Enterobacter pyrinus sp. nov., an Organism Associated with Brown Leaf Spot Disease of Pear Trees

YOUNG RYUN CHUNG,^{1*} DON J. BRENNER,² ARNOLD G. STEIGERWALT,² BYUNG SUP KIM,³
HEUNG TAE KIM,³ AND KWANG YUN CHO³

Department of Microbiology, Gyeongsang National University, Chinju 660-701,¹ and Agrochemical Screening Center, Korea Research Institute of Chemical Technology, Daejeon 305-606,³ Korea, and Meningitis and Special Pathogens Branch, Division of Bacterial and Mycotic Diseases, National Center for Infectious Diseases, Centers for Disease Control, Atlanta, Georgia 30333²

A new species, *Enterobacter pyrinus*, which was isolated from brown leaf spot lesions on pear trees, is described on the basis of the characteristics of seven strains. These bacteria are gram-negative, facultatively anaerobic, straight rods (0.6 to 1.0 by 1.6 to 2.3 μ m) that are motile and peritrichous. As determined by DNA hybridization (hydroxyapatite method), these seven strains were 97.5% related in both 60 and 75°C reactions, with no evidence of sequence divergence, indicating that they are members of a single species. *E. pyrinus* is most closely related to *Enterobacter gergoviae* (46%) and to *Enterobacter agglomerans* hybridization group XI (37%). *E. pyrinus* is differentiated from *E. gergoviae* by its growth in KCN broth, acid production from *myo*-inositol, and lack of acid production from raffinose. The type strain of *E. pyrinus* is strain KCTC 2520 (= CDC G6570 = ATCC 49851).

Brown leaf spot disease of pear trees was first observed in 1979 and has been epidemic since then in Korea, causing significant losses in pear yields (10). Recently, Chung et al. found that this disease is caused by gram-negative bacteria (8). These authors isolated the pathogenic bacteria from necrotic lesions of pear leaf spots and found them to be a new species that was similar to *Erwinia* species on the basis of morphological, physiological, and biochemical characteristics. The organism was named "*Erwinia pirina*" (8), although this name was never validated in the *International Journal of Systematic Bacteriology* and therefore has no standing in bacterial nomenclature.

Since the genus *Erwinia* is quite heterogeneous and since some species previously included in it have been transferred to the genus *Enterobacter*, it was necessary to further characterize the bacterial isolates from pears both biochemically and by DNA hybridization (4). In this paper we describe the results of these additional studies; on the basis of our results the name *Enterobacter pyrinus* sp. nov. is proposed for the agent of brown leaf spot disease of pears.

MATERIALS AND METHODS

Bacterial strains. A total of 28 strains were isolated from brown leaf spots of pear trees (*Pyrus pyrifolia* cv. Shingo and Mansamgil) in the Yusung area of Korea in 1988 (8). Seven of these strains, strains KCTC 2520^T (T = type strain), KCTC 2585, KCTC 2586, KCTC 2587, KCTC 2588, KCTC 2589, and KCTC 2590, were obtained from the Korean Collection for Type Cultures, Genetic Engineering Research Institute, Korea Institute of Science and Technology, Daejeon, Korea. *Enterobacter dissolvens* ATCC 23373^T, *Erwinia rhapontici* ATCC 29283^T, *Erwinia ananas* ATCC 33244^T, *Erwinia chrysanthemi* ATCC 11663^T, *Erwinia stewartii* ATCC 8199^T, and *Klebsiella pneumoniae* subsp. *oxytoca* ATCC 13182^T were obtained from the American Type Culture Collection, Rockville, Md. Unless noted otherwise,

all strains were maintained on medium containing 1% Casitone (Difco Laboratories, Detroit, Mich.), 0.3% yeast extract, 0.5% NaCl, and 0.7% agar or on nutrient agar at 30°C. All of the DNAs used in DNA hybridization experiments (Table 1) were obtained from strains in the culture collection of the Meningitis and Special Pathogens Laboratory Section, Centers for Disease Control, Atlanta, Ga. (4).

Phenotypic characteristics. The methods described by Schaad (14) were used for the following physiological and biochemical tests: catalase, oxidase, phosphatase, urease, indole production, acetoin production (Voges-Proskauer test), acid production from carbohydrates, utilization of organic compounds, H₂S production from cysteine, gelatin liquefaction, nitrate reduction, erythromycin susceptibility, growth at 36°C, potato soft rot, and tobacco hypersensitivity. Phenylalanine deaminase activity, DNase activity, casein hydrolysis, and motility were tested as described by Smibert and Krieg (15). Mucoid growth was tested on nutrient agar containing 5% sucrose, and tolerance to 5% NaCl was tested in nutrient broth. Tolerance to KCN was determined on Difco KCN broth. Commercial media were used whenever possible. Colonial characteristics and pigment formation were determined on nutrient agar. Cells and flagella were observed by phase-contrast light microscopy and electron microscopy. Inocula for biochemical and physiological tests were prepared from 24-h cultures grown on nutrient agar at 27°C, unless indicated otherwise.

