

Lactobacillus oligofermentans sp. nov., Associated with Spoilage of Modified-Atmosphere-Packaged Poultry Products

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Unidentified lactic acid bacterium (LAB) isolates which had mainly been detected in spoiled, marinated, modified atmosphere packaged (MAP) broiler meat products during two previous studies, were identified and analyzed for their phenotypic properties and the capability to produce biogenic amines. To establish the taxonomic position of these isolates, 16S rRNA gene sequence analysis, numerical analysis of ribopatterns, and DNA-DNA hybridization experiments were done. Unexpectedly for a meat-spoilage-associated LAB, the strains utilized glucose very weakly. According to the API 50 CHL test, arabinose and xylose were the only carbohydrates strongly fermented. None of the six strains tested for production of histamine, tyramine, tryptamine, phenylethylamine, putrescine, and cadaverine were able to produce these main meat-associated biogenic amines in vitro. The polyphasic taxonomy approach showed that these strains represent a new *Lactobacillus* species. The six isolates sequenced for the 16S rRNA encoding genes shared the highest similarity (95.0 to 96.3%) with the sequence of the *Lactobacillus durianis* type strain. In the phylogenetic tree, these isolates formed a distinct cluster within the *Lactobacillus reuteri* group, which also includes *L. durianis*. Numerical analyses of HindIII-EcoRI ribotypes placed all isolates together in a cluster with seven subclusters well separated from the *L. reuteri* group reference strains. The DNA-DNA hybridization levels between *Lactobacillus* sp. nov. isolates varied from 67 to 96%, and low hybridization levels (3 to 15%) were obtained with the *L. durianis* type strain confirming that these isolates belong to the same species different from *L. durianis*. The name *Lactobacillus oligofermentans* sp. nov. is proposed, with strain LMG 22743^T (also known as DSM 15707^T or AMKR18^T) as the type strain.

In recent years, the consumption of broiler meat has been increasing in Finland. Marinated broiler meat cuts packaged under a modified atmosphere (MA) are favored especially by consumers. Marinating in this context means mixing the meat cuts with acidic (acetic or citric-acid-containing) emulsified water-oil sauces which contain glucose or sucrose, NaCl, rheology-improving additives (like xanthan gum or guar gum), antimicrobial agents (sorbate and/or benzoate), aroma and flavor enhancers (sodium glutamate or yeast extract), and various spices. It has been estimated by Finnish meat producers that about 80% of the poultry meat is now sold at the retail level as marinated and MA packaged (MAP). Lactic acid bacteria (LAB), mainly *Lactobacillus* and *Leuconostoc* species, are usually the dominant spoilage organisms in cold-stored MAP meat products (8). However, although they also play a major role in raw MAP broiler products (6, 19), only three studies have to our knowledge dealt with the characterization of LAB species associated with these products (5, 6, 21).

Björkroth et al. (6) described an unusual spoilage phenomenon in MAP tomato-marinated broiler meat strips stored at 6°C. The products showed bulging due to gas formation already 5 days after packaging. On the last day of shelf life, the product pH was raised from the initial levels of 4.2 to 4.4

obtained by mixing with the acidic marinade to levels between 4.7 and 5.0. This was considered, but not verified, to indicate possible “protein swell spoilage” (17) since usually LAB lower the pH while utilizing carbohydrates present in the food. In protein swell, proteins are decomposed by proteolytic enzyme action and the subsequent decarboxylation of amino acids leads to the production of CO₂ and biogenic amines. Decrease in acidity has been attributed to the production of ammonia by the bacterial deamination of amino acids. To identify the spoilage organisms associated with this product, the 16 and 23S HindIII restriction fragment length polymorphism (RFLP) patterns (HindIII ribopatterns) of the isolates were compared to the corresponding patterns in the previously established LAB database (14) at the Department of Food and Environmental Hygiene, University of Helsinki, Helsinki, Finland. This database comprised about 2,400 isolates (nowadays, about 4,000) and type strains (about 200) of all relevant spoilage LAB in the genera of *Carnobacterium*, *Lactobacillus*, *Leuconostoc*, *Enterococcus*, and *Weissella* (2, 3, 4, 6, 14). The dominating organism was found to be a novel coccoid LAB species for which the name *Leuconostoc gasicomitatum* was proposed. A group of unidentified gram-positive, rod-shaped LAB was also detected in this study (6). The ribopatterns of these strains clustered together in the numerical analysis but remained apart from the typical meat spoilage LAB.

