-1599^T.

Genome sequence accession number: AZDM00000000.

16S rRNA gene accession number: AB205055.

Description of *Lentilactobacillus curieae* comb. nov.

Lentilactobacillus curieae (cu.rie'ae. N.L. fem. gen. n. *curieae* of Curie, named after Marie Curie, to acknowledge a role model for women in science).

Basonym: *Lactobacillus curieae* Lei et al. 2013, 2504^{VP}

Description: Growth is observed at 15 and 45°C and up to 8% NaCl [327]. The genome size of the type strain is 2.10 Mbp. The mol% GC content of DNA is 39.8.

Isolated from a stinky tofu brine, cocoa bean fermentations and from cheese curd powder.

The type strain is CCTCC M 2011381^T = S1L19^T = JCM 18524^T.

Genome sequence accession number: CP018906.

16S rRNA gene accession number: JQ086550.

Description of *Lentilactobacillus diolivorans* comb. nov.

Lentilactobacillus diolivorans (di.o.li.vo'rans. N.L. n. *diol* from 1,2-propanediol; L. pres. part. *vorans* eating; N.L. part. adj. *diolivorans* eating diols).

Basonym: *Lactobacillus diolivorans* Kroonemen et al. 2001, 645^{VP}

Growth is observed between 20 and 40°C, and between pH 3.8 and 7. *L. diolivorans* was the first lactic acid bacterium for which the metabolic pathway for propanediol and glycerol metabolism to propanol and propionate or 1,3 propanediol and 3-hydroxypropionate, respectively, was thoroughly described [328]. This metabolic pathway is functional is multiple other lactobacilli [14, 18]. The genome size of the type strain is 3.27 Mbp. The mol% GC content of DNA is 40.0.

Isolated from maize silage and as a spoilage organism in vegetable (cucumber) fermentations and fermented dairy products.

The type strain is JKD6^T = DSM 14421^T = JCM 12183^T = LMG 19667^T.

Genome sequence accession number: AZEY00000000.

16S rRNA gene accession number: AF264701.

Description of *Lentilactobacillus farraginis* comb. nov.

Lentilactobacillus farraginis (far.ra'gi.nis. L. gen. n. *farraginis* of mash, referring to soshu mash as an ingredient of the compost from which the type strain was isolated).

Basonym: *Lactobacillus farraginis* Endo and Okada 2007, 711^{VP}

Description: Growth is observed at 15 and 45°C and up to pH 9.0 for some strains [329]. The genome size of the type strain is 2.86 Mbp. The mol% GC content of DNA is 42.1.

Isolated from isolated from a compost of distilled shochu residue.

The type strain is DSM 18382^{T} = JCM 14108^{T} = NRIC 0676^{T}.

Genome sequence accession number: AZFY00000000.

16S rRNA gene accession number: AB262731.

Description of *Lentilactobacillus hilgardii* comb. nov.

Lentilactobacillus hilgardii (hil.gar'di.i. N.L. gen. n. *hilgardii* of Hilgard, named after E.W.Hilgard, a pioneer of enology in the State of California, U.S.A).

Basonym: *Lactobacillus hilgardii* Douglas and Cruess 1936, 115 (Approved Lists); the species was initially described in 1936; the description was emended in 1949 after the original type strain was lost [330, 331]

Strains grow optimally between pH 4.5 and 5.5 and in the range of 15 to 40°C [330, 331]. The genome size of the type strain is 2.60 Mbp. The mol% GC content of DNA is 39.6.

Isolated from spoiled wine, kefir grains, mezcal fermentations and silage.

The type strain is 9^{T} = ATCC 8290^{T} = CIP 103007^{T} = DSM 20176^{T} = JCM 1155^{T} = LMG 6895^{T}.

Genome sequence accession number: AZDF00000000.

16S rRNA gene accession number: M58821.

Description of *Lentilactobacillus kefiri* comb. nov.

Lentilactobacillus kefiri (ke.fi'ri. N.L. gen. n. *kefiri*, of kefir, referring to the source of isolation).

Basonym: *Lactobacillus kefir* Kandler and Kunath 1983, 672^{VL}

Characteristics are described in [332]. Growth is observed at 15 but not at 45 °C; the genome size of the type strain is 2.23 Mbp. The mol% GC content of DNA is 41.7.

Isolated from kefir as part of the core microbiota.

The type strain is A/K^{T} = ATCC 35411^{T}= CIP 103006^{T} = DSM 20587^{T} = JCM 5818^{T} = LMG 9480^{T}.

Genome sequence accession number: AYYV00000000.

16S rRNA gene accession number: AJ621553.

Description of *Lentilactobacillus kisonensis* comb. nov.

Lentilactobacillus kisonensis (ki.so.nen'sis. N.L. masc. adj. *kisonensis* from Kiso, the county in Japan, from where the type strain was isolated).

Basonym: *Lactobacillus kisonensis* Watanabe et al. 2009, 757^{VP}

Description. Growth is observed at 10 but not at 45 °C and between pH 4.5 to 8.0 [333]. The genome size of the type strain is 3.01 Mbp. The mol% GC content of DNA is 41.7.

Isolated from a pickle brine.

The type strain is YIT 11168^{T} = DSM 19906^{T} = JCM 15041^{T} = NRIC 074^{T}.

Genome sequence accession number: AZEB00000000.

16S rRNA gene accession number: AB366388.

Description of *Lentilactobacillus otakiensis* comb. nov.

Lentilactobacillus otakiensis (o.ta.ki.en'sis. N.L. masc. adj. *otakiensis* from Otaki, the village in Japan, from where the type strain was isolated).

Basonym: *Lactobacillus otakiensis* Watanabe et al. 2009, 758^{VP}

Physiological characteristics and origin are similar to *L. kisonensis* [333]. The genome size of the type strain is 2.35 Mbp. The mol% GC content of DNA is 42.4.

Isolated from sunki, a fermented turnip product and from kefir.

The type strain is YIT 11163^{T} = DSM 19908^{T} = JCM 15040^{T}= NRIC 0742^{T}.

Genome sequence accession number: AZED00000000.

16S rRNA gene accession number: AB366386.

Description of *Lentilactobacillus parabuchneri* comb. nov.

Lentilactobacillus (Gr. pref. *para* beside; N.L. gen. n. *buchneri* a species epithet; N.L. gen. n. *parabuchneri* beside *L. buchneri*, referring to the close relationship with this organism).

Basonym: *Lactobacillus parabuchneri* Farrow et al. 1988, 371^{VL}; strains of the species were previously classified as *L. ferintoshensis* [334] or *L. frigidus* [64, 335]

Characteristics are described in [278]; growth is observed at 10 and 40°C. The genome size of the type strain is 2.61 Mbp. The mol% GC content of DNA is 43.5.

Isolated from dairy products, saliva, silage, spoiled beer, and some strains were shown to persist over month in whiskey mashes in Scottish distilleries [334].

The type strain is 6E^{T} = ATCC 49374^{T}= DSM 5707^{T} = JCM 12493^{T} = LMG 11457^{T}.

Genome sequence accession number: AZGK00000000.

16S rRNA gene accession number: AB205056.

Description of *Lentilactobacillus parafarraginis* comb. nov.

Lentilactobacillus parafarraginis (Gr. pref. *para* beside; L. gen. n. *farraginis* a species epithet; N.L. gen. n. *parafarraginis* beside *L. farraginis*, referring to the close relationship with this organism).

Basonym: *Lactobacillus parafarraginis* Endo and Okada 2007, 711^{VP}

Physiological characteristics are similar to *L. farraginis* but growth is observed only between 20 and 37°C [329]. The genome size of the type strain is 3.08 Mbp. The mol% GC content of DNA is 45.2.

Isolated from a compost of distilled shochu residue, silage, fermented vegetables, and kefir grains.

The type strain is NRIC 0676^{T} = DSM 18390^{T} = JCM 14109^{T} = NRIC 0677^{T}.

Genome sequence accession number: AZFZ00000000.

16S rRNA gene accession number: AB262734.

Description of *Lentilactobacillus parakefiri* comb. nov.

Lentilactobacillus parakefiri (pa.ra.ke'fir.i. Gr. pref. *para* beside; N.L. gen. n. *kefiri* a species epithet; N.L. masc. adj. *parakefiri* beside *L. kefiri*, referring to the close relationship with this organism).

Basonym: *Lactobacillus parakefiri* Takizawa et al. 1994, 438^{VP}. The classification of *L. parakefiri* as separate species was disputed as the first published genome sequence of the type strain was virtually identical to *L. kefiri* [14, 16] but re-sequencing of the type strain supported classification of *L. parakefiri* as separate species [336]

Growth is observed at 15 but not at 45°C [101]. The genome size of the type strain is 4.91 Mbp. The mol% GC content of DNA is 42.6.

Isolated from kefir grains.

The type strain is GCL 1731^{T} = ATCC 51648^{T}= CCUG 39468^{T} = CIP 104242^{T} = DSM 10551^{T} = LMG 15133^{T}.

Genome sequence accession number: AZEN00000000.

16S rRNA gene accession number: AY026750.

Description of *Lentilactobacillus raoultii* sp. nov.

Lentilactobacillus raoultii (ra.oul'ti.i. N.L. gen. n. *raoultii* of Raoult, named after the microbiologist Didier Raoult).

The species was effectively but not validly published as *Lactobacillus raoultii* Nicaise et al. 2019 [337]. Growth is observed between 25 – 45°C and between pH 5 and 7.5; the genome size of the type strain is 3.07 Mbp. The mol% GC content of DNA is 41.4.

Isolated from the vagina of a healthy women.

The type strain is Strain Marseille P4006^{T} = CSUR P4006^{T} = LMG 31598^{T} = CCUG 71848^{T}.

Genome sequence accession number: OVSN00000000.

16S rRNA gene accession number: LT854294.

Description of *Lentilactobacillus rapi* comb. nov.

Lentilactobacillus rapi (ra'pi. L. gen. n. *rapi* of a turnip, the substrate for fermented sunki products).

Basonym: *Lactobacillus rapi* Watanabe et al. 2009, 759^{VP}

Origin and physiological properties are similar to *L. kisonensis* [333]. The genome size of the type strain is 2.86 Mbp. The mol% GC content of DNA is 43.0.

Isolated from sunki and other vegetable fermentations.

The type strain is YIT 11204^{T} = DSM 19907^{T} = JCM 15042^{T} = NRIC 0743^{T}.

Genome sequence accession number: AZEI00000000.

16S rRNA gene accession number: AB366389.

Description of *Lentilactobacillus senioris* comb. nov.

Lentilactobacillus senioris (se.ni.o'ris. L. gen. n. *senioris* of an elderly person, indicating the source of the type strain).

Basonym: *Lactobacillus senioris* Oki et al., 2012, 606^{VP}

Growth is observed at 15 and 37 °C but not at 45°C; the type strain was isolated from human feces [173]. *L. senioris* is the most distantly related member of the genus, has the smallest genome size (1.57 Mbp) and lowest GC content (39.9) among species in the genus, and does not share the signature genes that are shared by other lentilactobacilli, which may indicate that *L. senioris* transitions from a free-living to a host-adapted lifestyle.

Isolated from from the faeces of a 100-year-old female.

The type strain is YIT 12364^{T} = DSM 24302^{T} = JCM 17472^{T}.

Genome sequence accession number: AYZR00000000.

16S rRNA gene accession number: AB602570.

Description of *Lentilactobacillus sunkii* comb. nov.

Lentilactobacillus sunkii (sun'ki.i. N.L. gen. n. *sunkii* of sunki, non-salted Japanese traditional pickle).

Basonym: *Lactobacillus sunkii* Watanabe et al. 2009, 759^{VP}

Physiological properties and origin are comparable to *L. kisonensis* [333]. The genome size of the type strain is 2.69 Mbp. The mol% GC content of DNA is 42.1.

Isolated from sunki, a fermented turnip product, and from kefir.

The type strain is YIT 11161^{T} = DSM 19904^{T} = JCM 15039^{T} = NRIC 0744^{T}.

Genome sequence accession number: AZEA00000000.

16S rRNA gene accession number: AB366385.

NOTE ADDED IN PROOF

Species that were added at the proof stage:

Description of *Lapidilactobacillus achengensis* comb. nov.

Lapidilactobacillus achengensis (a.cheng.en´sis. N.L. masc. adj. *achengensis*, pertaining to Acheng, a county in Heilongjiang Province, P.R. China).

Basonym: *Lactobacillus achengensis* Long et al. 2020, 15^{VP}.

L. achengensis grows between 10 and 37°C but not at 5 and 45°C and metabolises several pentoses and a broad spectrum of disaccharides [338]. The genome size of the type strain is 2.64 Mbp. The mol% GC content of DNA is 49.0.

Isolated from a vegetable fermentation [338].

The type strain is 247-4^{T} = NCIMB 15155^{T} = CCM 8897^{T} = LMG 31059^{T} = CCTCC AB 2018410^{T}.

Genome sequence accession number: RHOV00000000.

16S rRNA gene accession number: MK110810.

Description of *Lapidilactobacillus gannanensis* comb. nov.

Lapidilactobacillus gannanensis (gan.nan.en´sis. N.L. masc. adj. *gannanensis*, pertaining to Gannan, a county in Heilongjiang Province, P.R. China).

Basonym: *Lactobacillus gannanensis* Long et al. 2020, 16^{VP}.

L. gannanensis grows between 15 and 37°C but not at 10 and 45°C; the strain produces acid from D-glucose, N-acetylglucosamine, salicin, cellobiose and gentiobiose but not from pentoses [338]. The genome size of the type strain is 2.39 Mbp. The mol% GC content of DNA is 40.8.

Isolated from a vegetable fermentation [338].

The type strain is 143-1^{T} = NCIMB 15157^{T} = CCM 8937^{T} = CCTCC AB 2018409^{T}.

Genome sequence accession number: RHOT00000000.

16S rRNA gene accession number: MK110813.

Description of *Lapidilactobacillus mulanensis* comb. nov.

Lapidilactobacillus mulanensis (mu.lan.en´sis. N.L. masc. adj. *mulanensis*, pertaining to Mulan, a county in Heilongjiang Province, P.R. China).

Basonym: *Lactobacillus mulanensis* Long et al. 2020, 14^{VP}.

L. mulanensis grows between 15 and 32°C; the strain produces acid from hexoses and disaccharides but not from pentoses [338]. The genome size of the type strain is 2.32 Mbp. The mol% GC content of DNA is 42.5.

Isolated from a vegetable fermentation [338].

The type strain is 143-6^T = NCIMB 15162^T = CCM 8951^T = JCM 33274^T = CCTCC AB 2018411^T.

Genome sequence accession number: RHOW00000000.

16S rRNA gene accession number: MK110808.

Description of *Lapidilactobacillus wuchangensis* comb. nov.

Lapidilactobacillus wuchangensis (wu.chang.en´sis. N.L. masc. adj. *wuchangensis*, pertaining to Wuchang, a county in Heilongjiang Province, P.R. China).

Basonym: *Lactobacillus wuchangensis* Long et al. 2020, 15^{VP}.

L. mulanensis grows between 15 and 37°C but not at 10 and 45°C; the strain produces L(+)-lactate from D-ribose, D-glucose, N-acetylglucosamine and cellobiose [338]. The genome size of the type strain is 2.53 Mbp. The mol% GC content of DNA is 41.7.

Isolated from a vegetable fermentation [338].

The type strain is 17-4^T = NCIMB 15161^T = CCM 8946^T = JCM 33271^T = CCTCC AB 2018406^T.

Genome sequence accession number: RHOU00000000.

16S rRNA gene accession number: MK110811.

Description of *Lacticaseibacillus daqingensis* comb. nov.

Lacticaseibacillus daqingensis (da.qing.en´sis. N.L. masc. adj. *daqingensis*, pertaining to Daqing, a city in in Heilongjiang Province, P.R. China).

Basonym: *Lactobacillus daqingensis* Long et al. 2020, 14^{VP}.

L. daqingensis grows at 10 - 37°C but not at 5° and 45°C [338]. The genome size of the type strain is 2.74 Mbp. The mol% GC content of DNA is 58.0.

Isolated from a vegetable fermentation [338].

The type strain is 143-4(a)^T = NCIMB 15173^T = CCM 8948^T = JCM 33273^T = CCTCC 2018390^T.

Genome sequence accession number: RHOH00000000.

16S rRNA gene accession number: MK110842.

Description of *Lacticaseibacillus hegangensis* comb. nov.

Lacticaseibacillus hegangensis (he.gang.en´sis. N.L. masc. adj. *hegangensis*, pertaining to Hegang, a city in Heilongjiang Province, P.R. China).

Basonym: *Lactobacillus hegangensis* Long et al. 2020, 12^{VP}.

Properties of *L. hegangensis* are similar to *L. daqingensis* [338]. The genome size of the type strain is 2.50 Mbp. The mol% GC content of DNA is 55.5.

Isolated from a vegetable fermentation [338].

The type strain is 73-4^T = NCIMB 15177^T = CCM 8912^T = CCTCC AB 2018407^T.

Genome sequence accession number: RHOL00000000.

16S rRNA gene accession number: MK110833.

Description of *Lacticaseibacillus suibinensis* comb. nov.

Lacticaseibacillus suibinensis (sui.bin.en´sis. N.L. masc. adj. *suibinensis*, pertaining to Suibin, a county in Heilongjiang Province, P.R. China).

Basonym: *Lactobacillus suibinensis* Long et al. 2020, 12^{VP}.

Properties of *L. suibiensis* are similar to *L. daqingensis* but *L. suibiensis* deaminates arginine [338]. The genome size of the type strain is 2.56 Mbp. The mol% GC content of DNA is 53.0.

Isolated from a vegetable fermentation [338].

The type strain is 247-3^T = NCIMB 15176^T = JCM 33275^T.

Genome sequence accession number: RHOK00000000.

16S rRNA gene accession number: MK110834.

Description of *Lacticaseibacillus yichunensis* comb. nov.

Lacticaseibacillus yichunensis (yi.chun.en´sis. N.L. masc. adj. *yichunensis*, pertaining to Yichun, a city in Heilongjiang Province, P.R. China).

Basonym: *Lactobacillus yichunensis* Long et al. 2020, 14^{VP}.

Properties of *L. yichunensis* are similar to *L. daqingensis*, but it does not grow at 37°C. [338]. The genome size of the type strain is 2.56 Mbp. The mol% GC content of DNA is 55.4.

Isolated from a vegetable fermentation [338].

The type strain is 33-1^T = NCIMB 15169^T = CCM 8947^T = JCM 33272^T = CCTCC 2018405^T.

Genome sequence accession number: RHOG00000000.

16S rRNA gene accession number: MK110845.

Description of *Loigolactobacillus binensis* comb. nov.

