Reclassification of *Xanthomonas*

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A comprehensive DNA-DNA hybridization study was performed by using 183 strains of the genus *Xanthomonas*. This genus was shown to comprise 20 DNA homology groups which are considered genomic species. Four groups corresponded to the previously described species *Xanthomonas albilineans*, *Xanthomonas fragariae*, *Xanthomonas oryzae*, and *Xanthomonas populi*. The previously described species *Xanthomonas campestris* was heterogeneous and was divided into 16 DNA homology groups. One of these groups exhibited a high level of DNA homology with *Xanthomonas axonopodis*. The 62 pathovars represented in this study were allocated to appropriate species. Our results, together with previous taxonomic data, supported a comprehensive revision of the classification of the genus *Xanthomonas*. The species *X. albilineans*, *X. fragariae*, *X. oryzae*, and *X. populi* are not affected. The type species of the genus, *X. campestris* (Pammel 1895) Dowson 1939, is emended to include only the pathovars obtained from crucifers (i.e., *X. campestris* pv. *aberrans*, *X. campestris* pv. *armoraciae*, *X. campestris* pv. *barbareae*, *X. campestris* pv. *campestris*, *X. campestris* pv. *incanae*, and *X. campestris* pv. *raphani*). *X. axonopodis* Starr and Garces 1950 is emended to include 34 former *X. campestris* pathovars. The following species names are proposed: *Xanthomonas arboricola* sp. nov., including *X. arboricola* pv. *corylina*, *X. arboricola* pv. *juglandis*, *X. arboricola* pv. *poinsettiiicola* (type C strains of the former *X. campestris* pathovar), *X. arboricola* pv. *populi*, and *X. arboricola* pv. *pruni*; *Xanthomonas bromi* sp. nov. for strains isolated from bromegrass; *Xanthomonas cassavae* (ex Wiehe and Dowson 1953) sp. nov., nom. rev.; *Xanthomonas codiae* sp. nov., including type B strains of the former taxon *X. campestris* pv. *poinsettiiicola*; *Xanthomonas cucurbitae* (ex Bryan 1926) sp. nov., nom. rev.; *Xanthomonas hortorum* sp. nov., including *X. hortorum* pv. *hederae*, *X. hortorum* pv. *pelargonii*, and *X. hortorum* pv. *vitians*; *Xanthomonas hyacinthi* (ex Wakker 1883) sp. nov., nom. rev.; *Xanthomonas melonis* sp. nov.; *Xanthomonas pisi* (ex Goto and Okabe 1958) sp. nov., nom. rev.; *Xanthomonas sacchari* sp. nov. for strains isolated from diseased sugarcane in Guadeloupe; *Xanthomonas theicola* sp. nov.; *Xanthomonas translucens* (ex Jones, Johnson, and Reddy 1917) sp. nov., nom. rev., including *X. translucens* pv. *arrhenatheri*, *X. translucens* pv. *cerealis*, *X. translucens* pv. *graminis*, *X. translucens* pv. *hordei*, *X. translucens* pv. *phlei*, *X. translucens* pv. *phleipratensis*, *X. translucens* pv. *poae*, *X. translucens* pv. *secalis*, *X. translucens* pv. *translucens*, and *X. translucens* pv. *undulosa*; *Xanthomonas vasicola* sp. nov., including *X. vasicola* pv. *holcicola* and *X. vasicola* pv. *vasculorum* (type B strains of the former taxon *X. campestris* pv. *vasculorum*); and *Xanthomonas vesicatoria* (ex Doidge 1920) sp. nov., nom. rev., which includes the type B strains of the former taxon *X. campestris* pv. *vesicatoria*. Differentiating characteristics were determined for the new species on the basis of metabolic activity on a range of carbon substrates by using the Biolog GN microplate system.

In the past, the taxonomy of bacteria has been dominated by a phenetic approach, and many classification systems have been and still are based on what were thought to be important phenotypic properties. The taxonomy of the genus *Xanthomonas* has followed this tendency in that a single phenotypic feature, host specificity, has determined the classification of the genus. Since the first report of a xanthomonad (55) until 1974, it was common practice to define a plant-pathogenic xanthomonad isolated from a new host plant as a new *Xanthomonas* species. The unreasonable number of nomenclatures resulting from this practice was drastically reduced by Dye and Lelliott (19), who justified their reclassification by referring to the impossibility of differentiating nomenclatures by any feature other than host specificity (10, 17). Later, names of former nomenclatures were preserved in a special-purpose classification (18) as *Xanthomonas campestris* pathovar names.

The original classification of the genus *Xanthomonas*, in which all of the phytopathological variants of *X. campestris* were recognized as separate species, was not sound taxonomically. With the exception of the ambiguous feature of host specificity, few biochemical and phenotypic characteristics were used to differentiate the species. In the last few years,

workers have provided evidence that the current classification, in which *X. campestris* contains more than 140 pathovars, is not a reflection of genomic relationships. The first DNA hybridization experiments performed with *Xanthomonas* nomenclatures were described by Murata and Starr (35), who observed that up to 50% of the DNA was characteristic for the nomenclatures which they studied. Schroth and Hildebrand (39) have stressed the need for genomic homology matrices to clarify the taxonomic relationships within the genera *Pseudomonas* and *Xanthomonas*. Extensive studies based on electrophoresis of proteins (48), gas chromatographic analysis of fatty acid methyl esters (FAME) (60), restriction fragment length polymorphisms of genomic DNA (32), restriction patterns of rRNAs (4), and DNA hybridization (28, 37, 49, 50) have shown that a number of more or less well-defined groups exist in *X. campestris* and that a number of pathovars are heterogeneous. Most of the DNA hybridization results that have been published are fragmentary (49, 50) or deal with specific groups, such as pathovars isolated from members of the Poaceae (51) or from citrus (52), and are part of a polyphasic study on the taxonomy of the genus *Xanthomonas* conducted in our laboratory. A global DNA homology matrix for the genus *Xanthomonas* should serve as a basis for reclassification of the species and pathovars of the genus (39, 49).

A classification system based solely on differences in overall genomic DNAs would in many cases be impractical for diag-

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nostic purposes, especially in laboratories in which phenotypic traits are routinely used for identification. Among the recent developments in bacterial taxonomy are ready-made phenotypic and chemotaxonomic fingerprinting systems which typically yield a large number of discriminating characteristics from a single experiment. Such techniques, combined with objective numerical comparisons and clustering algorithms in which computers are used, have enabled taxonomists to compare many characteristics of large numbers of organisms in a rational and unbiased way. Each of the conditions mentioned above (i.e., availability of fast fingerprinting systems, use of large numbers of strains, and numerical comparison) is very important in modern classification. On the other hand, DNA homology, as expressed by levels of hybridization of total cellular DNAs, remains the ultimate criterion for the circumscription of a bacterial species (56). Ideally, polyphasic taxonomy should be based on data from phenotypic, chemotaxonomic, and genotypic approaches, and classification schemes will be stable and useful only when the results obtained from all of these approaches converge to a reasonable degree.

Attempts have been made by Lee et al. (33) and Hildebrand et al. (27) to study phenotypic traits that differentiate the known genomic groups of the genus *Xanthomonas*. The commercial GN microplate assay (Biolog, Inc., Hayward, Calif.) was recently evaluated for its ability to identify members of the genus *Xanthomonas* and other plant-pathogenic bacteria (30), particularly *X. campestris* pv. citri (54) and *X. campestris* pv. vesicatoria (6). GN microplates are designed to fingerprint gram-negative bacteria by using tetrazolium violet as a redox indicator to reveal the metabolic activity of bacteria on 95 different carbon compounds (5). Although in previous studies (30, 54) the commercial database led to low percentages of correct identification, it was clearly shown that GN microplates distinguish between xanthomonads and may offer great potential for the identification of these organisms. In this study, a number of representatives of all previously described *Xanthomonas* genomic groups were characterized and compared by using the GN microplate assay.

