Nomenclatural Considerations of Certain Species of *Lactobacillus* Beijerinck

Request for an Opinion

MORRISON ROGOSA and P. ARNE HANSEN

National Institute of Dental Research, Laboratory of Microbiology, Bethesda, Maryland 20014,
and the University of Maryland, Department of Microbiology, College Park, Maryland 20742

The original description (2) of *Lactobacillus delbrueckii* (Leichmann) Beijerinck 1901 was confused with that of *L. fermentum* Beijerinck 1901. Although Opinion 38 of the Judicial Commission of the International Committee on Systematic Bacteriology (16, 17) accepts *L. delbrueckii* as the type species, the status of *L. fermentum* is unclear, and the name *L. fermentum* has probably not been validly published. To clarify matters, the synonymy and description of *L. delbrueckii* (neotype strain ATCC 9649) are herein up-dated; as a corollary, we request the Judicial Commission of the International Committee on Systematic Bacteriology to issue an Opinion conserving *L. fermentum* and associating its concept with the description of the herein designated neotype strain of *L. fermentum*, ATCC 14931. As a separate matter, a number of *Lactobacillus* species names have been erroneously attributed to Holland (74); these citations are appropriately reviewed and corrected as follows: *L. helveticus* (Orla-Jensen) Bergey et al. 1925—designated neotype strain ATCC 15009, *L. lactis* (Orla-Jensen) Bergey et al. 1934—designated neotype strain ATCC 12315, *L. bulgaricus* (Orla-Jensen) comb. nov.—designated neotype strain ATCC 11842, *L. plantarum* (Orla-Jensen) Bergey et al. 1923—type strain ATCC 14917. Concepts associated with the above names and with *L. leichmannii* (Henneberg) Bergey et al.—designated neotype strain ATCC 4797, *L. buchneri* (Henneberg) Bergey et al. 1923—designated neotype strain ATCC 4005, and *L. brevis* (Orla-Jensen) Bergey et al. 1934—designated neotype strain ATCC 14869, are discussed in a modern context. Basionyms and other synonyms, author citations, descriptions of type and neotype strains, and justifications of the proposals are presented.

A number of the presently recognized species in the genus *Lactobacillus* Beijerinck (2) do not have validly published names or lack type or neotype strains, or both. The purposes of this paper are (i) to review the names of these species and to propose new combinations where necessary, (ii) to list the objective (names based on the same type) and subjective (names based on different types) synonyms of these names, and (iii) to designate and describe type or neotype strains where indicated.

For those names listed as subjective synonyms, to our knowledge type or neotype strains have not been established. Therefore, the original descriptions serve as the types for these names. The subjective synonymies given

in that which follows have been determined on the basis of a comparison of the original descriptions associated with the names cited as subjective synonyms with the type or neotype strain of the species under discussion. There is one exception, however. The original description of *L. rudensis* Davis and Mattick (12) does not appear to be available. The subjective synonymy of this organism with *L. brevis* is based upon the later description of Davis and Mattick's organism by Breed and Pederson (9).

***Lactobacillus delbrueckii*.** Previously, *Lactobacillus caucasicus* Beijerinck 1901 has been accepted as the type species of the genus *Lactobacillus* Beijerinck. This organism is not recognizable, and no strains are extant. This is

also true for *L. longus* [probably identical with *L. bulgaricus* (22)], *L. fragilis*, and *L. conglomeratus*, the other species originally included by Beijerinck (2) in this genus. Recently, the Judicial Commission of the International Committee on Systematic Bacteriology issued Opinion 38 (16, 17) rejecting the previous type species and accepting, in its stead, *L. delbrueckii*. However, the confused status of *L. fermentum* Beijerinck [implicit in Beijerinck's (2) confused original description of *L. delbrueckii*] has not yet been resolved.

Beijerinck accepted Leichmann's (39) concept of *Bacillus Delbrücki* (sic) but regarded the organism as a variety of *L. fermentum*. Beijerinck (2) stated in a footnote (p. 229): "Le nom correct de cette bactérie serait *Lactobacillus fermentum* var. *delbrücki*. Pour la simplicité j'écris seulement *L. delbrücki*." Therefore, Beijerinck proposed the name *L. fermentum* for a species, with a variety *L. fermentum* var. *delbrücki*, the latter then being referred to colloquially (in a short-hand way) as *L. delbrücki* (sic).

Unfortunately, subsequent authors, apparently not cognizant of this footnote (reference 2, p. 229), have used *L. delbrücki* (corrected to *L. delbrueckii*) as the name of a species. To our knowledge, *L. delbrueckii* has never been validly published as the name of a species, although it has been used as such since Beijerinck's time.

