NOTES

Lactobacillus paraplantarum sp. nov., a New Species Related to *Lactobacillus plantarum*

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Four strains of facultatively heterofermentative lactobacilli isolated from beer and human feces have physiological characteristics similar to those of *Lactobacillus plantarum*. Unlike 66% of the *L. plantarum* strains tested (F. Bringel, M.-C. Curk, and J.-C. Hubert, Int. J. Syst. Bacteriol. 46:588–594, 1996), these strains do not catabolize α -methyl-D-mannoside. However, because they exhibit little DNA relatedness to *L. plantarum* and *Lactobacillus pentosus*, these four strains were classified as members of a new species, *Lactobacillus paraplantarum*; strain CNRZ 1885 (= CIP 104668) is the type strain.

The species *Lactobacillus plantarum* has been described as a taxon which exhibits phenotypic and genomic heterogeneity. Nucleic acid hybridization studies have clearly demonstrated the differences between *L. plantarum* and *Lactobacillus pentosus* (8, 18), and some strains have been shown to be neither *L. plantarum* nor *L. pentosus* strains (8). The taxonomic positions of these organisms have remained uncertain. When we studied the restriction fragment length polymorphisms of the de novo biosynthetic pyrimidine genes (2), four strains previously identified as *L. plantarum* strains (strains CNRZ 1885^T [T = type strain], CNRZ 1887, 61D, and ATCC 10776) produced peculiar restriction profiles. The *L. plantarum* strains produced three bands (at 7, 4, and 1 kb), whereas the *L. pentosus* strains produced only one band (at about 7 kb) and strains CNRZ 1885^T, CNRZ 1887, 61D, and ATCC 10776 produced two bands (at 4 and 1 kb). In this study, we found that the latter four strains appear to belong to a new species which differs from *L. plantarum* and *L. pentosus*. Below we propose the name *Lactobacillus paraplantarum* for this new species and present a description of it.

All strains (Table 1) were grown on MRS agar (9) at 30°C in a 4% CO₂-enriched atmosphere for 48 h and were stored at 4°C. For physiological tests, MRS broth (8 ml) was inoculated with lactobacilli from MRS agar plates, and the resulting culture was grown at 30°C in a 4% CO₂-enriched atmosphere for 24 h. This culture was subsequently used to inoculate MRS broth cultures incubated at 15, 30, 37, and 45°C when the growth temperature was tested, in a 4% CO₂-enriched atmosphere or under aerobic conditions when the effect of oxygen on growth was studied. To estimate the effect of NaCl on growth, cells were grown at 30°C in a 4% CO₂-enriched atmosphere in MRS broth preparations supplemented with 4, 6, 8, and 10% (wt/vol) NaCl. The effect of pH on growth was determined in MRS adjusted to pHs 4 and 5 with acetic acid and to pH 7 with NaOH. The production of gas from glucose was determined with MRS broth lacking beef extract, and the production of gas from gluconate was determined with MRS lack-

ing beef extract and glucose but containing gluconate (10 g liter⁻¹). The gas that was produced was trapped in Durham tubes. To study arginine degradation by the arginine deiminase pathway, cultures of strains on MRS agar were subcultured in MRS broth for 24 h and then in two tubes containing 5 ml of Niven medium (2 g of K₂HPO₄ per liter, 3 g of L-arginine per liter, 0.1% [vol/vol] Tween 80, 50 mg of MnSO₄ per liter; pH adjusted to 7); glucose at a final concentration of 2% (wt/vol) was added to one tube, and glucose at a final concentration of 0.05% (wt/vol) was added to the other tube (7). The cultures

TABLE 1. Strains studied^a

Strain	Source and/or other designation
<i>L. pentosus</i> NCFB 363 ^T	
<i>L. plantarum</i> ATCC 14917 ^T	Pickled cabbage
<i>L. paraplantarum</i> strains	
CNRZ 1885 ^T	CIP 104668; beer contaminant, obtained from the strain collection of TEPRAL (Brasseries Kronenbourg, Strasbourg, France) as strain CST 10961
CNRZ 1887	Beer contaminant, obtained from the strain collection of TEPRAL (Brasseries Kronenbourg, Strasbourg, France) as strain CST 10957
61D	CIP 104445; human feces (received from F. Gasser, Institut Pasteur, Paris, France)
ATCC 10776	CNRZ 1888
<i>L. paracasei</i> ATCC 334	Emmental cheese
<i>L. casei</i> NCIMB 11970 ^T	Cheese
<i>L. rhamnosus</i> DSM 20021 ^T	
<i>L. sake</i> INRA 300	Vacuum-packaged beef (obtained from M.-C. Montel, INRA, Theix, France)