In this paper we present and synthesize all of the available DNA homology data for the genus *Xanthomonas* and propose a new classification of *Xanthomonas* species in which both the genomic relationships and the needs of plant pathologists for a rational nomenclature are taken into account. Phenotypic data from previous studies and from the Biolog GN microplate fingerprint analysis are used to describe and differentiate the genomic groups.

MATERIALS AND METHODS

Bacterial strains. All of the strains used in this study were selected on the basis of the results of a fingerprint analysis of more than 1,000 *Xanthomonas* strains in which sodium dodecyl sulfate-polyacrylamide gel electrophoresis (SDS-PAGE) of proteins was used and on the basis of the results of a FAME analysis, as described previously (48, 49, 51, 52, 60). We verified that these organisms were authentic xanthomonads by determining their *Xanthomonas*-specific protein patterns and fatty acid contents (48, 60). A total of 183 strains representing all of the *Xanthomonas* species and 62 *X. campestris* pathovars were compared by performing DNA hybridization experiments. These strains are listed in Table 1. We used the following 252 strains representing all of the genomic groups described in this study for phenotypic characterization studies performed with Biolog GN microplates: *Xanthomonas albilineans* LMG 487, LMG 488, LMG 490, LMG 494^T (T = type strain), and LMG 482; *Xanthomonas axonopodis* LMG 539, LMG 540, LMG 538^T, LMG 537, and LMG 541; *X. campestris* LMG 8272 and LMG 8274 (isolated from bromegrass; received as *X. campestris* pv. graminis); *X. campestris* pv. alfalfae LMG 497* (* = pathovar reference strain), LMG 495, LMG 8018, LMG 8079, LMG 8080, LMG 8019, and LMG 8020; *X. campestris* pv. arrhenatheri LMG 7384, LMG 588, LMG 727*, LMG 591, and LMG 590; *X. campestris* pv. begoniae LMG 7194, LMG 7196, LMG 7595, LMG 552, and LMG 7303*; *X. campestris* pv. cajani LMG 7473, LMG 7387, and LMG 558*; *X. campestris* pv. campestris LMG 568^T, LMG 8121, LMG 8003, LMG 8035, LMG 8051, LMG

583, LMG 7514, LMG 7516, LMG 575, LMG 7662, LMG 571, LMG 8001, LMG 8119, LMG 8099, LMG 8112, LMG 8082, LMG 8055, LMG 8123, and LMG 8100; *X. campestris* pv. cassavae type A strains LMG 5246, LMG 5264, LMG 672, LMG 5270, and LMG 673*; *X. campestris* pv. cerealis LMG 880, LMG 679*, LMG 891, and LMG 887; *X. campestris* pv. citri A LMG 9176, LMG 9669, LMG 9671, LMG 682*, LMG 8657, LMG 9321, and LMG 8650; *X. campestris* pv. citri B LMG 9182, LMG 9183, and LMG 9179; *X. campestris* pv. citri C LMG 8655, LMG 8656, LMG 9181, LMG 9654, and LMG 9658; *X. campestris* pv. citri D LMG 9185; *X. campestris* pv. citri E LMG 9168, LMG 9160, LMG 9174, and LMG 9162; *X. campestris* pv. coracanae LMG 686* and LMG 7476; *X. campestris* pv. cucurbitae LMG 8661, LMG 8662, LMG 7480, LMG 7481, and LMG 690*; *X. campestris* pv. dieffenbachiae LMG 7399, LMG 8664, LMG 7484, LMG 695*, and LMG 7400; *X. campestris* pv. glycines LMG 8027, LMG 8126, LMG 8128, LMG 712*, and LMG 8026; *X. campestris* pv. graminis LMG 726* and LMG 595; *X. campestris* pv. hederiae LMG 7414, LMG 7413, LMG 734, LMG 733*, and LMG 8665; *X. campestris* pv. holcicola LMG 7489, LMG 736*, LMG 7416, LMG 8276, and LMG 8277; *X. campestris* pv. hordei LMG 882, LMG 879, LMG 737*, LMG 720, and LMG 884; *X. campestris* pv. hyacinthi LMG 740, LMG 7419, LMG 742, LMG 739*, and LMG 8042; *X. campestris* pv. juglandis LMG 8045, LMG 751, LMG 8046, LMG 747*, and LMG 750; *X. campestris* pv. malvacearum LMG 7430, LMG 7427, LMG 764, LMG 762, LMG 761*, and LMG 7427; *X. campestris* pv. manihotis LMG 782, LMG 768, LMG 780, LMG 769, and LMG 773*; *X. campestris* pv. melonis LMG 8671 and LMG 8674; *X. campestris* pv. pelargonii LMG 7354, LMG 7316, LMG 7715, LMG 7753, LMG 7764, LMG 7708, LMG 7690, LMG 820, LMG 7317, LMG 7318, LMG 7710, LMG 7315, LMG 7321, LMG 7356, LMG 7706, LMG 7763, LMG 7314*, LMG 7312, and LMG 7691; *X. campestris* pv. phaseoli LMG 7455*, LMG 8014, LMG 823, LMG 842, LMG 821, and LMG 829; *X. campestris* pv. phaseoli var. fuscans LMG 7459, LMG 7456, LMG 825, LMG 837, LMG 841, and LMG 8038; *X. campestris* pv. phlei LMG 730*, LMG 719, LMG 716, and LMG 723; *X. campestris* pv. phleipratensis LMG 843*; *X. campestris* pv. pisi LMG 8471* and LMG 8472*; *X. campestris* pv. poae LMG 728*; *X. campestris* pv. poinsetticola type A strain LMG 849*; *X. campestris* pv. poinsetticola type B strains LMG 8678 and LMG 8677; *X. campestris* pv. poinsetticola type C strain LMG 5402; *X. campestris* pv. pruni LMG 854, LMG 853, LMG 855, LMG 8679, LMG 852*, and LMG 7438; *X. campestris* pv. ricini LMG 7442, LMG 861*, LMG 7443, and LMG 7444; *X. campestris* pv. secalis LMG 883*; *X. campestris* pv. theicola LMG 6886, LMG 8684*, and LMG 8685; *X. campestris* pv. translucens LMG 876*, LMG 5259, LMG 5260, LMG 5262, and LMG 875; *X. campestris* pv. undulosa LMG 8283, LMG 885, LMG 888, and LMG 886; *X. campestris* pv. vasculorum type A strains LMG 903, LMG 8285, LMG 901*, LMG 899, and LMG 894; *X. campestris* pv. vasculorum type B strains LMG 896, LMG 8284, LMG 900, and LMG 902; *X. campestris* pv. vesicatoria type A strains LMG 668, LMG 667, LMG 909, LMG 910, LMG 906, LMG 905, LMG 929, LMG 913, LMG 922, LMG 932, and LMG 914; *X. campestris* pv. vesicatoria type B strains LMG 935, LMG 925, LMG 919, LMG 917, LMG 916, LMG 911*, and LMG 920; *X. campestris* pv. vitians type A strain LMG 937*; *X. campestris* pv. vitians type B strains LMG 7508, LMG 7510, LMG 8688, LMG 8690, and LMG 8689; *Xanthomonas fragariae* LMG 706 and LMG 708^T; *Xanthomonas oryzae* pv. oryzae LMG 5047^T, LMG 795, LMG 641, LMG 806, and LMG 803; *X. oryzae* pv. oryzicola LMG 661, LMG 797*, LMG 665, LMG 793, and LMG 657; *Xanthomonas populi* LMG 970^T (= LMG 5743^T) and LMG 975; and strains LMG 476 and LMG 471 from sugarcane received as *X. albilineans*.