Beijerinck (2) clearly had occasional mixed cultures of *L. delbrueckii* and *L. fermentum* and claimed reversible "transformations" from one to the other, dependent on shifts in temperature, anaerobiosis, or both. These "transformations" involved entire or large parts of the cell populations and went from homofermentations to heterofermentations and vice versa; from lack of ability to produce mannitol from fructose to such positive ability and vice versa; and included distinctive but incomplete changes in the mixtures of colonial and cellular morphologies.

Despite all of this, Beijerinck (2) also described *L. delbrueckii* and *L. fermentum* as if they were separate organisms or separate, transformed phases of the same organism (it is often not clear which was meant). These individual descriptions, within their scope, agree with current concepts of the two species. Furthermore, Smit (64), who worked in Beijerinck's laboratory and must have been aware of Beijerinck's concepts, had a distinctive concept of *L. fermentum*, and the presently proposed neotype strain is in agreement with Smit's characteristics. Thus, Smit (64), like Henneberg

(30) previously, and others since (including one of us, M. R.), never observed Beijerinck's "transformations," but rather surely recognized the distinctions between *L. fermentum* and *L. delbrueckii*.

Because the original description of *L. fermentum* by Beijerinck (2) is rather confused, there may be some question as to whether the name was validly published [see Rule 14a (3) of the International Code of Nomenclature of Bacteria (32)]. Therefore, we here ask the Judicial Commission for an Opinion conserving the name *Lactobacillus fermentum* Beijerinck. This would be a common-sense action in the interest of stability in nomenclature.

The synonymy of the name of the type species of *Lactobacillus* Beijerinck and a citation of the neotype strain of this species follow.

***Lactobacillus delbrueckii* (Leichmann) Beijerinck 1901, 229.**

Objective synonyms: *Bacillus Delbrücki* (sic) Leichmann 1896, 284 (basionym). *Bacterium delbrücki* (sic) (Leichmann) Migula 1900, 406. *Lactobacillus delbrücki* (sic) (Leichmann) Beijerinck 1901, 230. *Lactobacterium delbrücki* (sic) (Leichmann) van Steenberghe 1920, 816. *Ulvina delbrücki* (sic) (Leichmann) Pribram 1933, 75. *Plocamobacterium delbrücki* (sic) (Leichmann) Pribram 1933, 77.

Subjective synonyms: *Bacillus acidificans longissimus* Lafar 1896, 195. *Thermobacterium cereale* Orla-Jensen 1919, 164.

Leichmann's (39) description, the separate description by Beijerinck (2), and further descriptions by Henneberg (30) are of a recognizable organism which has been frequently reisolated. Supplemental descriptions (23, 57, 58) agree with these early descriptions. The strain designated as the neotype (17) agrees with the description by Henneberg (30) in all 19 fermentation reactions. The neotype strain fermented maltose on isolation but lost this property after one year's cultivation in the laboratory; other strains have also occasionally done this. The weak galactose fermentation noted by Henneberg (30) does not occur with most strains; "pure" galactose in 1903 would generally contain varying amounts of glucose.

ATCC 9649, the neotype strain (17), was isolated by Rogosa from sour grain mash (Calvert Distillery, Baltimore, Md.). The characteristics of the neotype strain (23, 57, 58) are not inconsistent with those recorded in the original description of *Bacillus Delbrücki* (sic) by Leichmann (39) and agree with the present concept of the species (23, 57, 58). The neotype strain is described in Table 1.

SECTION 1: GENERAL INFORMATION

01004: Collection Number in the World Directory of Culture Collections
(if known):

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01005: Postal Address: (Leave one space between each word or number.
If applicable, use exact World Directory address.)

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SECTION 1: GENERAL INFORMATION

01006: Category of microbe being described (Use following code):

AL = Algae	BT = Bacteria	VA = Viruses - Animal
FN = Fungi	BR = Rickettsia	VB = Viruses - Bacterial
FY = Yeasts	BM = Mycoplasma	VI = Viruses - Insect
PZ = Protozoa	QQ = Other	VP = Viruses - Plant

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01007: Name of Genus (or arbitrary numerical code for Group* or Group name*):

NOTE 1: Completely different sets of CODE SHEETS must be used for each Genus or Group.

NOTE 2: If the data being submitted for strains is arranged under SUBGENERA, completely different sets of CODE SHEETS must be used for each SUBGENUS. The generic name must be inserted for question 01007 in each set.

*NOTE 3: If the genus name is not known and data is being submitted for any arbitrary group of organisms, use (a) an arbitrary numerical code, e.g., "Group 22" or simply "22" OR (b) a group name, e.g., CORYNEFORMS. See DIRECTIONS for further explanation.

L A C T O B A C I L L U S | | | | | | | | | | | | | | | |
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01008: Name of Subgenus: (Insert the name ONLY if data being submitted for strains is arranged under Subgenera, otherwise, leave this answer blank).