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^a ATCC, American Type Culture Collection, Rockville, Md.; CNRZ, Centre National de Recherches Zootechniques, Jouy-en-Josas, France; DSM, Deutsche Sammlung von Mikroorganismen, Braunschweig, Germany; NCFB, National Collection of Food Bacteria, Reading, United Kingdom; NCIMB, National Collection of Industrial and Marine Bacteria, Aberdeen, Scotland, United Kingdom; INRA, Institut National de la Recherche Agronomique.

TABLE 2. DNA base compositions, thermal stabilities, and levels of DNA hybridization for *L. paraplantarum* strains and other *Lactobacillus* strains

Strain	G+C content (mol%)	Thermal stability (°C) of duplexes formed with ³ H-labeled CNRZ 1885 ^T DNA	% Relative binding with [³ H]DNA from:					
			<i>L. paraplantarum</i> CNRZ 1885 ^T	<i>L. pentosus</i> NCFB 363 ^T	<i>L. plantarum</i> ATCC 14917 ^T	<i>L. paracasei</i> ATCC 334	<i>L. casei</i> NCIMB 11970 ^T	<i>L. rhamnosus</i> DSM 20021 ^T
<i>L. paraplantarum</i> CNRZ 1885 ^T	44	0	100	14	42	0	9	3
<i>L. paraplantarum</i> CNRZ 1887	44		100	15	43	0	9	3
<i>L. paraplantarum</i> 61D	44	0.6	72	20	41			
<i>L. paraplantarum</i> ATCC 10776	45		100	23	56			
<i>L. plantarum</i> ATCC 14917 ^T	41	7	29	15	100			
<i>L. pentosus</i> NCFB 363 ^T	42	13	26	100	20			

were centrifuged, and 1 ml of distilled water, 1 ml of H₂SO₄/H₃PO₄ (1:3), and 0.13 ml of 3% (wt/vol) diacetylmonoxime were added to 1 ml of the culture supernatant. An orange color appeared after the preparations were boiled for 10 min, and this allowed us to detect the arginine degradation product, citrulline. *Lactobacillus sake* INRA 300 was used as the positive control. Strains were tested for their sugar fermentation abilities by using the API 50 CHL system (bioMérieux). The inocula were taken directly from MRS agar. The test preparations were incubated at 30°C, and readings were obtained after 24, 48, and 72 h. For the peptidoglycan analysis we used cells obtained from MRS agar that were cultivated in 40 ml of MRS broth for 24 h at 30°C in a CO₂-enriched atmosphere. The method used to prepare and hydrolyze cell walls was the rapid screening method described by Schleifer and Kandler (16). The cell walls were partially hydrolyzed with 4 M HCl for 2 h and analyzed by thin-layer chromatography (15). The hydrolysates were spotted onto a Silica Gel G layer (20 by 20 cm; Polygram SIL G/UV₂₅₄; Macherey-Nagel) and separated by using a CHCl₃-methanol-17% NH₃ (2:2:1, vol/vol/vol) solvent system for 5 to 6 h. Spots were made visible with ninhydrin (15). To assay the isomers of lactic acid, cells were subcultured in 8 ml of MRS broth under the conditions described above. A 0.1-ml portion of growth medium supernatant was assayed to determine its D-(-)- and L-(+)-lactic acid contents by using D-(-)-lactate dehydrogenase from *Lactobacillus leichmannii*