The following abbreviations for culture collections are used in strain designations in this paper: LMG, Laboratorium voor Microbiologie Culture Collection, Universiteit Gent, Ghent, Belgium; NCPBP, National Collection of Plant Pathogenic Bacteria, Harpenden, Hertfordshire, United Kingdom; ICMP, International Collection of Microorganisms from Plants, Department of Scientific and Industrial Research Mount Albert Research Centre, Auckland, New Zealand; ATCC, American Type Culture Collection, Rockville, Md.; DSM, Deutsche Sammlung von Mikroorganismen und Zellkulturen GmbH, Braunschweig, Germany; CFBP, Collection Française de Bactéries Phytopathogènes, Institut National de la Recherche Agronomique, Station de Pathologie Végétale et Phytobactériologie, Angers, France.

DNA hybridization. DNAs were extracted and purified as described by Murmur (34). The levels of DNA binding were determined from the initial renaturation rates by using a spectrophotometer (13). The renaturation rates were determined in 2× SSC at the optimal renaturation temperature, 80.8°C, which was calculated from the G+C contents as described by De Ley (12) (1× SSC is 0.15 M NaCl plus 0.015 M sodium citrate).

Phenotypic analysis with the Biolog GN microplate system. Stock cultures were subcultured on nutrient agar (0.1% [wt/vol] Lab Lemco, 0.2% [wt/vol] yeast extract, 0.5% [wt/vol] peptone, 0.5% [wt/vol] NaCl, 2% [wt/vol] bacteriological agar) for 72 h at room temperature. A small quantity of cells was streaked onto Trypticase soy agar plates and incubated for 24 h at 28 ± 0.5°C. Since *X. populi* does not grow at 28°C, strains of this species were incubated at 19 ± 0.5°C.

To prepare inocula, sterile cotton sticks were carefully dipped into the colonies, and the cells were suspended in sterile saline. The optical density of each inoculum was determined spectrophotometrically at 590 nm and was adjusted to 0.190 to 0.210. The Biolog GN microplates were preincubated at 28°C and inoculated with 150 µl of suspension per reaction well; they were incubated at 28 ± 0.5°C.

TABLE 1. DNA homology groups, pathovars and strains analyzed in DNA hybridization experiments, and proposed species names

Group	DNA binding value (%) ^a	Name as received	Strain	Mean DNA binding value within group (%)	No. of values determined ^b	Proposed name
1 (<i>X. fragariae</i>)	91	<i>X. fragariae</i>	LMG 706	91	1	<i>X. fragariae</i>
			LMG 708 ^T	91	1	
2 (<i>X. hortorum</i>)	92 ± 10	<i>X. campestris</i> pv. pelargonii	LMG 7314*	96	4	<i>X. hortorum</i> pv. pelargonii
			LMG 7356	102	1	
			LMG 7585	96	2	
			LMG 7712	96	2	
		<i>X. campestris</i> pv. hederæ	LMG 733*	77	1	<i>X. hortorum</i> pv. hederæ
		<i>X. campestris</i> pv. vitians type B ^c	LMG 938	81	2	<i>X. hortorum</i> pv. vitians
3 (<i>X. populi</i>)	96 ± 1	<i>X. populi</i>	LMG 974	97	2	<i>X. populi</i>
			LMG 5743 ^T	96	2	
			LMG 5753	97	2	
4 (<i>X. arboricola</i>)	79 ± 15	<i>X. campestris</i> pv. corylina	LMG 688	89	3	<i>X. arboricola</i> pv. corylina
			LMG 689*	82	6	
			LMG 8658	86	2	
			LMG 8660	92	3	
		<i>X. campestris</i> pv. juglandis	LMG 747*	79	4	<i>X. arboricola</i> pv. juglandis
			LMG 8047	82	1	
		<i>X. campestris</i> pv. poinsetticola type C ^c	LMG 5403	68	3	<i>X. arboricola</i> pv. poinsetticola
		<i>X. campestris</i> pv. populi	LMG 12141*	57	4	<i>X. arboricola</i> pv. populi
		<i>X. campestris</i> pv. pruni	LMG 852*	82	5	<i>X. arboricola</i> pv. pruni
			LMG 8680	97	1	
5 (<i>X. cassavae</i>)	94 ± 2	<i>X. campestris</i> pv. cassavae type A ^c	LMG 670	95	2	<i>X. cassavae</i>
			LMG 672	95	1	
			LMG 673*	94	3	
			LMG 5264	93	2	
6 (<i>X. codiae</i>)	99	<i>X. campestris</i> pv. poinsetticola type B ^c	LMG 8677	99	1	<i>X. codiae</i>
			LMG 8678	99	1	
7 (<i>X. bromi</i>)	88 ± 6	<i>X. campestris</i> pv. ?	LMG 947	84	1	<i>X. bromi</i>
		" <i>X. campestris</i> pv. graminis"	LMG 8269	88	2	
			LMG 8272	92	1	
8 (<i>X. cucurbitae</i>)	88	<i>X. campestris</i> pv. cucurbitae	LMG 690*	88	1	<i>X. cucurbitae</i>
			LMG 8662	88	1	
9 (<i>X. axonopodis</i>)	77 ± 15	<i>X. axonopodis</i>	LMG 5381 ^T	66	9	<i>X. axonopodis</i> pv. axonopodis
			LMG 539	94	1	
		<i>X. campestris</i> pv. alfalfae	LMG 497*	72	14	<i>X. axonopodis</i> pv. alfalfae
			LMG 8079	81	3	
		<i>X. campestris</i> pv. bauhiniae	LMG 548*	72	8	<i>X. axonopodis</i> pv. bauhiniae
		<i>X. campestris</i> pv. begoniae	LMG 551	96	3	<i>X. axonopodis</i> pv. begoniae
			LMG 7178	87	4	
			LMG 7188	88	3	
			LMG 7226	95	3	
			LMG 7303*	81	11	
			LMG 7304	87	3	
			LMG 7601	73	7	
		<i>X. campestris</i> pv. cajani	LMG 558*	74	10	<i>X. axonopodis</i> pv. cajani
			LMG 7387 ^{t1}	77	1	
		<i>X. campestris</i> pv. cassavae type B ^c	LMG 8049	87	1	<i>X. axonopodis</i> pv. cassavae
		<i>X. campestris</i> pv. cassiae	LMG 675*	76	6	<i>X. axonopodis</i> pv. cassiae
		<i>X. campestris</i> pv. citri A ^d	LMG 681	91	6	<i>X. axonopodis</i> pv. citri
			LMG 682*	70	17	
			LMG 8650	89	5	
			LMG 8654	89	4	
			LMG 8657	86	6	
			LMG 9176	80	7	
			LMG 9321	93	2	
			LMG 9665	91	3	
			LMG 9671	84	7	
		<i>X. campestris</i> pv. citri B (<i>X. campestris</i> pv. aurantifolii) ^{d,e}	LMG 9179	94	4	<i>X. axonopodis</i> pv. aurantifolii
			LMG 9183	78	2	
		<i>X. campestris</i> pv. citri C (<i>X. campestris</i> pv. aurantifolii) ^{d,e}	LMG 8655	78	8	
			LMG 9181	71	15	
			LMG 9658	86	3	