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|26|27|28|29|30|31|32|33|34|35|36|37|38|39|40|41|42|43|44|45|46|

01009: For how many subgenera of the genus are you submitting data?

| | |
|47|48|

01010: Specific epithet of type species for this genus:

D E L B R U E C K I I | | | | | | | | | | | | | | | |
|49|50|51|52|53|54|55|56|57|58|59|60|61|62|63|64|65|66|67|68|69|70|

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01011: Are the organisms of this genus procaryotic? 1
|01|

01012: Has a type species ever been established for this genus? 1
|02|

01013: Has a type culture ever been established for the type species? 1
|03|

01014: Is the type culture of the type species (of the genus) in living form? 0
|04|

01015: Is any strain of the type species in living form? 0
|05|

TABLE 1. *Selected characteristics of type and neotype strains^a*

Organism	Status of strain	GC mean %	Gas from glucose	Gas from gluconate	Acid from ribose	Aldolase	Lactic acid enantio-morph	Acid in milk (%)	NH ₃ from arginine	Growth		Serological group	Requirement for		Carbohydrate utilization																					
										15 C	45 C		Thiamine	Riboflavine	Pyridoxal	Folic acid	Thymidine	Aesculin	Amygdalin	Arabinose	Cellobiose	Fructose	Galactose	Lactose	Maltose	Mannitol	Mannose	Melezitose	Melibiose	Raffinose	Salicin	Sucrose	Trehalose	Xylose		
<i>L. delbrueckii</i> ATCC 9649	NT	50.0	—	—	—	+	D(—)	0	+	—	+	?	—	+	—	—	—	—	—	+	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>L. fermentum</i> ATCC 14931	DNT	53.4	+	+	+	—	DL	0.03-0.28	+	—	+	F	+	—	—	—	—	—	—	+	+	+	—	—	—	—	—	—	—	—	—	—	+	—	—	—
<i>L. helveticus</i> ATCC 15009	DNT	39.3	—	—	—	+	DL	2.7	—	—	+	A	—	+	+	—	—	—	—	+	+	+	—	—	—	—	—	—	—	—	—	—	+	—	—	—
<i>L. lactis</i> ATCC 12315	DNT	50.2	—	—	—	—	D(—)	1.4-1.7	—	—	+	E	—	+	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>L. leichmannii</i> ATCC 4797	DNT	50.8	—	—	—	+	D(—)	0	+	—	+	?	—	—	—	+	—	+	+	—	+	+	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>L. bulgaricus</i> ATCC 11842	DNT	50.3	—	—	—	+	D(—)	1.7	—	—	+	E	—	+	—	—	—	—	—	+	+	+	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>L. plantarum</i> ATCC 14917	T	45.0	—	+	+	+	DL	0.1-0.28	—	+	—	D	—	+	—	—	—	—	—	+	+	+	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>L. buchneri</i> ATCC 4005	DNT	44.8	+	+	+	—	DL	0.04-0.24	+	+	—	E	+	—	—	—	—	—	—	+	+	+	+	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>L. brevis</i> ATCC 14869	DNT	42.7	+	+	+	—	DL	0.09-0.31	+	+	—	E	+	—	—	+	—	—	—	+	+	+	+	—	—	—	—	—	—	—	—	—	—	—	—	—

^a All strains listed here are gram-positive, straight, unbranched rods, width < 1 μ m, length of varying dimensions. All are negative for catalase, indole, nitrate reductase, oxidase, and benzidine reactions. All strains attack glucose and produce lactic acid as the major product; strains producing gas from glucose, however, produce about 50% lactate with CO₂, acetate, ethanol as additional significant products. None ferment adonitol, dulcitol, erythritol, glycerol, glycogen, inositol, inulin, sorbose, starch. Only strain 14917 ferments α -methyl-D-glucoside, α -methyl-D-mannoside, sorbitol, and exhibits weak or variable fermentation of rhamnose. All strains require niacin and pantothenate. Great care has been taken to make certain that the data shown are for pure cultures of these specific strains only; the data are not statistical or summary data; such information on groups of strains may be found elsewhere (57, 58). The included data are from repeated testings (generally 4 to 12 during the past 20 years or more; even the guanine plus cytosine (GC) data are the means of duplicate determinations and, in a number of cases, repeated determinations with new cell crops. Symbols: +, consistently positive reaction in all repeated testings; —, consistently negative reaction in all repeated testings; $\pm$, variable or weak reaction in our laboratory or disagreement of results from different collaborating laboratories or both; $\mp$, generally negative but occasionally weak reaction; DNT, herein designated neotype strain; NT, previously designated neotype strain; T, previously designated type strain.

Lactobacillus fermentum. The name *Lactobacillus fermentum* Beijerinck has the following synonymy.

Lactobacillus fermentum Beijerinck 1901, 233 (proposed *nomen conservandum*).

