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Transfer of *Enterobacter agglomerans* (Beijerinck 1888) Ewing and Fife 1972 to *Pantoea* gen. nov. as *Pantoea agglomerans* comb. nov. and Description of *Pantoea dispersa* sp. nov.

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Deoxyribonucleic acid (DNA)-DNA hybridization was performed with 10 strains belonging to the "*Erwinia herbicola-Enterobacter agglomerans* complex" by using the competition method on nitrocellulose filters. These strains exhibited more than 75% DNA binding to *Erwinia herbicola* ATCC 14589^T (T = type strain) and constitute DNA hybridization group 14589 (including strains ATCC 14589^T and CDC 1429-71 from DNA hybridization group III [D. J. Brenner, G. R. Fanning, J. K. Leete Knutson, A. G. Steigerwalt, and M. J. Krichevsky, Int. J. Syst. Bacteriol. 34:45–55, 1984]). The high level of genomic relatedness of these strains was confirmed by the similarities observed in their electrophoretic protein patterns. On the basis of our data, DNA hybridization group 14589 constitutes a discrete species within the family *Enterobacteriaceae*. Its closest relative is DNA hybridization group 27155 (41 to 53% DNA relatedness), which was previously defined and includes the type strains, among others, of *Enterobacter agglomerans*, *Erwinia herbicola*, and *Erwinia milletiae* (A. Beji, J. Mergaert, F. Gavini, D. Izard, K. Kersters, H. Leclerc, and J. De Ley, Int. J. Syst. Bacteriol. 38:77–88, 1988). We propose to unite DNA hybridization groups 14589 and 27155 in a single genus, *Pantoea* gen. nov. *Pantoea agglomerans* (Beijerinck 1888) comb. nov. is proposed to contain most strains of DNA hybridization group 27155 (including DNA hybridization group XIII of Brenner et al.), and its type strain is strain ATCC 27155 (= NCTC 9381 = LMG 1286). *Pantoea dispersa* sp. nov. is proposed to contain DNA hybridization group 14589, and its type strain is strain ATCC 14589 (= LMG 2603). Descriptions of the genus and its two species are given.

On the basis of a numerical phenotypic analysis of 169 strains belonging to the "*Erwinia herbicola-Enterobacter agglomerans* complex," Gavini et al. (11) described five major groups that were divided into 15 subgroups. Verdonck et al. (32) classified about 140 strains of *Erwinia herbicola*, *Erwinia milletiae*, and *Enterobacter agglomerans* into 23 different phena. Brenner et al. (3) studied levels of deoxyribonucleic acid (DNA) relatedness among 124 strains and found that 90 of these strains were distributed over 13 DNA hybridization groups. Using a similar hybridization technique, Lind and Ursing (23) showed that 52 of 86 *Enterobacter agglomerans* clinical isolates were closely related to each other and to the type strain of the species, as well as to the type strains of *Erwinia herbicola* and *Erwinia milletiae*. More recently, the study of Beji et al. (1) conducted with strains belonging to phenotypic groups B4 of Gavini et al. (11) and 7B and 8 of Verdonck et al. (32) pointed out the high levels of DNA relatedness (72 to 97% DNA binding) among the type strains of these three species, 21 strains belonging to group B4, and two strains belonging to DNA hybridization group XIII of Brenner et al. (3). A somewhat lower level of DNA binding (62%) was noticed with strain CDC 3482-71, a member of group V of Brenner et al. (3). The synonymy of the species names *Enterobacter agglomerans*, *Erwinia herbicola*, and *Erwinia milletiae*, which was suspected based on the high protein electrophoretic and phenotypic similarities among the type strains of these species (27, 32) and was demonstrated by DNA hybridization (23), was confirmed by Beji et al. (1). An emended description of these species, defined as DNA hybridization group 27155, was given by these authors (1). Previously, groups E2, E3, and E5 of Gavini et al. (11) and DNA hybridization group XI of Brenner et al. (3) were shown to constitute the species *Escherichia adecarboxylata* (14). In contrast to the findings of Izard et al. (15) and Brenner et al. (3), Tamura et al. (31) found only very low levels of DNA binding (less than 13%) between strains belonging to *Escherichia adecarboxylata* and strains of *Enterobacter* species and renamed the former taxon *Leclercia adecarboxylata*.

The aim of this study was to analyze another phenotypic group, group B5 of Gavini et al. (11), four strains of which were present in phenotypic group 10 of Verdonck et al. (32). We determined (i) whether the eight strains of group B5 and four additional strains belonging to phenotypic group 10 of Verdonck et al. (32) could be characterized as a single genomic, protein electrophoretic, and phenotypic subset of the *Erwinia herbicola-Enterobacter agglomerans* complex, (ii) whether this subset could be separated at the species level from DNA hybridization group 27155 as defined by Beji et al. (1), and (iii) the levels of genomic relatedness of these strains to other groups within the *Erwinia herbicola-Enterobacter agglomerans* complex (3, 11), to other species of the genera *Erwinia* and *Enterobacter*, and to other species of the family *Enterobacteriaceae*.