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TABLE 1—Continued

Group	DNA binding value (%) ^a	Name as received	Strain	Mean DNA binding value within group (%)	No. of values determined ^b	Proposed name
10 (<i>X. oryzae</i>)	91 ± 7	<i>X. campestris</i> pv. citri D (<i>X. campestris</i> pv. aurantifolii) ^{d,e}	LMG 9182	83	6	
		<i>X. campestris</i> pv. citri E (<i>X. campestris</i> pv. citrumelo) ^{d,e}	LMG 9160	69	13	<i>X. axonopodis</i> pv. citrumelo
			LMG 9167	88	2	
			LMG 9172	81	5	
			LMG 9175	76	4	
			LMG 9325	91	2	
		<i>X. campestris</i> pv. clitoriae	LMG 9045*	69	4	<i>X. axonopodis</i> pv. clitoriae
		<i>X. campestris</i> pv. coracanae	LMG 686*	65	4	<i>X. axonopodis</i> pv. coracanae
			LMG 7476	81	4	
		<i>X. campestris</i> pv. cyamopsidis	LMG 691*	76	8	<i>X. axonopodis</i> pv. cyamopsidis
		<i>X. campestris</i> pv. desmodii	LMG 692*	74	7	<i>X. axonopodis</i> pv. desmodii
		<i>X. campestris</i> pv. desmodiigangetici	LMG 693*	90	3	<i>X. axonopodis</i> pv. desmodiigangetici
		<i>X. campestris</i> pv. desmodiilaxiflori	LMG 9046*	66	8	<i>X. axonopodis</i> pv. desmodiilaxiflori
		<i>X. campestris</i> pv. desmodiitundifolii	LMG 6941*	79	9	<i>X. axonopodis</i> pv. desmodiitundifolii
		<i>X. campestris</i> pv. dieffenbachiae	LMG 6951*	70	8	<i>X. axonopodis</i> pv. dieffenbachiae
			LMG 7399	66	2	
			LMG 8664	99	1	
		<i>X. campestris</i> pv. erythrinae	LMG 698*	81	4	<i>X. axonopodis</i> pv. erythrinae
		<i>X. campestris</i> pv. glycines	LMG 712*	79	12	<i>X. axonopodis</i> pv. glycines
			LMG 8125	88	2	
		<i>X. campestris</i> pv. lespedezae	LMG 757*	74	9	<i>X. axonopodis</i> pv. lespedezae
		<i>X. campestris</i> pv. malvacearum	LMG 761*	74	3	<i>X. axonopodis</i> pv. malvacearum
			LMG 7429	77	3	
		<i>X. campestris</i> pv. manihotis	LMG 771	75	3	<i>X. axonopodis</i> pv. manihotis
			LMG 773*	73	9	
			LMG 778	80	2	
			LMG 784*	78	5	
		<i>X. campestris</i> pv. patelii	LMG 8111*	83	7	<i>X. axonopodis</i> pv. patelii
		<i>X. campestris</i> pv. phaseoli	LMG 7455*	66	14	<i>X. axonopodis</i> pv. phaseoli
			LMG 8014	99	1	
		<i>X. campestris</i> pv. phaseoli var. fuscans	LMG 8371	94	1	<i>X. axonopodis</i> pv. phaseoli var. fuscans
			LMG 7511	97	1	
			LMG 8036	78	6	
		<i>X. campestris</i> pv. phyllanthi	LMG 8441*	72	3	<i>X. axonopodis</i> pv. phyllanthi
		<i>X. campestris</i> pv. poinsetticola type A ^c	LMG 849*	74	7	<i>X. axonopodis</i> pv. poinsetticola
		<i>X. campestris</i> pv. rhynchosiae	LMG 8021*	78	3	<i>X. axonopodis</i> pv. rhynchosiae
		<i>X. campestris</i> pv. ricini	LMG 861*	82	4	<i>X. axonopodis</i> pv. ricini
			LMG 862	85	4	
			LMG 7441	83	4	
			LMG 7443	83	3	
		<i>X. campestris</i> pv. sesbaniae	LMG 867*	68	6	<i>X. axonopodis</i> pv. sesbaniae
		<i>X. campestris</i> pv. tamarindi	LMG 869	73	7	<i>X. axonopodis</i> pv. tamarindi
			LMG 955*	84	5	
		<i>X. campestris</i> pv. vasculorum type A ^f	LMG 895	89	2	<i>X. axonopodis</i> pv. vasculorum
			LMG 899	90	2	
			LMG 901*	73	5	
			LMG 903	82	3	
		<i>X. campestris</i> pv. vesicatoria type A ^g	LMG 905	87	3	<i>X. axonopodis</i> pv. vesicatoria
			LMG 910	97	2	
			LMG 9291	82	4	
		<i>X. campestris</i> pv. vignaeradiatae	LMG 936*	65	9	<i>X. axonopodis</i> pv. vignaeradiatae
		<i>X. campestris</i> pv. vignicola	LMG 828	99	2	<i>X. axonopodis</i> pv. vignicola
			LMG 8139	98	1	
			LMG 8752*	71	9	
		<i>X. campestris</i> pv. vitians type A ^c	LMG 937*	63	2	<i>X. axonopodis</i> pv. vitians
		<i>X. oryzae</i> pv. oryzae	LMG 795	91	2	<i>X. oryzae</i> pv. oryzae
			LMG 5047 ^T	86	3	
			LMG 6518	87	1	
		<i>X. oryzae</i> pv. oryzicola	LMG 665	96	2	<i>X. oryzae</i> pv. oryzicola
			LMG 793	96	1	
			LMG 797*	92	3	