Objective synonyms: *Bacillus* δ von Freudenreich 1895, 173. *Bacillus casei* δ von Freudenreich and Thöni 1904, 532. *Lactobacterium fermentum* (Beijerinck) van Steenberge 1920, 816. *Lactobacillus fermenti* (sic) Beijerinck (reference 3, p. 252). *Betabacterium Jensenii* (sic) Frank 1936 (reference 50, p. 91).

Subjective synonyms: *Bacterium gayoni* Müller-Thurgau and Osterwalder 1917, 34. *Betabacterium longum* Orla-Jensen 1919, 175. *Lactobacillus gayoni* (Müller-Thurgau and Osterwalder) Pederson 1929a, 23. *Lactobacillus longus* (Orla-Jensen) Bergey et al. 1934, 312. *Lactobacterium longum* (Orla-Jensen) Krasil'nikov 1949, 220.

Designated neotype strain: ATCC 14931. [This strain was recommended as the neotype (23), with the understanding that the official designation be made in this journal. Therefore, ATCC 14931 is here designated as the neotype.]

This strain is Orla-Jensen's original *Betabacterium longum* no. 28, which he isolated from fermented beets and described (49, 50) in a very recognizable manner.

These descriptions are not inconsistent with the separate description of *L. fermentum* by Beijerinck (2) or with the description by Smit (64). The neotype strain and hundreds of others identical or similar to the neotype strain have been extensively described (23, 28, 52–55, 57, 58); a description of this strain is also given in Table 1.

In addition to the foregoing, some of the names of other presently recognized species in the genus *Lactobacillus* have not been validly published (10). These include the following combinations attributed to Holland (74) (see Rule 12a): *L. bulgaricus* (Massol) Holland 1920; *L. helveticus* (Orla-Jensen 1916) Holland 1920; *L. lactis* (Orla-Jensen 1919) Holland 1920; and *L. plantarum* (Orla-Jensen 1919) Holland 1920. The names *L. casei* and *L. acidophilus*, previously not validly published by Holland, have recently been validly published (25 and 26, respectively).

"*L. leichmanni* (sic) (Henneberg)," "*L. buchneri* (Henneberg)," and "*L. plantari* (sic) (Orla-Jensen)" were given by Bergey et al. (3). Although it is not clear that these names were being proposed as new combinations by Bergey et al. (3), the subsequent editions of *Bergey's Manual*, edited by Bergey et al., cite Bergey et

al. (3) as the authors of these names. This leaves no doubt that Bergey et al. (3) intended to propose these new combinations. *L. brevis* was given in the 4th ed. of *Bergey's Manual* (6) as a new combination. *L. bulgaricus* is presented herein as a new combination, and the concept of the species is discussed.

The synonymies and the nomenclatural types of the above-mentioned species are as follows.

Lactobacillus helveticus.

Lactobacillus helveticus (Orla-Jensen) Bergey et al. 1925, 184.

Objective synonyms: *Bacillus* ϵ von Freudenreich 1895, 173; 1895, 211. *Bacillus casei* ϵ von Freudenreich and Thöni 1904, 532. *Caseobacterium* ϵ Orla-Jensen 1909, 337. *Thermobacterium helveticum* Orla-Jensen 1919, 164 (basonym). *Bacterium casei* ϵ Holland 1920, 221. *Lactobacillus helveticum* (sic) (Orla-Jensen) Bergey et al. 1925, 184. *Plocamobacterium casei* Pribram 1933, 77. *Plocamobacterium helveticum* (Orla-Jensen) Pribram 1933, 78. *Lactobacterium helveticum* (Orla-Jensen) Krasil'nikov 1949, 212.

This organism was correctly and adequately described by Orla-Jensen (49); supplemental descriptions (23, 57, 58) confirmed and expanded Orla-Jensen's description. Bergey et al. (4) refer to the description by Orla-Jensen; however, some erroneous characters, e.g. gas formation, were mentioned. These were corrected in the next edition (5) and in all subsequent editions. The many strains known as *Thermobacterium Jugurt* (sic) Orla-Jensen 1919 (synonym *L. jugurti* (sic) Rogosa and Sharpe 1959) differ from the type strain (and hundreds like it) only in not fermenting maltose. Thus, these may be maltose-negative mutants of *L. helveticus*.

Designated neotype strain: ATCC 15009. This is Orla-Jensen's (49) *Thermobacterium helveticum* no. 12, which he isolated from Emmental (Swiss) cheese. [This strain was cited by Hansen (23) as the type; however, this strain cannot be the type because it is not one of the strains on which the original (von Freudenreich) description of this organism was based, and so it is here designated as the neotype.] A description of this strain is given in Table 1.

Lactobacillus lactis.

Lactobacillus lactis (Orla-Jensen) Bergey et al. 1934, 303.