Later, in three independent studies of other MAP broiler products, several new isolates resembled the initial 12 isolates by their ribotypes. Thirty-seven isolates were found during an

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TABLE 1. Sources and references of the isolates and their division between the six ribogroups

HindIII ribogroup	Producer	No. of strains	Product type	Reference, if exists (group ^a)
I	A	2	Broiler leg, marinated	6 (unknown)
		9	Broiler leg, tomato marinated	
IIa	B	7	Broiler leg, marinated	5 (UVIIIb)
IIb	B	8	Broiler leg, marinated	5 (UVIIIa)
III	A	2	Broiler leg and breast filet, both nonmarinated	6 (unknown)
		4	Broiler leg, three marinated and one nonmarinated	
IV	C	2	Broiler leg, nonmarinated	5 (UVII)
		1	Broiler meat strips, marinated	
		22	Broiler leg, marinated	
V	B	2	Broiler leg, tomato marinated	6 (unknown)
		6	Five filet strips and one breast filet, all nonmarinated	
		2	Minced meat	

^a Name of the corresponding group in the reference.

investigation of initial (three isolates) and spoilage (34 isolates) bacterial populations in marinated MAP broiler legs (5). One isolate had been detected in a study of bacterial population of marinated MAP broiler meat strips analyzed on sell-by day (21). Eighteen isolates have recently been found in marinated (five isolates) and nonmarinated (13 isolates) MAP broiler products (legs, meat strips, breast filet, or minced meat) also analyzed at the end of shelf life (unpublished data). These studies involved products manufactured by three completely distinct large-scale plants purchasing the broiler chickens from contract farmers supplying to only one manufacturer.

Due to the continuous detection in spoiled or late-shelf-life products, this study was carried out to clarify the taxonomic status of these unidentified isolates and to evaluate if they form biogenic amines from the typical meat-associated amino acids. A polyphasic approach, including numerical analysis of ribopatterns (16 and 23S rRNA gene RFLP patterns), 16S rRNA gene sequence analysis, DNA-DNA hybridization, and examination of phenotypic properties, was used for species description, and the formation of histamine, tyramine, tryptamine, phenylethylamine, putrescine, and cadaverine was measured by a high-performance liquid chromatography (HPLC) technique.

MATERIALS AND METHODS

Bacterial strains, the use of strains in different phases of the study, and culturing of these strains. Sixty-seven isolates with similar HindIII ribopatterns were detected in the earlier studies. In the preliminary numerical analyses, these isolates were divided into six different groups (I, IIa, IIb, III, IV, and V) according to their HindIII ribopatterns. Table 1 shows the source and reference (if existing) of the isolates and their division between the six ribogroups. To the present study, four to six isolates were selected randomly from each ribogroup unless the group contained only two isolates (I and III).

The HindIII ribotyping of the selected 26 isolates was repeated, and they were also subjected to EcoRI ribotyping. Sets of 6 to 11 isolates, representing each of the HindIII-deficient clusters (Fig. 1), were selected for further studies. Pheno-

typical testing was carried out using 11 isolates (1-1, 5-14, 406, 423, 518, 533, 557, AMKR18^T, AMKR26, AMKR33, MARL13) with the exception of determination of lactic acid configuration, which was studied using six isolates (5-14, 423, 557, AMKR18^T, AMKR26, MARL13). The HPLC analysis of biogenic amine forming capacity was carried out using six isolates (5-14, 423, 533, AMKR18^T, AMKR26, MARL13). The phylogenetic analysis based on 16S rRNA gene sequences was carried out using six isolates and GenBank entries of type strains belonging to the *Lactobacillus reuteri* group (Fig. 2). For the DNA-DNA hybridization experiments, eight isolates (Table 2) and the *Lactobacillus durianis* type strain LMG 19193^T were selected on the basis of the results obtained in the BLAST search of 16S rRNA gene sequences.

All isolates were routinely cultured at 25°C either overnight in MRS broth (Difco, BD Diagnostic Systems, Sparks, MD) or for 5 days on MRS agar plates (Oxoid, Hampshire, United Kingdom). The plates were incubated under an anaerobic CO₂ atmosphere (9 to 13% CO₂ according to the manufacturer; Anaerogen, Oxoid). All isolates were maintained in MRS broth (Difco) at -70°C.