Continued on following page

TABLE 1—Continued

Group	DNA binding value (%) ^a	Name as received	Strain	Mean DNA binding value within group (%)	No. of values determined ^b	Proposed name
11 (<i>X. vasicola</i>)	90 ± 4	<i>X. campestris</i> pv. holcicola	LMG 736t2*	92	3	<i>X. vasicola</i> pv. holcicola
			LMG 7416	92	1	
			LMG 7489	92	2	
		<i>X. campestris</i> pv. vasculorum type B ^f	LMG 900	89	3	<i>X. vasicola</i> pv. vasculorum
			LMG 902	86	2	
12 (<i>X. pisi</i>)	88	<i>X. campestris</i> pv. pisi	LMG 8284	93	1	<i>X. pisi</i>
		<i>X. campestris</i> pv. melonis	LMG 847t1*			
			LMG 8670t1*	88	1	
13 (<i>X. melonis</i>)	88	<i>X. campestris</i> pv. melonis	LMG 8672	88	1	<i>X. melonis</i>
			LMG 911t1*	99	1	
			LMG 920t1	99	1	
14 (<i>X. vesicatoria</i>)	99	<i>X. campestris</i> pv. vesicatoria type B ^f	LMG 9037*	81	4	<i>X. vesicatoria</i>
			LMG 535*	86	6	
			LMG 7383t2	89	2	
15 (<i>X. campestris</i>)	87 ± 7	<i>X. campestris</i> pv. aberrans	LMG 547*	86	7	<i>X. campestris</i> pv. aberrans
			LMG 7385	95	2	
		<i>X. campestris</i> pv. armoraciae	LMG 567	96	3	<i>X. campestris</i> pv. armoraciae
			LMG 568 ^T	90	10	
		<i>X. campestris</i> pv. barbareae	LMG 571	89	4	<i>X. campestris</i> pv. barbareae
			LMG 573	87	3	
		<i>X. campestris</i> pv. campestris	LMG 583	87	5	<i>X. campestris</i> pv. campestris
			LMG 7514	86	3	
		<i>X. campestris</i> pv. incanae	LMG 8032	92	2	<i>X. campestris</i> pv. incanae
			LMG 7421	95	2	
		<i>X. campestris</i> pv. raphani	LMG 7490*	83	6	<i>X. campestris</i> pv. raphani
			LMG 860t1*	84	7	
		<i>X. campestris</i> pv. raphani	LMG 7505	86	4	<i>X. campestris</i> pv. raphani
			LMG 8134	87	2	
		<i>X. campestris</i> pv. arrhenatheri	LMG 588	76	6	<i>X. translucens</i> pv. arrhenatheri
			LMG 727t1*	80	3	
16 (<i>X. translucens</i>)	78 ± 11	<i>X. campestris</i> pv. cerealis	LMG 679*	67	8	<i>X. translucens</i> pv. cerealis
			LMG 880	82	1	
		<i>X. campestris</i> pv. graminis	LMG 713	88	1	<i>X. translucens</i> pv. graminis
			LMG 726*	75	7	
		<i>X. campestris</i> pv. hordei	LMG 737*	77	10	<i>X. translucens</i> pv. hordei
			LMG 879	84	2	
		<i>X. campestris</i> pv. hordei	LMG 882	81	3	<i>X. translucens</i> pv. hordei
			LMG 8279	75	1	
		<i>X. campestris</i> pv. phlei	LMG 716	85	4	<i>X. translucens</i> pv. phlei
			LMG 730*	97	1	
		<i>X. campestris</i> pv. phleipratensis	LMG 843*	72	3	<i>X. translucens</i> pv. phleipratensis
			LMG 594	90	1	
		<i>X. campestris</i> pv. poae	LMG 728*	78	10	<i>X. translucens</i> pv. poae
			LMG 883*	77	9	
		<i>X. campestris</i> pv. secalis	LMG 7507t1	84	1	<i>X. translucens</i> pv. secalis
			LMG 876*	80	8	
17 (<i>X. hyacinthi</i>)	98 ± 2	<i>X. campestris</i> pv. translucens	LMG 5259	69	2	<i>X. translucens</i> pv. translucens
			LMG 5260t1	90	1	
		<i>X. campestris</i> pv. undulosa	LMG 885	98	1	<i>X. translucens</i> pv. undulosa
			LMG 888	85	3	
		<i>X. campestris</i> pv. undulosa	LMG 892*	77	10	<i>X. translucens</i> pv. undulosa
			LMG 739*	97	2	
		<i>X. campestris</i> pv. hyacinthi	LMG 742	99	2	<i>X. hyacinthi</i>
			LMG 8041	99	2	
		<i>X. campestris</i> pv. theicola	LMG 8684*			<i>X. theicola</i>
			LMG 471	98	1	
		<i>X. campestris</i> pv. theicola	LMG 476	98	1	<i>X. sacchari</i>
			LMG 482	97	1	
		<i>X. albilineans</i>	LMG 494 ^T	97	1	<i>X. albilineans</i>
			LMG 958 ^T			
		<i>S. maltophilia</i>				<i>S. maltophilia</i>

^a Mean ± standard deviation DNA binding value for the group.^b Number of DNA hybridization values determined for a strain within the group.^c Genomic types of the same pathovar as determined in this study.^d Groups defined by Hartung and Civerolo (24).^e The pathovar names in parentheses are pathovar names proposed by Gabriel et al. (22).^f Types defined by Vauterin et al. (51).^g Types defined by Vauterin et al. (49).

FIG. 1. Average DNA binding values within and between 20 *Xanthomonas* DNA homology groups and *S. maltophilia*. The standard deviations are indicated in parentheses, and the numbers of values determined are indicated below the DNA binding values.

DNA homology groups and their significance. In general, the levels of DNA binding for strains belonging to the same group were high, ranging from 80 to 100%. The average levels of DNA binding between strains belonging to different *Xanthomonas* DNA homology groups (Fig. 1) were generally low; typically, the levels of DNA homology were less than 40%. Higher levels of homology, about 50%, were found between groups 2 and 3, between groups 5 and 6, between groups 5 and 7, and between group 10 and groups 11, 16, 17, and 18. These findings led to the hypothesis that two major classes of DNA homology could be differentiated in the genus *Xanthomonas*, a class of genomically almost unrelated strains and a class of genomically highly related strains exhibiting levels of DNA

RESULTS AND DISCUSSION

DNA hybridization. A total of 790 DNA hybridization values were determined for 183 strains. All of the values presented below are the averages of the values from at least two independent measurements. The overall experimental error of the method was $\pm 5.8\%$ DNA binding, as determined from the standard deviations of the replications. Since the complete matrix of DNA homology values was too large and uninformative in its original form, strains which exhibited average homology values (DNA binding values) of at least 60% were grouped together. This resulted in 20 genomic groups (groups 1 through 20) and a separate group (group 21) for the type strain of *Stenotrophomonas maltophilia* Palleroni and Bradbury 1993 (36) (formerly *Xanthomonas maltophilia* Swings, De Vos, Van den Mooter, and De Ley 1983 [42]). Since our preliminary description of six DNA homology groups in the genus *Xanthomonas* (49), a number of additional groups have been identified. In order to present the genomic groups in a natural sequence, they were ordered and numbered on the basis of their levels of relatedness. The strains which we studied and

FIG. 2. Distribution of 790 DNA homology values determined for 183 strains of the genus *Xanthomonas*. % D, DNA binding value.

homology of more than 80%. To verify this hypothesis, all 790 hybridization values were divided into classes of 10%, a value which was chosen because it was significantly larger than the overall error of the method (5.8%). These classes were used to construct a bar graph (Fig. 2), and this graph showed that there were two clear maxima, at 20 to 30% and at 90 to 100%. A third less pronounced maximum occurred at 60 to 70%; as discussed below, this peak could be explained by the presence of several subgroups in major homology groups 9 and 16. A significant minimum occurred between 40 and 60% on the frequency graph, which is consistent with the definition of genomic groups at an internal homology value of 60% (49), as maintained in this study.

Among the 20 *Xanthomonas* DNA homology groups, group 1 represented *X. fragariae*; the DNA binding value for two strains of this organism was 91%. This species is known to be phenotypically homogeneous and distinct from the other xanthomonads (46).

Group 2 was a very homogeneous group (DNA binding value, 92%) and included *X. campestris* pv. *pelargonii*, *X. campestris* pv. *hederae*, and *X. campestris* pv. *vitians* type B. *X. campestris* pv. *vitians* type B contained most of the strains which we studied but did not contain the pathovar reference strain. This heterogeneity was observed previously in a comparative protein electrophoresis study of *X. campestris* pathovars (48).

Group 3 corresponded to the species *X. populi*; the DNA binding value for three strains of this species was 96%. *X. populi* has been shown to differ from other xanthomonads in a number of phenotypic features (46).

In group 4, *X. campestris* pv. *corylina*, *X. campestris* pv. *juglandis*, and *X. campestris* pv. *pruni* were all highly related (average DNA homology value, 89%). Quinate metabolism was found to be a characteristic that distinguishes these pathovars from strains belonging to most of the other DNA homology groups (33). *X. campestris* pv. *populi* and *X. campestris* pv. *poinsetticola* type C were related to the other group 4 pathovars at average DNA homology values of 57 and 74%, respectively. However, the individual DNA homology values with other group 4 strains ranged from 48 to 76%.