Objective synonyms: *Bacillus lactis acidi* Leichmann 1896, 283. *Bacterium lactis acidi* (Leichmann) Leichmann 1896, 778. *Thermobacterium lactis* Orla-Jensen 1919, 164 (basio-

SECTION 1: GENERAL INFORMATION

- 01016: Has a neotype strain of the type species been established? 1
|06|
- 01017: Has any strain of the type species been studied
extensively in the last 20 years? 1
|07|
- 01018: Have nucleic acid homologies been measured among any
of the strains of species of this genus? 1
|08|
- 01019: Have nucleic acid homologies been measured between any
strains of species of this genus and those of other genera? 0
|09|
- 01020: Has bacteriophage typing been used in this genus? 0
|10|
- 01021: Has transduction been demonstrated among any strains of
species of this genus? 0
|11|
- 01022: Has transduction been demonstrated between any strains of
species of this genus and those of other genera? 0
|12|
- 01023: Has transformation been demonstrated among any strains of
species of this genus? 0
|13|
- 01024: Has transformation been demonstrated between any strains of
species of this genus and those of other genera? 0
|14|
- 01025: Have studies of the geographical distribution of any
strains of the genus been carried out? 1
|15|
- 01026: Have studies of the ecological distribution of any strains
of species of this genus been carried out? 1
|16|
- 01027: Have studies of the ecological interactions within a
habitat of any strains of species of this genus been
carried out? 1
|17|
- 01028: Have studies of ecological distribution on any level
been used for taxonomy of this genus? 1
|18|
- 01029: Have immunological criteria been used for taxonomy of
this genus? 1
|19|
- 01030: Have any strains of species of this genus been reported as 1
pathogenic? If any strains for which you are submitting
data are pathogenic, please supply the following information
on a separate sheet of paper: (a) strains by specific
epithets, (b) hosts (both common and scientific names), and
(c) diseases. Identify each sheet of paper with the World
Directory of Culture Collections Number, if applicable, and
also the same information as required in the top right
corner of CODE SHEET-1. 20
|20|
- 01031: What is the total number of CODE SHEETS-1, II plus III you
are submitting for strains of this genus (or subgenus or
arbitrary group)? (Note: all CODE SHEETS-A, B, C, D, I, II, III for
the genus must be securely fastened together.)

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nym). *Lactobacillus lactis* (Orla-Jensen) Holland 1920, 223 [not validly published (Rule 12c)]. *Lactobacillus lactis-acidi* (Leichmann) Bergey et al. 1923, 248. *Lactobacillus lactis-acidi* (Leichmann) Holland (reference 4, p. 182). *Lactobacterium caucasicum* var. *lactis* (Orla-Jensen) Krasil'nikov 1949, 211. Note: *Lactobacillus lactis* was cited on page 303 in the 4th ed. of *Bergey's Manual* (6) as a comb. nov., and the intent seems clear as it was included in the 5th ed. (1939) with a correct reference to Bergey et al. (6). Strangely enough, the 6th ed. (8) and the 7th ed. (1957) cite Holland as the author of the name. Clearly, Bergey et al. (6) are the authors. Descriptions by Orla-Jensen (49), Rogosa et al. (57), and Rogosa and Sharpe (58) permit recognition of the organism.

Designated neotype strain: ATCC 12315. This is Orla-Jensen's (49) *Thermobacterium lactis* no. 10, which he isolated from Emmmental (Swiss) cheese. [This strain was cited by Hansen (23) as the type; however this strain cannot be the type because it is not one of the strains on which the original (Leichmann) description of this organism was based, and so it is here designated as the neotype.] A description of this strain is given by Hansen (23) and in Table 1.

***Lactobacillus leichmannii*.**

Lactobacillus leichmannii (Henneberg) Bergey et al. 1923, 249.

Objective synonyms: *Bacillus leichmanni* (sic) Henneberg 1903, 163, 164 (basionym), (includes Henneberg's *B. leichmanni* I and III). *Lactobacillus leichmanni* (sic) (Henneberg) Bergey et al. 1923, 249. *Bacterium leichmanni* I (sic) (Henneberg) Henneberg 1926, 107. *Lactobacterium leichmannii* (Henneberg) Krasil'nikov 1949, 215.

Designated neotype strain: ATCC 4797. This strain was deposited at the ATCC by E. B. Fred (his strain F59) but the source is unknown; it probably was isolated from corn mash. The neotype strain has been studied (23, 57, 58) and has characteristics generally consistent with Henneberg's (30) description. The neotype strain differs from Henneberg's description in the following minor respects. (i) Galactose is variably or weakly fermented (30); galactose is not fermented (neotype strain); (ii) lactose is not fermented in milk or doubtfully in other media (30); lactose is not fermented in milk but is fermented in other suitable media (neotype strain); (iii) mannitol is weakly fermented (30); mannitol is not fermented (neotype strain); and (iv) α -methyl-D-glucoside is variably fermented

(30) and is not fermented (neotype strain). These differences are trivial and are no greater than those between *B. leichmanni* I and *B. leichmanni* III of Henneberg. A description of the neotype strain is given in Table 1.