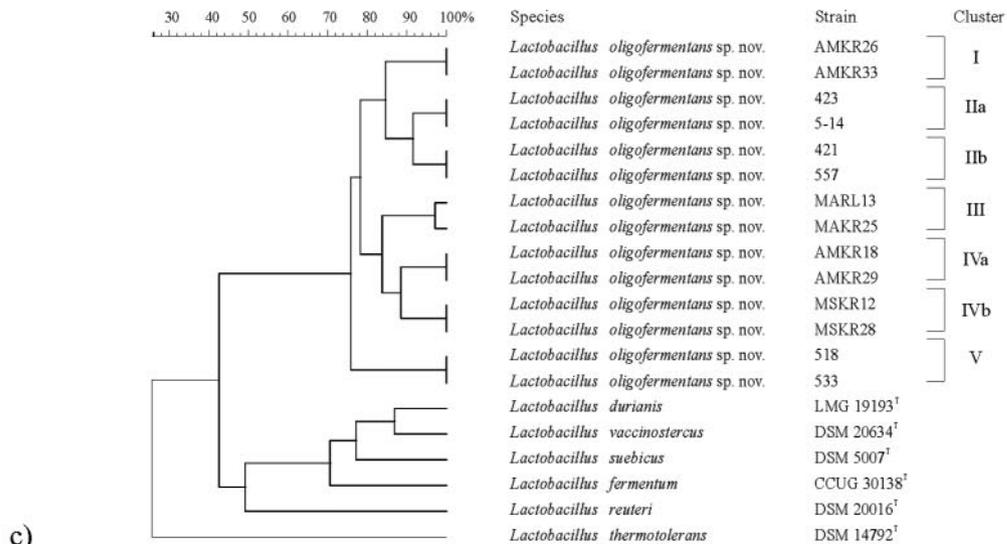
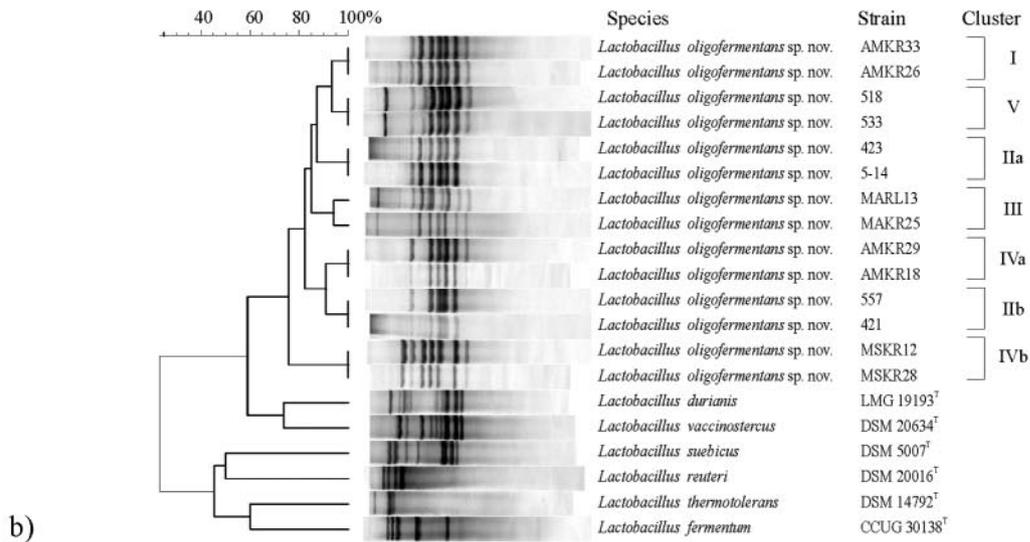
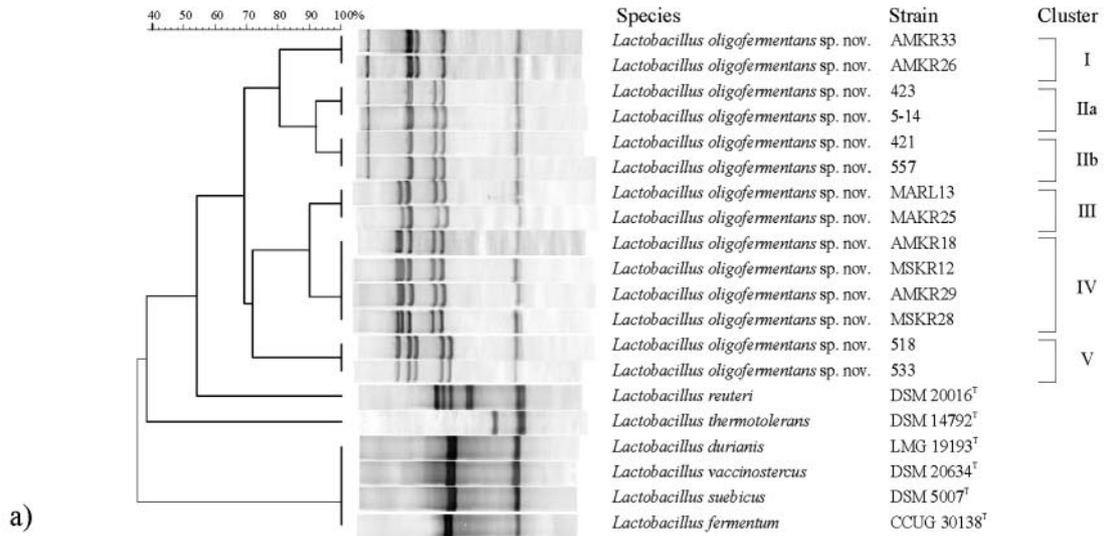
DNA isolation and 16S rRNA gene sequence analysis. DNA for all DNA-based analyses was isolated as previously described by Björkroth et al. (2). The nearly complete (at least 1,400 bases sequenced) 16S rRNA gene was amplified by PCR with a universal primer pair, F8-27 (5'-AGAGTTTGATCCTGGCTGAG-3') and R1541-1522 (5'-AAGGAGGTGATCCAGCCGCA-3'). Sequencing of the purified (QIAquick PCR purification kit; QIAGEN, Venlo, The Netherlands) PCR product from both directions was performed by Sanger's dideoxynucleotide chain termination method using primers F19-38 (5'-CTGGC TCAGGAYGAACGCTG-3'), F926 (5'-AACTCAAAGGAATTGACGG-3'), R519 (5'-GTATTACCGCGGCTGCTG-3'), and R1541-1522. Samples were run in a Global IR² sequencing device with e-Seq 2.0 software (LiCor, Lincoln, NE) according to the manufacturer's instructions. The consensus sequences of these strains (created with AlignIR software; LiCor) and representative strains belonging to the same phylogenetic group (retrieved from GenBank [http://www.ncbi.nlm.nih.gov], using BLASTN 2.2.6 [1]) were aligned, and a phylogenetic tree was constructed based on the neighbor-joining method using the BioNumerics 3.5 software package (Applied Maths, Sint-Martens-Latem, Belgium). Figure 2 shows the accession numbers of the 16S rRNA gene sequences used and deposited during the study.