Group 5 contained most of the *X. campestris* pv. *cassavae* strains (DNA binding value, 94%). The exceptions were three isolates obtained from Niger (unpublished data); one of these isolates was used for DNA hybridization experiments and fell

into group 9. The authentic *X. campestris* pv. *cassavae* strains, including the pathovar reference strain, were assigned to type A, whereas the isolates obtained from Niger were designated type B strains. *X. campestris* pv. *cassavae* was previously shown to be distinct from other xanthomonads on the basis of the results of SDS-PAGE of proteins (48).

Two strains received as *X. campestris* pv. *poinsetticola*, which were designated type B strains and were isolated from *Codiaeum variegatum*, were not related to the other *X. campestris* pv. *poinsetticola* strains and belonged to a separate DNA homology group, group 6. These strains were previously shown to be very similar to each other and to differ from other *X. campestris* pv. *poinsetticola* strains on the basis of the results of SDS-PAGE of proteins (48).

Strains isolated from *Bromus* spp. in different countries and received as *X. campestris* pv. *graminis* or as *X. campestris* strains not allocated to any pathovar were not related to any other pathovar isolated from members of the Poaceae but clustered together in a separate, homogeneous DNA homology group, group 7, at a DNA binding value of 88%. This confirmed previous results obtained in a comparative study of pathovars isolated from members of the Poaceae (51).

Group 8 included *X. campestris* pv. *cucurbitae* strains that were related at a DNA binding value of 88%. This pathovar could also be distinguished from other xanthomonads on the basis of the results of SDS-PAGE of proteins (48).

Group 9 was the largest and most heterogeneous *Xanthomonas* genomic group identified. This group contained 34 *X. campestris* pathovars and *X. axonopodis*, and all of the strains were related at an average level of homology of 77%. It has been reported previously (48) that many of the pathovars in group 9, particularly those isolated from members of the Fabaceae, are related on the basis of their SDS-PAGE protein profiles. Within group 9, many strains or subgroups were related to each other at degrees of binding ranging from 60 to 70%. This group was mainly responsible for the peak at 60 to 70% on the graph showing the distribution of DNA hybridization values (Fig. 2). Within group 9, *X. campestris* pv. *citri* is an example of a taxon containing strains belonging to different subgroups that can be delineated at DNA binding values of 60 to 70% (20, 52). Considered separately, these subgroups correlated well with the pathogenicities of the strains (i.e., group A, the cluster of groups B, C, and D, and group E in *X. campestris* pv. *citri*) (21, 24, 25). However, other *X. campestris* pathovars were related at very high levels of DNA homology to some of these groups. *X. campestris* pv. *glycines* and *X. campestris* pv. *cajani* were related at levels of more than 90% to pathogenicity group A of *X. campestris* pv. *citri*, whereas *X. campestris* pv. *alfalfae* exhibited more than 82% DNA homology with group E strains (data from the original homology matrix not shown). *X. campestris* pv. *dieffenbachiae* was shown previously to consist of two types on the basis of SDS-PAGE protein profiles (48). These types contained strains isolated from *Anthurium* species in Brazil and *Dieffenbachia* species in the United States. Although both types fell into the same DNA homology group, their level of DNA homology was 66% (data not shown), which confirmed the previous findings. The same types were also described by Berthier et al. (4) on the basis of rRNA gene restriction patterns. These types may represent different pathovars within the same genomic group. *X. campestris* pv. *vasculorum* has been subdivided previously into two types, types A and B (51). *X. axonopodis* and *X. campestris* pv. *vasculorum* type A were highly related to each other and distinct from other xanthomonads associated with members of the Poaceae (51). Both of these taxa were assigned to group 9 on the basis of an overall level of DNA homology of 58% with

other strains belonging to group 9, although individual values ranged from 47 to 71%.

Group 10 was represented by *X. oryzae* pv. *oryzae* and *X. oryzae* pv. *oryzicola*. The species *X. oryzae* was recently revived by Swings et al. (43) on the basis of phenotypic characteristics and DNA hybridization data. Its separate position in the homology matrix supports this reclassification.

Group 11 was composed of *X. campestris* pv. *holcicola* and the type B strains of *X. campestris* pv. *vasculorum*, which were defined at a DNA binding level of 90%. This confirmed previous results based on SDS-PAGE of proteins, FAME analysis, and DNA hybridization (48).

Group 12 was defined by one strain, the pathovar reference strain of *X. campestris* pv. *pisi*. In terms of relatedness at the species level, this strain exhibited low levels of DNA homology with all of the other groups studied. Vauterin et al. showed that this strain could be distinguished by protein electrophoresis data (48). It has been subdivided into two stable types on the basis of colony morphology, and these types are indistinguishable phenotypically and genotypically.

Group 13 was composed only of *X. campestris* pv. *melonis* strains, which exhibited a distinct, homogeneous genotype.

Group 14 contained the type B strains of *X. campestris* pv. *vesicatoria*. Vauterin et al. (49) reported that this pathovar is composed of two unrelated genotypes, which were designated types A and B. These types were later confirmed by protein electrophoresis data (48). The pathovar reference strain is a type B strain, which was shown in this study to belong to a separate *Xanthomonas* homology group.

In group 15, all of the pathovars isolated from crucifers (members of the family Brassicaceae) are related at a level of DNA binding of 87%. The striking homogeneity of this group of pathovars has been shown previously by FAME fingerprinting (60) and protein electrophoresis (unpublished data).

Ten pathovars isolated from members of the Poaceae were related at a level of 78% and were placed in group 16. This DNA homology group has been studied in detail by Vauterin et al. (51).

Group 17 was a very homogeneous group with a distinct genotype, and contained *X. campestris* pv. *hyacinthi* strains. This group is also distinct and homogeneous on the basis of the SDS-PAGE protein profiles of the strains (48).

Group 18 was represented by *X. campestris* pv. *theicola* and is another distinct group as determined by both DNA hybridization and protein electrophoresis (48).

Group 19 contained strains from Guadeloupe which were received as *X. albilineans* but were members of a different homology group belonging to the genus *Xanthomonas*. These strains have been discussed in detail previously and have been shown to have distinct protein and FAME profiles (51).

The original *X. albilineans* strains constituted group 20. The characteristics and homogeneity of this species were studied in detail by Yang et al. (59).

The type strain of *S. maltophilia* in group 21 exhibited levels of DNA binding of less than 25% with members of all of the *Xanthomonas* DNA homology groups.

Correlation between genomic groups and pathogenic specialization. In an attempt to relate the DNA homology groups to the phytopathogenic specialization of the strains, we found two clear cases in which pathovars that attack related hosts belong to the same genomic group. The first example involved the six pathovars obtained from crucifers (members of the family Brassicaceae), *X. campestris* pv. *campestris*, *X. campestris* pv. *aberrans*, *X. campestris* pv. *armoraciae*, *X. campestris* pv. *barbareae*, *X. campestris* pv. *incanae*, and *X. campestris* pv. *raphani*, which constituted group 15. Group 15 was defined at

a DNA binding value of 87% and exhibited low levels of DNA homology with all of the other groups. The second example involved pathovars which were obtained from grasses and cereals (members of the family Poaceae) and belonged to group 16 (51). Group 16 included *X. campestris* pv. *arrhenatheri*, *X. campestris* pv. *cerealis*, *X. campestris* pv. *graminis*, *X. campestris* pv. *hordei*, *X. campestris* pv. *phlei*, *X. campestris* pv. *phleipraensis*, *X. campestris* pv. *poae*, *X. campestris* pv. *secalis*, *X. campestris* pv. *translucens*, and *X. campestris* pv. *undulosa*. Only the following three known *X. campestris* pathovars isolated from members of the Poaceae did not belong to group 16: *X. campestris* pv. *coracanae*, *X. campestris* pv. *holcicola*, and *X. campestris* pv. *vasculorum*. It is also interesting that of the 21 pathovars obtained from legumes (members of the family Fabaceae), only *X. campestris* pv. *pisi* did not belong to group 9. However, group 9 is a heterogeneous group which includes pathovars obtained from nonleguminous hosts, such as *X. campestris* pv. *citri*, *X. campestris* pv. *manihotis*, *X. campestris* pv. *begoniae*, *X. campestris* pv. *malvacearum*, and the species *X. axonopodis*, which were isolated from various hosts.