***Lactobacillus bulgaricus*.**

Lactobacillus bulgaricus (Orla-Jensen) comb. nov. Not *Lactobacillus bulgaricus* (Massol) Holland 1920, 233 (not validly published).

Objective synonym: *Thermobacterium bulgaricum* Orla-Jensen 1919, 81 (basionym).

Names of organisms whose relationship to *L. bulgaricus* is uncertain: *Lactobacillus longus* Beijerinck 1901, 217. Bacille A Grigoroff 1905, 716. *Bacillus bulgaricus* Luerssen and Kühn 1907, 241. *Bacterium bulgaricum* (Luerssen and Kühn) Buchanan and Hammer 1915, 250. *Lactobacillus bulgaricus* (Grigoroff) Holland (as cited and described by Bergey et al. 1923, 244 and all subsequent editions). *Acidobacterium bulgaricum* (Luerssen and Kühn) Schlirf 1925, 116. *Plocamobacterium bulgaricum* (Luerssen and Kühn) Lehmann and Neumann 1927, 511. *Bacterium giogurt* de Rossi 1927, 743. *Lactobacterium bulgaricum* (Luerssen and Kühn) Krasil'nikov 1949, 212.

Descriptions of *L. bulgaricus* (Orla-Jensen) comb. nov. have already been published (13, 14, 22, 49, 58).

Luerssen and Kühn's (40) *Bacillus bulgaricus* is not recognizable except as a member of the genus *Lactobacillus* of the group named *Thermobacterium* by Orla-Jensen. The organism was a homofermentative, lactic-acid producing rod, growing at 45 to 50 C but not at 22 C or below, and acidified and clotted milk. Claimed production of L(+) lactic acid is unbelievable: the determinations were done in clarified whey without extracting the lactic acid; from the total acid produced there was more than 3% residual lactose, which in itself, could account for the dextrorotation. Microscopic and colonial morphology are consistent with the characteristics of any of four members of *Thermobacterium* Orla-Jensen. There are no extant strains of *Bacillus bulgaricus* Luerssen and Kühn, and we shall never know what this organism really was.

Bergey et al. (3) described an organism under the name *Lactobacillus bulgaricus* and attributed the origin of the epithet *bulgaricus* to Grigoroff (21). This was incorrect. Bergey et al. (4) also attributed the name *L. bulgaricus* to Holland. However, as previously pointed out, this name was not validly published by Holland. The organism described by Grigoroff was named Bacille A (and nothing else) by

Grigoroff. Also, the characteristics of this non-recognizable, nonextant organism are internally contradictory for a thermophilic, homofermentative lactobacillus (being an alcohol-producing, denitrifying, mannitol-fermenting strain), and it has never been reisolated. The organism was most probably a sporeforming gram-positive rod, and the use of *Bacillus* (Bacille) would be acceptable today for an organism with these characteristics.

To date, all *Bergey's Manual* descriptions of *L. bulgaricus* clearly were composite descriptions of two organisms, one producing D(-) and the other producing DL-lactic acid; the sugar fermentations of this "organism" reported from various sources are also in conflict with each other. From studies of the actual strains on which the *Bergey's Manual* descriptions of this "organism" were based, it is definite that the two organisms involved are *L. bulgaricus* and *L. jugurti*.

At least 19 strains identical with Orla-Jensen's strain no. 14 (the designated neotype) have been isolated from Bulgarian, Russian, Greek, Syrian, and Armenian yogurts (13, 14, 22, 58); the cited authors also confirmed the uniqueness of *L. bulgaricus* and *L. jugurti* (*Thermobacterium jugurti* Orla-Jensen) and the frequent simultaneous presence of these organisms and sometimes also *Lactobacillus lactis* and other lactobacilli in such sour milks.

Kulp and Rettger (35) and Sherman and Hodge (62) named their strains *Lactobacillus bulgaricus*. Rogosa et al. (57) restudied these strains and found them to be identical with *L. jugurti* (*Thermobacterium jugurti*). Nevertheless, Rogosa et al. (57) mistakenly followed the *Manual* and continued to use the name *L. bulgaricus*.

Designated neotype strain: ATCC 11842. This is Orla-Jensen's (49) *Thermobacterium bulgaricum* No. 14, which he isolated from Bulgarian yogurt. A description of this strain is given by Hansen (23) and in Table 1.

***Lactobacillus plantarum*.**

Lactobacillus plantarum (Orla-Jensen) Bergey et al. 1923, 250. Not *Lactobacillus plantarum* (Orla-Jensen) Holland 1920, 225 (not validly published).