DNA base composition and DNA-DNA hybridization. For the determination of the G+C content, DNA was enzymatically degraded into nucleosides as described by Mesbah et al. (16). The obtained nucleoside mixture was then separated by HPLC using a Waters SymmetryShield C₈ column thermostated at 37°C. The solvent was 0.02 M NH₄H₂PO₄ with 1.5% acetonitrile. Nonmethylated λ phage DNA (Sigma) was used as the calibration reference. DNA-DNA hybridizations were performed with photobiotin-labeled probes in microplate wells as described by Ezaki et al. (10) using an HTS7000 bioassay reader (Perkin-Elmer) for the fluorescence measurements. The hybridization temperature was 35°C in 50% formamide.

Ribotyping and numerical analyses of ribopatterns. HindIII and EcoRI enzymes were used for the digestion of DNA as specified by the manufacturer (New England Biolabs, Beverly, MA). Restriction enzyme analysis, Southern blotting, hybridization, and detection of the digoxigenin label were performed as described previously (2). Labeling of the cDNA probe used was done by avian myeloblastosis virus reverse transcription (Promega) and Dig labeling kit; Roche Molecular Biochemicals, Mannheim, Germany) (7).

Scanned (Hewlett Packard Scan Jet 4c/T, Palo Alto, CA) ribopatterns were analyzed using the BioNumerics 3.5 software package. The similarity between all pairs was expressed by the Dice coefficient correlation, and unweighted-pair group method using average linkages clustering was used for construction of the dendrograms. Based on the use of internal controls, a position tolerance of 1.5% was allowed for the bands.

Morphology and phenotypical tests. All strains were Gram stained. For the size and precise morphology determination by transmission electron microscopy, cells of strains AMKR26, AMKR18^T, and 557 were suspended in physiological NaCl, negatively stained with 1% phosphotungstic acid, and examined using the JEM 100 electron microscope (JEOL, Toyo, Japan). All the phenotypical tests were done at 25°C, unless otherwise stated, and each test was carried out at least twice. Growth at different temperatures (4, 15, and 37°C) or in the presence of NaCl (2%, 4%, and 6.5%, wt/vol) was tested in MRS broth (Difco) incubated until growth was observed or otherwise at least for 21 days. Configuration of lactic acid was determined enzymatically by using the UV method according to Hohorst (12) and Stetter (20). Carbohydrate fermentation profiles were tested using API 50 CHL (bioMérieux, Marcy l'Etoile, France) according to the manufacturer's instructions. Gas formation from glucose was tested according to the method of Gibson and Abdel-Malek (11).