Loigolactobacillus binensis (bin.en´sis. N.L. masc. adj. *binensis*, pertaining to Bin, a county in Heilongjiang Province, P.R. China).

Basonym: *Lactobacillus binensis* Long et al. 2020, 16^{VP}.

L. binensis grows between 10 and 37°C but not at 5 and 45°C; the strain produces acid from several hexoses, sugar alcohols and maltose, but not from pentoses [338]. The genome size of the type strain is 2.85 Mbp. The mol% GC content of DNA is 43.5.

Isolated from a vegetable fermentation [338].

The type strain is 735-2^T = NCIMB 15190^T = CCM 8925^T = LMG 31186^T.

Genome sequence accession number: BJDN00000000.

16S rRNA gene accession number: LC438524.

Description of *Lactiplantibacillus garii* comb. nov.

Lactiplantibacillus garii (ga'ri.i N.L. gen. n. *garii* of *gari*, the fermented cassava product from which the type strain was isolated).

Basonym: *Lactobacillus garii* Diaz et al. 2020, 5^{VP}.

L. garii grows in the temperature range of 6 – 42 °C and in the pH range of 4.0 to 8.8. The type strain produces D(-)-lactate from a wide spectrum of pentoses, hexoses, and disaccharides [339]. The genome size of the type strain is 2.97 Mbp. The mol% GC content of DNA is 48.3.

Isolated from *gari*, a fermented cassava product [339].

The type strain is $FI11369^T$ = NCIMB 15148^T = DSM 108249^T.

Genome sequence accession number: QWZQ00000000.

16S rRNA gene accession number: MN81791.

Description of *Levilactobacillus angrenensis* comb. nov.

Levilactobacillus angrenensis (ang.ren.en´sis. N.L. masc. adj. *angrenensis*, pertaining to Angren, a county in the Tibet Autonomous Region, PR China, where the bacterium was isolated).

Basonym: *Lactobacillus angrenensis* Long et al. 2020, 16^{VP}.

L. angrenensis grows between 10 and 37°C but not at 5 and 45°C [338]. The genome size of the type strain is 2.80 Mbp. The mol% GC content of DNA is 50.5.

Isolated from a fermented dairy beverage [338].

The type strain is M1530-1^T = NCIMB 15150^T = CCM 8893^T = LMG 31046^T = CCTCC AB 2018402^T.

Genome sequence accession number: RHOB00000000.

16S rRNA gene accession number: MK110858.

Description of *Levilactobacillus enshiensis* comb. nov.

Levilactobacillus enshiensis (en.shi.en'sis. N.L. masc. adj. *enshiensis* pertaining to Enshi, the prefecture in Hubei Province of the P.R. China where strain was isolated).

Basonym: *Lactobacillus enshiensis* Zhang et al. 2020, 6^{VP}.

L. enshiensis grows in the pH range of 4.0 to 10 and between 20 and 45°C but not at 15 and 50°C [340]. Acid is produced from a wide spectrum of pentoses, hexoses, disaccharides and several sugar alcohols; citrate is converted to malate [340]. *In silico* analyses presented in the species new description suggest a functional glycolytic pathway, however, phosphofructokinase, a key enzyme of glycolysis that is absent in virtually all heterofermentative lactobacilli [14] is also absent in the genome of *L. enshiensis* and the spectrum of metabolites from glucose demonstrate heterofermentative metabolism [340]. The genome size of the type strain is 3.07 Mbp. The mol% GC content of DNA is 47.8.

Isolated from Zha-Chili, a fermented product from mustard greens [340].

The type strain is $HBUAS57009^T$ = GDMCC 1.1664^T = KACC 21424^T.

Genome sequence accession number: SULH00000000.

16S rRNA gene accession number: MN082021.

AUTHOR STATEMENTS

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Ethical statement. The study did not use animals or humans for research.

Conflicts of interest. The authors declare no conflict of interest. Bruno Pot is employed by Yakult Europe but has no conflict of interest for this paper.

ABBREVIATIONS

AAI, pairwise amino acid identity

cAAI, pairwise amino acid identity of conserved genes

ANI, average nucleotide identity.

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FIGURES AND TABLES

Figure 1. Cumulative number of species described in the genera *Pediococcus* and *Lactobacillus* until Jan. 2020*.* The species decribed in Jan. 2020 is included in the 2010 – 2019 count.

Figure 2. Core genome phylogenetic tree of *Lactobacillaceae*. The phylogenomic analysis is based on the concatenated alignment of protein sequences for the 114 single-copy core genes. The maximum likelihood tree was inferred by RAxML as described [14] using the 244 *Lactobacillus* and *Pediococcus* species for which genome sequence data was available on the NCBI database on August 19th, 2019. The tree was rooted via midpoint rooting. Bootstrap support values were calculated from 500 replicates, and only values above 90% were labelled. Members of the same phylogenetic group that are the basis for the proposed taxonomy are indicated by the same color for branches, and the type strain of each group is printed in bold. Outer rings provide information on genomic features and the inferred lifestyle of the species. The color gradient in red represents the GC content of each genome sequence; higher GC contents are indicated by darker shading*.* The solid circles in brown represent genome sizes; the area of the circle correlates with the genome size. The second ring indicates the inferred natural habitats of the species as vertebrate host-adapted (red), insect-adapted (orange), nomadic (green), free-living (blue) or unassigned (white). This assignment of species to lifestyle was based on [17].

Figure 3. Box plot of the intra-family and inter-family cAAI values in the families *Leuconostocaceae* and *Lactobacillaceae*. The reference line is drawn at a cAAI of 59% in both panels.

Figure 4. Frequency distribution of pairwise cAAI in *Lactobacillaceae* and *Leuconostocaceae*. Inter-genus cAAI values are shown in descending order; Intra-genus cAAI values are shown in ascending order for the current taxonomy (dotted lines) and for the proposed taxonomy that divides the genus *Lactobacillus* in 25 genera (solid lines). Genera are color coded; *Lactobacillus*; *Pediococcus*, *Leuconostoc*, and *Weissella*. The number of pairwise cAAI values that is represented by the lines is indicated in the figure legend. Owing to the low number of values, intra-genus cAAI values for *Fructobacillus*, *Oenococcus* and *Convivina* are not shown. The data used for the graph is provided in online supplementary Table S3.

Figure 5. Range of pairwise intra-genus cAAI values for all current and proposed genera in the families *Lactobacillaceae* and *Leuconostocaceae*. The dotted line designates the lowest cAAI value for current genera excluding *Lactobacillus*. Bars and symbols are coloured gray if the genus is exclusive, i.e. if the lowest intra-genus cAAI is higher than any inter-genus cAAI of species in that genus. Bars and symbols are coloured red and green, respectively, if the genus is non-exclusive, i.e. if the lowest intra-genus cAAI is lower than the highest inter-genus cAAI of species in that genus. Trivial values (100% for self to self comparison) are shown only for genera that include one species. The data used for the graph is provided in online supplementary Table S3. The y-axis label uses the proposed taxonomy as follows *Lentilactobacillus* - *L. buchneri* group; *Secundilactobacillus* - *L. collinoides* group; *Levilactobacillus* - *L. brevis* group; *Fructilactobacillus* - *L. fructivorans* group; *Acetilactobacillus*, no prior designation; *Apilactobacillus* - *L. kunkeei* group; *Limosilactobacillus* – *L. reuteri* group; *Paucilactobacillus* – *L. vaccinostercus* group; *Furfurilactobacillus* – *L. rossiae* group; *Lactiplantibacillus* – *L. plantarum* group; *Ligilactobacillus* – part of *L. salivarius* group; *Liquorilactobacillus* - part of *L. salivarius* group; *Dellaglioa – L. algidus; Loigolactobacillus* – *L. coryniformis* group; *Paralactobacillus – L. selangorensis; Latilactobacillus* – *L. sakei* group; *Lacticaseibacillus* – *L. casei* group; *Agrilactobacillus* – *L. composti*; *Schleiferilactobacillus* – *L. perolens* group; *Lapidilactobacillus – L. dextrinicus / convacus; Companilactobacillus* – *L. alimentarius* group; *Bombilactobacillus* – *L. mellifer / mellis* group; *Lactobacillus* – *L. delbrueckii* group; *Amylolactobacillus* – *L. amylophilus* group; *Holzapfelia* – *L. florum*.

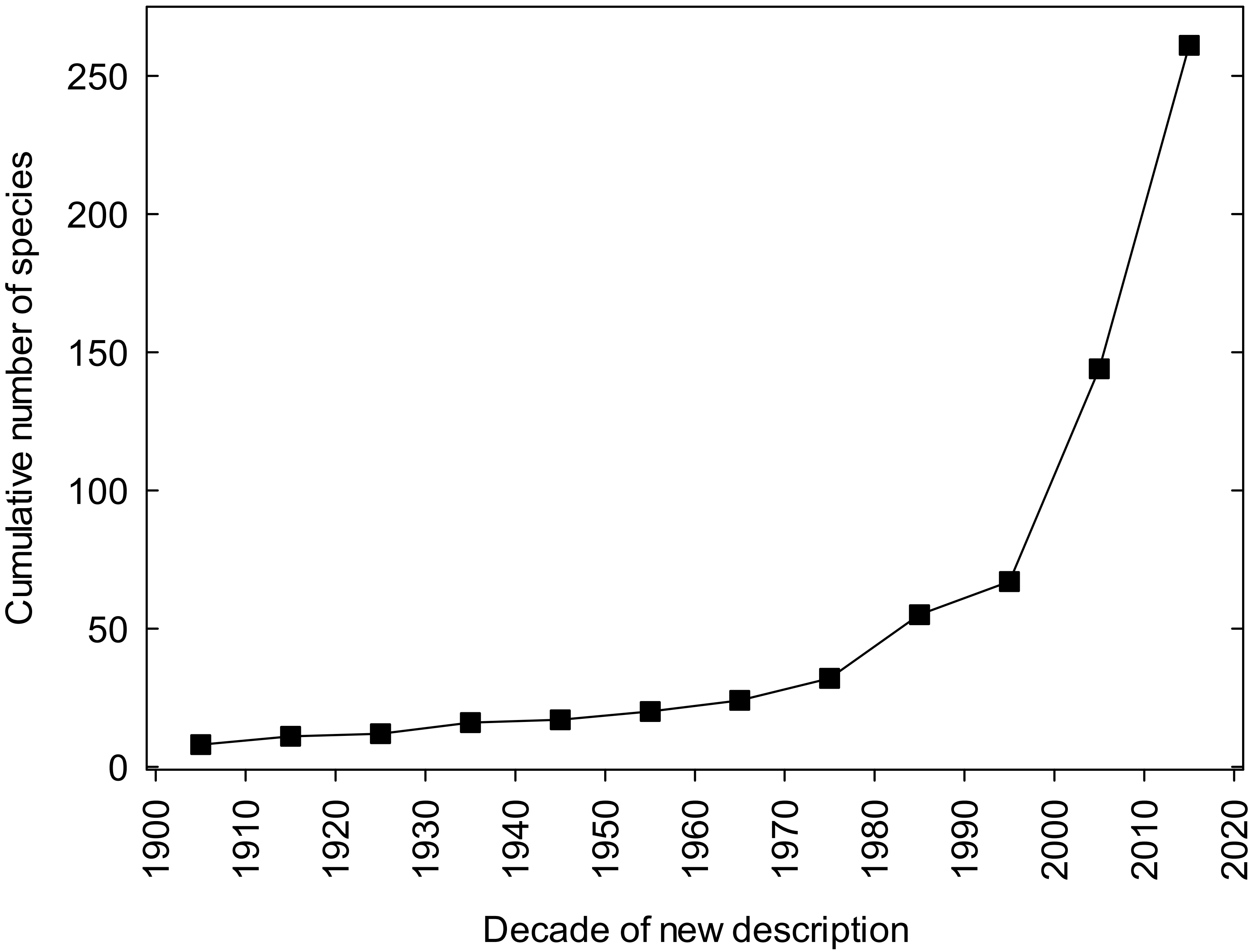
Figure 6. Gene family presence/absence patterns in *Lactobacillaceae* and *Leuconostocaceae*. Each column represents a gene family presence/absence pattern in species of *Lactobacillaceae* and *Leuconostoaceae*, where presence is indicated with a dot. The absolute number of gene families that conform to each pattern is visualized in the marginal bar plot at the top. Separations between phylogroups are indicated with horizontal black lines. We defined genes that were present in all genomes of a clade and in none of the genomes outside of that clade as "signature genes" (dark blue); other genes are shown in light blue). Only presence/absence patterns followed by four or more gene families are shown. Patterns of presence in a single species or all species are not shown. Unassigned species are clusters of closely related genomes which could not be assigned to a known species due to low whole-genome similarity to a type strain and / or low 16S rRNA similarity to a type strain.

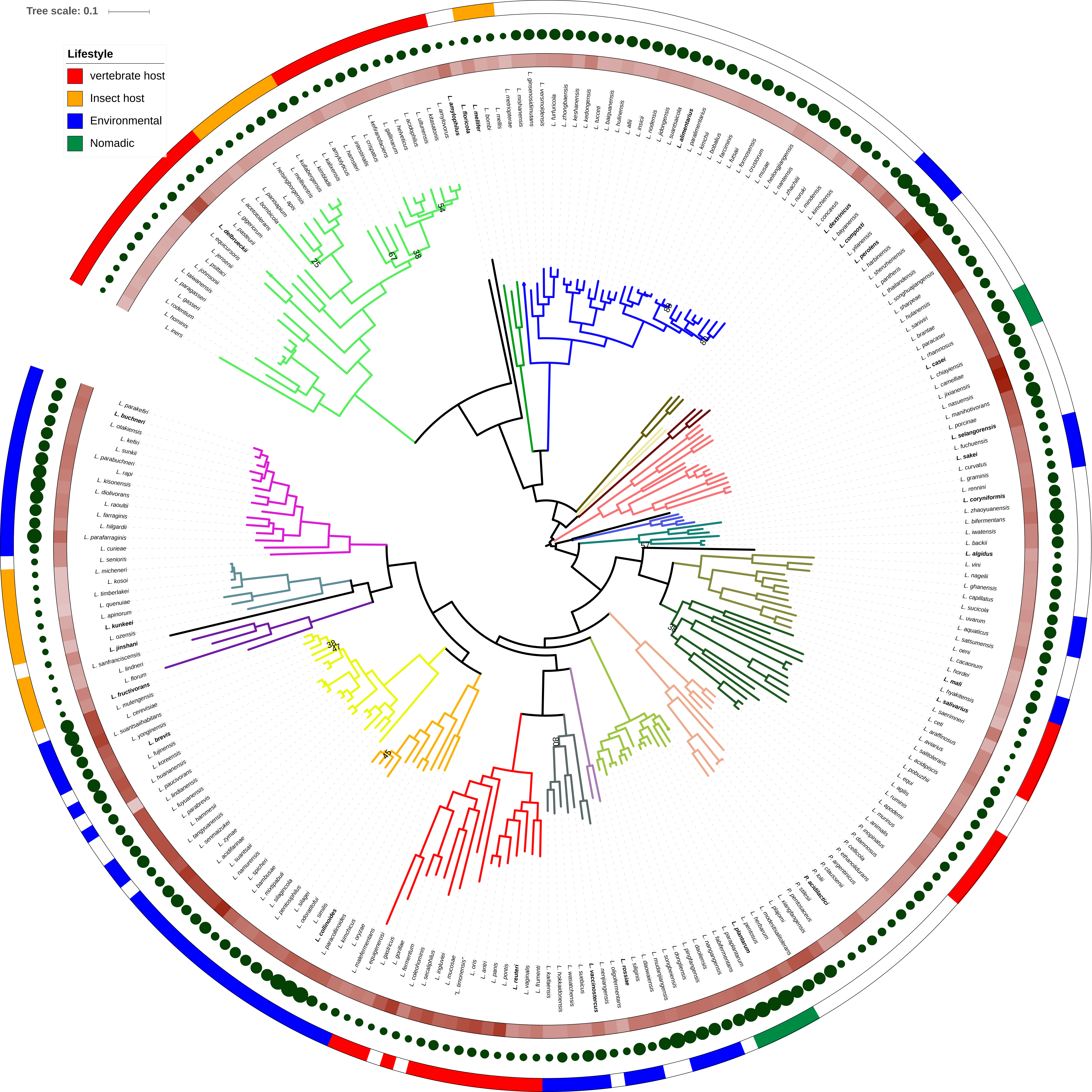
Figure 7.

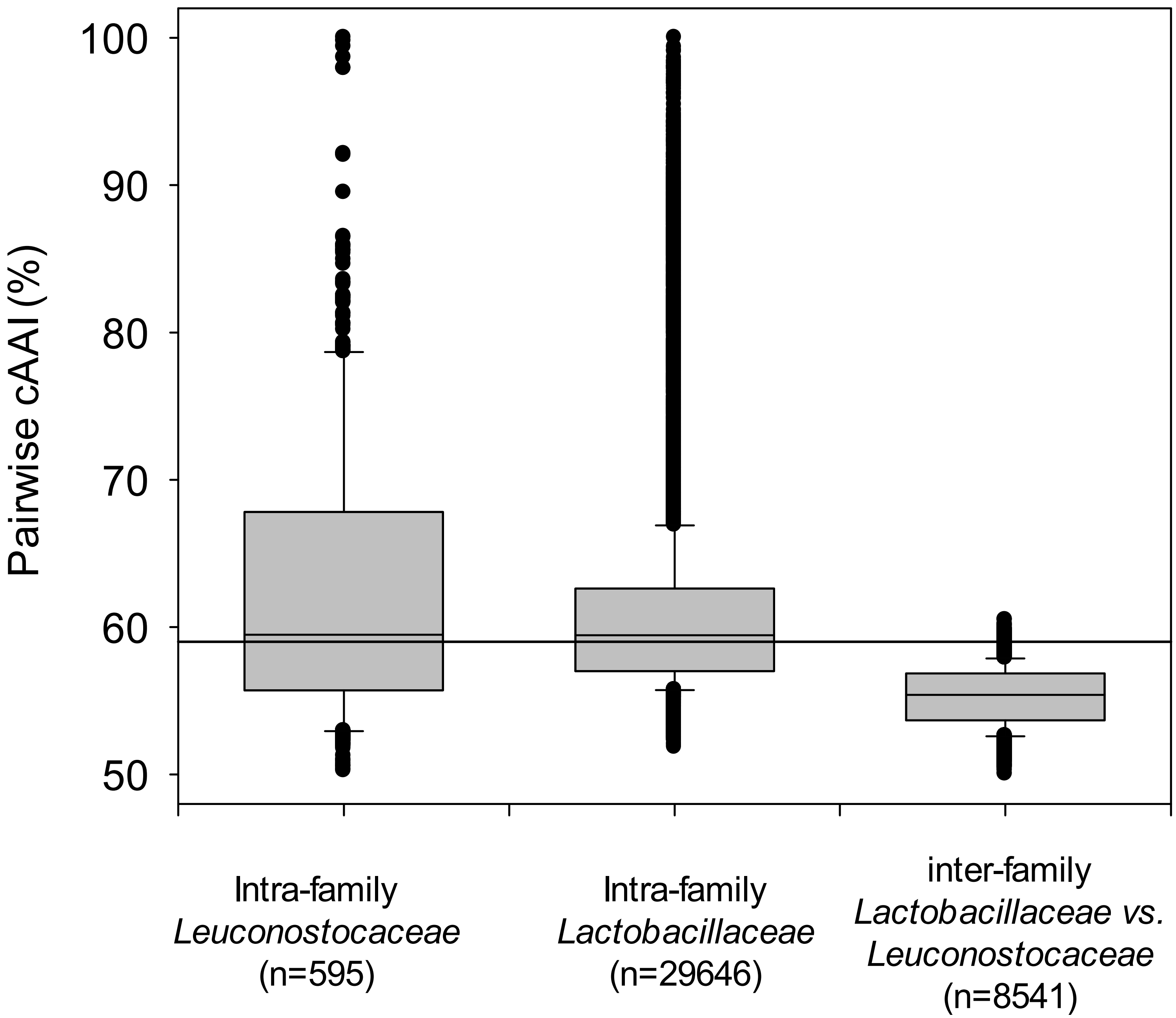
Panel (a). Core genome phylogenetic tree with the type strains of 25 phylogenetic groups of the genus *Lactobacillus*, 31 type strains of other genera in the *Lactobacillales,* and 8 type strains from *Bacillales* as outgroup. The phylogenomic analysis is based on the concatenated protein sequences of 170 single copy core genes. The maximum likelihood tree was inferred by RAxML as described (12). Bootstrap support values were calculated from 500 replicates, and only values of > 80% are labeled. Members of the same bacterial families are colour coded.