DNA methods. Guanine-plus-cytosine (G+C) contents were determined spectrophotometrically by the method of Marmur and Doty (13) and are reported below to the nearest 0.5 mol%. The methods used to extract and purify DNA and the hydroxyapatite hybridization method for determining levels of DNA relatedness have been described previously (5). Strain KCTC 2520^T was labeled enzymatically in vitro with [³²P]dCTP by using a nick translation reagent kit (Bethesda Research Laboratories, Inc., Gaithersburg, Md.) as directed by the manufacturer. Each G+C content determination and DNA hybridization reaction was done at least twice, and the values obtained were averaged.

* Corresponding author.

TABLE 1. Levels of DNA relatedness between *Enterobacter pyrinus* isolates and between *Enterobacter pyrinus* KCTC 2520^T and representative strains of members of the *Enterobacteriaceae*

Source of unlabeled DNA ^a	Labeled DNA from <i>Enterobacter pyrinus</i> KCTC 2520 ^T		
	Relative binding ratio at 60°C ^b	% Divergence ^b	Relative binding ratio at 75°C
<i>Enterobacter pyrinus</i> KCTC 2520 ^T	100	0.0	100
<i>Enterobacter pyrinus</i> KCTC 2588	100	0.0	100
<i>Enterobacter pyrinus</i> KCTC 2586	99	0.0	99
<i>Enterobacter pyrinus</i> KCTC 2585	99	0.0	97
<i>Enterobacter pyrinus</i> KCTC 2589	97	0.0	96
<i>Enterobacter pyrinus</i> KCTC 2590	96	0.0	96
<i>Enterobacter pyrinus</i> KCTC 2587	94	0.0	97
<i>Enterobacter gergoviae</i> IP 76.01	46	— ^c	
<i>Enterobacter agglomerans</i> CDC 5378-71	37		
<i>Enterobacter gergoviae</i> CDC 2863-76	34		
<i>Cedecea davisae</i> CDC 3278-77	34		
<i>Enterobacter agglomerans</i> CDC 4388-71	33		
<i>Enterobacter aerogenes</i> CDC 1627-66	33		
<i>Enterobacter gergoviae</i> CDC 607-77	32		
<i>Escherichia vulneris</i> CDC 2898-73	32		
<i>Klebsiella pneumoniae</i> CDC 2	29		
<i>Klebsiella terrigena</i> CDC 9001-81	29		
<i>Enterobacter dissolvens</i> ATCC 23373	27		
<i>Enterobacter intermedius</i> CDC 9001-82	26		
<i>Enterobacter agglomerans</i> CDC 2780-70	26		
<i>Klebsiella pneumoniae</i> subsp. <i>rhinoscleromatis</i>	26		
<i>Erwinia milletiae</i> CDC 9572-82	26		
<i>Erwinia herbicola</i> CDC 9571-82	26		
<i>Erwinia persicinus</i> CDC 9108-82	25		
<i>Enterobacter agglomerans</i> CDC 3123-70	25		
<i>Enterobacter agglomerans</i> CDC 219-71	25		
<i>Enterobacter agglomerans</i> CDC 6003-71	24		
<i>Enterobacter nimipressuralis</i> CDC 9912	24		
<i>Enterobacter sakazakii</i> CDC 4562-70	24		
<i>Enterobacter taylorae</i> CDC 2126-81	24		
<i>Klebsiella planticola</i> CDC 4245-72	24		
<i>Cedecea lapagei</i> CDC 485-76	24		
<i>Kluyvera ascorbata</i> CDC 408-78	24		
<i>Erwinia rhapontici</i> ATCC 29283	23		
<i>Enterobacter cloacae</i> CDC 1347-71	23		
<i>Serratia marcescens</i> CDC 868-57	23		
<i>Erwinia amylovora</i> EA178	22		
<i>Erwinia ananas</i> ATCC 33244	22		
<i>Enterobacter agglomerans</i> CDC 5422-69	22		
<i>Enterobacter amnigenus</i> CDC 1325-74	22		
<i>Citrobacter freundii</i> CDC 460-61	22		
<i>Salmonella typhimurium</i> LT2	22		
<i>Klebsiella pneumoniae</i> subsp. <i>oxytoca</i> ATCC 13282	22		
<i>Erwinia chrysanthemi</i> ATCC 11663	21		
<i>Enterobacter agglomerans</i> CDC 1741-71	21		
<i>Serratia ficaria</i> CDC 1165-77	20		
<i>Erwinia stewartii</i> ATCC 8199	20		
<i>Buttiauxella agrestis</i> CDC 1180-81	20		
<i>Edwardsiella tarda</i> CDC 3592-64	20		
<i>Erwinia cypripedii</i> EC155	19		
<i>Erwinia carotovora</i> ATCC 15713	19		
<i>Escherichia blattae</i> CDC 9005-74	19		
<i>Erwinia rubrifaciens</i> ER105	18		
<i>Enterobacter agglomerans</i> CDC 1620-71	18		
<i>Escherichia hermannii</i> CDC 980-72	18		
<i>Leminorella grimontii</i> 1944-81	18		
<i>Shigella flexneri</i> CDC 2746-71	18		
<i>Erwinia carnegieana</i> EC186	17		
<i>Erwinia mallotivora</i> ATCC 2851	17		
<i>Erwinia quercina</i> EQ102	17		
<i>Erwinia psidii</i> CDC 435-84	17		
<i>Enterobacter agglomerans</i> CDC 1429-71	17		
<i>Enterobacter agglomerans</i> CDC 3482-71	17		
<i>Enterobacter agglomerans</i> CDC 6070-69	17		
<i>Obesumbacterium proteus</i> CDC 4302-74	17		