We propose a new genus, *Pantoea*, which includes the following two species: *Pantoea agglomerans* comb. nov. for most strains belonging to DNA hybridization group 27155 of Beji et al. (1) (including the type strains, among others, of

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TABLE 1. Strains used and levels of relative binding of their DNAs to [^{3}H]DNA from *Pantoea dispersa* ATCC 14589^T

Group	Species name as received	Strain[a]	% of relative DNA binding to [^{3}H]DNA from strain ATCC 14589^T[b]
Strains assigned by us to *Pantoea dispersa* (DNA hybridization group 14589)	*Erwinia herbicola*	ATCC 14589^T[c]	100
	Enterobacter agglomerans	Lille 214-6	92
	Enterobacter agglomerans	Gilardi 961	89
	Erwinia herbicola	Graham G146	88
	Enterobacter agglomerans	Gilardi 968	87
	Erwinia herbicola	NCPPB 2279 (= LMG 2601)	87
	Enterobacter agglomerans	CDC 1429-71[c]	85
	Enterobacter agglomerans	Goullet 29.2.80	81
	Erwinia herbicola	NCPPB 2285 (= LMG 2602)	78
	Erwinia herbicola	IPO 445 (= LMG 2604)	76
Strains assigned by us to *Pantoea agglomerans*	*Erwinia herbicola*	ICPB 2953	53
	Erwinia herbicola	Graham G150 (= LMG 2581)	52
	Enterobacter agglomerans	ATCC 12287[d]	49
	Erwinia milletiae	NCPPB 2519^T (= LMG 2660^T)	46
	Enterobacter agglomerans	ATCC 27155^T (= NCTC 9381^T = LMG 1286^T)	44
	Erwinia herbicola	NCPPB 2971^T (= LMG 2565^T)	41
Other strains belonging to phenotypic group B5 of Gavini et al. or group 10 of Verdonck et al.[e]	*Enterobacter agglomerans*	Gilardi 1030	44
	Enterobacter agglomerans	Gilardi 953	41
	Erwinia herbicola	Angers B.6.2	39
Other phenotypic groups within the *Erwinia herbicola-Enterobacter agglomerans* complex according to Gavini et al.[f]			
B1	*Erwinia herbicola*	Angers 243-3	32
B2	*Erwinia herbicola*	Angers A.17.6	27
B6	*Enterobacter agglomerans*	Gilardi 959	30
B7	*Enterobacter agglomerans*	Richard 13–78	16
B9	*Erwinia herbicola*	Angers 217-8	37
E1	Atypical coliform	Gavini 98	32
Other DNA hybridization groups within the *Erwinia herbicola-Enterobacter agglomerans* complex according to Brenner et al.[g]			
II	*Enterobacter agglomerans*	CDC 3123-70	43
IV	*Enterobacter agglomerans*	CDC 1741-71	45
V	*Enterobacter agglomerans*	CDC 3482-71	43
VI	*Enterobacter agglomerans*	CDC 6070-69	29
VII	*Enterobacter agglomerans*	CDC 6003-71	47
VIII	*Enterobacter agglomerans*	CDC 5422-69	43
IX	*Enterobacter agglomerans*	CDC 4388-71	21
X	*Enterobacter agglomerans*	CDC 1600-71	20
XII	*Enterobacter agglomerans*	CDC 219-71	31
Other *Erwinia* species	*Erwinia stewartii*	NCPPB 2295^T	51
	Erwinia uredovora	NCPPB 800^T	47
	Erwinia ananas	NCPPB 1846^T	39
	Erwinia carotovora	ATCC 15713^T	28
	Erwinia amylovora	ATCC 15580^T	28
Other *Enterobacter* species	*Enterobacter dissolvens* (*synonym, Erwinia dissolvens*)	NCPPB 1850^T	35
	Enterobacter amnigenus	ATCC 33072^T	24
	Enterobacter sakazakii	ATCC 29544^T	23
	Enterobacter aerogenes (synonym, *Klebsiella mobilis*)	ATCC 13048^T	22
	Enterobacter asburiae	ATCC 35953^T	21
	Enterobacter cloacae	ATCC 13047^T	20
		CDC 1347-71	18
	Enterobacter gergoviae	CIP 76.01^T	19
	Enterobacter taylorae	ATCC 35313^T	17
	Enterobacter intermedium	CIP 79.27^T	15

Continued on following page

TABLE 1—*Continued*

Group	Species name as received	Strain[a]	% of relative DNA binding to [^{3}H]DNA from strain ATCC 14589^{T}[b]
Other members of the *Enterobacteriaceae*	*Escherichia blattae*	ATCC 29907^T	37
	Citrobacter diversus	CDC 3613-63	37
	Escherichia hermannii	ATCC 33650^T	36
	Kluyvera cryocrescens	ATCC 33435^T	32
	Leclercia adecarboxylata	CDC 5378-71	30
		Leclerc 35	26
	Klebsiella pneumoniae	ATCC 13882	28
	Escherichia vulneris	ATCC 33821^T	27
	Salmonella typhimurium	ATCC 23565	26
	Serratia liquefaciens	ATCC 27592^T	25
	Cedecea neteri	ATCC 33855^T	25
	Levinea amalonatica	CDC 25406	24
	Serratia grimesii	ATCC 14460^T	23
	Hafnia alvei	ATCC 13337^T	23
	Cedecea lapagei	CIP 80.35^T	23
	Ewingella americana	ATCC 33852^T	23
	Leminorella grimontii	ATCC 33999	23
	Cedecea davisae	CIP 80.34^T	22
	Tatumella ptyseos	ATCC 33301^T	22
	Kluyvera ascorbata	ATCC 33433^T	21
	Serratia fonticola	ATCC 29844^T	20
	Klebsiella planticola	ATCC 33531^T	19
	Buttiauxella agrestis	ATCC 33320^T	19
	Citrobacter freundii	ATCC 8090	18
	Klebsiella oxytoca	ATCC 13182^T	18
	Serratia odorifera	CDC 1979-77^T	18
	Escherichia coli	ATCC 10536	17
	Klebsiella terrigena	CIP 80.07^T	17
	Koserella trabulsii	CDC 3349-72^T	16
	Serratia marcescens	ATCC 13880^T	16
	Edwardsiella tarda	ATCC 15947^T	15
	Escherichia fergusonii	CDC 0568-73^T	13
	Yersinia enterocolitica	CIP 80.27^T	11
	Proteus vulgaris	ATCC 13315	10
	Budvicia aquatica	ATCC 35567^T	1
	Rahnella aquatilis	ATCC 30701^T	9
	Serratia ficaria	ATCC 33105^T	9
	Leminorella richardii	ATCC 33998^T	4