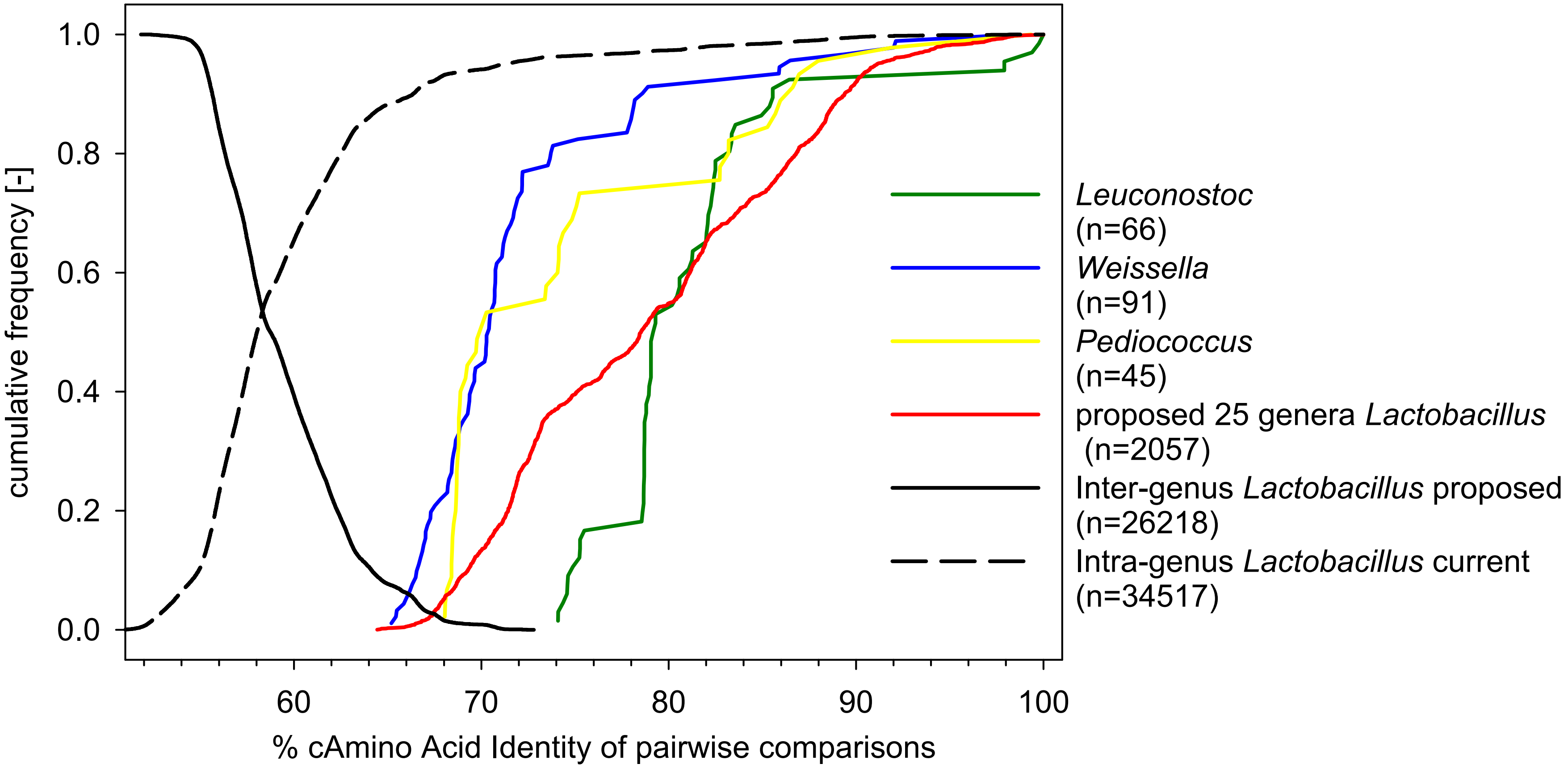
Panel (b). Overview tree of phylogroups of *Lactobacillaceae* and *Leuconostocaceae*. Subtree of the tree shown in Figure S4; only the branches corresponding to type species of phylogroups of *Lactobacillaceae* or genera of *Leuconostocaceae* are shown.

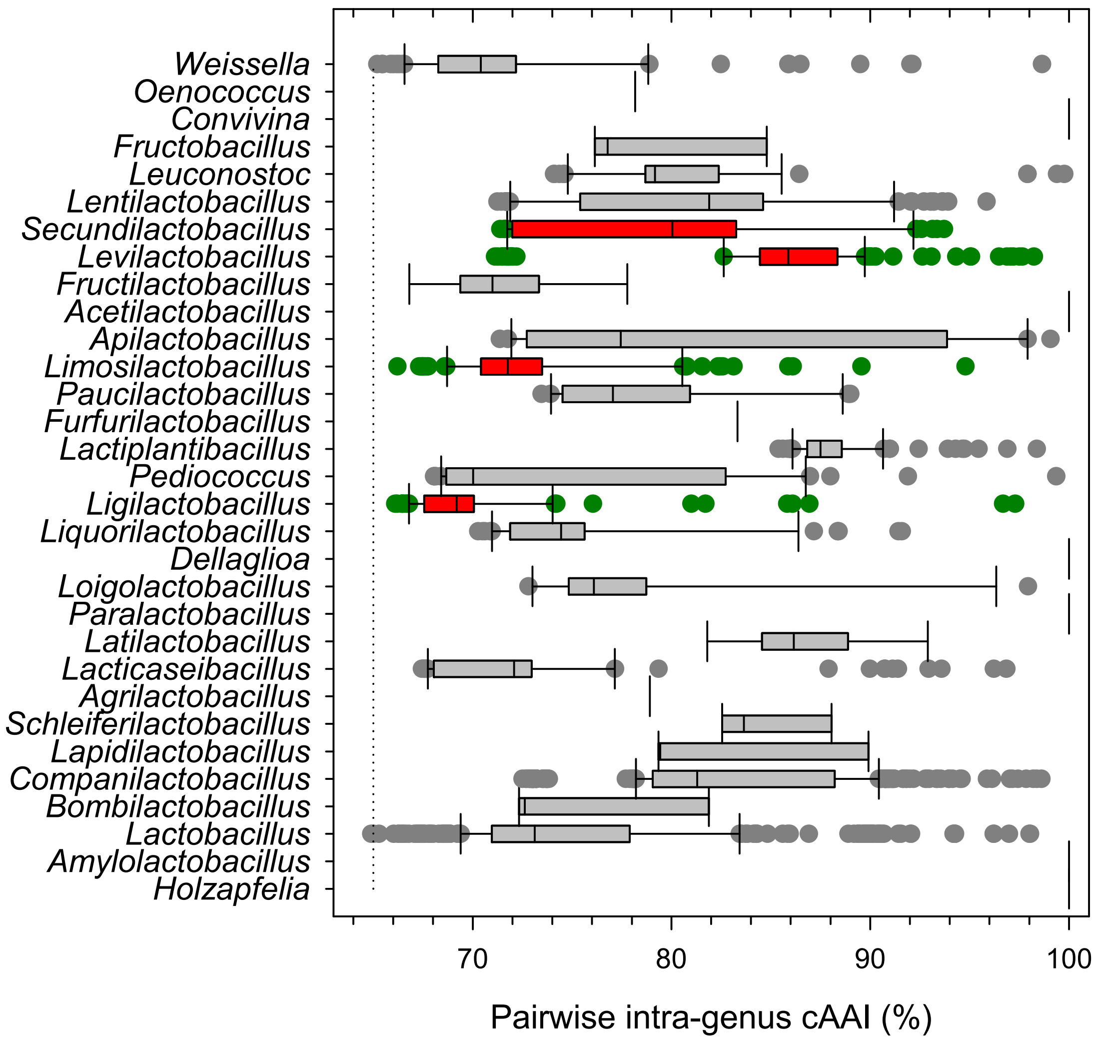
Figure 8. Heat map depicting the cAAI values of the 38782 pairwise comparisons of all species in the families *Leuconostocaceae* and *Lactobacillaceae* for which genome sequence data was available in August 2019. The source file is provided as Table S3.


Cumulative number of species
0
50
100
150
200
250
1900
1910
1920
1930
1940
1950
1960
1970
1980
1990
2000
2010
2020
Decade of new description


Tree scale: 0.1
Lifestyle
🟥 vertebrate host
🟧 Insect host
🟦 Environmental
🟩 Nomadic
L. iners
L. hominis
L. rodentium
L. gasseri
L. paragasseri
L. taiwanensis
L. johnsonii
L. psittaci
L. jensenii
L. equicursoris
L. delbrueckii
L. pasteurii
L. gigeriorum
L. acetotolerans
L. bombicola
L. panisapium
L. apis
L. helsingborgensis
L. melliventris
L. kullabergensis
L. kimbladii
L. kalixensis
L. amylolyticus
L. hamsteri
L. intestinalis
L. crispatus
L. kefiranofaciens
L. gallinarum
L. helveticus
L. acidophilus
L. ultunensis
L. kitasatonis
L. amylovorus
L. amylophilus
L. floricola
L. mellifer
L. bombi
L. mellis
L. metriopterae
L. mishanensis
L. ginsenosidimutans
L. versmoldensis
L. furfuricola
L. zhongbaensis
L. keshanensis
L. kedongensis
L. tucceti
L. baiquanensis
L. hulinensis
L. allii
L. insicii
L. nodensis
L. jidongensis
L. suantsaicola
L. alimentarius
L. paralimentarius
L. kimchii
L. bobalius
L. farciminis
L. futsaii
L. formosensis
L. crustorum
L. musae
L. heilongjiangensis
L. nantensis
L. zhachilii
L. nuruki
L. mindensis
L. kimchiensis
L. concavus
L. dextrinicus
L. bayanensis
L. composti
L. yilanensis
L. perolens
L. harbinensis
L. shenzhenensis
L. pantheris
L. thailandensis
L. songhuajiangensis
L. sharpeae
L. hulanensis
L. saniviri
L. brantae
L. paracasei
L. rhamnosus
L. casei
L. chiayiensis
L. camelliae
L. jixianensis
L. nasuensis
L. manihotivorans
L. porcinae
L. selangorensis
L. fuchuensis
L. sakei
L. curvatus
L. graminis
L. rennini
L. coryniformis
L. zhaoyuanensis
L. bifermentans
L. iwatensis
L. backii
L. algidus
L. vini
L. nagelii
L. ghanensis
L. capillatus
L. sucicola
L. uvarum
L. aquaticus
L. satsumensis
L. oeni
L. cacaonum
L. hordei
L. mali
L. hyakitensis
L. salivarius
L. saerimneri
L. ceti
L. araffinosus
L. aviarius
L. salitolerans
L. acidipiscis
L. pobuzihii
L. equi
L. agilis
L. ruminis
L. apodemi
L. murinus
L. animalis
P. inopinatus
P. damnosus
P. cellicola
P. ethanolidurans
P. argentinicus
P. claussenii
P. lolii
P. acidilactici
P. stilesii
P. pentosaceus
L. xiangfangensis
L. plajomi
L. modestisalitolerans
L. herbarum
L. pentosus
L. plantarum
L. paraplantarum
L. fabifermentans
L. nangangensis
L. daoliensis
L. pingfangensis
L. dongliensis
L. songbeiensis
L. mudanjiangensis
L. daowaiensis
L. siliginis
L. rossiae
L. oligofermentans
L. nenjiangensis
L. vaccinostercus
L. suebicus
L. wasatchensis
L. hokkaidonensis
L. kaifaensis
L. frumenti
L. vaginalis
L. reuteri
L. pontis
L. panis
L. antri
L. oris
"L. timonensis"
L. mucosae
L. ingluviei
L. secaliphilus
L. coleohominis
L. fermentum
L. gorillae
L. gastricus
L. equigenerosi
L. malefermentans
L. oryzae
L. kimchicus
L. paracollinoides
L. collinoides
L. similis
L. odoratitofui
L. silagei
L. pentosiphilus
L. silagincola
L. mixtipabuli
L. bambusae
L. spicheri
L. namurensis
L. suantsaii
L. acidifarinae
L. zymae
L. senmaizukei
L. tangyuanensis
L. hammesii
L. parabrevis
L. fuyuanensis
L. lindianensis
L. paucivorans
L. huananensis
L. koreensis
L. fujinensis
L. brevis
L. yonginensis
L. suantsaiihabitans
L. cerevisiae
L. mulengensis
L. fructivorans
L. florum
L. lindneri
L. sanfranciscensis
L. jinshani
L. ozensis
L. kunkeei
L. apinorum
L. quenuiae
L. timberlakei
L. kosoi
L. micheneri
L. senioris
L. curieae
L. parafarraginis
L. hilgardii
L. farraginis
L. raoultii
L. diolivorans
L. kisonensis
L. rapi
L. parabuchneri
L. sunkii
L. kefiri
L. otakiensis
L. buchneri
L. parakefiri
25
67
38
54
68
48
57
33
80
45
38
47


Pairwise cAAI (%)
100
90
80
70
60
50
Intra-family *Leuconostocaceae* (n=595)
Intra-family *Lactobacillaceae* (n=29646)
inter-family *Lactobacillaceae vs. Leuconostocaceae* (n=8541)


1.0
0.8
0.6
0.4
0.2
0.0
cumulative frequency [-]
60
70
80
90
100
% cAmino Acid Identity of pairwise comparisons
Leuconostoc (n=66)
Weissella (n=91)
Pediococcus (n=45)
proposed 25 genera *Lactobacillus* (n=2057)
Inter-genus *Lactobacillus* proposed (n=26218)
Intra-genus *Lactobacillus* current (n=34517)


Weissella
Oenococcus
Convivina
Fructobacillus
Leuconostoc
Lentilactobacillus
Secundilactobacillus
Levilactobacillus
Fructilactobacillus
Acetilactobacillus
Apilactobacillus
Limosilactobacillus
Paucilactobacillus
Furfurilactobacillus
Lactiplantibacillus
Pediococcus
Ligilactobacillus
Liquorilactobacillus
Dellaglioa
Loigolactobacillus
Paralactobacillus
Latilactobacillus
Lacticaseibacillus
Agrilactobacillus
Schleiferilactobacillus
Lapidilactobacillus
Companilactobacillus
Bombilactobacillus
Lactobacillus
Amylolactobacillus
Holzapfelia
70
80
90
100
Pairwise intra-genus cAAI (%)