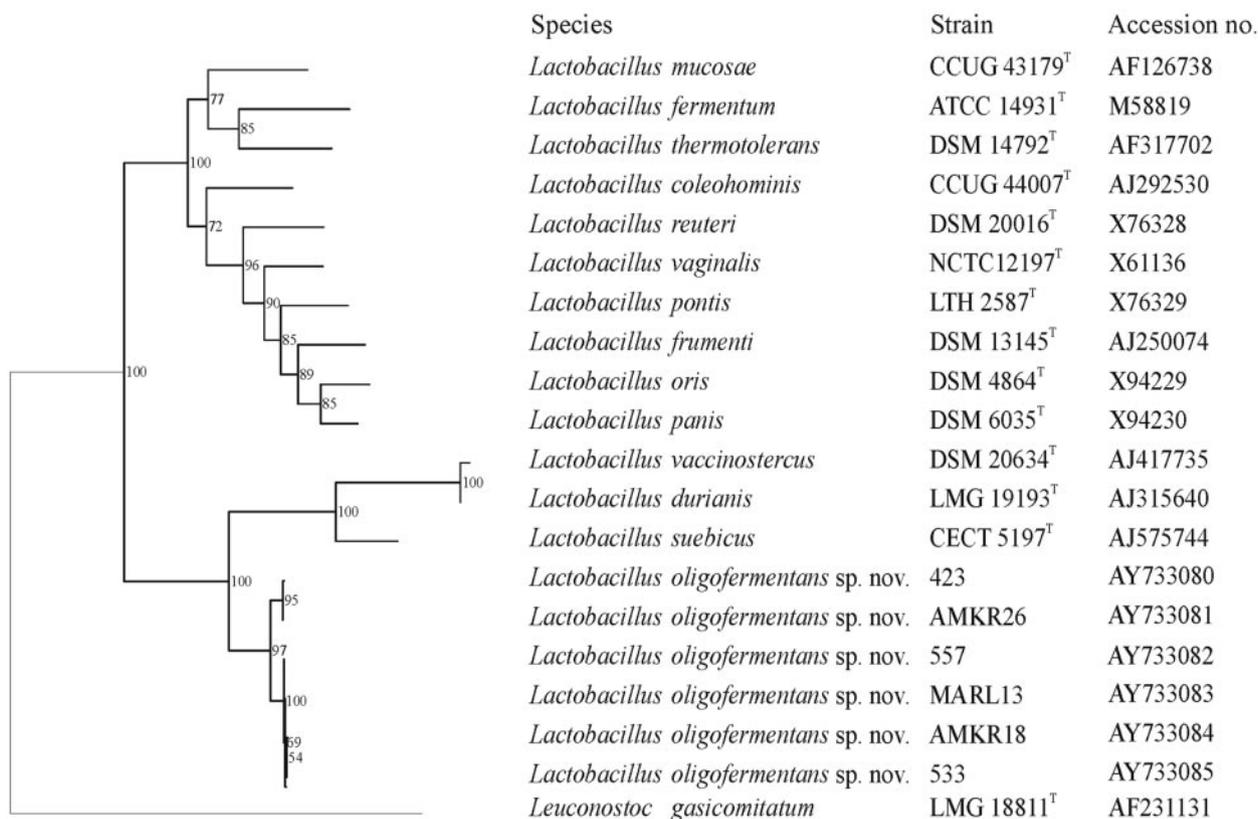


FIG. 2. Phylogenetic tree based on homologies of the almost entire 16S rRNA gene sequences (at least 1,400 bp) of *Lactobacillus oligofermentans* sp. nov. and its phylogenetic neighbors. Bootstrap probability values from 500 trees resampled are given at the branch points.

Confirmation of biogenic amine formation. The amine-forming capacity was studied by a liquid chromatographic method described by Maijala and Eerola (15) and Eerola et al. (9). The potential formation of histamine, tyramine, tryptamine, phenylethylamine, putrescine, and cadaverine was tested.

Strains were adapted for 24 h at 25°C in MRS broth (pH 6.3) containing 2.0 g/liter of each precursor amino acid (separately). The precursor amino acids were L-histidine, L-tyrosine, L-tryptophane, L-phenylalanine, L-lysine (monohydrochloride), and L-ornithine (monohydrochloride). Next, 100 µl of broth was further transferred to another tube of the same medium and incubated at 25°C for 48 h. One ml of each fermented broth was extracted with (0.4%) perchloric acid and analyzed by accredited the high-performance liquid chromatography method (SFS-EN ISO/IEC 17025) by their dansyl derivatives using a Hewlett Packard (Waldbronn, Germany) HPLC system 1090 M. The results were confirmed by positive controls.