[a] Abbreviations and sources: ATCC, American Type Culture Collection, Rockville, Md.; Angers, Laboratoire de Phytophathologie, Angers, France; CDC, Centers for Disease Control, Atlanta, Ga.; CIP, Collection de l'Institut Pasteur, Paris, France; Gavini, F. Gavini, Unite 146, Institut National de la Santé et de la Recherche Médicale, Villeneuve d'Ascq, France (11); Gilardi, G. L. Gilardi, Hospital for Joint Diseases and Medical Center, New York, N.Y. (12); Goullet, P. Goullet, Laboratoire de Microbiologie, Faculté de Médecine Xavier Bichat, Université de Paris, Paris, France; Graham, D. C. Graham, Department of Agriculture and Fisheries for Scotland, Agricultural Scientific Services, Edinburgh, Scotland (13); ICPB, International Collection of Phytopathogenic Bacteria, University of California, Davis; IPO, Instituut voor Plantenziektenkundig Onderzoek, Wageningen, The Netherlands; Leclerc, H. Leclerc, Unite 146, Institut National de la Santé et de la Recherche Médicale, Villeneuve d'Ascq, France (20); Lille, Laboratoire d'Hydrobiologie, Institut Pasteur, Lille, France; LMG, Culture Collection, Laboratorium voor Microbiologie, Ghent, Belgium; NCPPB, National Collection of Plant Pathogenic Bacteria, Harpenden, England; NCTC, National Collection of Type Cultures, London, England; Richard, C. Richard, Service des Entérobactéries, Institut Pasteur, Paris, France (28).

[b] Experiments were performed at the optimal renaturation temperature (see Materials and Methods).

[c] Strain belonging to DNA hybridization group III of Brenner et al. (3).

[d] Strain belonging to DNA hybridization group XIII of Brenner et al. (3).

[e] See references 11 and 32.

[f] See reference 11.

[g] See reference 3.

Enterobacter agglomerans, *Erwinia herbicola*, and *Erwinia milletiae*) and *Pantoea dispersa* sp. nov. for DNA hybridization group 14589, as defined below.

MATERIALS AND METHODS

Strains used. The 87 strains used in this study are listed in Table 1.

DNA-DNA hybridization. To prepare DNA, cells were grown in nutrient broth at 30°C for 24 h with shaking. *Erwinia herbicola* ATCC 14589^T (T = type strain) was selected for the preparation of DNA labeled with [^{3}H]thymidine. A modification of the method of Marmur (24) as described by Ferragut and Leclerc (10) was used to prepare both unlabeled and ^{3}H-labeled DNAs. Unlabeled high-molecular-weight DNA was fixed and denaturated on nitrocellulose filters by using the technique described by De Ley and Tytgat (7). Fragmentation of DNA was carried out by using a French pressure cell at 20,000 lb/in^2. DNA-DNA reassociation was done in 2× SSC (1× SSC is 0.15 M NaCl plus 0.015 M trisodium citrate, pH 7.0) containing 30% dimethyl sulfoxide. The optimal temperature of renaturation in 2× SSC containing 30% dimethyl sulfoxide ($T_{OR,D}$) was calculated by using the following equation of De Ley and Tytgat (7): $T_{OR,D}$ = (0.51 × guanine-plus-cytosine content)

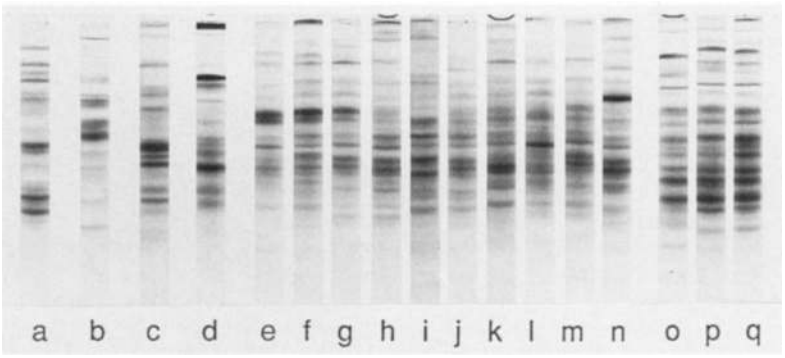

FIG. 1. Normalized protein electropherograms for 10 strains of *Pantoea dispersa*, for *Pantoea agglomerans* NCTC 9381^T, and for six strains belonging to other, related taxa. Lane a, *Erwinia ananas* NCPPB 1846^T; lane b, *Erwinia uredovora* NCPPB 800^T; lane c, *Erwinia stewartii* NCPPB 2295^T; lane d, *Pantoea agglomerans* NCTC 9381^T; lanes e through n, *Pantoea dispersa* NCPPB 2285, IPO 445, Gilardi 968, Gilardi 961, ATCC 14589^T, NCPPB 2279, Graham G146, CDC 1429-71, Lille 214-6, and Goullet 29.2.80, respectively; lane o, *Enterobacter agglomerans* Gilardi 1030; lane p, *Erwinia herbicola* Angers B.6.2; lane q, *Enterobacter agglomerans* Gilardi 953.

+ 28.0. The mean guanine-plus-cytosine content of the labeled DNA of strain ATCC 14589^T was 56.5 ± 0.5 mol% (three determinations), as determined by the thermal denaturation method (6, 25). Consequently, the optimal temperature of renaturation was 56.8°C. The rate of reassociation was calculated by using the formula of De Ley and Tytgat (7).