75
50
25
0
Lactobacillus buchneri
Lactobacillus parakefiri
Lactobacillus otakiensis
Lactobacillus sunkii
Lactobacillus kefiri
Lactobacillus parabuchneri
Lactobacillus kisonensis
Lactobacillus rapi
Lactobacillus diolivorans
Lactobacillus farraginis
Lactobacillus raoultii
Lactobacillus hilgardii
Lactobacillus parafarraginis
Unassig. species 1
Lactobacillus curieae
Lactobacillus senioris
Lactobacillus kunkeei
Unassig. species 5
Lactobacillus apinorum
Unassig. species 11
Lactobacillus timberlakei
Lactobacillus quenuiae
Lactobacillus ozensis
Lactobacillus sanfranciscensis
Lactobacillus lindneri
Lactobacillus florum
Lactobacillus fructivorans
Unassig. species 2
Lactobacillus brevis
Lactobacillus koreensis
Lactobacillus parabrevis
Lactobacillus hammesii
Lactobacillus paucivorans
Lactobacillus senmaizukei
Lactobacillus spicheri
Lactobacillus namurensis
Lactobacillus zymae
Lactobacillus acidifarinae
Lactobacillus bambusae
Lactobacillus mixtipabuli
Lactobacillus silagincola
Lactobacillus pentosiphilus
Lactobacillus silagei
Lactobacillus odoratitofui
Lactobacillus similis
Lactobacillus paracollinoides
Lactobacillus collinoides
Lactobacillus kimchicus
Lactobacillus malefermentans
Lactobacillus oryzae
Lactobacillus plantarum
Lactobacillus paraplantarum
Lactobacillus pentosus
Lactobacillus herbarum
Lactobacillus xiangfangensis
Unassig. species 8
Unassig. species 9
Lactobacillus fabifermentans
Leuconostoc citreum
Leuconostoc lactis
Leuconostoc kimchii
Leuconostoc gelidum
Leuconostoc carnosum
Leuconostoc mesenteroides
Leuconostoc pseudomesenteroides
Leuconostoc fallax
Fructobacillus tropaeoli
Fructobacillus pseudoficulneus
Fructobacillus ficulneus
Fructobacillus fructosus
Fructobacillus durionis
Convivina intestini
Oenococcus oeni
Oenococcus kitaharae
Weissella hellenica
Unassig. species 14
Unassig. species 13
Weissella paramesenteroides
Weissella thailandensis
Weissella cibaria
Weissella confusa
Weissella halotolerans
Weissella ceti
Weissella viridescens
Weissella minor
Weissella oryzae
Weissella koreensis
Weissella kandleri
Weissella soli
Lactobacillus rossiae
Lactobacillus siliginis
Lactobacillus antri
Lactobacillus oris
Lactobacillus panis
Lactobacillus pontis
Unassig. species 7
Lactobacillus reuteri
Unassig. species 16
Lactobacillus vaginalis
Lactobacillus frumenti
Lactobacillus fermentum
Lactobacillus gorillae
Lactobacillus gastricus
Lactobacillus equigenerosi
Lactobacillus coleohominis
Lactobacillus secaliphilus
Lactobacillus ingluviei
Lactobacillus mucosae
'Lactobacillus timonensis'
Lactobacillus suebicus
Lactobacillus vaccinostercus
Lactobacillus hokkaidonensis
Lactobacillus wasatchensis
Lactobacillus oligofermentans
Pediococcus pentosaceus
Pediococcus stilesii
Pediococcus acidilactici
Pediococcus claussenii
Pediococcus argentinicus
Pediococcus ethanolidurans
Pediococcus parvulus
Pediococcus cellicola
Pediococcus damnosus
Pediococcus inopinatus
Lactobacillus murinus
Lactobacillus animalis
Lactobacillus apodemi
Lactobacillus ruminis
Unassig. species 15
Lactobacillus equi
Lactobacillus agilis
Lactobacillus pobuzihii
Lactobacillus acidipiscis
Lactobacillus araffinosus
Lactobacillus aviarius
Lactobacillus salivarius
Lactobacillus hayakitensis
Lactobacillus ceti
Lactobacillus saerimneri
Lactobacillus hordei
Lactobacillus mali
Lactobacillus cacaonum
Lactobacillus satsumensis
Lactobacillus oeni
Lactobacillus uvarum
Lactobacillus aquaticus
Lactobacillus sucicola
Lactobacillus capillatus
Lactobacillus nagelii
Lactobacillus ghanensis
Lactobacillus vini
Lactobacillus algidus
Lactobacillus kimbladii
Lactobacillus kullabergensis
Lactobacillus melliventris
Lactobacillus helsingborgensis
Lactobacillus bombicola
Unassig. species 12
Lactobacillus panisapium
Lactobacillus apis
Lactobacillus acetotolerans
Lactobacillus amylovorus
Lactobacillus kitasatonis
Lactobacillus ultunensis
Lactobacillus kefiranofaciens
Lactobacillus helveticus
Lactobacillus gallinarum
Lactobacillus acidophilus
Lactobacillus crispatus
Lactobacillus intestinalis
Lactobacillus amylolyticus
Lactobacillus kalixensis
Lactobacillus hamsteri
Unassig. species 6
Lactobacillus gigeriorum
Lactobacillus pasteurii
Lactobacillus delbrueckii
Lactobacillus equicursoris
Unassig. species 3
Unassig. species 4
Lactobacillus jensenii
Lactobacillus psittaci
Lactobacillus gasseri
Lactobacillus taiwanensis
Lactobacillus johnsonii
Lactobacillus hominis
Lactobacillus rodentium
Lactobacillus iners
Lactobacillus amylophilus
Lactobacillus floricola
Lactobacillus nantensis
Unassig. species 10
Lactobacillus heilongjiangensis
Lactobacillus mindensis
Lactobacillus kimchiensis
Lactobacillus nuruki
Lactobacillus crustorum
Lactobacillus musae
Lactobacillus formosensis
Lactobacillus futsaii
Lactobacillus farciminis
Lactobacillus paralimentarius
Lactobacillus kimchii
Lactobacillus alimentarius
Lactobacillus nodensis
Lactobacillus allii
Lactobacillus tucceti
Lactobacillus ginsenosidimutans
Lactobacillus versmoldensis
Lactobacillus metriopterae
Lactobacillus mellis
Lactobacillus bombi
Lactobacillus mellifer
Lactobacillus concavus
Lactobacillus dextrinicus
Lactobacillus shenzhenensis
Lactobacillus harbinensis
Lactobacillus perolens
Lactobacillus composti
Lactobacillus rhamnosus
Lactobacillus casei
Lactobacillus paracasei
Lactobacillus nasuensis
Lactobacillus manihotivorans
Lactobacillus camelliae
Lactobacillus brantae
Lactobacillus saniviri
Lactobacillus pantheris
Lactobacillus thailandensis
Lactobacillus sharpeae
Lactobacillus curvatus
Lactobacillus graminis
Lactobacillus sakei
Lactobacillus fuchuensis
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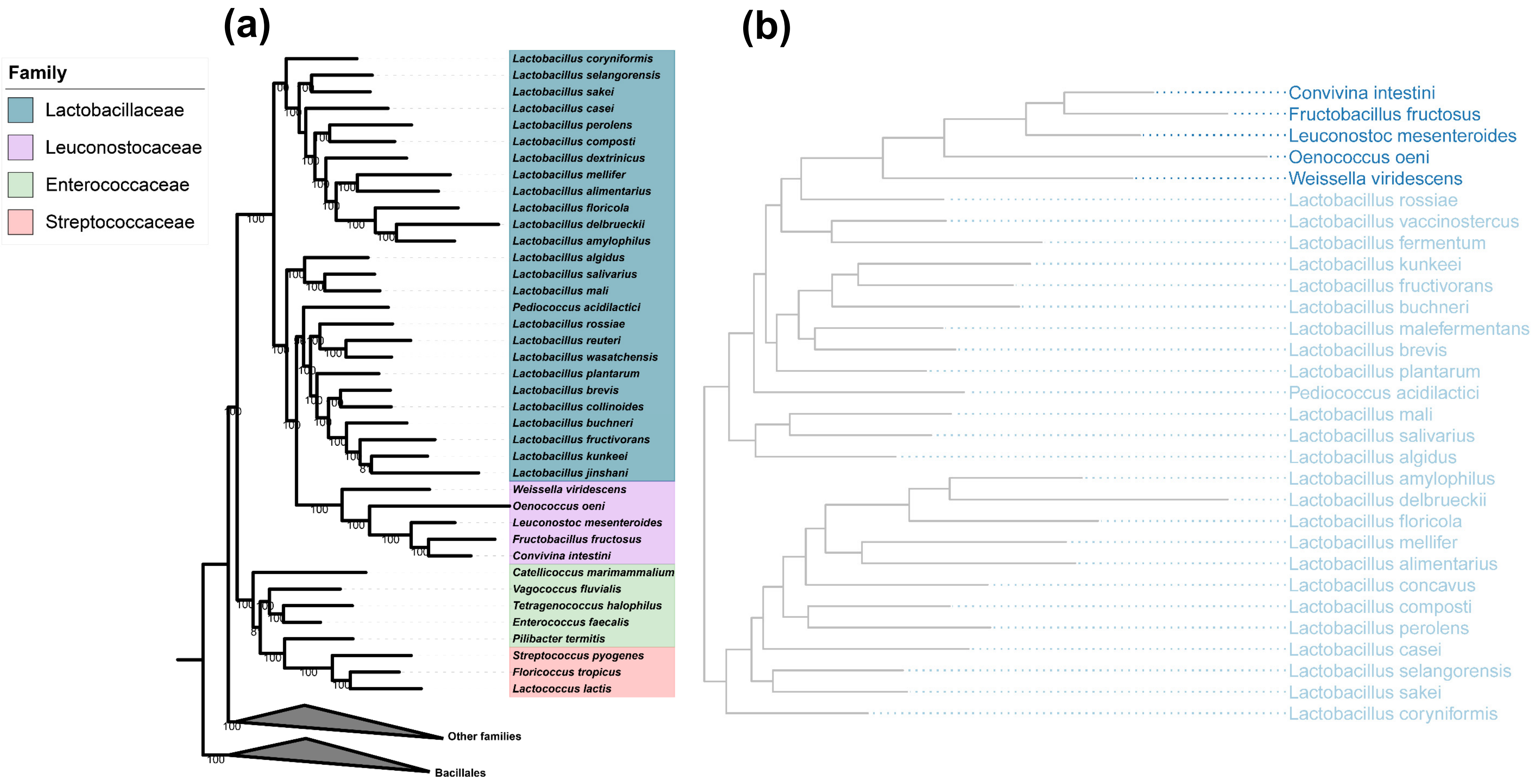
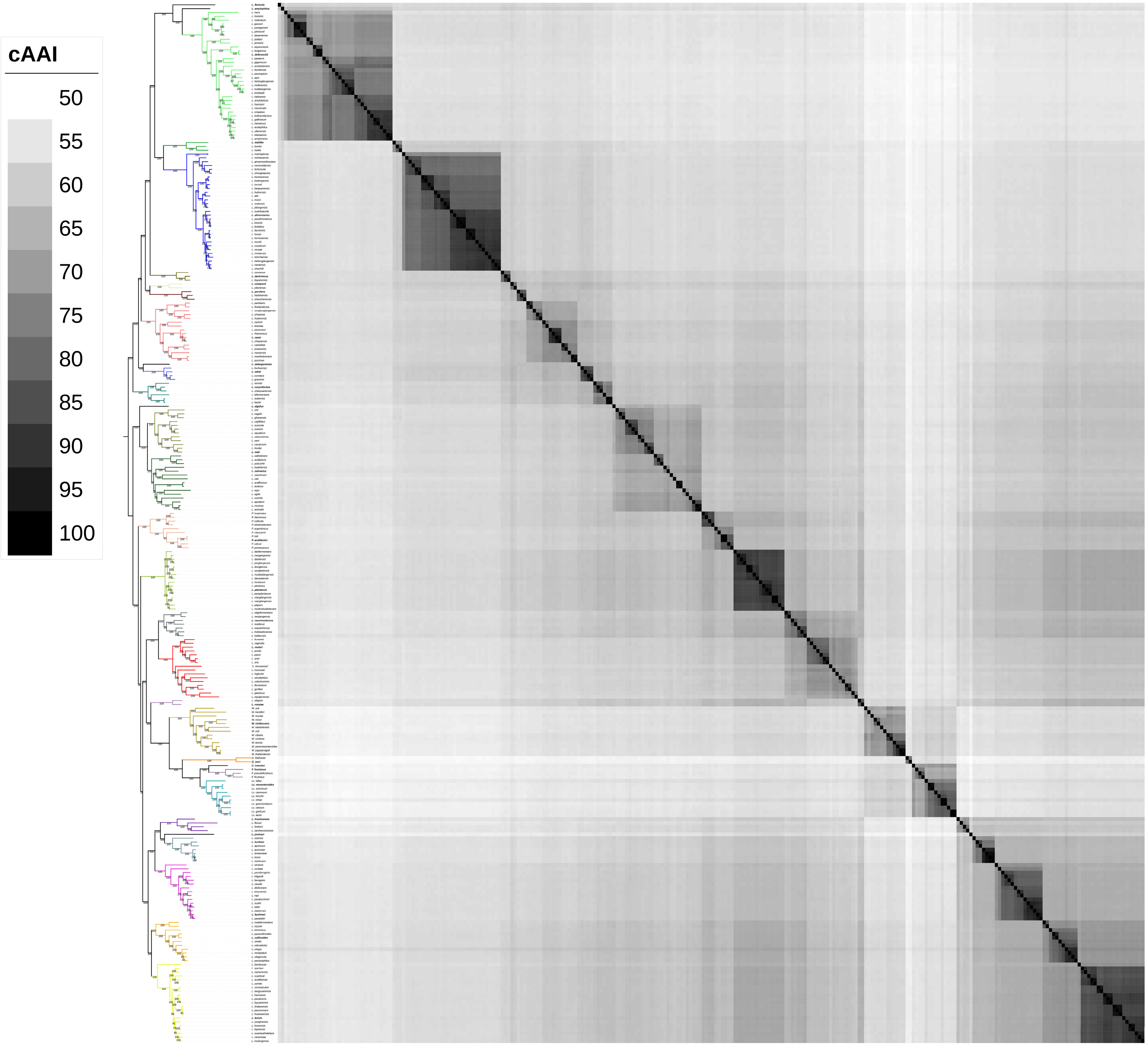
Lactobacillus coryniformis
Lactobacillus rennini
Lactobacillus bifermentans
Lactobacillus backii


(a)
(b)
Family
Lactobacillaceae
Leuconostocaceae
Enterococcaceae
Streptococcaceae
Lactobacillus coryniformis
Lactobacillus selangorensis
Lactobacillus sakei
Lactobacillus casei
Lactobacillus perolens
Lactobacillus composti
Lactobacillus dextrinicus
Lactobacillus mellifer
Lactobacillus alimentarius
Lactobacillus floricola
Lactobacillus delbrueckii
Lactobacillus amylophilus
Lactobacillus algidus
Lactobacillus salivarius
Lactobacillus mali
Pediococcus acidilactici
Lactobacillus rossiae
Lactobacillus reuteri
Lactobacillus wasatchensis
Lactobacillus plantarum
Lactobacillus brevis
Lactobacillus collinoides
Lactobacillus buchneri
Lactobacillus fructivorans
Lactobacillus kunkeei
Lactobacillus jinshani
Weissella viridescens
Oenococcus oeni
Leuconostoc mesenteroides
Fructobacillus fructosus
Convivina intestini
Catellicoccus marimammalium
Vagococcus fluvialis
Tetragenococcus halophilus
Enterococcus faecalis
Pilibacter termitis
Streptococcus pyogenes
Floricoccus tropicus
Lactococcus lactis
Other families
Bacillales
Convivina intestini
Fructobacillus fructosus
Leuconostoc mesenteroides
Oenococcus oeni
Weissella viridescens
Lactobacillus rossiae
Lactobacillus vaccinostercus
Lactobacillus fermentum
Lactobacillus kunkeei
Lactobacillus fructivorans
Lactobacillus buchneri
Lactobacillus malefermentans
Lactobacillus brevis
Lactobacillus plantarum
Pediococcus acidilactici
Lactobacillus mali
Lactobacillus salivarius
Lactobacillus algidus
Lactobacillus amylophilus
Lactobacillus delbrueckii
Lactobacillus floricola
Lactobacillus mellifer
Lactobacillus alimentarius
Lactobacillus concavus
Lactobacillus composti
Lactobacillus perolens
Lactobacillus casei
Lactobacillus selangorensis
Lactobacillus sakei
Lactobacillus coryniformis


cAAI
50
55
60
65
70
75
80
85
90
95
100

A taxonomic note on the genus *Lactobacillus*: Description of 24 novel genera, emended description of the genus *Lactobacillus* Beijerinck 1901, and union of *Lactobacillaceae* and *Leuconostocaceae*

Jinshui Zheng[1,$], Stijn Wittouck[2,$], Elisa Salvetti[3, $], Charles M.A.P. Franz[4], Hugh M.B. Harris[5], Paola Mattarelli[6], Paul O'Toole[5], Bruno Pot[7], Peter Vandamme[8], Jens Walter[9, 10], Koichi Watanabe[11, 12], Sander Wuyts[2], Giovanna E. Felis[3, #*], Michael G. Gänzle[9, 13#*], Sarah Lebeer[2 #]

Online supplementary figures and tables.

Table S1. List of species and subspecies of *Lactobacillaceae* and *Leuconostocaceae* that were included in analyses. Lister are the type strains, the lifestyle of the organisms, accession numbers for genome sequence data and 16S rRNA sequence data, and the proposed new taxonomic position.

The file listing all species in the Lactobacillaceae is also available on https://site.unibo.it/subcommittee-lactobacillus-bifidobacterium/en; the file hosted on the website will be periodically updated by adding new species that have been validly published.

Table S2. Genomes used for the iqtree phylogenetic analysis and the gene presence/absence analyses.

Table S3. Pairwise comparison of cAAI values of species in the *Lactobacillaceae* and *Leuconostocaceae***.**

Table S4. Pairwise comparison of AAI values of species in the *Lactobacillaceae* and *Leuconostocaceae***.**

Table S5. Signature genes and number of species of phylogroups.

Figure S1. Box plot of intra-family and inter-family AAI values in the families *Leuconostocaceae* and *Lactobacillaceae*.

Figure S2. Frequency distribution of pairwise amino acid identity (AAI) in *Lactobacillaceae* and *Leuconostocaceae*.

Figure S3. Range of pairwise intra-genus amino acid identity (AAI) values for all proposed genera in the families *Lactobacillaceae* and *Leuconostocaceae*.

Figure S4. Full phylogenetic species tree of *Lactobacillaceae*, *Leuconostocaceae* and outgroups. The figure is provided as separate image file.

Figure S5. Core genome phylogenetic tree of *Lactobacillaceae* and *Leuconostococaceae*. The figure is provided as separate image file.

Figure S6. Phylogenetic tree on the basis of 16S rRNA gene sequences of the proposed species of *Lactobacillaceae* with three or more species.

Figure S7. Top amino acid identity (AAI) values of genomes to genera.

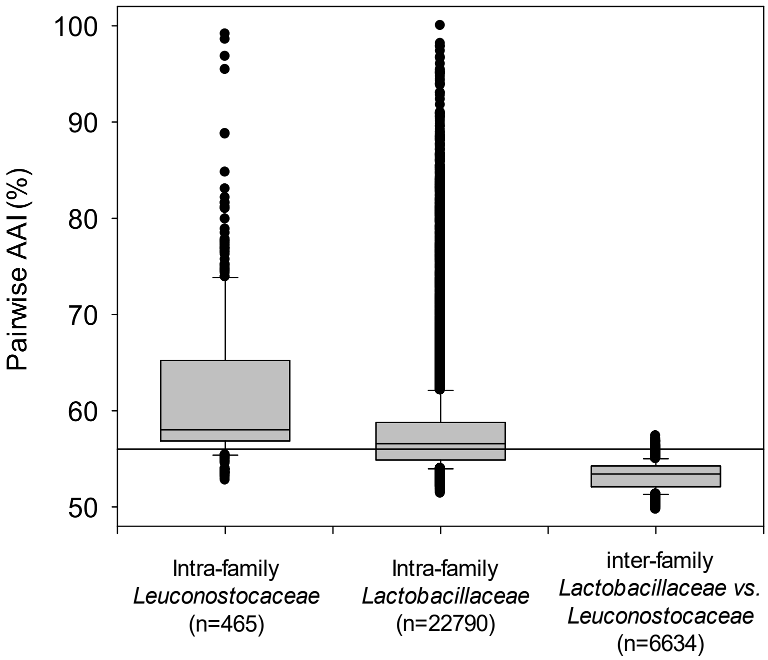


Figure S1. Box plot of intra-family and inter-family AAI values in the families *Leuconostocaceae* and *Lactobacillaceae*. The analysis was performed with genome sequence data that was available in May 2019. The reference line is drawn at an AAI of 56%.