In group 4, the genomic relatedness of *X. campestris* pv. *corylina*, *X. campestris* pv. *juglandis*, and *X. campestris* pv. *pruni* can be correlated with the infection mechanism rather than with the botanical relatedness of the host plants. These three pathovars, which were related at a level of 89%, attack hazelnuts, walnuts, and stone fruits, respectively, which are all trees which grow in temperate regions. The very high level of genomic relatedness of these organisms suggests that they may have originated from the same organism, an organism which had the ability to infect and colonize trees in temperate regions.

Examples of the opposite situation, where *X. campestris* pathovars pathogenic for closely related hosts or even the same host occurred in different DNA homology groups, were also found. *X. campestris* pv. *cassavae* type A and *X. campestris* pv. *manihotis* (44) are members of groups 5 and 9, respectively. *X. campestris* pv. *coracanae*, *X. campestris* pv. *vasculorum*, and *X. campestris* pv. *holcicola* do not belong to group 16, which includes all other pathogens of members of the Poaceae (51). *X. campestris* pv. *cucurbitae* in group 8 and *X. campestris* pv. *melonis* in group 13 are both pathogenic for members of the family Cucurbitaceae and have overlapping host ranges (8, 26).

Strains that had different origins grouped together in group 9, which contained 21 *X. campestris* pathovars obtained from members of the Fabaceae and 13 pathovars obtained from other hosts. Furthermore, *X. campestris* pv. *pelargonii*, *X. campestris* pv. *vitians* B, and *X. campestris* pv. *hederae*, which are associated with three different plant families, grouped together in group 2.

Homogeneity and heterogeneity of *X. campestris* pathovars. Most of the *X. campestris* pathovars which we studied were phenotypically and genotypically homogeneous. However, our data revealed that a number of pathovars are composed of two or more unrelated genotypes, which were designated type A, type B, etc. Unless indicated otherwise, type A contained the pathovar reference strain. *X. campestris* pv. *vesicatoria* consisted of two unrelated types, types A and B, confirming previous DNA hybridization data (49) and data obtained from SDS-PAGE of cellular proteins (48). Type A fell into DNA homology group 9, whereas type B, containing the pathovar reference strain, fell into a different DNA homology group, group 14. Both groups have been characterized by diverse genotypic (40) and phenotypic methods (6). Similarly, *X. campestris* pv. *vasculorum* consisted of types A and B (51).

Type A belonged to DNA homology group 9, whereas type B was related to *X. campestris* pv. *holcicola* in group 11. The most heterogeneous pathovar studied was *X. campestris* pv. *poinsettiicola*, which was composed of types A, B, and C. Type A occurred in group 9, whereas type C was related to the pathogens of trees in group 4. Type B strains constituted a separate DNA homology group, group 6. Most *X. campestris* pv. *cassavae* strains (type A) formed a homogeneous group; the exceptions were strains obtained from Niger (type B), which produced a characteristic brown soluble pigment in GYCA medium. A special case of a heterogeneous pathovar was represented by *X. campestris* pv. *vitians*. As shown previously (48, 60), most strains of this pathovar are similar; the exception is the aberrant pathovar reference strain, strain LMG 937. The authentic *X. campestris* pv. *vitians* strains (designated type B) fell into DNA group 2, whereas the pathovar reference strain belonged to group 9. A number of strains isolated from bromegrass in New Zealand and France, which were received as *X. campestris* pv. *graminis* (51), were not related to *X. campestris* pv. *graminis* but belonged to a separate DNA homology group, group 7.

Phenotypic analysis of the genomic groups. When we used an incubation time of 24 h as recommended by the manufacturer of the GN microplates, we found that the color reactions were often not sufficiently developed to allow accurate readings. This was particularly true for some slowly growing species and pathovars, such as *X. fragariae*, *X. populi*, *X. oryzae* pv. *oryzae*, *X. campestris* pv. *hyacinthi*, and *X. campestris* pv. *theicola*. In addition, a level of reproducibility which was unacceptably low for our purposes was obtained when fingerprints of duplicate incubation mixtures were compared. The color reactions were generally much better developed, easier to read, and hence more reliable after 48 h. Readings obtained after 72 h were very similar to those obtained after 48 h. For these reasons we decided to use the data obtained after 48 h of incubation in this study.

The level of reproducibility of the procedure which we used was estimated by culturing and inoculating 10 strains in duplicate. In this study the duplicate strains exhibited an average level of reproducibility of 94% after 48 h of incubation.

In an attempt to characterize the genomic groups in the genus *Xanthomonas* phenotypically, the percentages of positive reactions were calculated for all of the substrates for the strains belonging to each group. This resulted in the values shown in Table 2, which lists the average levels of metabolic activity observed with 95 carbon sources for each genomic group. The values in Table 2 are based on a sample of 252 strains. For example, for groups 1, 3, 6, 7, 12, 13, and 19 the average values were based on only two profiles. However, either these groups were known to be very homogeneous as determined by both their SDS-PAGE protein patterns (48; unpublished data) and their FAME profiles (60) or only a few strains were available. An exceptional species in this respect was *Xanthomonas pisi*; only two distinct colony types of one strain of this species were available. The number of strains used for each species is listed in Table 3.

It is obvious that some DNA homology groups were more homogeneous than others and hence were more accurately defined. In order to get an idea of the consistency of the profiles within each of the groups, the average level of internal homogeneity (h) was calculated by using the following formula:

$$h = 2 \sum_{i=1}^{95} \frac{|0.5 - x_{m,i}|}{95}$$

where

$$x_{m,i} = \sum_{j=1}^n \frac{x_{ij}}{n}$$

where x_{ij} is the i th reaction of strain j and n is the total number of strains tested in the group. The h value is 1 if a group is perfectly consistent (i.e., if all of the strains exhibit the same reaction with each carbon substrate) and zero if 50% of the strains are positive for each substrate. The resulting values are shown in Table 3. Among the least consistent or most variable groups were group 3, group 7, and particularly group 9. Group 3 (*X. populi*) strains exhibited poor color reactions after 48 h. Ambiguous readings rather than differences in substrate utilization may have been responsible for the apparent heterogeneity of this species. The heterogeneity found for group 9 was based on a total of 99 strains and reliably reflects the genomic diversity of this group.