The ΔT_m (the difference, in degrees Celsius, between the T_m [the temperature at which 50% of the DNA was denatured] of the hybrid molecule and the T_m of the homologous DNA) was determined for *Erwinia herbicola* NCPPB 2285 and IPO 445. This experiment was performed by using the technique described by De Ley et al. (8).

Polyacrylamide gel electrophoresis of soluble proteins. Protein electropherograms were prepared as described previously (26).

Characterization of strains by the API 20E system. Tests in API 20E strips (API System, Montalieu-Vercieu, France) were performed at 30°C by using procedures described previously (27). Results were coded and interpreted by using APILAB computer program V2.0.

RESULTS

DNA hybridizations. Radioactive DNA from *Erwinia herbicola* ATCC 14589^T was hybridized to filter-bound DNAs of 34 strains belonging to the *Erwinia herbicola-Enterobacter agglomerans* complex, to the DNAs of the type strains of five other *Erwinia* species, to DNAs from 10 strains belonging to other *Enterobacter* species, and to DNAs from 38 strains representing 37 other species belonging to the family *Enterobacteriaceae* (Table 1).

Five strains belonging to phenotypic group B5 (11) and three strains belonging to phenotypic group 10 (32) exhibited 76 to 92% DNA binding to *Erwinia herbicola* ATCC 14589^T. A high level of relative DNA binding (85%) was also observed with strain CDC 1429-71, which represents DNA hybridization group III of Brenner et al. (3). The differences in thermal elution midpoints (ΔT_m) between homologous and heterologous duplexes were 0.5 and 2.6°C for two of these strains (strains NCPPB 2285 and IPO 445, respectively). These 10 strains constitute a genomic group provisionally referred to as DNA hybridization group 14589.

The two remaining strains of phenotypic group B5 (strains Gilardi 953 and Angers B.6.2) (11) and strain Gilardi 1030, a member of phenotypic group 10 (32), exhibited only 41, 39, and 44% DNA binding, respectively, to reference strain ATCC 14589^T.

The levels of DNA binding between strain ATCC 14589^T and six strains belonging to DNA hybridization group 27155, as previously defined by Beji et al. (1), were between 41 and 53%; the levels of DNA binding were less than 38% with strains belonging to other phenotypic groups (groups B1, B2, B6, B7, B9, and E1) of Gavini et al. (11). Representative strains belonging to DNA hybridization groups II, IV, V to X, and XII of Brenner et al. (3) exhibited 20 to 47% DNA binding to strain ATCC 14589^T.

DNA binding levels of 51, 47, and 39% were obtained with the type strains of *Erwinia stewartii*, *Erwinia uredovora*, and *Erwinia ananas*, respectively, and DNA binding levels of 28 and 19% were observed with the type strains of *Erwinia carotovora* and *Erwinia amylovora* (type species [29]), respectively. A DNA binding level of 35% was observed with the type strain of *Enterobacter dissolvens* (synonym, *Erwinia dissolvens* [4]); DNA binding levels of less than 25% were obtained with strains belonging to other *Enterobacter* species (including the type species, *Enterobacter cloacae* [29]), and DNA binding levels of less than 38% were observed with strains belonging to 37 other species of the family *Enterobacteriaceae*.

Comparison of protein electropherograms. Protein electropherograms were prepared from eight strains belonging to phenotypic group B5 (11), four additional strains belonging to phenotypic group 10 (32), reference strain CDC 1429-71 of DNA hybridization group III of Brenner et al. (3), and type strains *Enterobacter agglomerans* NCTC 9381 (= ATCC 27155), *Erwinia ananas* NCPPB 1846, *Erwinia uredovora* NCPPB 800, and *Erwinia stewartii* NCPPB 2295. Normalized photographs of the protein electropherograms are shown in Fig. 1.

It is apparent that the 10 strains belonging to DNA hybridization group 14589, as delineated above, have many similarities in their protein patterns. The electropherograms of these strains differ significantly from the electropherograms of *Enterobacter agglomerans* NCTC 9381^T (= ATCC 27155^T), *Erwinia ananas* NCPPB 1846^T, *Erwinia uredovora* NCPPB 800^T, and *Erwinia stewartii* NCPPB 2295^T.

Strains Gilardi 953 and Angers B.6.2 (which were classified in group B5 [11]) and strain Gilardi 1030 (a member of phenotypic group 10, but classified outside group B5 by Gavini et al. [11, 29]) constitute a separate, homogeneous

TABLE 2. Phenotypic characteristics of *Pantoea agglomerans* and *Pantoea dispersa* (DNA hybridization group 14589)[a]