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TABLE 1—Continued

Source of unlabeled DNA ^a	Labeled DNA from <i>Enterobacter pyrinus</i> KCTC 2520 ^T		
	Relative binding ratio at 60°C ^b	% Divergence ^b	Relative binding ratio at 75°C
<i>Erwinia salicis</i> ATCC 15712	16		
<i>Erwinia uredovora</i> CDC 9574-82	16		
<i>Escherichia coli</i> K-12	16		
<i>Erwinia tracheiphila</i> ATCC 33245	15		
<i>Erwinia atroseptica</i> ATCC 33260	15		
<i>Erwinia carotovora</i> subsp. <i>atroseptica</i> ATCC 496	15		
<i>Ewingella americana</i> CDC 1468-78	15		
<i>Klebsiella ozaenae</i> CDC 1660-71	15		
<i>Leminorella richardii</i> CDC 978-82	15		
<i>Rahnella aquatilis</i> CDC 1327-79	12		
<i>Yersinia ruckeri</i> CDC 4535-69	12		
<i>Erwinia carotovora</i> subsp. <i>wasabiae</i> ATCC 43316	11		
<i>Erwinia carotovora</i> subsp. <i>betavasculorum</i> ATCC 8061	11		
<i>Hafnia alvei</i> CDC 5632-72	11		
<i>Budvicia aquatica</i> CDC 440-84	11		
<i>Morganella morganii</i> ATCC 25830	11		
<i>Enterobacter agglomerans</i> CDC 1645-71	10		
<i>Yersinia enterocolitica</i> CDC 497-70	10		
<i>Yokenella regensburgei</i> CDC 329-73	10		
<i>Tatumella ptyseos</i> CDC H36	8		
<i>Xenorhabdus luminescens</i> CDC 9016-80	6		
<i>Providencia rustigiani</i> CDC 2896-68	6		
<i>Xenorhabdus nematophilus</i> CDC 9012-80	5		
<i>Moellerella wisconsensis</i> CDC 2896-78	5		
<i>Proteus mirabilis</i> CDC PR14	5		
<i>Providencia alcalifaciens</i> CDC 3370-67	5		
<i>Providencia rettgeri</i> ATCC 1163	5		
<i>Providencia stuartii</i> CDC 132-68	4		

^a ATCC, American Type Culture Collection, Rockville, Md.; CDC, Centers for Disease Control, Atlanta, Ga.; KCTC, Korean Collection for Type Cultures, Korea Institute of Science and Technology, Daejeon, Korea; IP, Institut Pasteur, Paris, France.

^b Relative binding ratios were calculated as follows: (percentage of heterologous DNA bound to hydroxyapatite/percentage of homologous DNA bound to hydroxyapatite) × 100. The relative binding ratios and divergence values are averages from at least two experiments.

^c —, a blank space indicates that the reaction was not done.