(Boehringer Mannheim) and L-(+)-lactate dehydrogenase from rabbit muscle (Boehringer Mannheim). A 0.1-ml portion of the cell-free supernatant was mixed with a solution containing 0.3 ml of 0.5 M hydrazine-0.6 M glycine buffer (pH 9.2), 0.6 ml of distilled water, 1.5 mg of NAD, and 7.5 µl of L-(+)- or D-(-)-lactate dehydrogenase. After incubation for 15 min at 37°C, the A₃₄₀ was determined with a Uvikon 930 spectrophotometer (Kontron Instruments). In the control, the supernatant was replaced with distilled water. DNA was extracted by the method of Brenner et al. (1), as modified by Champomier et al. (4). Our determination of the G+C content of the DNA (14) was based on the fact that the absorbance of DNA is similar to the absorbance of nucleotides at pH 3. Therefore, the ratio of the molar extinction coefficient at 260 nm to the molar extinction coefficient at 280 nm of a DNA solution determined in 0.1 M acetic acid (pH 3) is a function of the G+C content of the DNA. The absorbance profiles of 50-µg/ml DNA solutions were determined by using a Uvikon 930 spectrophotometer (Kontron Instruments). The DNA used for DNA-DNA hybridization experiments was labeled with [³H]dCTP (30 Ci mmol⁻¹) by using a nick translation kit (Amersham) as recommended by the manufacturer. The methods used for dialysis and S1 nuclease hydrolysis of the probe have been described by Grimont et al. (12). Preparations were hybridized at 70°C in 0.42 M NaCl for 16 h. We used the S1 nuclease-trichloroacetic acid method (6) as modified by Gri-

TABLE 3. Physiological and biochemical characteristics of *L. paraplantarum* strains and *L. plantarum* and *L. pentosus* type strains^a

Strain	Growth in MRS medium containing:				Growth at:							Peptidoglycan type	Lactic acid isomers	Gas produced from glucose	Gas produced from gluconate	Degradation of arginine
	4% NaCl	6% NaCl	8% NaCl	10% NaCl	pH 4	pH 5	pH 7	15°C	30°C	37°C	45°C					
ATCC 14917 ^T	+	+	+	-	-	+	+	+	+	+	-	mDAP	D,L	-	+	-
NCFB 363 ^T	+	+	+	-	-	+	+	+	+	+	-	mDAP	D,L	-	+	-
CNRZ 1885 ^T	+	+	+	-	-	+	+	+	+	+	-	mDAP	D,L	-	+	-
CNRZ 1887	+	+	+	-	-	+	+	+	+	+	-	mDAP	D,L	-	+	-
61D	+	+	+	-	-	+	+	+	+	+	-	mDAP	D,L	-	+	-
ATCC 10776	+	+	+	-	-	+	+	+	+	+	-	mDAP	D,L	-	+	-

^a +, positive reaction or growth; -, negative reaction or no growth; mDAP, meso-diaminopimelic acid; D, D-(-)-lactic acid; L, L-(+)-lactic acid. Strains CNRZ 1885^T and CNRZ 1887 grew poorly when gluconate was the sole source of carbohydrate. Strains ATCC 14917^T, NCFB 363^T, and 61D grew faster (24 to 48 h) than the other strains (72 h) in MRS medium containing 8% NaCl.

mont et al. (12). When the thermal stability of duplexes was tested, the temperature was raised in 5°C increments after hybridization at 70°C. Each time that the temperature was raised, a 100-μl sample of reassociated DNA was hydrolyzed with S1 nuclease (15 μl) and then treated as described above in the liquid DNA-DNA hybridization procedure. We then extrapolated the temperature at which 50% of the double-stranded DNA was denatured (T_m). The ΔT_m was the difference between the T_m of the homologous duplex and that of the heterologous duplex.