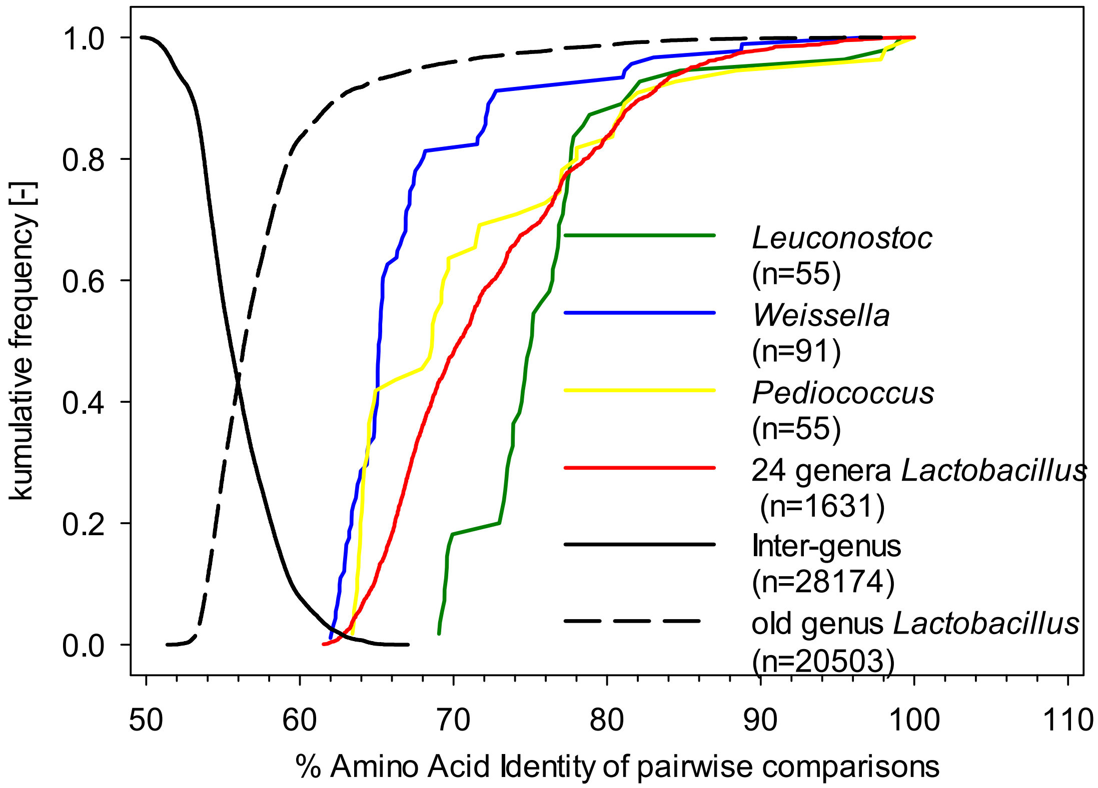


Figure S2. Frequency distribution of pairwise amino acid identity (AAI) in *Lactobacillaceae* and *Leuconostocaceae*. Inter-genus AAI values are shown in descending order; Intra-genus AAI values are shown in ascending order for the current taxonomy (dotted lines) and for the proposed taxonomy that divides the genus *Lactobacillus* in 24 genera (solid lines). All genomes that were available in May 2019 were used for the analysis, excluding *L. jinshani* (proposed genus *Acetilactobacillus*). Genera are color coded; *Lactobacillus*; *Pediococcus*, *Leuconostoc*, and *Weissella*. The number of pairwise AAI values that is represented by the lines is indicated in the figure legend. Owing to the low number of values, intra-genus AAI values for *Fructobacillus*, *Oenococcus* and *Convivina* are not shown. The data used for the graph is provided in online supplementary Table S4.

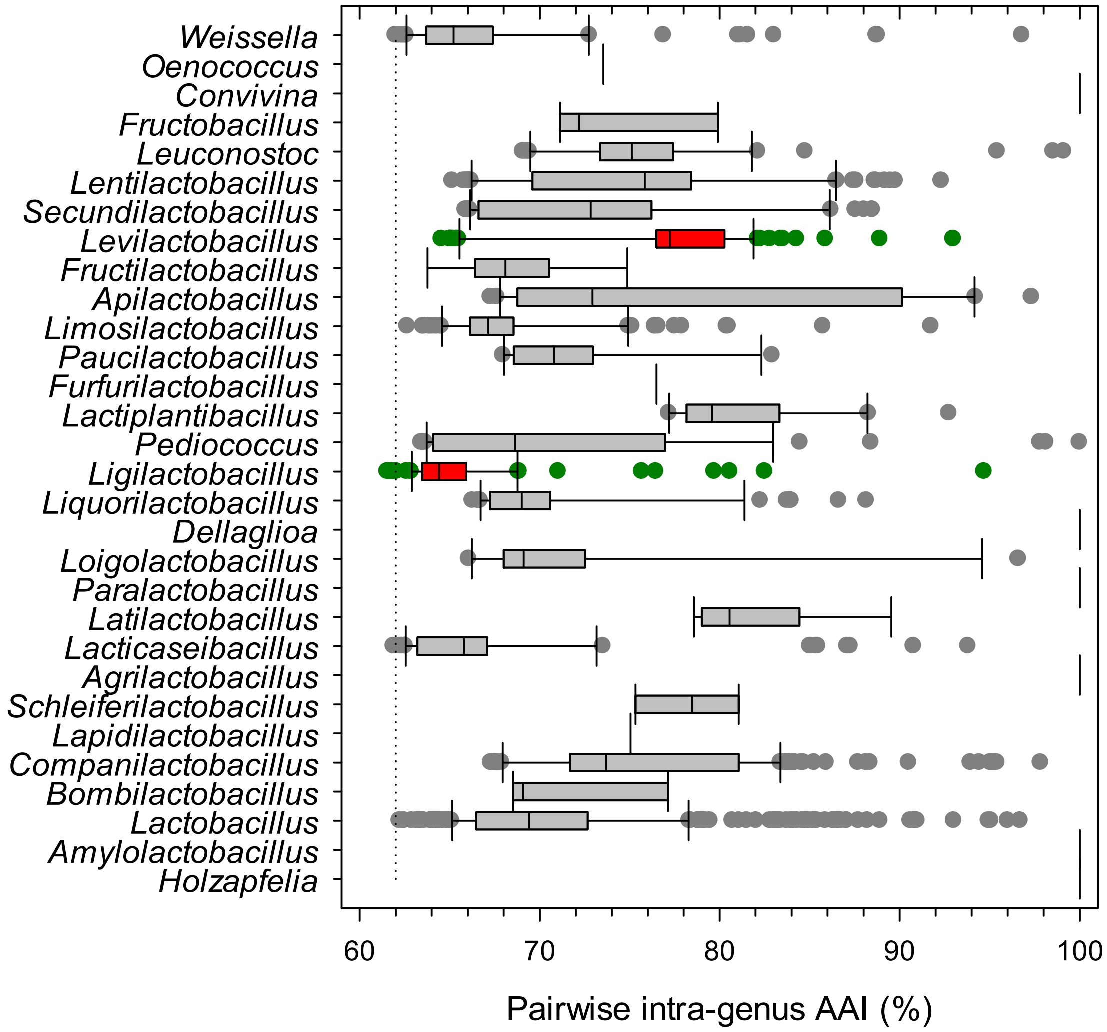


Figure S3. Range of pairwise intra-genus amino acid identity (AAI) values for all proposed genera in the families *Lactobacillaceae* and *Leuconostocaceae*. The dotted line designates the lowest AAI value for current genera excluding *Lactobacillus*. Bars and symbols are coloured gray if the genus is exclusive, i.e. if the lowest intra-genus AAI is higher than any inter-genus AAI of species in that genus. Bars and symbols are coloured red and green, respectively, if the genus is non-exclusive, i.e. if the lowest intra-genus AAI is lower than the highest intra-genus AAI of species in that genus. All genomes that were available in May 2019 were used for the analysis, excluding *L. jinshani* (proposed genus *Acetilactobacillus*). The data used for the graph is provided in online supplementary Table S3.

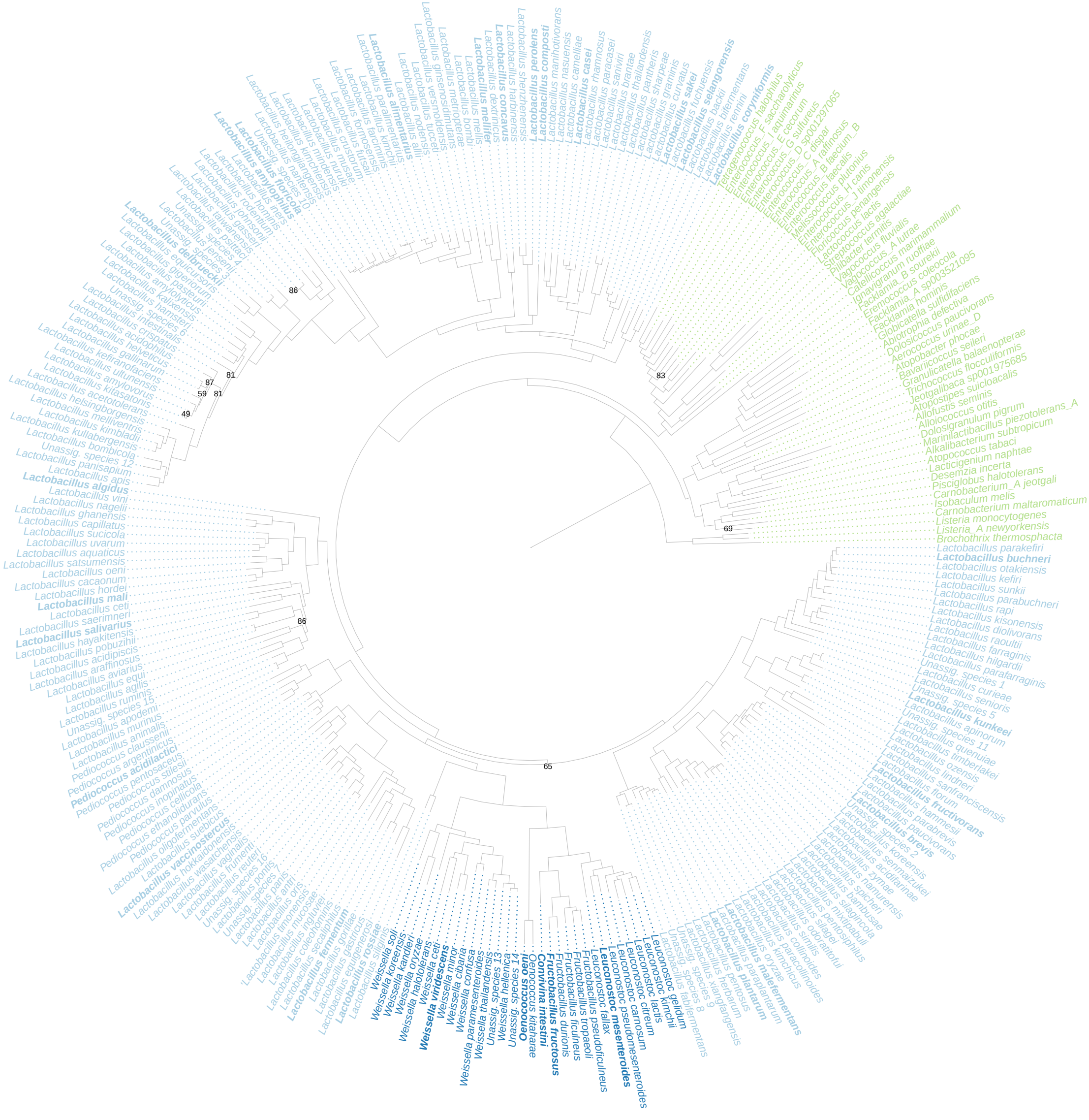

Lactobacillus parakefiri
Lactobacillus buchneri
Lactobacillus otakiensis
Lactobacillus kefiri
Lactobacillus sunkii
Lactobacillus parabuchneri
Lactobacillus rapi
Lactobacillus kisonensis
Lactobacillus diolivorans
Lactobacillus raoultii
Lactobacillus farraginis
Lactobacillus hilgardii
Lactobacillus parafarraginis
Unassig. species 1
Lactobacillus curieae
Lactobacillus senioris
Unassig. species 5
Lactobacillus kunkeei
Lactobacillus apinorum
Unassig. species 11
Lactobacillus quenuiae
Lactobacillus timberlakei
Lactobacillus ozensis
Lactobacillus lindneri
Lactobacillus sanfranciscensis
Lactobacillus florum
Lactobacillus fructivorans
Lactobacillus hammesii
Lactobacillus parabrevis
Lactobacillus paucivorans
Lactobacillus brevis
Unassig. species 2
Lactobacillus koreensis
Lactobacillus senmaizukei
Lactobacillus acidifarinae
Lactobacillus zymae
Lactobacillus namurensis
Lactobacillus spicheri
Lactobacillus bambusae
Lactobacillus silagincola
Lactobacillus mixtipabuli
Lactobacillus pentosiphilus
Lactobacillus silagei
Lactobacillus odoratitofui
Lactobacillus similis
Lactobacillus collinoides
Lactobacillus paracollinoides
Lactobacillus kimchicus
Lactobacillus oryzae
Lactobacillus paraplantarum
Lactobacillus malefermentans
Lactobacillus plantarum
Lactobacillus pentosus
Lactobacillus herbarum
Lactobacillus xiangfangensis
Unassig. species 9
Unassig. species 8
Lactobacillus fabifermentans
Leuconostoc gelidum
Leuconostoc kimchii
Leuconostoc lactis
Leuconostoc citreum
Leuconostoc carnosum
Leuconostoc pseudomesenteroides
Leuconostoc mesenteroides
Leuconostoc fallax
Lactobacillus pseudoficulneus
Fructobacillus tropaeoli
Fructobacillus ficulneus
Fructobacillus durionis
Fructobacillus fructosus
Convivina intestini
Oenococcus kitaharae
Oenococcus oeni
Unassig. species 14
Weissella hellenica
Unassig. species 13
Weissella thailandensis
Weissella paramesenteroides
Weissella confusa
Weissella cibaria
Weissella minor
Weissella viridescens
Weissella ceti
Weissella halotolerans
Weissella oryzae
Weissella kandleri
Weissella koreensis
Weissella soli
Lactobacillus siliginis
Lactobacillus rossiae
Lactobacillus equigenerosi
Lactobacillus gastricus
Lactobacillus gorillae
Lactobacillus fermentum
Lactobacillus secaliphilus
Lactobacillus coleohominis
Lactobacillus ingluviei
Lactobacillus mucosae
Lactobacillus timonensis
'Lactobacillus oris'
Lactobacillus antri
Lactobacillus panis
Unassig. species 7
Lactobacillus pontis
Unassig. species 16
Lactobacillus reuteri
Lactobacillus frumenti
Lactobacillus vaginalis
Lactobacillus wasatchensis
Lactobacillus hokkaidonensis
Lactobacillus vaccinostercus
Lactobacillus suebicus
Lactobacillus oligofermentans
Pediococcus parvulus
Pediococcus ethanolidurans
Pediococcus cellicola
Pediococcus inopinatus
Pediococcus damnosus
Pediococcus stilesii
Pediococcus pentosaceus
Pediococcus acidilactici
Pediococcus argentinicus
Pediococcus claussenii
Lactobacillus animalis
Lactobacillus murinus
Lactobacillus apodemi
Unassig. species 15
Lactobacillus ruminis
Lactobacillus agilis
Lactobacillus equi
Lactobacillus aviarius
Lactobacillus araffinosus
Lactobacillus acidipiscis
Lactobacillus pobuzihii
Lactobacillus hayakitensis
Lactobacillus salivarius
Lactobacillus saerimneri
Lactobacillus ceti
Lactobacillus mali
Lactobacillus hordei
Lactobacillus cacaonum
Lactobacillus oeni
Lactobacillus satsumensis
Lactobacillus aquaticus
Lactobacillus uvarum
Lactobacillus sucicola
Lactobacillus capillatus
Lactobacillus ghanensis
Lactobacillus nagelii
Lactobacillus vini
Lactobacillus algidus
Lactobacillus apis
Lactobacillus panisapium
Unassig. species 12
Lactobacillus bombicola
Lactobacillus kullabergensis
Lactobacillus kimbladii
Lactobacillus melliventris
Lactobacillus helsingborgensis
Lactobacillus acetotolerans
Lactobacillus kitasatonis
Lactobacillus amylovorus
Lactobacillus ultunensis
Lactobacillus kefiranofaciens
Lactobacillus gallinarum
Lactobacillus helveticus
Lactobacillus acidophilus
Lactobacillus crispatus
Lactobacillus intestinalis
Unassig. species 6
Lactobacillus hamsteri
Lactobacillus kalixensis
Lactobacillus amylolyticus
Lactobacillus pasteurii
Lactobacillus gigeriorum
Lactobacillus equicursoris
Lactobacillus delbrueckii
Unassig. species 3
Lactobacillus jensenii
Unassig. species 4
Lactobacillus psittaci
Lactobacillus taiwanensis
Lactobacillus gasseri
Lactobacillus johnsonii
Lactobacillus rodentium
Lactobacillus hominis
Lactobacillus iners
Lactobacillus amylophilus
Lactobacillus floricola
Unassig. species 10
Lactobacillus nantensis
Lactobacillus heilongjiangensis
Lactobacillus kimchiensis
Lactobacillus mindensis
Lactobacillus nuruki
Lactobacillus musae
Lactobacillus crustorum
Lactobacillus futsaii
Lactobacillus formosensis
Lactobacillus farciminis
Lactobacillus kimchii
Lactobacillus paralimentarius
Lactobacillus alimentarius
Lactobacillus allii
Lactobacillus nodensis
Lactobacillus tucceti
Lactobacillus versmoldensis
Lactobacillus ginsenosidimutans
Lactobacillus metriopterae
Lactobacillus bombi
Lactobacillus mellis
Lactobacillus mellifer
Lactobacillus dextrinicus
Lactobacillus concavus
Lactobacillus harbinensis
Lactobacillus shenzhenensis
Lactobacillus perolens
Lactobacillus composti
Lactobacillus manihotivorans
Lactobacillus nasuensis
Lactobacillus camelliae
Lactobacillus casei
Lactobacillus rhamnosus
Lactobacillus paracasei
Lactobacillus saniviri
Lactobacillus brantae
Lactobacillus thailandensis
Lactobacillus pantheris
Lactobacillus sharpeae
Lactobacillus graminis
Lactobacillus curvatus
Lactobacillus sakei
Lactobacillus fuchuensis
Lactobacillus selangorensis
Lactobacillus backii
Lactobacillus bifermentans
Lactobacillus rennini
Lactobacillus coryniformis
Tetragenococcus halophilus
Enterococcus_F saccharolyticus
Enterococcus_I aquimarinus
Enterococcus_E cecorum
Enterococcus_G sulfureus
Enterococcus_D sp001297065
Enterococcus_C dispar
Enterococcus_A raffinosus
Enterococcus_B faecium_B
Enterococcus faecalis
Melissococcus plutonius
Enterococcus_H canis
Enterococcus_J timonensis
Floricoccus penangensis
Lactococcus lactis
Streptococcus agalactiae
Pilibacter termitis
Vagococcus fluvialis
Vagococcus_A lutrae
Catellicoccus marimammalium
Ignavigranum ruoffiae
Facklamia_B sourekii
Eremococcus coleocola
Facklamia_A sp003521095
Facklamia hominis
Globicatella sulfidifaciens
Abiotrophia defectiva
Dolosicoccus paucivorans
Aerococcus urinae_D
Atopobacter phocae
Bavariicoccus seileri
Granulicatella balaenopterae
Trichococcus flocculiformis
Jeotgalibaca sp001975685
Atopostipes suicloacalis
Allofustis seminis
Alloiococcus otitis
Dolosigranulum pigrum
Marinilactibacillus piezotolerans_A
Alkalibacterium subtropicum
Atopococcus tabaci
Lacticigenium naphtae
Desemzia incerta
Pisciglobus halotolerans
Carnobacterium_A jeotgali
Isobaculum melis
Carnobacterium maltaromaticum
Listeria monocytogenes
Listeria_A newyorkensis
Brochothrix thermosphacta
86
81
87
59
81
49
86
83
69
65

Figure S4. Full phylogenetic species tree of *Lactobacillaceae*, *Leuconostocaceae* and outgroups. The tree was inferred on a protein supermatrix of 294 single-copy core genes, all of which were present in a single copy in at least 99% of the genomes. Bootstrap support values were calculated based on 1000 replicates; only support values of less than 90% are shown. Labels are colored according to the family of the species; light blue for *Lactobacillaceae*, dark blue for *Leuconostocaceae* and light green for the outgroup species (one for each genus of the order *Lactobacillales*). Type species of phylogroups are shown in bold.