Objective synonyms: *Streptobacterium plantarum* Orla-Jensen 1919, 174 (basionym). *Lactobacillus plantari* (sic) (Orla-Jensen) Bergey et al. 1923, 250. *Lactobacterium plantarum* (Orla-Jensen) Krasil'nikov 1949, 216.

Subjective synonyms: *Lactobacillus arabinosus* Fred et al. 1921, 410. *Lactobacillus pentosus* Fred et al. 1921, 410. *Lactobacillus rudensis* Davis and Mattick (reference 9, p.

667); also see subjective synonymy of *L. brevis*. *Lactobacillus plantarum* var. *rudensis* (Davis and Mattick) Breed and Pederson 1938, 667. *Lactobacillus plantarum* var. *mobilis* Harrison and Hansen 1950, 446.

Names of organisms whose relationship to *L. plantarum* is uncertain: *Bacillus pabuli acidi* II Weiss 1899, 599. *Bacillus Beijerincki* (sic) Henneberg 1903, 22 and 159. *Bacillus Listeri* (sic) Henneberg 1903, 22 and 161. *Bacillus Wortmanni* (sic) Henneberg 1903, 162. *Bacillus Leichmanni* II (sic) Henneberg 1903, 164. *Bacillus Maerckeri* (sic) Henneberg 1903, 165. *Bacillus cucumeris fermentati* Henneberg 1903, 22 and 166. *Bacterium brassicae* Wehmer 1903, 628. *Lactobacterium listeri* (Henneberg) van Steenberghe 1920, 814. *Lactobacillus brassicae* (Wehmer) Le Fevre 1922, 25. *Lactobacillus pabuli-acidi* (Weiss) Bergey et al. 1923, 247. *Lactobacillus Beijerincki* (sic) (Henneberg) Bergey et al. 1923, 248. *Lactobacillus listeri* (Henneberg) Bergey et al. 1923, 248. *Lactobacillus cucumeris* (Henneberg) Bergey et al. 1923, 250. *Lactobacillus pabuli-acidi* (Weiss) Bergey et al. 1925, 181. *Lactobacillus cucumeris* Bergey et al. 1925, 182. *Bacterium busae asiaticae* Tschekan 1929, 89. *Lactobacillus busaeasiaticus* (Tschekan) Bergey et al. 1930, 288. *Lactobacillus wortmanni* (sic) (Henneberg) Bergey et al. 1930, 288.

The description by Orla-Jensen (49) permits recognition of the species. Confirmation and expansion of Orla-Jensen's description have been made (23, 50, 57, 58). Additional characteristics of the species are: growth in 4% sodium taurocholate, diaminopimelic acid in the cell wall, and a guanine plus cytosine content of the deoxyribonucleic acid of 45 ± 1.0 moles per cent (buoyant density; Mandel, *personal communication*).

Type strain (subsequent designation by Hansen (23)): ATCC 14917. This is Orla-Jensen's (49) *Streptobacterium plantarum* no. 39, which he isolated from pickled cabbage. A description of this strain is given in Table 1.

***Lactobacillus buchneri*.**

Lactobacillus buchneri (Henneberg) Bergey et al. 1923, 251.

Objective synonyms: *Bacillus Buchneri* (sic) Henneberg 1903, 163 (basionym). *Lactobacillus lycopersici* Mickle 1924, 404. *Bacterium buchneri* (Henneberg) Henneberg 1926, 111. *Ulvina buchneri* (Henneberg) Pribram 1933, 75. *Lactobacterium buchneri* (Henneberg) Krasil'nikov 1949, 218.

Subjective synonyms: *Bacillus Hayducki* (sic) Henneberg 1903, 163. *Bacillus Wehmeri* (sic) Henneberg 1903, 165. *Bacterium man-*

nitopoeum Müller-Thurgau 1908, 396. *Lactobacillus mannitopoeus* (Müller-Thurgau) Pederson 1929a, 31. *Lactobacillus mannitopoeus* var. *fermentus* Iwasaki 1940, 148.

Henneberg's (30) original description of *Bacillus Buchneri* (sic) and the strain here designated as the neotype have remarkably similar characteristics. The 90 strains of Rogosa et al. (57) have morphological and fermentation characteristics in agreement with Henneberg's (30) original description. Henneberg's description of maximum and optimal growth temperatures (30) is unclear, if not contradictory. He says that the maximum temperature was over 47°C in mash and that the optimum was at first 39 to 40°C and later 23 to 30°C. The latter optimum is consistent with the behavior of presently known strains. Henneberg (30) did not test xylose, melibiose, or melezitose. However, both Pederson (54) and Rogosa et al. (57) agreed that all strains fermented melezitose and that xylose was usually not fermented. The neotype strain, however, ferments xylose, as shown in Table 1. Further descriptions of this species are given by Rogosa and Sharpe (58) and Hansen (23).