We found that strains CNRZ 1885^T, CNRZ 1887, ATCC 10776, and 61D had a Southern-type hybridization profile different from that of the *L. plantarum* type strain, strain ATCC 14917 (2). The results of DNA-DNA hybridization experiments performed with these strains are shown in Table 2. If two strains belong to the same species, the level of relative binding of their DNAs is more than 70% (17) and the thermal stability of the heteroduplex is less than 5°C (11). The four strains which we studied exhibited 41 to 56% relatedness to the *L. plantarum* type strain and 14 to 23% relatedness to the *L. pentosus* type strain. Dellaglio et al. (8) have previously observed low levels of DNA hybridization between strain ATCC 10776 and the *L. plantarum* and *L. pentosus* type strains. We chose CNRZ 1885^T as the reference strain; strains ATCC 10776, 61D, and CNRZ 1887 exhibited 72 to 100% relatedness to CNRZ 1885^T (Table 2). Since strain 61D had the lowest level of relative binding (72%), the thermal stability of the heteroduplex was determined, and the value obtained was 0.6°C; therefore, the four strains which we studied belong to one genotypic taxon. Since some strains of *Lactobacillus casei*, *Lactobacillus rhamnosus*, and *Lactobacillus paracasei* have physiological characteristics similar to those of *L. plantarum*, CNRZ 1885^T and CNRZ 1887 were hybridized with these lactobacilli, and the levels of relative binding obtained were less than 9% (Table 2). Moreover, the thermal stability value of the *L. plantarum* type strain-strain CNRZ 1885^T heteroduplex was 7°C and the thermal stability value of the *L. pentosus* type strain-strain CNRZ 1885^T heteroduplex was 13°C. These data confirmed that CNRZ 1885^T belongs to a distinct species which differs from the closely related species *L. plantarum* and *L. pentosus*. The four strains which we studied also had G+C contents of 44 to 45 mol%; these values were somewhat higher than the values obtained for *L. plantarum* and *L. pentosus* (41 and 42 mol%, respectively) (Table 2). Other *Lactobacillus* species have similar G+C contents, as follows: *Lactobacillus graminis*, 41 to 44 mol%; *Lactobacillus murinus*, 43 to 44 mol%; and *L. sake* and *Lactobacillus curvatus*, 42 to 44 mol%. On the basis of the results of a 16S rRNA sequence phylogenetic analysis, Collins et al. (5) showed that within the *L. casei*-*Pediococcus* cluster *L. graminis*, *L. curvatus*, and *L. sake* form a clade which does not include *L. plantarum*. A partial 16S rRNA sequence of strain ATCC 10776 has been shown to be identical to sequences of *L. plantarum* and *L. pentosus*, confirming that *L. paraplantarum* is distinct from *L. sake*, *L. curvatus*, and *L. graminis* (13). *L. paraplantarum* is also distinct from *L. murinus* as shown by the results of a restriction fragment length polymorphism analysis of the pyrimidine genes (2) performed with *L. murinus* type strain CNRZ 220^T (data not shown).

We also studied physiological and biochemical characteristics of strains CNRZ 1885^T, CNRZ 1887, 61D, and ATCC 10776 (Table 3). These four strains could not be distinguished from the *L. pentosus* and *L. plantarum* type strains on the basis of the data obtained for most of the physiological and biochemical characteristics studied; none of the strains grew in the presence of NaCl concentrations greater than 8%, at pH 4, or

TABLE 4. Carbohydrate utilization profiles of *L. paraplantarum* strains and *L. plantarum* and *L. pentosus* type strains

Strain	Utilization of "a"																			
	Glycerol	L-Arabinose	Ribose	D-Xylose	Galactose	D-Glucose	D-Fructose	D-Mannose	Rhamnose	Mannitol	Sorbitol	α-Methyl-D-mannoside	N-Acetylglucosamine	Amygdalin	Arbutin	Esculin	Salicin	Cellobiose	Maltose	Lactose
ATCC 14917 ^T	-	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
NCFB 363 ^T	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
ATCC 10776	-	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
CNRZ 1887	-	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
CNRZ 1885 ^T	-	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
61D	-	+	+	-	+	+	+	+	-	+	+	+	+	+	+	+	+	+	+	+

"a" +, positive reaction; +, weakly positive reaction; -, negative reaction. None of the strains utilized the following substances: adonitol, D-arabinose, L-arabitol, dulcitol, erythritol, D-fructose, L-fucose, glycogen, inositol, inulin, 2-keto-gluconate, 5-keto-gluconate, D-lyxose, β-methyl-xyloside, α-methyl-D-glucoside, L-sorbose, starch, D-tagatose, xylitol, and L-xylose.