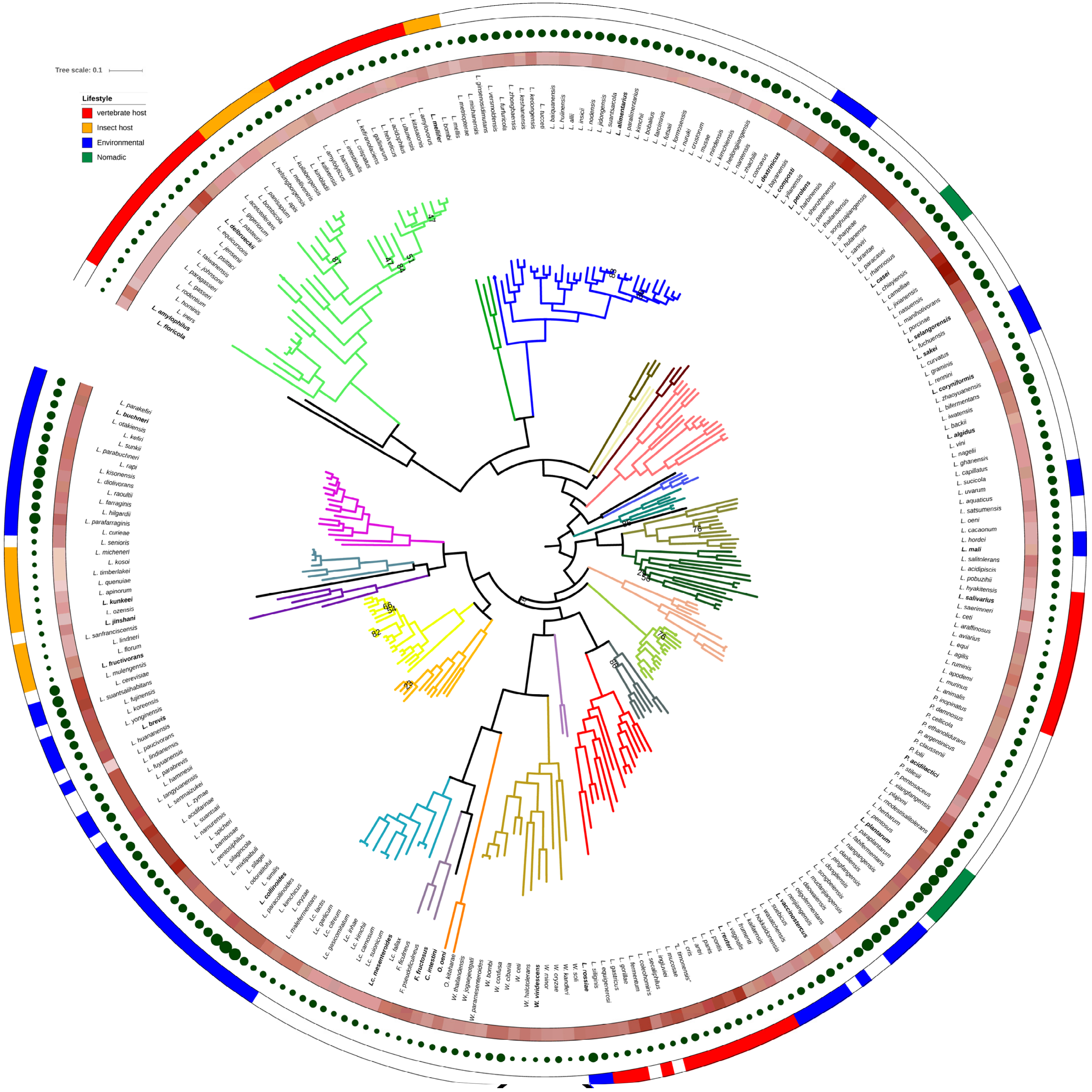

Tree scale: 0.1
Lifestyle
vertebrate host
Insect host
Environmental
Nomadic

Figure S5. Core genome phylogenetic tree of *Lactobacillaceae* and *Leuconostococaceae*. The phylogenomic analysis is based on the concatenated protein sequences of 101 single-copy core genes. The maximum likelihood tree was inferred by RAxML as described (12) using the 297 species for which genome sequence data was available on the NCBI database in August, 2019. All nodes have more than 92% bootstrap support. Members of the same phylogenetic group are indicated by the same color for branches, and the type strain of each group is printed in bold. Outer rings provide information on genomic features and the lifestyle of the species. The color gradient in red represents the GC content of each genome sequence; higher GC contents are indicated by darker shading. The solid circles in brown represent genome sizes; the area of the circle correlates with the genome size. The second ring indicates the natural habitats of the species as vertebrate host-adapted (red), insect-adapted (orange), nomadic (green), environmental (blue) or unassigned (white). The assignment of species to lifestyle was based on (11).

Fig. S6A

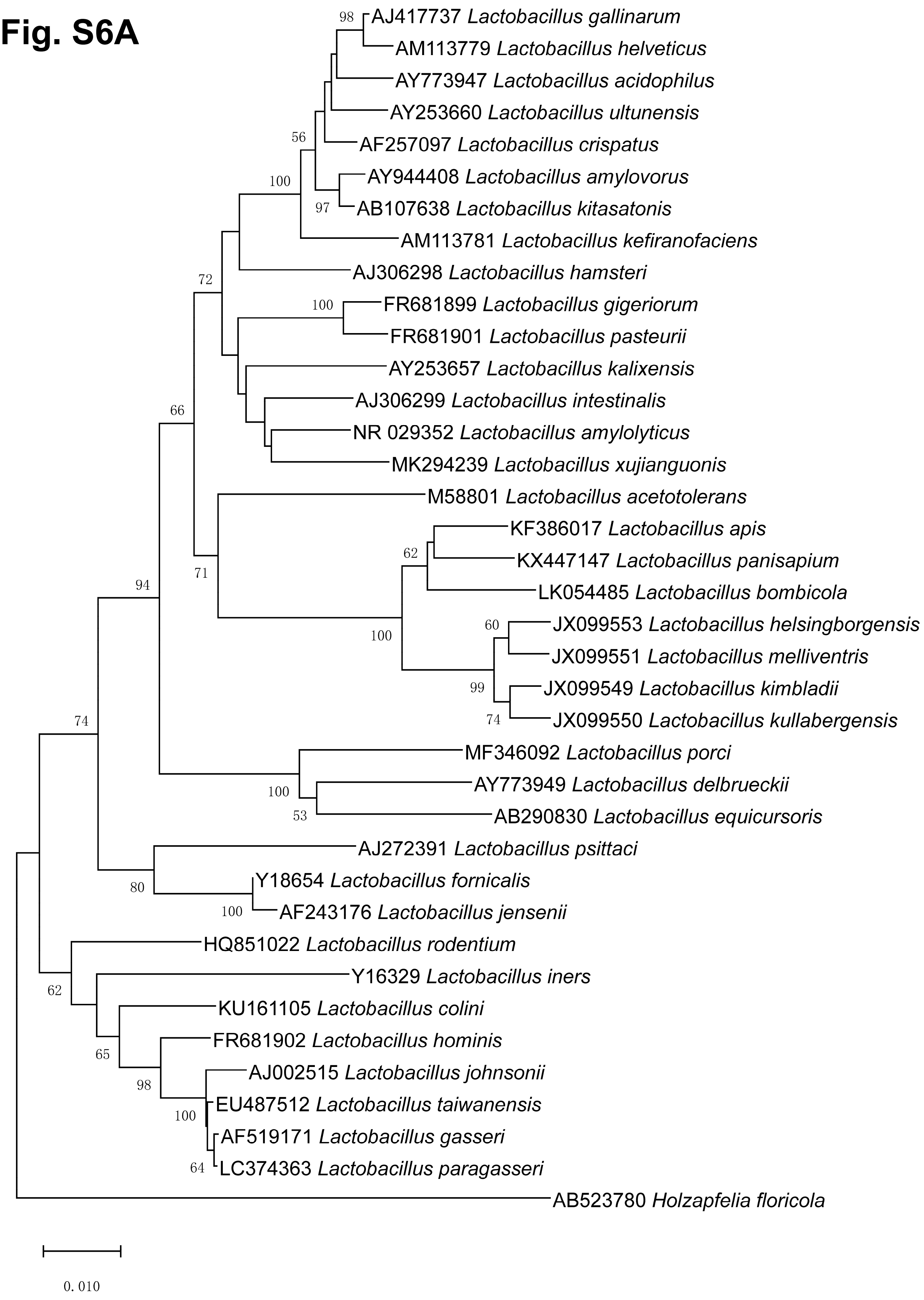

98
AJ417737 *Lactobacillus gallinarum*
AM113779 *Lactobacillus helveticus*
AY773947 *Lactobacillus acidophilus*
AY253660 *Lactobacillus ultunensis*
56
AF257097 *Lactobacillus crispatus*
100
AY944408 *Lactobacillus amylovorus*
97
AB107638 *Lactobacillus kitasatonis*
AM113781 *Lactobacillus kefiranofaciens*
AJ306298 *Lactobacillus hamsteri*
72
100
FR681899 *Lactobacillus gigeriorum*
FR681901 *Lactobacillus pasteurii*
AY253657 *Lactobacillus kalixensis*
66
AJ306299 *Lactobacillus intestinalis*
NR 029352 *Lactobacillus amylolyticus*
MK294239 *Lactobacillus xujianguonis*
M58801 *Lactobacillus acetotolerans*
KF386017 *Lactobacillus apis*
62
KX447147 *Lactobacillus panisapium*
94
71
LK054485 *Lactobacillus bombicola*
60
JX099553 *Lactobacillus helsingborgensis*
100
JX099551 *Lactobacillus melliventris*
99
JX099549 *Lactobacillus kimbladii*
74
74
JX099550 *Lactobacillus kullabergensis*
MF346092 *Lactobacillus porci*
AY773949 *Lactobacillus delbrueckii*
100
53
AB290830 *Lactobacillus equicursoris*
AJ272391 *Lactobacillus psittaci*
Y18654 *Lactobacillus fornicalis*
80
100
AF243176 *Lactobacillus jensenii*
HQ851022 *Lactobacillus rodentium*
Y16329 *Lactobacillus iners*
62
KU161105 *Lactobacillus colini*
FR681902 *Lactobacillus hominis*
65
AJ002515 *Lactobacillus johnsonii*
98
EU487512 *Lactobacillus taiwanensis*
100
AF519171 *Lactobacillus gasseri*
64
LC374363 *Lactobacillus paragasseri*
AB523780 *Holzapfelia floricola*
0.010