Characteristic	*Pantoea agglomerans* (16 strains)			*Pantoea dispersa* (10 strains)			*Pantoea agglomerans* ATCC 27155[Tb]	*Pantoea dispersa* ATCC 14589[T]
	Reaction	% of strains positive	% of strains having slow reaction	Reaction	% of strains positive	% of strains having slow reaction		
Production of yellow pigment	+	100		+ or −	60		+	+
Growth at 4°C	(+) or +	12	81	−	0		(+)(5)	−
Growth at 41°C	− or (+)	0	12	+	90	10	−	+
Growth at 44°C	−	0		−	0	10	−	−
Motility	+	100		+	90	10	+	+
KCN (growth)	+ or −	75		+	90		+	−
Gelatin liquefaction	(+)		100	(+)	0	90	(+)(15)	(+)(16)
Indole production	−	0		−	0		−	−
Voges-Proskauer reaction	+	94		+	100		+	+
Nitrate reduced to nitrite	+	94		+ or −	70		+	−
H_2S production	−	0		−	0		−	−
Hydrolysis of esculin	+	100		−	0		+	−
Gas produced from D-glucose	−	0		−	0		−	−
Arginine dihydrolase (Moeller)	−	0		−	0		−	−
Lysine decarboxylase (Moeller)	−	0		−	0		−	−
Ornithine decarboxylase (Moeller)	− or +	31		−	10		−	+
Phenylalanine deaminase	+ or −	86		−	0		−	−
Tetrathionate reductase	− or +	12		−	0		−	−
Deoxyribonuclease	−	0		−	0		−	−
β-Xylosidase	−	0		−	0		−	−
β-Galactosidase	+	100		+	100		+	+
Urease	−	0		−	0		−	−
Utilization of:								
Citrate (Simmons)	+	94		+	100		+	+
Malonate	+	100		−	10		+	+
D-Tartrate (Kauffman)	−	6		− or +	30		+	−
L-Tartrate (Kauffman)	−	0		+ or −	50		−	−
meso-Tartrate (Kauffman)	−	0		+ or −	80		−	+
Mucate (Kauffman)	−	0		− or +	40		−	−
Acid produced from:								
L-Arabinose	+	100		d	60	10	+	+
D-Ribose	+	100		+	100		+	+
D-Xylose	+	100		+	100		+	+
D-Fructose	+	100		+	100		+	+
D-Mannose	+	100		+	100		+	+
L-Rhamnose	+	95	5	+	100		+	+
L-Sorbose	−	0		−	0		−	−
D-Cellobiose	d	44	44	+ or (+)	50	50	(+)(12)	(+)(8)
D-Galactose	+	100		+	100		+	+
Lactose	d	19	6	−	0	10	−	−
Maltose	+	100		+	100		+	+
Melibiose	−	0	6	d	10	30	−	+
Sucrose	+	100		+	100		+	+
Trehalose	+	100		+	100		+	+
Melezitose	−	0		−	0		−	−
Raffinose	d	6	19	−	0		−	−
Glycerol	(+)		100	(+) or +	20	70	(+)(4)	+
meso-Erythritol	−	0		−	0	10	−	−
Adonitol	−	0	6	−	0		(+)(12)	−
Dulcitol	−	0		−	0	10	−	−
Inositol	− or (+)	0	37	d	60	20	(+)(15)	+
D-Mannitol	+	100		+	100		+	+
D-Sorbitol	−	0		−	0		−	−
α-Methyl-D-glucoside	−	0		−	0		−	−
Salicin	+	100		− or (+)	0	50	+	−
Glycogen	−	0		− or +	40		−	−
Inulin	− or +	12		−	0		−	−
Tartrate (Jordan)	−	0		− or +	40		−	−

[a] +, Reaction present in at least 90% of the strains within 24 to 48 h; −, reaction absent in at least 90% of the strains after 2 days; (+), slow reaction (between 2 and 30 days; the numbers in parentheses indicate the numbers of days necessary for the reaction to occur); d, different reactions. When more than one symbol is used (e.g., (+ or −), the first symbol indicates the most frequent result. Tests were done at 30°C, unless indicated otherwise.

[b] Data from reference 1.

TABLE 3. Differential characteristics of *Pantoea agglomerans*, *Pantoea dispersa*, and the species previously assigned or phenotypically related to the *Erwinia herbicola-Enterobacter agglomerans* complex[a]

Characteristic	*Pantoea agglomerans*	*Pantoea dispersa*	*Erwinia uredovora*	*Erwinia ananas*	*Erwinia stewartii*	*Leclercia adecarboxylata*	*Escherichia hermannii*	*Escherichia vulneris*	*Enterobacter sakazakii*	*Rahnella aquatilis*	*Ewingella americana*
Production of yellow pigment	+	d	+	+	+	+	+	d	+	−	−
Indole production	−	−	+	+	−	+	+	−	(−)	−	−
Voges-Proskauer reaction	+	+	+	+	−	−	−	−	+	+	+
Arginine dihydrolase	−	−	−	−	−	−	−	d	+	−	−
Lysine decarboxylase	−	−	−	−	−	−	−	(+)	−	−	−
Ornithine decarboxylase	d	−	−	−	−	−	+	−	+	−	−
Acid produced from:											
D-Cellobiose	d	d	+	+	+	+	+	+	+	+	+
Lactose	d	−	+	+	+	+	d	(−)	+	+	d
Maltose	+	+	+	+	−	+	+	+	+	+	+
Melibiose	−	d	+	+	+	+	−	+	+	+	NT
Raffinose	d	−	+	+	+	+	d	+	+	+	−
Sucrose	+	+	+	+	+	+	d	−	+	+	−
Adonitol	−	−	+	−	−	+	−	−	−	−	−
Dulcitol	−	−	−	−	−	+	(−)	−	−	(+)	−
Sorbitol	−	−	+	+	+	−	−	−	−	+	−
α-Methyl-D-glucoside	−	−	−	−	−	−	−	d	+	−	−
Salicin	+	−	d	+	−	+	d	d	+	+	+

[a] +, Reaction present in at least 90% of the strains; −, reaction absent in at least 90% of the strains; (+), reaction present in 76 to 89% of the strains; (−), reaction present in 11 to 25% of the strains; d, reaction present in 26 to 75% of the strains; NT, not tested. Data were obtained after 48 h of incubation at 30°C (*Pantoea* and *Erwinia* species) or 36 ± 1°C (other species). See references 2, 21, and 22.

electrophoretic group, with protein patterns that are very different from those of all other strains examined.