RESULTS

The G+C contents were as follows: 57.5 mol% for strain KCTC 2520^T; 58.5 mol% for strains KCTC 2585, KCTC 2586, KCTC 2587, and KCTC 2589; 60 mol% for strain KCTC 2588; and 61 mol% for strain KCTC 2590.

The levels of relatedness between labeled DNA from strain KCTC 2520^T and unlabeled DNAs from the six other pear leaf strains and from type or reference strains of 89 genospecies belonging to the family *Enterobacteriaceae* are shown in Table 1. The average level of relatedness of the pear leaf strains was 97.5% in both 60 and 75°C reactions. There was no evidence of divergence within the related sequences. DNA from strain KCTC 2520^T exhibited 46% relatedness to *Enterobacter gergoviae* IP 76.01^T DNA and was 37% or less related to the DNAs of all of the other members of the *Enterobacteriaceae* tested (Table 1).

All of the strains of pear leaf bacteria were gram-negative, straight rods (0.6 to 1.1 by 1.6 to 2.3 µm) and were facultatively anaerobic. The cells were motile and peritrichous; four to six flagella were usually discernible (Fig. 1). After 48 h of incubation on nutrient agar, the pear leaf bacteria formed yellowish white, circular, convex, smooth, translucent, butyrous colonies that were approximately 1.5 to 4.0 mm in diameter. The seven strains were homogeneous in their physiological and biochemical properties, which are listed below in the description of the new species.

Biochemically and physiologically, the pear leaf strains were most similar to strains of *Enterobacter gergoviae*,

Enterobacter aerogenes, *Erwinia cypripedii*, and *Erwinia rhapontici* (Table 2). The pear leaf strains were differentiated from *Enterobacter gergoviae* by their ability to produce H₂S, to grow in KCN broth, and to ferment *myo*-inositol and by their inability to ferment raffinose. Reactions that differentiate the pear leaf strains from their other closest phenotypic relatives are shown in Table 2.

DISCUSSION

The seven strains isolated from pear brown leaf spots were homogeneous in their biochemical characteristics and G+C

FIG. 1. Electron micrograph of a negatively stained cell of *Enterobacter pyrinus* KCTC 2520^T. Bar = 1 µm.

TABLE 2. Biochemical and physiological characteristics of *Enterobacter pyrinus* and biochemically similar species

Characteristic	<i>Enterobacter pyrinus</i>	<i>Enterobacter gergoviae</i> ^a	<i>Enterobacter aerogenes</i> ^a	<i>Erwinia cypripedii</i> ^a	<i>Erwinia rhapontici</i>
Motility	+	+	+	+	+
Pink pigment	—	—	—	—	+
Yellow pigment	—	—	—	—	—
Gas produced from D-glucose	+	+	+	+	—
Nitrate reduction	+	+	+	+	+
Indole production	—	—	—	—	—
Voges-Proskauer test	+	+	+	—	+
Growth in KCN broth	+	—	+	+	+
Urease activity	+	+	—	—	—
Gelatin liquefaction	—	—	—	—	—
Acid produced from:					
Melibiose	+	+	+	+	+
myo-Inositol	+	—	+	+	+
Raffinose	—	+	+	—	+
Inulin	—	ND	ND	—	—
Starch	—	ND	ND	—	—
Maltose	+	+	+	+	+
L-Arabinose	+	+	+	+	+
D-Sorbitol	—	—	+	+	+
Ribose	+	ND	ND	+	+
Mannose	+	+	+	+	+
D-Mannitol	+	+	+	+	+
Cellobiose	+	+	+	+	+
Lactose	—	d	+	—	+
L-Rhamnose	+	+	+	+	+
Esculin	+	+	+	+	+
Salicin	+	+	+	+	+
D-Xylose	+	+	+	+	w
Trehalose	+	+	+	+	+
Dulcitol	—	—	—	—	—
Glycerol	+	ND	ND	d	+
Sucrose	+	+	+	—	w
Adonitol	—	—	+	—	+
Dextrin	—	ND	ND	—	—
Melezitose	—	ND	ND	—	+
α -Methyl-D-glucoside	—	—	+	—	+
Utilization of:					
Citrate (Simmons)	+	+	+	+	+
L-Tartrate	—	ND	ND	+	—
Malonate	+	+	+	d	+
Galacturonate	+	ND	+	+	+
H ₂ S production ^c	+	—	—	+	+
DNase activity	—	—	—	—	—
Phenylalanine deaminase activity	—	—	—	+	—

^a Data from reference 1.^b +, 80% or more of the strains are positive; —, 20% or less of the strains are positive; d, 21 to 79% of the strains are positive; w, weak reaction; ND, insufficient or no data.^c Data for *Enterobacter gergoviae* and *Enterobacter aerogenes* are results obtained on triple sugar iron agar, and the reactions of the *Erwinia* species were determined by using cysteine.

contents, which fell within the phenotypic definition of the family *Enterobacteriaceae*. These strains were closely related as determined by DNA hybridization. Therefore, both phenotypically and genetically, these strains represent a single species.