Designated neotype strain: ATCC 4005. This strain was isolated by Mickle (42) from tomato pulp. A description of this strain is given by Rogosa et al. (57) and in Table 1.

***Lactobacillus brevis*.**

Lactobacillus brevis (Orla-Jensen) Bergey et al. 1934, 312.

Objective synonyms: *Bacillus* γ von Freudenreich 1891, 22. *Bacillus casei* γ von Freudenreich and Thöni 1904, 532. *Betabacterium breve* Orla-Jensen 1919, 175 (basionym). *Lactobacterium breve* (Orla-Jensen) Krasil'nikov 1949, 217.

Subjective synonyms: *Saccharobacillus pastorianus* var. *berolinensis* Henneberg 1901, 383. *Bacillus lindneri* Henneberg 1901, 384. *Bacillus fasciformis* Schönfeld and Rommel 1902, 585. *Bacillus brassicae fermentatae* Henneberg 1903, 167. *Bacillus panis fermentati* Henneberg 1903, 168. *Bacterium soya* Saito 1907, 20. *Bacillus acidophil-aerogenes* Torrey and Rahe 1915, 437. *Lactobacillus pentoaceticus* Fred et al. 1919, 357. *Lactobacillus acidophil-aerogenes* (Torrey and Rahe) Holland 1920, 216. *Lactobacillus lindneri* (Henneberg) Bergey et al. 1923, 245. *Lactobacillus berolinensis* (Henneberg) Bergey et al. 1923, 246. *Lactobacillus panis* (Henneberg) Bergey et al. 1923, 251. *Lactobacillus soya* (Saito) Bergey et al. 1923, 251. *Lactobacillus fermentatae* Bergey et al. 1923, 252. *Lactobacillus panis* Bergey et al. 1925, 185. *Bacterium lindneri* (Henneberg)

Henneberg 1926, 123. *Saccharobacillus pastorianus* var. *berolinensis fasciformis* Henneberg 1926, 123. *Saccharobacillus berolinensis fasciformis* (Henneberg) Henneberg 1926, 123. *Plocamobacterium pentoaceticum* (Fred et al.) Pribram 1933, 78. *Betabacterium arabinosaceum* Frank 1936 (as cited by Orla-Jensen 1943, 91). *Lactobacillus rudensis* Davis and Mattick 1936, 3 (reference 9, p. 667); also see subjective synonymy of *L. plantarum*. *Lactobacillus brevis* var. *rudensis* (Davis and Mattick) Breed and Pederson 1938, 667. *Bacillus belorinensis* (sic) (Henneberg) Otani 1939, 149. *Lactobacillus pentoaceticus* var. *magnus* Iwasaki 1940, 148. *Lactobacterium fasciformis* (Schönfeld and Rommel) Krasil'nikov 1949, 219. *Lactobacterium lindneri* (Henneberg) Krasil'nikov 1949, 219. *Lactobacillus pastorianus* var. *brownii* Shimwell 1949, 26. *Lactobacillus brownii* (Shimwell) Shimwell 1949, 29. *Lactobacillus pastorianus* var. *diastaticus* Andrews and Gilliland 1952, 195. *Lactobacillus frigidus* Bhandari and Walker 1953, 332.

Name of organism whose relationship to *L. brevis* is uncertain: *Saccharobacillus pastorianus* van Laer 1892, 4.

Objective synonyms: *Bacillus pastorianus* (van Laer) Macé 1901, 957. *Lactobacterium pastorianum* (van Laer) van Steenberge 1920, 816. *Lactobacillus pastorianus* (van Laer) Bergey et al. 1923, 246. The latter organism is unrecognizable. Van Laer's description is inadequate and is of an organism, or more likely organisms, alternately reported to behave like a homofermentative strain as often as it or they were heterofermentative.

Bacillus caucasicus von Freudenreich 1897, 135 and *Betabacterium caucasicum* Orla-Jensen 1919, 173 are closely related but ferment fewer sugars. Strains designated as *Lactobacillus pastorianus* or many synonyms thereof are not different from *L. brevis*. The International Subcommittee on Lactobacilli and Closely Related Organisms recommended rejection of the name *Lactobacillus pastorianus* Bergey et al. 1923, 246 (Minute 7, Moscow, July 22, 1966).

Designated neotype strain: ATCC 14869. This is Orla-Jensen's (49) *Betabacterium breve* no. 14, which he isolated from human feces. [This strain was cited by Hansen (23) as the type; however, this strain cannot be the type because it is not one of the strains on which the original (von Freudenreich) description of this organism was based, and so it is here designated as the neotype.] A description is given by Orla-Jensen (49) and by Hansen (23) and appears in Table 1.

Variable galactose and lactose fermentations by the neotype strain agree with Orla-Jensen's

(49, 50) description. Hundreds of other strains identical or very similar to the neotype strain have been described (52-55, 57, 58).

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