API 20E seven-digit codes. The strains of DNA hybridization group 14589, as delineated above, were tested by using the API 20E system. Five strains gave the numerical code 1205173; strains NCPPB 2285 and Goullet 29.2.80 differed because of negative reactions in the API 20E amygdalin test and gave the code 1205172. Both of these codes were identified by the APILAB program as *Enterobacter agglomerans* or *Erwinia* sp. Strains Lille 214-6 and ATCC 14589^T did not produce acid from L-rhamnose in API 20E strips and gave the code 1205163. Strain CDC 1429-71 produced acid from inositol and sorbitol but did not utilize citrate in the API 20E strips; consequently, code 1005773 was obtained. The latter two codes could not be identified unambiguously by the APILAB program, even when additional tests were taken into account; *Enterobacter agglomerans* was listed as one of the possibilities.

For comparison, strains Gilardi 953, Gilardi 1030, and Angers B.6.2, which were phenotypically similar to the strains belonging to DNA hybridization group 14589 (11, 32) but were genomically and electrophoretically different (Table 1 and Fig. 1), were also examined by using the API 20E system. Strains Gilardi 953 and Angers B.6.2 yielded codes different from those mentioned above. Strain Gilardi 1030 gave the code 1205172, which was also found for two strains belonging to DNA hybridization group 14589 (see above).

DISCUSSION

The following 10 strains exhibited more than 75% DNA binding to *Erwinia herbicola* ATCC 14589^T: 6 strains belonging to phenotypic group B5 of Gavini et al. (11) (strains ATCC 14589^T, Lille 214-6, Gilardi 961, Gilardi 968, Graham G146, and Goullet 29.2.80), 3 strains belonging to phenotypic group 10 of Verdonck et al. (32) (strains NCPPB 2279, NCPPB 2285, and IPO 445), and strain CDC 1429-71 (Table 1). The ΔT_m, determined for strains NCPPB 2285 and IPO 445, was less than 2.7°C. We provisionally referred to this group as DNA hybridization group 14589, which includes strains belonging to DNA hybridization group III of Brenner et al. (3) (strains ATCC 14589^T and CDC 1429-71). In the opinion of Brenner et al. (3), each of their DNA hybridization groups constitutes a unique species. The high level of genomic relatedness of the strains belonging to DNA hybridization group 14589 was confirmed by the similarities observed in their electrophoretic protein patterns (Fig. 1).

Levels of DNA binding less than 54% were observed between strain ATCC 14589^T and all of the other strains tested, including three strains (strains Gilardi 953, Gilardi 1030, and Angers B.6.2) which have been classified in the same phenotypic groups as the strains belonging to DNA hybridization group 14589 (Table 1) (11, 32). These strains constituted a separate electrophoretic group (Fig. 1).

On the basis of the present data it is clear that DNA hybridization group 14589 constitutes a discrete species within the family *Enterobacteriaceae*. The closest relative of this species is DNA hybridization group 27155, as defined by Beji et al. (1), with which it exhibits up to 53% DNA relatedness. The latter group consists of strains received as *Enterobacter agglomerans*, *Erwinia herbicola*, and *Erwinia milletiae*, including the type strains of these three species, and reference strains belonging to DNA hybridization groups V and XIII of Brenner et al. (1, 3). The degrees of genomic relatedness (levels of DNA binding) observed by Brenner et al. (3) between their DNA hybridization group III (which corresponds to our group 14589) and their DNA hybridization groups V and XIII (corresponding together to group 27155 [1]) were 50 to 56%, which is in good agreement with our results (Table 1). Beji et al. suggested (1) that DNA hybridization group 27155 might constitute a single species within a new enterobacterial genus, but this suggestion was not implemented by nomenclatural proposals. As discussed by Beji et al. (1), a problem arose with the delineation of DNA hybridization group 27155 as a single species. Reference strain CDC 3482-71 belonging to DNA hybridization

group V of Brenner et al. (3) exhibited only 62% DNA binding to *Enterobacter agglomerans* ATCC 27155^T, which is in good agreement with the percentages found by Brenner et al. (3) and Lind and Ursing (23) with other, genomically comparable reference strains. Lind and Ursing also reported a ΔT_m of 13.8°C (in their experiments at 60°C) and only 38% DNA binding when the incubation temperature was increased to 75°C. Thus, DNA hybridization group 27155 (1) does not meet the definition of a species as recommended by Wayne et al. (33). Therefore, we have to exclude strain CDC 3482-71. As the latter strain is a representative of protein profile group II of Beji et al. (1), the three other strains of this protein profile group also have to be excluded. It has been shown that strains with similar protein electropherograms are genomically highly related and should not be classified in different species (15–17; this paper). As the three other strains of protein profile group II exhibited up to 77% DNA binding to *Enterobacter agglomerans* ATCC 27155^T (1), we also provisionally delete the four strains of protein profile group VII of Beji et al. (1), because strains of the latter protein profile group exhibited less than 77% DNA binding to *Enterobacter agglomerans* ATCC 27155^T (1).

DNA hybridization group 14589 (Table 1) and DNA hybridization group 27155 (with protein profile groups II and VII [1] and DNA hybridization group V of Brenner et al. [3] excluded) should be united as separate species in a single, new genus, because they form a distinct genomic (1, 3, 23) (Table 1) and phenotypic (11, 27, 32) entity within the family *Enterobacteriaceae*.