RESULTS

16S rRNA gene sequence comparison, mean base composition of DNA, and DNA-DNA reassociation studies. In the BLAST analysis, the 16S rRNA gene sequences of the isolates 423, 553, 557, MARL13, AMKR26, and AMKR18^T possessed the highest similarities with *L. durianis* type strain LMG 19193^T (similarity between 95.0 and 96.3%), *Lactobacillus vaccinostercus* (92.7%), and *Lactobacillus suebicus* (from 95.8 to

96.0%). These species belongs to the *L. reuteri* phylogenetic group of the genus *Lactobacillus*. Figure 2 shows the distance matrix tree based on the 16S rRNA gene similarities, and the accession numbers of the 16S rRNA gene sequences used and deposited are also shown in the figure. However, it should be noted that the sequence (AJ417735) of *L. vaccinostercus* deposited into GenBank is relatively short (508 bp) compared to the other sequences (about 1,500 bp) used in the study.

The C+G content of the strains studied was 35.3 to 39.9%. Table 2 presents the DNA-DNA hybridization results. Reassociation values between *Lactobacillus oligofermentans* isolates and *L. durianis* LMG 19193^T varied from 3 to 15%, whereas values among the eight *L. oligofermentans* isolates varied from 67 to 96%.

Numerical analyses of ribopatterns. Figure 1a to c shows the dendrograms and banding patterns based on the HindIII (Fig. 1a) and EcoRI (Fig. 1b) ribotypes together with the dendrogram obtained by combining the unweighted pattern information of both EcoRI and HindIII ribotypes into one numerical analysis (Fig. 1c). In all numerical analyses, *L. oligofermentans* strains clustered together but clearly apart from the other

FIG. 1. Panels a, b, and c present numerical analysis of 16 and 23S RFLP patterns (ribotypes) generated by HindIII, EcoRI, and an analysis combining the information of both restriction enzymes, respectively. Numerical analyses of the patterns are presented as dendrograms; the left side of the HindIII and EcoRI banding patterns possesses high molecular sizes, <23 kbp; the right side of the banding patterns possesses low molecular sizes, >1,000 bp in HindIII patterns and >2,300 bp in EcoRI patterns.

TABLE 2. Results of *L. oligofermentans* sp. nov. DNA-DNA reassociation experiments

HindIII cluster	Strain	% DNA-DNA reassociation with:						
		LMG 19193 ^{Ta}	423	5-14	557	518	MARL13	AMKR18
IIa	423	3						
IIa	5-14	6	93					
IIb	557	7	90	90				
V	518	14	ND ^b	ND	90			
V	533	15	ND	ND	80	96		
III	MARL13	8	ND	ND	ND	ND		
IV	AMKR18	8	74	ND	72	ND	67	
I	AMKR26	4	82	ND	79	ND	90	72

^a LMG 19193^T, *Lactobacillus durianis* type strain.

^b ND, not determined.

species. The strain division between the different *L. oligofermentans* EcoRI clusters resembled the division between the six HindIII clusters detected earlier, with the exception that HindIII-deficient cluster IV was further divided into two subclusters, IVa and IVb. The pattern similarity levels among the *L. oligofermentans* clusters varied from 70.1 to 75.8%, depending on the analysis. The highest similarity between the *L. oligofermentans* clusters and the other species was with the patterns of *L. reuteri* (56.4% in HindIII and 42.5% in combined HindIII-EcoRI) or the *L. durianis* and *Lactobacillus vaccinostercus* (59.0% in EcoRI) type strains.

Phenotypic properties. All isolates studied were gram-positive rods. Figure 3 shows the transmission electron microscopy picture of cells of isolates AMKR26, AMKR18^T, and 557. All isolates grew at 4 and 15°C; none grew at 37°C, indicating the psychrotrophic nature of these strains. All isolates grew in the presence of 2% NaCl but none in the presence of 6.5% NaCl. According to the Gibson and Abdel-Malek (11) test, all isolates produced gas from glucose. However, in the API 50 CHL test, the utilization of D-glucose, gluconate, and N-acetylglucosamine was very weak or delayed. Positive reactions were obtained after a 5-day incubation period, and even then, some of the strains produced weak reactions. Detailed results of the utilization of carbohydrates are given in the species description below. The ratio of L- and D-lactic acids produced was approximately 70/30. None of the isolates produced ammonia from arginine.

DISCUSSION

The results of the present study indicate that the LAB strains detected in various MAP broiler meat products belong to a novel species to which we propose the name *Lactobacillus oligofermentans* sp. nov. (see the species description below). Phylogenetic analysis (Fig. 2) clearly assigned this novel species to the genus *Lactobacillus* and, specifically, to the *L. reuteri* phylogenetic group, with *L. durianis*, *L. vaccinostercus*, and *L. subebicus* as its closest neighbors. The DNA-DNA reassociation experiments, however, clearly distinguished *L. oligofermentans* strains and *L. durianis* type strain LMG 19193^T as two different species. This finding was expected because of the relatively low (identities, 96.3 to 96.2%) 16S rRNA gene sequence similari-