Fig. S6B

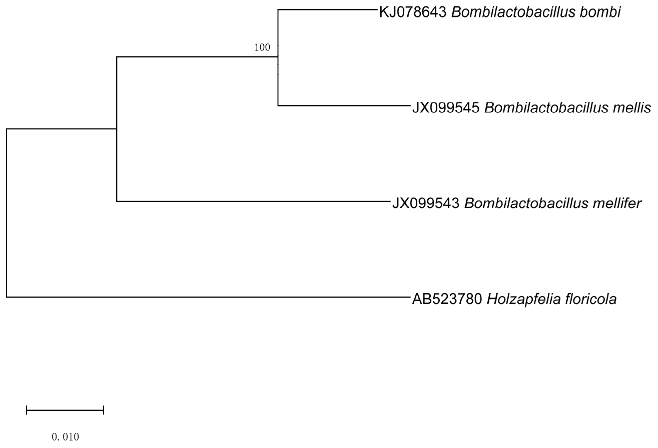


Fig. S6C

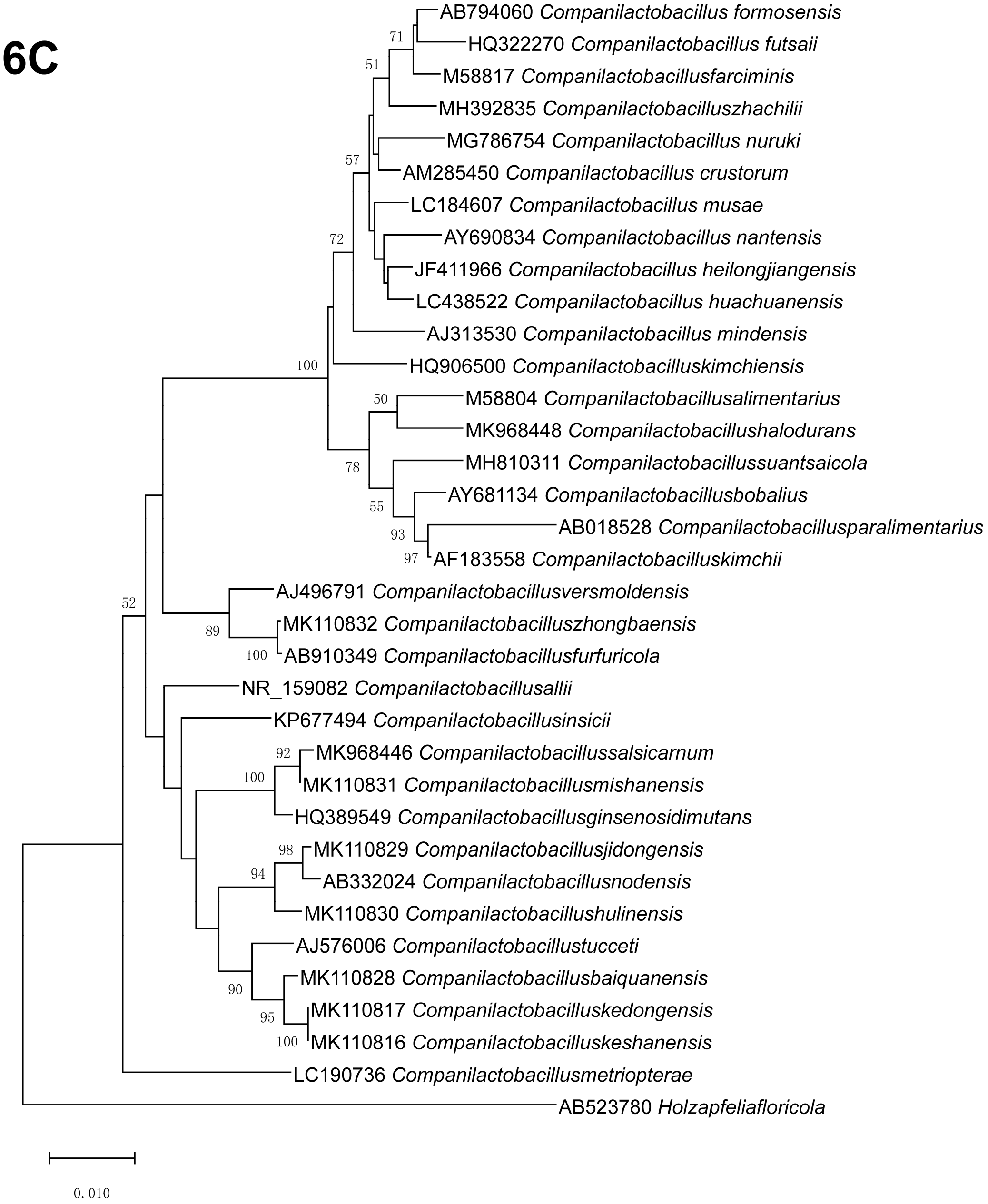


Fig. S6D

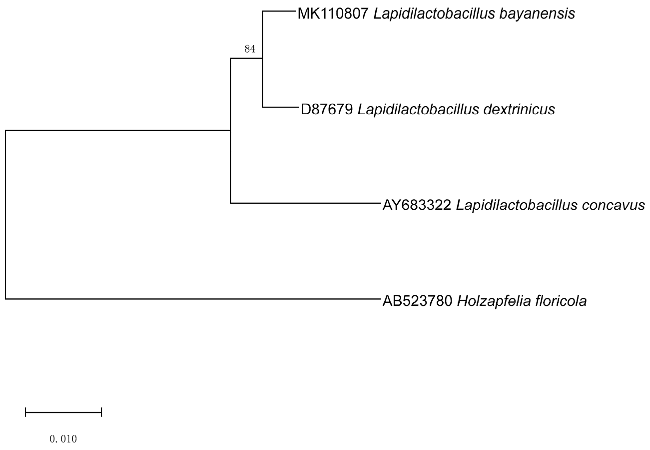


Fig. S6E

Fig. S6F

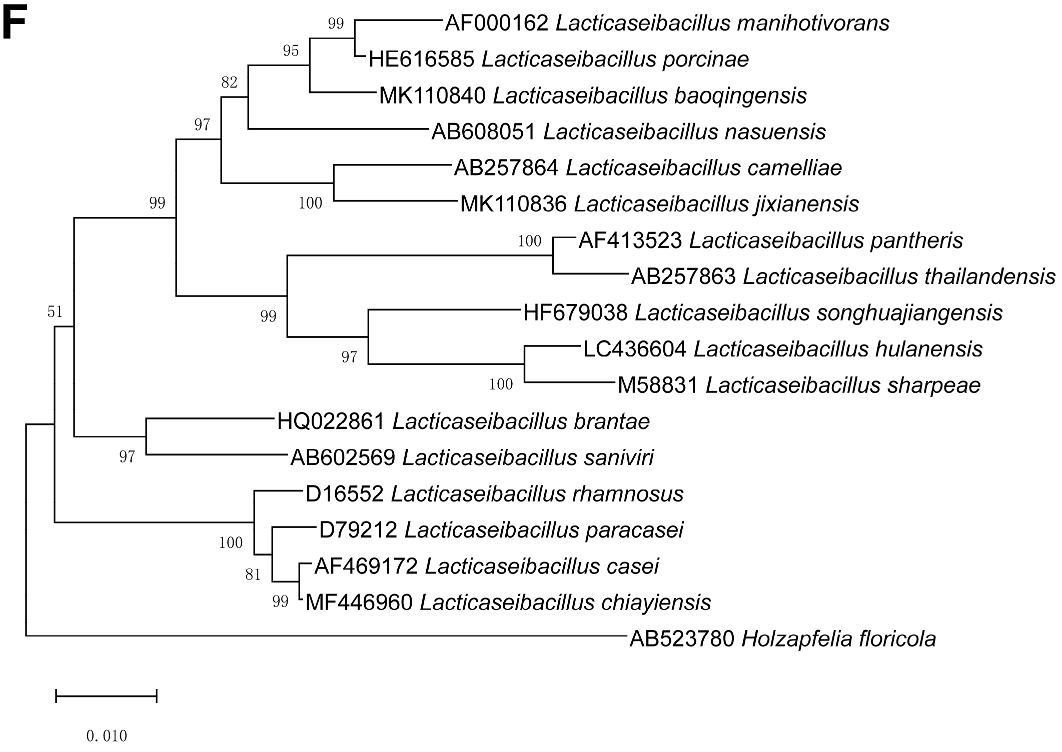


Fig. S6G

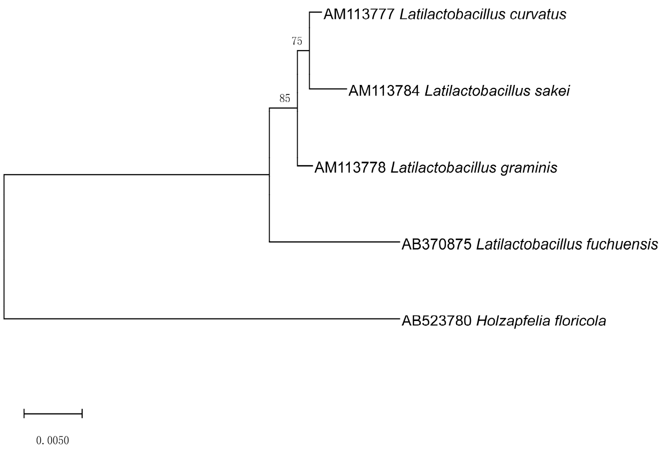


Fig. S6H

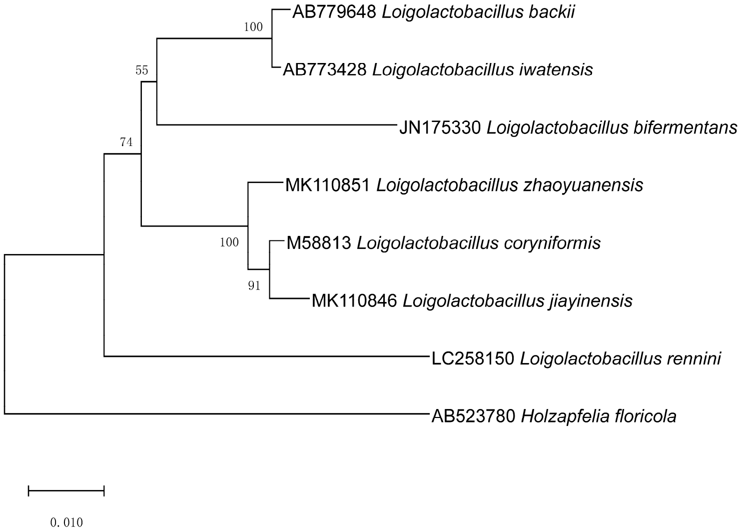


Fig. S6I

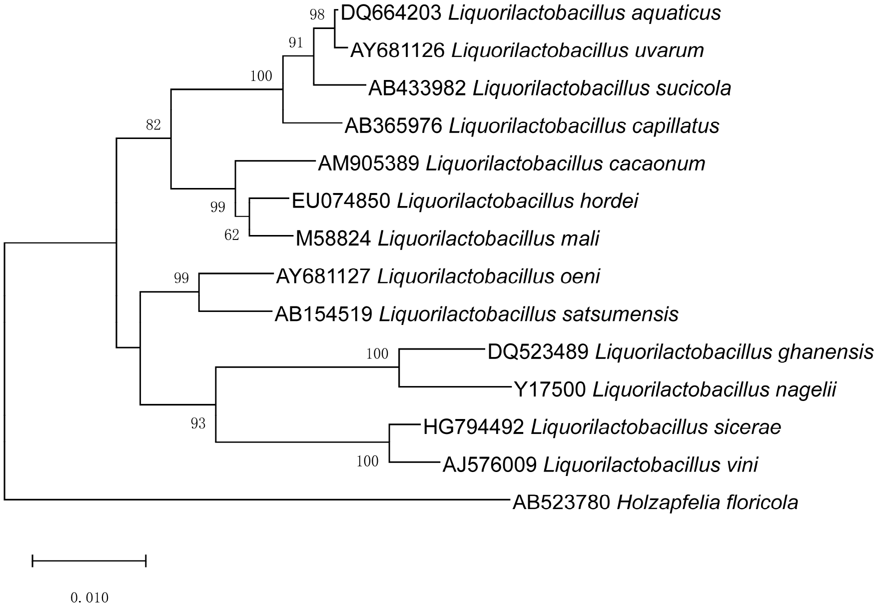


Fig. S6J

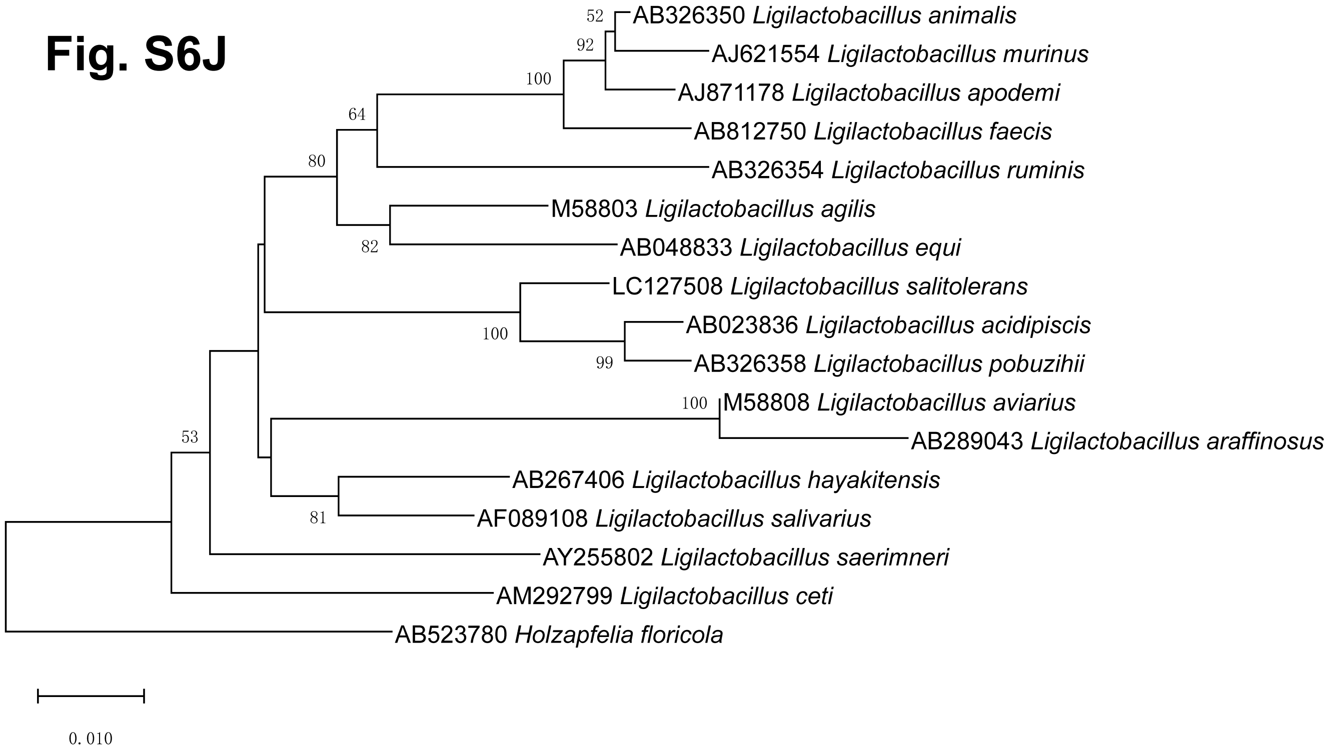


Fig. S6K

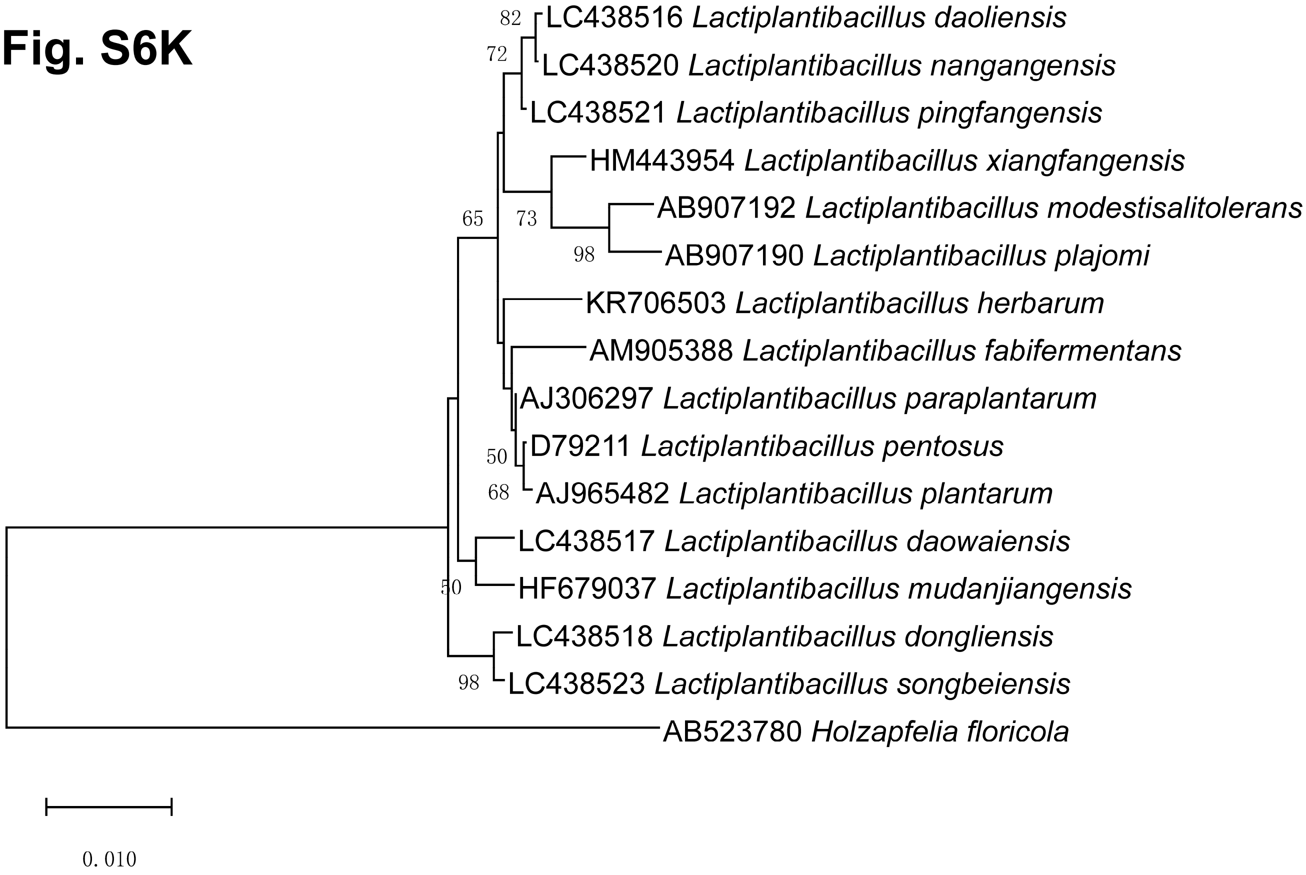


Fig. S6L

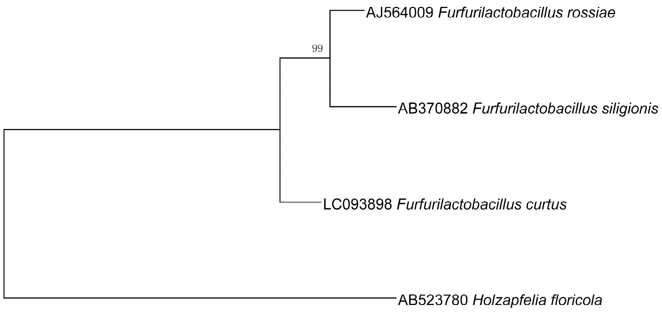


Fig. S6M

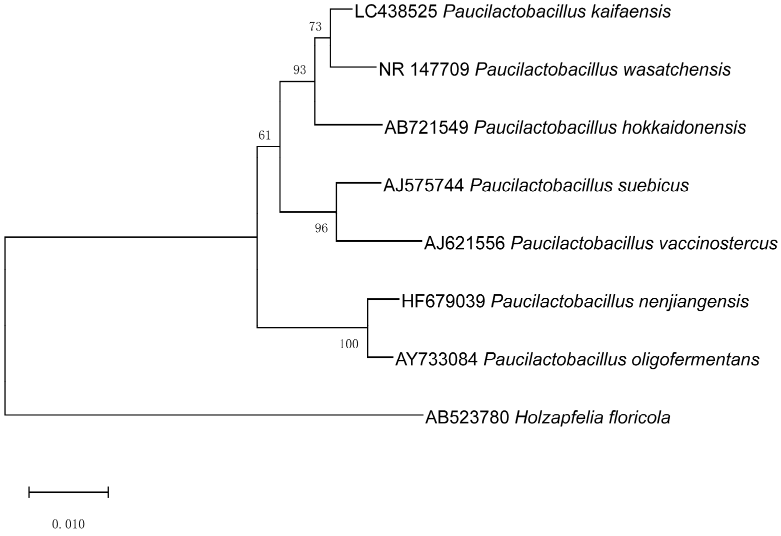


Fig. S6N

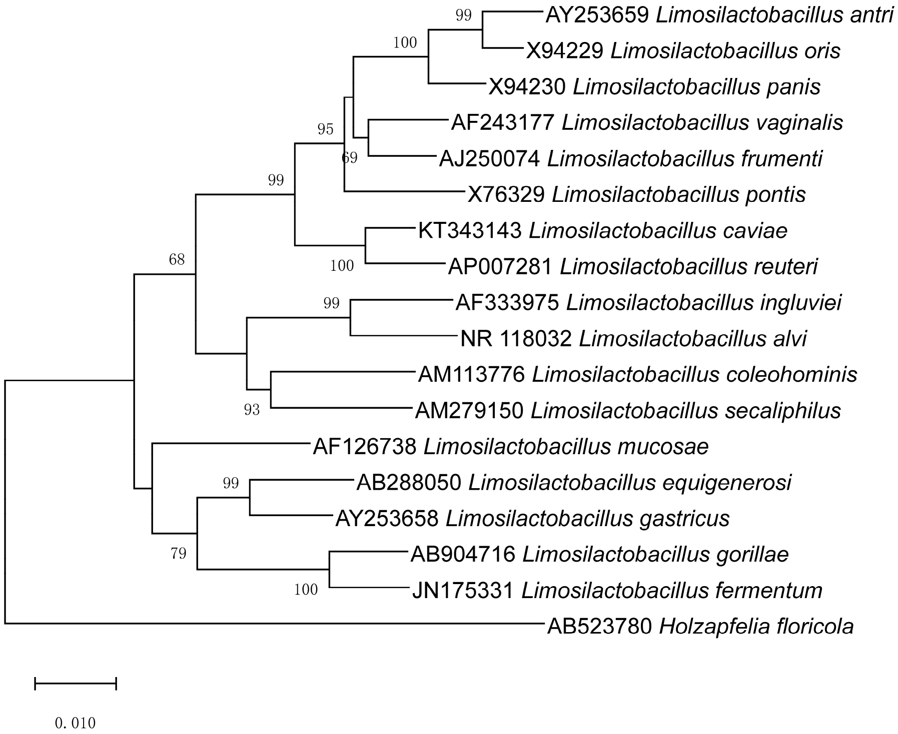


Fig. S6O

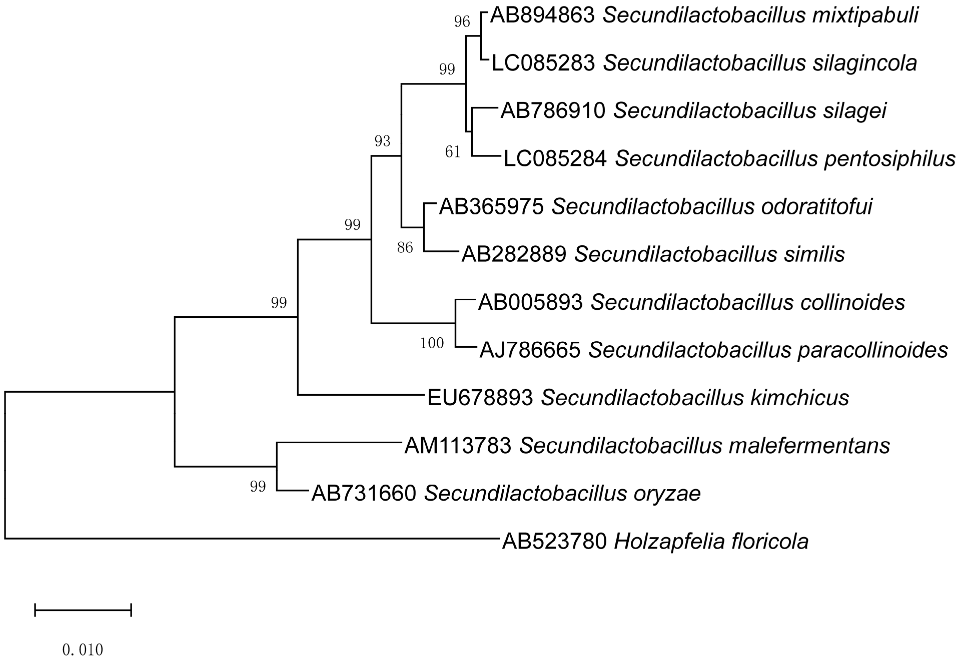


Fig. S6P

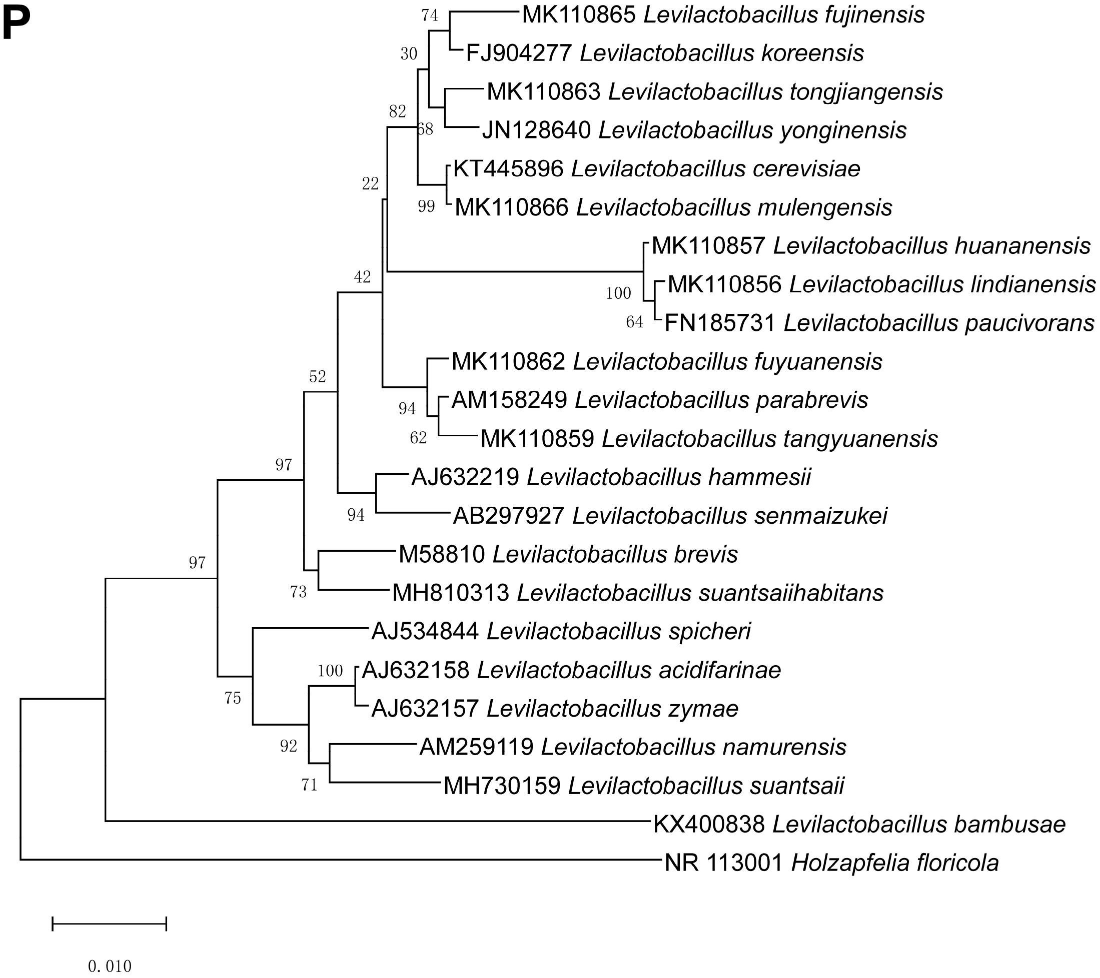


Fig. S6Q

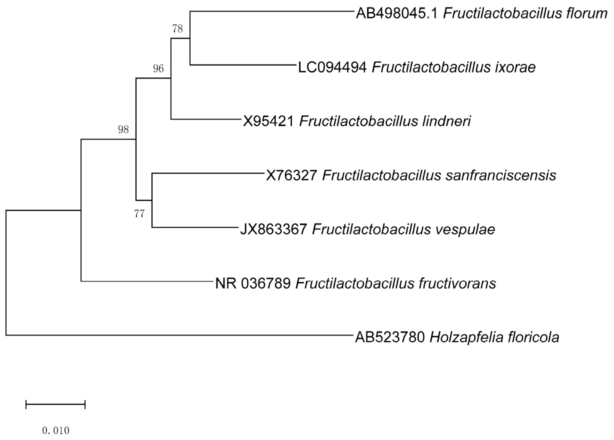


Fig. S6R

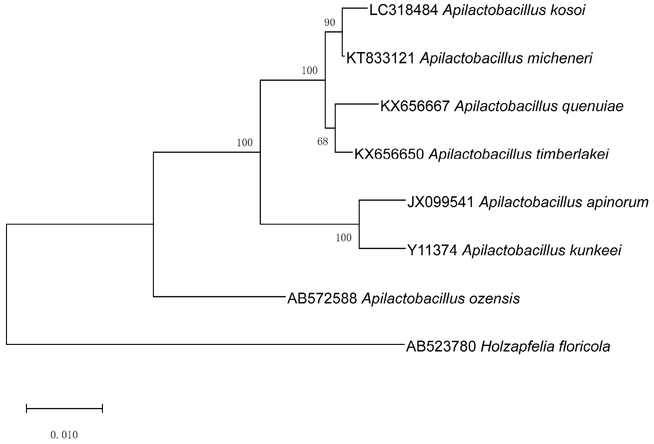


Fig. S6S

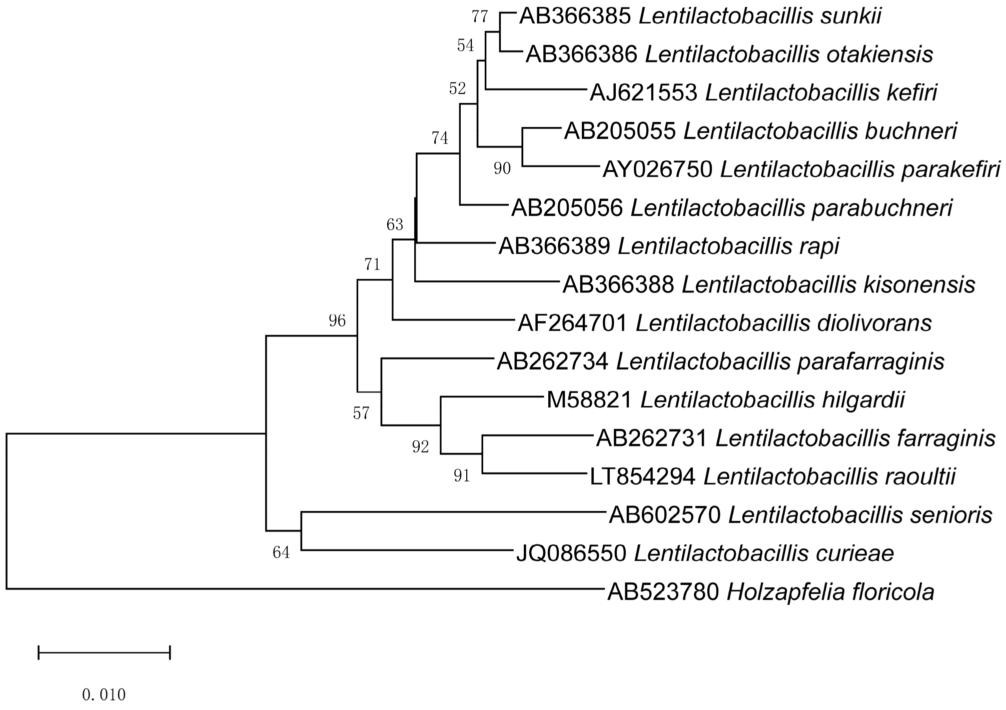
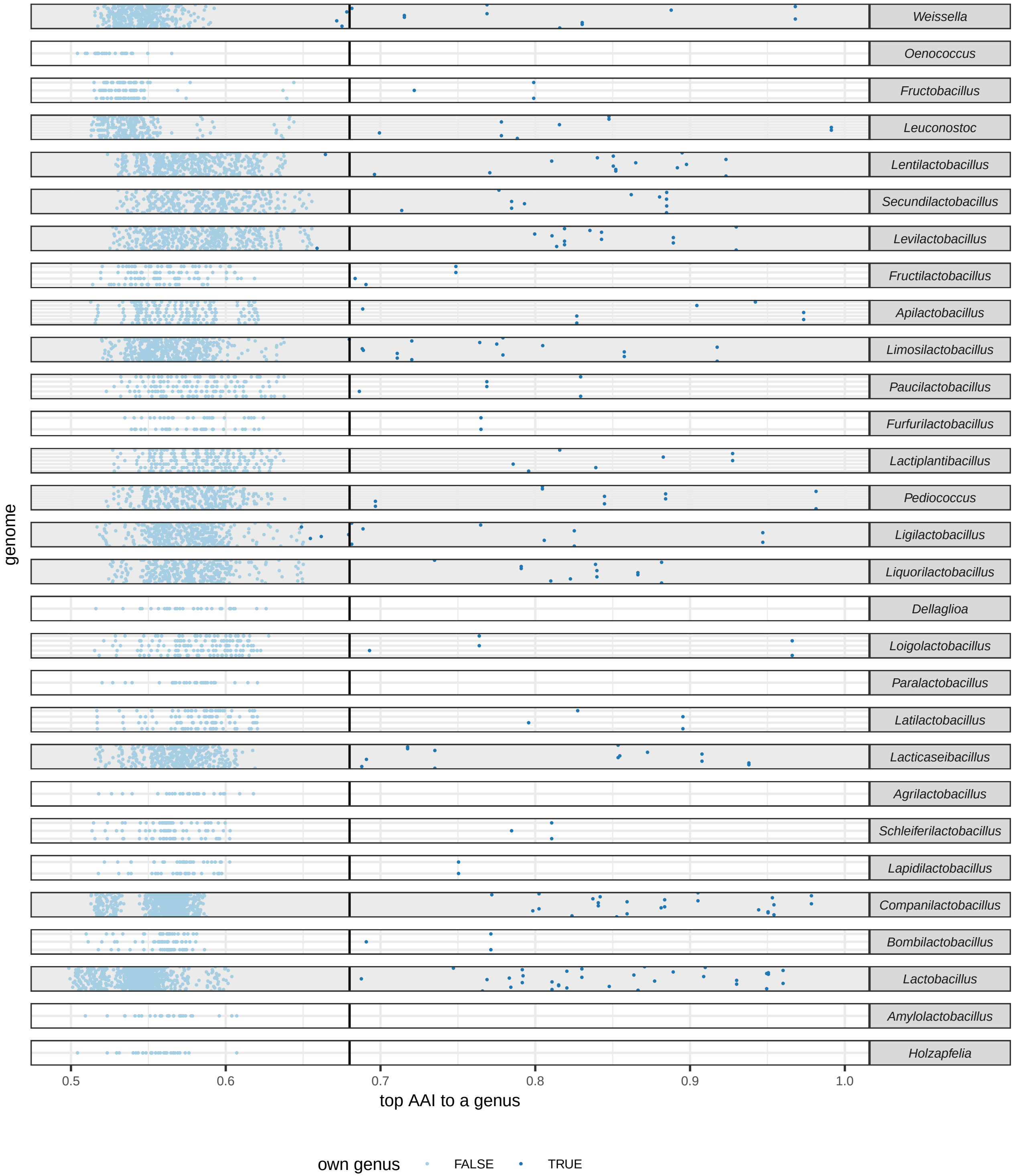


Figure S6. Phylogenetic tree on the basis of 16S rRNA gene sequences of the proposed species of *Lactobacillaceae* with three or more species. *Holzapfelia floricola* was used as outgroup for all trees. The Figure includes all species that were effectively or validly published species as of Dec. 12th, 2019. Shown are the following proposed genera: **Panel A,** emended genus *Lactobacillus;* **Panel B,** *Bombilactobacillus***;** **Panel C**, *Companilactobacillus;* **Panel D,** *Lapidilactobacillus;* **Panel E,** *Schleiferilactobacillus;* **Panel F,** *Lacticaseibacillus;* **Panel G,** *Latilactobacillus;* **Panel H,** *Loigolactobacillus;* **Panel I,** *Liquorilactobacillus;* **Panel J,** *Ligilactobacillus;* **Panel K,** *Lactiplantibacillus;* **Panel