We propose the name *Pantoea* gen. nov., for the new taxon, with the two species described below. The name *Pantoea dispersa* sp. nov. is proposed for the 10 strains belonging to DNA hybridization group 14589 (Table 1); from the data of Brenner et al. (3) it follows that the strains belonging to their DNA hybridization group III should also be included in this species, as both groups have strains in common. The name *Pantoea agglomerans* comb. nov. is proposed for the 52 strains belonging to protein electrophoretic profile groups I and III to VI as defined by Beji et al. (1); this species includes the strains belonging to DNA hybridization group XIII of Brenner et al. (3) and the 52 strains genomically identified as *Enterobacter agglomerans* by Lind and Ursing (23). *Pantoea agglomerans* includes the type strains of *Enterobacter agglomerans* (Beijerinck 1888) Ewing and Fife 1972, *Erwinia herbicola* (Löhnis 1911) Dye 1964, and *Erwinia milletiae* (Kawakami and Yoshida 1920) Magrou 1937 (29). According to the *International Code of Nomenclature of Bacteria* (19), the species epithet *agglomerans* has priority over the epithets *herbicola* and *milletiae* and was consequently selected for the new combination *Pantoea agglomerans*. The strains belonging to protein electrophoretic profile groups II and VII of Beji et al. (1) and DNA hybridization group V of Brenner et al. (3) are provisionally classified as *Pantoea* sp., until their interrelatedness is elucidated.

The data presented here and previously (1, 3, 23) suggest that other groups within the so-called *Erwinia herbicola-Enterobacter agglomerans* complex might also be included as additional species in the genus *Pantoea*. Strains representing some other DNA hybridization groups of Brenner et al. (3) and the type strains of *Erwinia stewartii* and *Erwinia uredovora* exhibited about 50% DNA binding to the two *Pantoea* species (Table 1) (1). Slightly less DNA binding (39 to 49%) was observed with strains Gilardi 1030, Gilardi 953, and Angers B.6.2 (Table 1) (1), which constituted a separate protein electrophoretic group (Fig. 1) but were found to be phenotypically close to *Pantoea dispersa* strains (11, 32). *Erwinia ananas* NCPPB 1846^T was found to be 56% related to *Pantoea agglomerans* ATCC 27155^T (1), but only 39% related to *Pantoea dispersa* ATCC 14589^T (Table 1). More data on more strains are needed to confirm these observations and to clarify the taxonomic position of these groups and species.

Finally, data presented here or published previously (1, 27) strongly suggest that extreme caution should be used in identification of strains as *Enterobacter agglomerans*, *Erwinia herbicola*, or *Pantoea* sp. when researchers rely solely on rapid, commercialized identification systems. With one such system, API 20E test strips, we were unable to differentiate unequivocally among some strains of *Pantoea dispersa* and *Pantoea agglomerans*, other named *Enterobacter agglomerans* and *Erwinia herbicola* strains, and strains of other *Erwinia* species or of other genera (1, 27; this paper). Some helpful additional discriminating features, which are not contained in some of the rapid systems, are shown in Tables 2 and 3.

Description of *Pantoea* gen. nov. *Pantoea* (Pan. toe'a. Gr. adj. *pantoios*, of all sorts and sources; M. L. fem. n. *Pantoea*, [bacteria] from diverse [geographical and ecological] sources). Gram-negative, noncapsulated, nonspore-forming straight rods measuring 0.5 to 1.0 by 1.0 to 3.0 μm. Most are motile and are peritrichously flagellated. Colonies on nutrient agar are smooth, translucent, and more or less convex with entire margins. Colonies may or may not be yellow pigmented. Facultatively anaerobic; oxidase negative. Acid is produced from D-xylose, D-ribose, maltose, D-galactose, D-mannose, D-fructose, trehalose, and D-mannitol. Isolated from plant surfaces, seeds, soil, and water, as well as from humans (wounds, blood, urine, internal organs) and animals, in several parts of the world.

The guanine-plus-cytosine content of the DNA is 55.1 to 60.6 mol% (1, 5, 9, 30; Mergaert, unpublished data), as determined by the T_m method.

The type species is *Pantoea agglomerans* (Beijerinck 1888) comb. nov.

Description of *Pantoea agglomerans*. *Pantoea agglomerans* (Beijerinck 1888) comb. nov. (*Enterobacter agglomerans* (Beijerinck 1888) Ewing and Fife 1972) (ag. glo' mer. ans. L.v. *agglomerare*, to form into a ball; L. part. adj. *agglomerans*, forming into a ball).

The species has all of the characteristics of the genus. The specific description below is mainly based on 16 strains studied by conventional methods by Gavini et al. (11).

Culture conditions. Strains grow well on nutrient agar at 30°C but not at 44°C.

Biochemical characteristics. The biochemical characteristics at 30°C (11) are shown in Tables 2 and 3.

Nutritional characteristics. The following carbon sources are utilized at 30°C by 90 to 100% of the strains within 5 days: glycerol, *meso*-inositol, D-mannitol, L-arabinose, D-ribose, D-xylose, D-galactose, D-glucose, D-fructose, D-mannose, L-rhamnose, D-maltose, sucrose, trehalose, salicin, *N*-acetyl-D-glucosamine, D-gluconate, 2-keto-D-gluconate, succinate, fumarate, DL-glycerate, D-malate, L-malate, *meso*-tartrate, *cis*-aconitate, L-glutamate, L-proline, DL-4-aminobutyrate, and glucosamine.