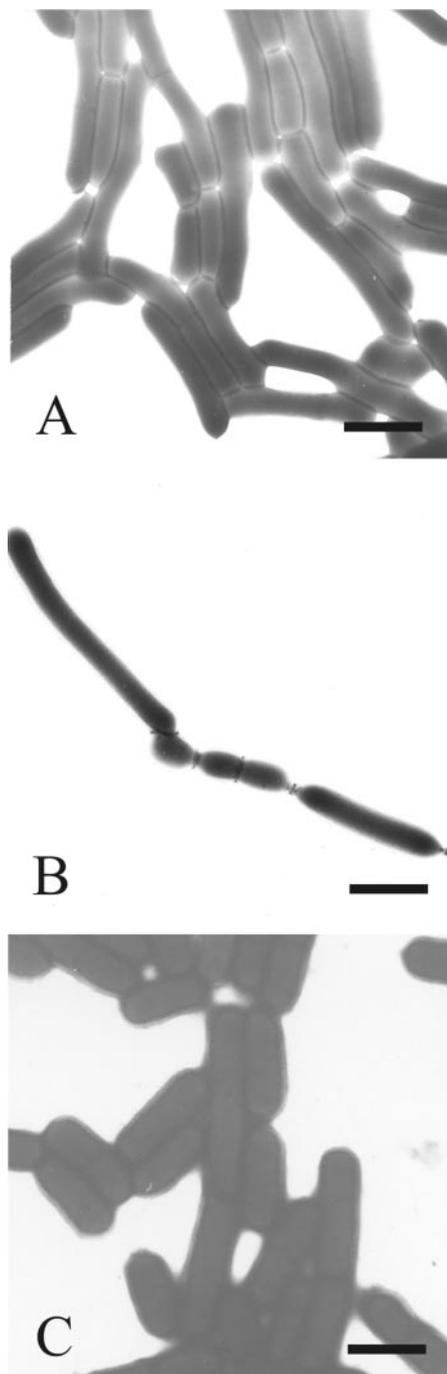


FIG. 3. Transmission electron microscopy picture of negatively stained (1% of phosphotungstic acid) cells of *Lactobacillus oligofermentans* sp. nov. strains AMKR26, AMKR18^T, and 557. Bar length, 2 μ m.

ties between the 6 *L. oligofermentans* strains and the *L. durianis* type strain.

Also in the numerical analysis based on ribotyping, *L. oligofermentans* strains were distinguished from the *L. reuteri* phylogenetic group reference strains (Fig. 1). However, depending on the analysis, *L. oligofermentans* strains possessed pattern variability between 24.3 and 29.9% (Fig. 1). In the DNA-DNA

reassociation experiments, reassociation levels varying from 67 to 96% were detected. Between the strains from same RFLP cluster or subclusters, DNA-DNA reassociation values from 93 to 96% were obtained (Table 2) whereas the lowest value, 67%, was obtained between strains representing clusters III and IV. The variation in the DNA-DNA reassociation results, in the G+C content (35.3 to 39.9%), and in ribopatterns may indicate that *L. oligofermentans* is a heterogeneous species.

All of our *L. oligofermentans* isolates originated from MAP broiler meat products. We have not detected this species from other meat sources. These MAP broiler meat products have included various kinds of nonmarinated and marinated products, such as legs, meat strips, breast filets, and minced meat. Even though the products harboring *L. oligofermentans* have been variable, most (46 of the 67 total) isolates originate from marinated products. We have not yet, however, detected this or other spoilage LAB species in the marinades used for poultry products. It is currently not clear to us why marinating supports the growth of *L. oligofermentans*. The other species, *L. durianis*, *L. vaccinofermentans*, and *Lactobacillus suebicus*, located in the same phylogenetic branch with *L. oligofermentans* based on the 16S rRNA gene sequences (Fig. 2) have been detected in fermented durian fruits (tempoyak), apple and pear mashes, and dried cow dung, respectively. A common feature of these species is that they prefer pentose carbohydrates to hexoses and they all ferment xylose well and glucose poorly.

L. oligofermentans has been detected both in the initial LAB population associated with marinated MAP broiler legs (5) and in late-shelf-life (21) or spoiled products (6). However, two-thirds of the strains have been isolated from spoiled products where the total LAB counts have varied from 10^8 to 10^{10} CFU/g (6). Even though the levels of *L. oligofermentans* have been high in those products, this species has never dominated the spoilage LAB populations. In the studies of Björkroth et al. (5, 6), *L. oligofermentans* formed 10 (as unidentified) and 18% (as Unknown VII, VIIIa, and VIIIb) of the spoilage LAB while the dominating species were *Leuconostoc gasicomitatum* (6) or *Carnobacterium* sp. (5), respectively. As neither broiler meat nor the marinades contain any of the carbohydrates favored by *L. oligofermentans* (ribose, L-arabinose and D-xylose) and the utilization of glucose is slower compared to the glucose utilization of *Leuconostoc gasicomitatum* and carnobacteria, it is not clear how *L. oligofermentans* is able to grow and compete in this mixed population. Instead of competition, some kind of positive growth interaction may exist for *L. oligofermentans*, *Leuconostoc gasicomitatum*, and/or carnobacteria often detected simultaneously.