Phenotypically, the pear brown leaf spot strains can be differentiated from their closest relatives by four or more tests. The levels of DNA relatedness between pear brown leaf spot strain KCTC 2520^T and 89 strains representing other species of the *Enterobacteriaceae* were in all cases less than 50%, a value far lower than the level of relatedness recommended for phylogenetic definition of a species (70% or more) (17). These data confirm that the pear brown leaf spot strains constitute a new species.

Because these strains are the causative agent of brown leaf

spot disease in pear trees, it was natural to consider classifying them in the genus *Erwinia*, the genus that contains phytopathogenic species of the *Enterobacteriaceae* (8). It has been known for a long time that the genus *Erwinia* is phenotypically and genetically heterogeneous and that the boundary separating the genera *Erwinia* and *Enterobacter* is quite subjective (1–4, 7, 11, 12, 16). A number of species originally classified in the genus *Erwinia* have now been reclassified in other genera, most notably the genus *Enterobacter* and the new genus *Pantoea* (4, 9, 12). For purposes of comparison with previous work, strains belonging to the *Erwinia herbicola*-*Enterobacter agglomerans* group, some of which have now been reclassified in the genus *Pantoea*, are referred to in Table 1 as *Enterobacter agglomerans* hybridization groups I to XIII (2). DNA hybridization stud-

ies showed that the pear brown leaf spot strains are most closely related to *Enterobacter gergoviae* (6). Therefore, we propose the name *Enterobacter pyrinus* sp. nov. for the pear brown leaf spot strains.

Description of *Enterobacter pyrinus* sp. nov. *Enterobacter pyrinus* (pyr' i.nus. N. L. n. *pyrus*, pear; L. suff. *-inus*, belonging to; N. L. adj. *pyrinus*, from pears). Cells are gram-negative, oxidase-negative, catalase-positive, fermentative rods (0.6 to 1.0 by 1.6 to 2.3 μ m) that are motile and peritrichous. Grows well on nutrient agar, yeast extract-dextrose-CaCO₃ agar, and other common bacteriological media. Colonies on nutrient agar are circular, entire, convex, smooth, translucent, and 1.5 to 5.0 mm in diameter after 48 h of incubation at 27°C. Growth occurs at 36°C and in the presence of 5% (wt/vol) NaCl. Positive in tests for acetoin production (Voges-Proskauer test), H₂S production from cysteine, gluconate oxidation, gas production from D-glucose, KCN tolerance, nitrate reduction, phosphatase activity, reducing substances produced from sucrose, and urease activity. Negative in tests for casein hydrolysis, DNase activity, erythromycin susceptibility, gelatin liquefaction, growth factor requirement, indole production, mucoid growth, pectinase activity, phenylalanine deaminase activity, pigment production, potato rot, and tobacco hypersensitivity. The strains utilize citrate, formate, lactate, galacturonate, and malonate as sole carbon sources, but not L-tartrate. Acid is produced from L-arabinose, cellobiose, esculin, glycerol, myo-inositol, maltose, D-mannitol, mannose, melibiose, ribose, L-rhamnose, salicin, trehalose, and D-xylose. Acid is not produced from adonitol, dextrin, dulcitol, inulin, lactose, melezitose, α -methyl-D-glucoside, palatinose, raffinose, D-sorbitol, and starch. Phenotypic tests that are useful for differentiating *Enterobacter pyrinus* from other *Enterobacter* and *Erwinia* species are shown in Table 2.

The G+C content of the DNA is 57.5 to 61 mol% (as determined by the thermal denaturation method).

Strains were isolated from pear leaves and cause brown leaf spot disease of pear trees (*P. pyrifolia* Nakai).

Description of the type strain. The type strain of *Enterobacter pyrinus* is strain KCTC 2520 (= CDC 6570 = ATCC 49851). This strain was isolated from diseased pear (*P. pyrifolia* cv. Mansamgil) leaves at Yusung, Korea, in 1988. The biochemical characteristics of this strain are identical to those of the species, and the G+C content of its DNA is 57.5 mol%.

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