at 45°C, all strains had *meso*-diaminopimelic acid in the peptidoglycan and produced DL-lactic acid, and none of the strains deaminated arginine (Table 3). All of the strains were facultatively heterofermentative. Thus, the four strains which we studied could not be distinguished from *L. plantarum* or *L. pentosus* by these physiological characteristics but could be distinguished from the other streptobacterial species. Gasser (10) showed that the lactic acid dehydrogenase zymogram of strain 61D differed from the lactic acid dehydrogenase zymograms of *L. plantarum* strains. Strain 61D has one-NAD-dependent L(-)-lactic acid dehydrogenase and one NAD-independent D(+)-lactic acid dehydrogenase, while *L. plantarum* has two NAD-dependent L(-)- and D(+)-lactic acid dehydrogenases. Strain 61D contains many plasmids, and one of them is similar to plasmid pLP1 isolated from *L. plantarum* CCM 1904 (3). Sugar fermentation profiles (Table 4) revealed that the four strains which we studied and *L. plantarum* can be differentiated from the type strain of *L. pentosus* and most of the strains of this species (2) by glycerol and D-xylose fermentation and not by melezitose fermentation. The four strains which we studied (Table 4) could be distinguished from *L. plantarum* by the fact that 66% of the *L. plantarum* strains but none of the four strains which we studied were able to use α -methyl-D-mannoside, as shown by Bringel et al. (2).

L. plantarum, *L. pentosus*, and the four strains which we studied are difficult to distinguish on the basis of phenotypic characteristics. On the other hand, strains CNRZ 1885^T, CNRZ 1887, 61D, and ATCC 10776 can be clearly differentiated from *L. plantarum* and *L. pentosus* by using DNA similarity values. We decided to name the new species *L. paraplantarum* because of its phenotypic similarity to *L. plantarum*. A description of *L. paraplantarum* is given below.

Description of *Lactobacillus paraplantarum* sp. nov. *Lactobacillus paraplantarum* (pa. ra. plan. tar' um. Gr. prep. para, resembling; L. gen. n. *plantarum*, specific epithet of *L. plantarum*; M. L. adj. *paraplantarum*, resembling *L. plantarum*). Cells are rod shaped and occur singly, in pairs, and sometimes in short chains. Colonies grown on MRS agar are round, smooth, dome shaped, and creamy colored. Cells are nonmotile, Gram positive, catalase negative, and facultatively anaerobic. Grows at 15 (slowly), 30, and 37°C, but not at 45°C. Grows in MRS medium at pHs 5 and 7, but not at pH 4. Grows in MRS medium containing NaCl up to a concentration of 8%. Facultatively heterofermentative, producing D(-)- and L-(+)-lactic acids. All strains ferment ribose, galactose, D-glucose, D-fructose, D-mannose, mannitol, N-acetylglucosamine, amygdalin, arbutin, salicin, cellobiose, maltose, lactose, melibiose, sucrose, trehalose, melezitose, β -gentiobiose, and gluconate. All strains do not ferment glycerol, erythritol, D-arabinose, D-xylose, L-xylose, adonitol, β -methyl-xyloside, L-sorbose, dulcitol, inositol, α -methyl-D-mannoside, α -methyl-D-glucoside, inulin, starch, glycogen, xylitol, D-lyxose, D-tagatose, D-fucose, L-fucose, L-arabitol, 2-keto-gluconate, and 5-keto-gluconate. Some strains ferment L-arabinose, L-(+)-rhamnose, sorbitol, D-raffinose, D-turanose, and D-arabitol. Esculin is hydrolyzed. Arginine is not deaminated. The peptidoglycan is characterized by the presence of *meso*-diaminopimelic acid. The G+C content of the DNA ranges from 44 to 45 mol%. Strains have

been isolated from beer and human feces in France. The type strain is CNRZ 1885. In most respects, the description of the type strain resembles that of the species. The type strain was isolated from beer, ferments D-raffinose, and does not ferment L-arabinose, sorbitol, D-turanose, and D-arabitol. Its DNA G+C content is 44 mol%.

We thank F. Gasser and M.-C. Montel for sending strains and M. Simon for technical assistance. We also thank P. Tailleux for communicating data prior to publication.

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