The following carbon sources are not utilized at 30°C by 90 to 100% of the strains within 5 days: adonitol, dulcitol, sorbitol, *meso*-xylitol, L-arabitol, *meso*-erythritol, L-xylose, L-sorbose, melibiose, gentiobiose, D-melizitose, D-tagatose, D-fucose, L-fucose, D-turanose, α-methyl-D-mannoside, α-methyl-D-glucoside, β-methyl-D-xyloside, amygdalin, arbu-

tin, esculin, inulin, starch, glycogen, acetate, propionate, butyrate, isobutyrate, *n*-valerate, isovalerate, *n*-caproate, heptanoate, caprylate, pelargonate, caprate, oxalate, malate, glutarate, adipate, pimelate, suberate, azelate, sebacate, glycolate, DL-3-hydroxybutyrate, levulinate, citraconate, itaconate, mesaconate, phenylacetate, benzoate, *o*-hydroxybenzoate, *m*-hydroxybenzoate, *p*-hydroxybenzoate, D-mandelate, L-mandelate, phthalate, isophthalate, terephthalate, glycine, L-leucine, L-norleucine, DL-2-aminobutyrate, L-threonine, L-methionine, L-phenylalanine, L-tyrosine, D-tryptophan, L-tryptophan, trigonelline, L-ornithine, L-lysine, L-citrulline, L-arginine, DL-kynurenine, betaine, creatin, β-alanine, DL-3-aminobutyrate, DL-5-aminovalerate, DL-2-aminobenzoate, DL-3-aminobenzoate, DL-4-aminobenzoate, urea, acetamide, sarcosine, ethylamine, butylamine, amylamine, ethanolamine, benzylamine, putrescine, spermine, histamine, and tryptamine.

DNA base composition. The guanine-plus-cytosine contents of 21 strains range from 55.1 to 56.8 mol% (5, 27; Mergaert, unpublished data), as determined by the T_m method.

Habitat. Isolated from plant surfaces, seeds, and water, as well as from humans (wounds, blood, urine, internal organs) and animals. Some strains (synonym, *Erwinia milletiae*) have been reported to cause galls on *Wisteria floribunda* and *Wisteria japonica*, some strains have been reported to cause galls on *Gypsophila paniculata*, and some strains have been reported to cause stalk and leaf necrosis on onions (14).

The strain is strain ATCC 27155 (= CDC 1461-67 = NCTC 9381 = LMG 1286 = ICPB 3435), which was isolated from a knee laceration in Zimbabwe.

Description of *Pantoea dispersa* sp. nov. *Pantoea dispersa* (dis. per' sa. L. v. *dispergere*, to spread, to scatter; L. fem. part. adj. *dispersa*, spread, scattered). The species has all of the characteristics of the genus, as well as the characteristics described below.

Culture conditions. Strains grow at neither 4 nor 44°C, but grow well on nutrient agar at 30 and 41°C.

Biochemical characteristics. The biochemical characteristics at 30°C (11) are shown in Tables 2 and 3.

Nutritional characteristics. The following carbon sources are utilized at 30°C by 90 to 100% of the strains within 5 days: glycerol, *meso*-erythritol, *meso*-inositol, D-arabitol, D-mannitol, L-arabinose, D-ribose, D-xylose, D-galactose, D-glucose, D-fructose, D-mannose, L-rhamnose, amygdalin, D-cellobiose, D-maltose, sucrose, trehalose, gentiobiose, D-lyxose, D-gluconate, 2-keto-D-gluconate, 5-keto-D-gluconate, succinate, fumarate, DL-lactate, DL-glycerate, L-malate, L-tartrate, *meso*-tartrate, *cis*-aconitate, citrate, L-histidine, L-aspartate, L-glutamate, DL-4-aminobutyrate, and glucosamine.

The following carbon sources are not utilized at 30°C by 90 to 100% of the strains within 5 days: adonitol, dulcitol, sorbitol, *meso*-xylitol, L-arabitol, L-xylose, L-sorbose, lactose, melibiose, D-melizitose, D-raffinose, D-tagatose, D-fucose, L-fucose, D-turanose, β-methyl-D-xyloside, α-methyl-D-mannoside, α-methyl-D-glucoside, inulin, starch, glycogen, propionate, butyrate, isobutyrate, *n*-valerate, isovalerate, *n*-caproate, heptanoate, caprylate, pelargonate, caprate, oxalate, malonate, maleate, glutarate, adipate, pimelate, suberate, azelate, sebacate, glycolate, DL-3-hydroxybutyrate, D-tartrate, levulinate, citraconate, itaconate, mesaconate, phenylacetate, benzoate, *o*-hydroxybenzoate, *m*-hydroxybenzoate, *p*-hydroxybenzoate, D-mandelate, L-mandelate, phthalate, isophthalate, terephthalate, glycine, L-leucine, L-isoleucine, L-norleucine, L-valine, DL-norvaline, DL-2-aminobutyrate, L-threonine, L-methionine, L-phenylalanine, L-tyrosine, D-tryptophan, L-tryptophan, trigonelline, L-lysine, L-citrulline, L-arginine, DL-kynurenine, betaine, creatin, β-alanine, DL-3-aminobutyrate, DL-5-aminovalerate, DL-2-aminobenzoate, DL-3-aminobenzoate, DL-4-aminobenzoate, urea, acetamide, sarcosine, butylamine, benzylamine, putrescine, spermine, histamine, and tryptamine.

DNA base composition. The guanine-plus-cytosine contents of four strains are 56.5 mol% (strain ATCC 14589^T) (this paper), 58.6 mol% (strain Graham G146) (5), 59.1 mol% (strain NCPPB 2285) (Mergaert, unpublished data), and 60.6 mol% (strain IPO 445) (9), as determined by the T_m method.

Habitat. Isolated from plant surfaces, seeds, humans, and the environment.

Type strain. The type strain is strain ATCC 14589 (= LMG 2603), which was isolated from soil in Japan (18).

The biochemical characteristics of type strains *Pantoea agglomerans* ATCC 27155 and *Pantoea dispersa* ATCC 14589 are shown in Table 2.

Differential characteristics for *Pantoea agglomerans*, *Pantoea dispersa*, and the species previously classified in or phenotypically related to the *Erwinia herbicola-Enterobacter agglomerans* complex are shown in Table 3. Additional differential characteristics that differentiate *Pantoea agglomerans* and *Pantoea dispersa* are utilization of *meso*-erythritol, amygdalin, and gentiobiose as carbon sources within 5 days at 30°C (absent in the former species and present in the latter species).

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