L,** *Furfurilactobacillus;* **Panel M,** *Paucilactobacillus;* **Panel N,** *Limosilactobacillus;* **Panel O,** *Secundilactobacillus;* **Panel P,** *Levilactobacillus;* **Panel Q,** *Fructilactobacillus;* **Panel R,** *Apilactobacillus;* **Panel S,** *Lentilactobacillus*.



Weissella
Oenococcus
Fructobacillus
Leuconostoc
Lentilactobacillus
Secundilactobacillus
Levilactobacillus
Fructilactobacillus
Apilactobacillus
Limosilactobacillus
Paucilactobacillus
Furfurilactobacillus
Lactiplantibacillus
Pediococcus
Ligilactobacillus
Liquorilactobacillus
Dellaglioa
Loigolactobacillus
Paralactobacillus
Latilactobacillus
Lacticaseibacillus
Agrilactobacillus
Schleiferilactobacillus
Lapidilactobacillus
Companilactobacillus
Bombilactobacillus
Lactobacillus
Amylolactobacillus
Holzapfelia
genome
0.5
0.6
0.7
0.8
0.9
1.0
top AAI to a genus
own genus
FALSE
TRUE

Figure S7. Top amino acid identity (AAI) values of genomes to genera. For each genome in genome dataset 2, we selected the highest AAI value with respect to each genus. Dark blue points represent top AAI values of species in the genera that the genomes belong to; light blue points represent top AAI values to species that are classified different genera. When a top AAI value of a genome to a genus is higher than 68%, the genome always belongs to that genus for the genomes in our dataset. Genomes are grouped per genus.

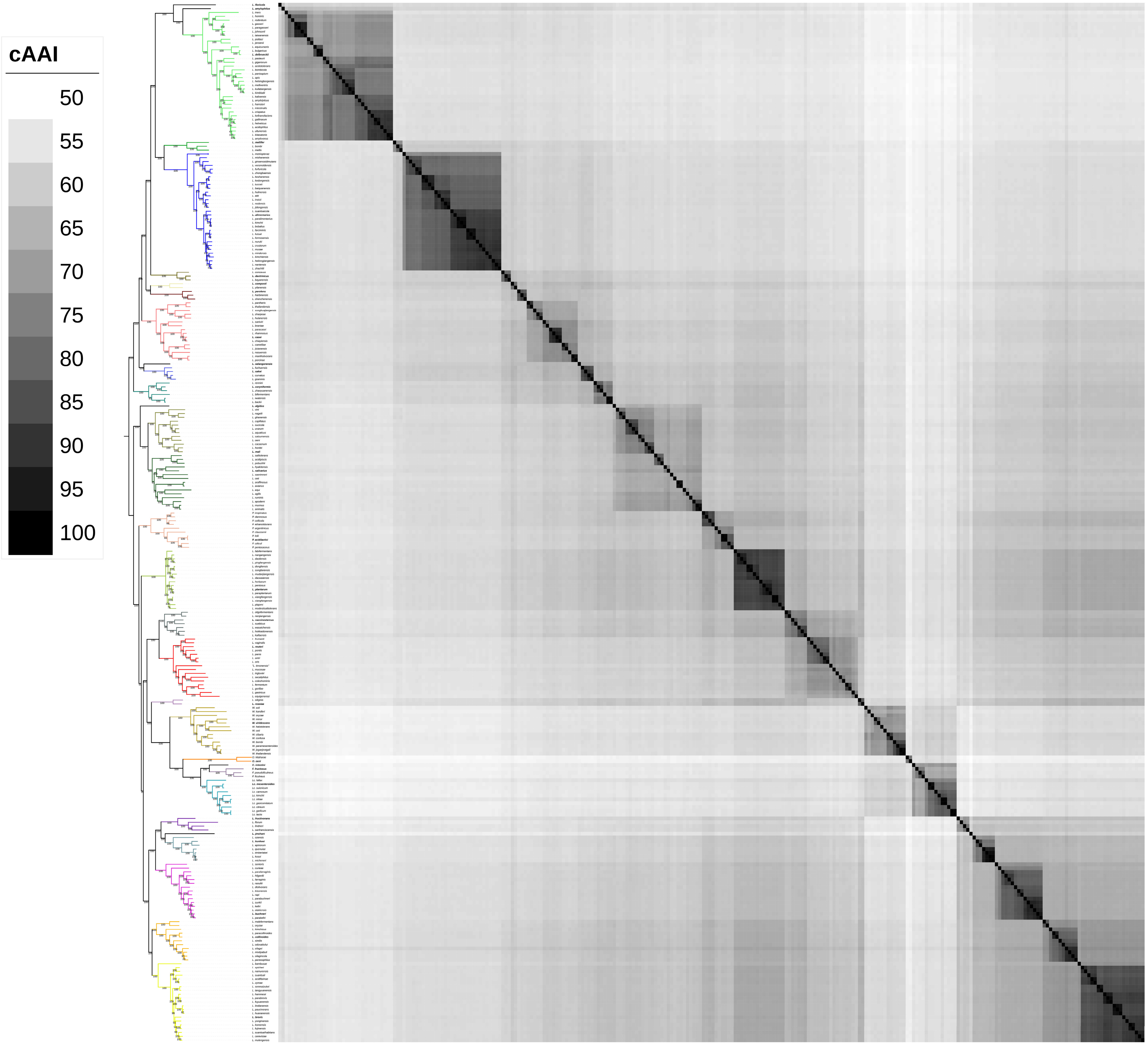

cAAI
50
55
60
65
70
75
80
85
90
95
100

Figure S8. High resolution rendition of Figure 8. Heat map depicting the cAAI values of the 38782 pairwise comparisons of all species in the families Leuconostocaceae and Lactobacillaceae for which genome sequence data was available in August 2019. The source file is provided as Table S3.