Rokka et al. (18) studied the formation of biogenic amines in MA-packaged nonmarinated broiler cuts stored at several constant (from 3.4 to 7.7°C) or variable (several temperature schemes mimicking the distribution chain and mean temperatures from 2.9 to 8.3°C) temperatures. They detected tyramine, putrescine, and/or cadaverine after 5 to 9 days of storage, regardless of the storage temperature. Cadaverine was detected not at all or only in insignificant concentrations in packages stored below 6.1°C. Putrescine and tyramine formation was detected also in temperatures below 6°C, but the rate was slower than that at temperatures above 6.1°C. They concluded that the growth of *Enterobacteriaceae*, proteolytic bacteria, and

hydrogen-sulfide-producing bacteria was in association with the amine production. According to their results, the LAB component is not associated with the biogenic amine formation in these products. This is in harmony with our findings since the six *L. oligofermentans* strains tested in this study did not biogenic amines from meat-associated amino acids in vitro form, neither have we associated this ability with *Leuconostoc gasicomitatum* since 20 strains tested by same HPLC approach have all yielded negative results (unpublished results).

Our results show that microbial ecology in marinated MAP poultry products is poorly understood. We have now detected altogether three novel LAB species in these products (6, 13), and our next goal is to understand the metabolism of these species. Glucose has always been considered one of the main substrates of meat-associated LAB, but the poor glucose utilization of *L. oligofermentans*, together with the ability to grow up to high levels, is intriguing. These results indicate that the metabolic properties, and hence the role of *L. oligofermentans* in the spoilage of these products, as well as the interaction of other bacteria with *L. oligofermentans*, are still indistinct and need to be studied further.

Description of *Lactobacillus oligofermentans* sp. nov. *Lactobacillus oligofermentans* (o.li.go.fer.men' tans, Gr. adj. oligos few or little, L. part. adj. fermentans fermenting, N.L. part. adj. oligofermentans fermenting few [substrates]).

Strains are gram-positive, round-ended rods. Size varies extremely, between 0.8 to 3.1 μm in width and 5.0 to 27.0 μm in length, when grown in MRS broth (Fig. 3). Colonies on MRS agar are white, the size varying from 0.5 mm to 2.5 mm. Strains grow well at 15°C and more slowly at 4°C, but no growth is observed at 37°C. All strains grow well in the presence of 2% NaCl, and most (not strains 406 and 423) in the presence of 4% NaCl. None of the strains grows in the presence of 6.5% NaCl.

L- and D-lactic acids are produced at a ratio of 70/30. All strains produced acid from ribose, L-arabinose, and D-xylose, but not from D-arabinose or L-xylose. Utilization of maltose, gluconate, D-glucose, and N-acetylglucosamine is weak or delayed. Strains were negative for adonitol, amidon, amygdalin, arbutine, cellobiose, dulcitol, erythritol, esculine, galactose, glycerol, glycogene, inositol, inuline, lactose, mannitol, melibiose, melezitose, rhamnose, saccharose, salicine, sorbitol, trehalose, xylitol, D-fructose, D-lyxose, D-mannose, D-raffinose, D-tagatose, D-turanose, L-sorbose, D- and L-fucose, D- and L-arabitol, α -methyl-D-mannoside, α -methyl-D-glucoside, β -gentiobiose, β methyl-xyloside, 2 and 5 ceto-gluconate.

The G+C content of DNA is from 35.3 to 39.9%. The type strain is LMG 22743^T (also known as DSM 15707^T or AMKR18^T) isolated from late-shelf-life, modified-atmosphere-packaged, marinated broiler legs. Its G+C content is from 35.9%. Strains 406, 518, and AMKR33 have been deposited in the Belgian Coordinated Collections of Microorganisms LMG Bacteria Collection (Laboratorium voor Microbiologie, Ghent, Belgium) as LMG 22744^T, LMG 22745, and LMG 22746, respectively. Strains 423, 557, AMKR26, 5-14, and MARL13 have been deposited to the German Collection of Microorganisms and Cell Cultures as DSM 15704, DSM 15705, DSM 15706, DSM 15708, and DSM 15709, respectively. The strains originate from MAP raw broiler chicken products.

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