Tests which differentiated two genomic groups were defined as those tests which yielded at least 90% positive reactions in one group and less than 10% positive reactions in the other group. By using this definition, an estimate of the "unicity" of each DNA homology group was calculated by determining the total number of species from which the group could be differentiated by at least one test when the 90% discrimination level was used as described above. The resulting values are shown in Table 3 and indicate that by using the Biolog GN microplate system we were able to differentiate most of the *Xanthomonas* genomic groups from one another. However, as the results which we obtained were based on sampling, the results could certainly change slightly for some characters if more strains were added to each of the groups. Identification criteria that unambiguously distinguish the 20 *Xanthomonas* genomic groups may not exist. It has been pointed out by using *Xanthomonas* strains as examples that attempts to divide biological populations into clear taxa is inconsistent with the real biological space, which harbors a continuum of cloudy condensed nodes rather than discrete taxa (47), and therefore it may be impossible to provide keys to unambiguously identify such taxa. Nevertheless, we believe that our results illustrate that the Biolog GN microplate system is a sensitive technique for differentiating the plant-pathogenic xanthomonads and that it is a useful tool for helping locate unknown xanthomonads in the new genomic classification.

It is obvious from Tables 2 and 3 that some groups are identified more reliably than others. There are a number of distinguishing tests that can be used for groups such as group 12 (*X. campestris* pv. *pisi*), group 19 (Guadeloupe strains obtained from sugarcane), and group 20 (*X. albilineans*), whereas other groups, such as groups 9, 11, 14, and 16 are less well-characterized. However, when the average data in Table 2 are used for identification, many reactions that do not fulfill the 90% discrimination criterion can also be useful for identifying unknown strains. The best identification is certainly obtained when whole fingerprints are compared.

Other interesting features include the carbon compounds which are positive or negative for all or most xanthomonads. These compounds may be descriptive for the genus. Features which were either positive or negative for more than 90% of the strains and at the same time did not differentiate any of the 20 species were considered characteristic for the genus. The average reactions for *Xanthomonas* strains are shown in Fig. 3, and the determinative characteristics are indicated. Reactions which were negative or positive for at least 90% of the strains but did not distinguish any of the groups are also indicated.

TABLE 2. Average metabolic activities of the 20 *Xanthomonas* DNA homology groups on 95 carbon sources in the Biolog GN microplate assay

Designation	Carbon substrate Name	% of positive strains in DNA homology group:																			
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
A2	α -Cyclodextrin	0	3	0	0	0	0	0	0	8	0	0	0	0	0	0	3	20	67	0	0
A3	Dextrin	100	83	100	100	80	100	100	100	90	100	89	100	100	100	100	94	100	100	100	0
A4	Glycogen	100	38	100	92	80	100	50	100	82	70	78	100	100	57	89	78	100	100	100	0
A5	Tween 40	0	21	0	75	80	100	50	60	68	30	22	100	100	71	84	38	20	100	100	20
A6	Tween 80	0	66	0	92	80	100	50	80	77	40	44	100	100	100	79	50	20	100	100	0
A7	<i>N</i> -Acetyl-D-galactosamine	0	0	0	0	20	0	0	0	12	0	0	100	0	14	0	3	0	0	0	0
A8	<i>N</i> -Acetyl-D-glucosamine	50	69	50	100	80	100	100	20	69	40	33	100	100	86	95	78	80	0	100	100
A9	Adonitol	0	0	0	0	0	0	50	0	5	0	0	0	0	0	0	0	0	33	0	0
A10	L-Arabinose	0	7	0	8	40	0	50	0	15	20	0	100	0	0	0	41	20	67	100	20
A11	D-Arabitol	0	3	0	0	0	0	50	0	6	0	0	0	0	0	0	0	0	0	50	0
A12	Cellobiose	0	97	0	100	80	100	100	100	93	90	89	100	100	86	100	78	100	100	100	60
B1	<i>meso</i> -Erythritol	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
B2	D-Fructose	100	100	100	100	100	100	100	100	98	100	100	100	100	100	100	100	100	100	100	100
B3	L-Fucose	50	86	0	92	100	0	50	60	84	30	78	100	100	100	89	31	0	100	100	80
B4	D-Galactose	50	72	50	100	60	100	100	40	87	40	56	100	100	0	95	47	100	100	100	0
B5	Gentiobiose	100	100	50	92	100	100	100	0	91	70	89	100	100	100	100	62	100	100	100	0
B6	α -D-Glucose	100	100	100	100	100	100	100	100	98	100	89	100	100	100	100	100	100	100	100	100
B7	<i>meso</i> -Inositol	0	0	0	0	0	0	0	0	3	0	0	0	0	14	0	3	0	0	0	0
B8	α -D-Lactose	0	0	0	42	0	100	50	0	14	0	0	100	50	0	0	3	0	0	100	0
B9	Lactulose	0	69	0	67	20	100	50	0	65	0	11	100	100	71	89	28	0	0	100	0
B10	Maltose	100	97	100	100	100	100	100	100	94	100	89	100	100	100	100	100	100	100	100	0
B11	D-Mannitol	0	0	50	0	0	50	50	0	12	0	11	100	0	14	0	0	0	0	50	0
B12	D-Mannose	100	100	100	100	100	100	100	100	94	90	89	100	100	86	95	100	100	100	100	100
C1	D-Melibiose	0	97	0	83	100	100	50	80	72	0	0	100	100	86	100	3	0	0	100	0
C2	β -Methyl-D-glucoside	0	3	50	0	0	100	50	0	9	0	0	100	50	0	0	3	20	0	100	0
C3	D-Psicose	100	97	100	100	80	100	100	100	91	90	100	100	100	100	95	97	100	100	100	0
C4	D-Raffinose	0	31	0	0	0	50	0	0	37	0	11	100	50	0	53	0	0	0	0	0
C5	L-Rhamnose	0	0	0	0	0	0	50	0	8	0	0	100	0	14	0	0	0	33	0	0
C6	D-Sorbitol	0	10	50	33	0	50	50	0	28	10	0	100	0	14	0	3	0	33	0	0
C7	Sucrose	50	79	100	75	20	100	100	0	82	70	22	100	100	43	58	47	100	0	100	100
C8	D-Trehalose	100	100	100	100	100	100	100	100	98	100	89	100	100	100	100	100	100	67	100	0
C9	Turanose	50	24	50	58	40	100	100	0	51	40	33	100	50	29	26	41	80	67	100	0
C10	Xylitol	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0
C11	Methylpyruvate	100	100	50	100	100	100	100	100	99	100	100	100	100	100	100	100	100	100	100	100
C12	Monomethylsuccinate	0	100	50	92	100	100	100	100	95	70	89	100	100	100	95	81	100	67	100	0
D1	Acetic acid	0	55	50	92	80	100	50	0	73	0	22	0	100	43	37	9	0	33	100	0
D2	<i>cis</i> -Aconitic acid	0	38	50	67	20	100	0	0	64	10	44	100	100	0	16	3	0	0	100	0
D3	Citric acid	0	38	50	75	40	100	50	0	39	10	11	100	100	14	53	16	0	0	100	0
D4	Formic acid	0	0	0	0	0	0	0	0	9	0	0	100	0	0	0	0	0	0	50	0
D5	D-Galactonic acid lactone	0	0	0	0	0	0	0	0	10	0	0	100	0	0	0	0	0	0	50	0
D6	D-Galacturonic acid	0	0	0	0	0	0	0	0	9	0	0	100	0	14	0	0	0	0	50	0
D7	D-Gluconic acid	0	3	50	0	0	0	50	0	11	0	0	100	0	0	5	0	0	0	50	0
D8	D-Glucosaminic acid	0	0	0	0	0	0	0	0	4	0	0	50	0	14	0	0	0	0	0	0
D9	D-Glucuronic acid	0	0	0	0	0	0	100	0	10	0	0	100	0	0	0	0	0	0	50	0
D10	α -Hydroxybutyric acid	0	55	0	67	0	50	0	60	56	10	11	100	50	71	21	19	0	33	100	0
D11	β -Hydroxybutyric acid	0	0	0	17	0	50	50	0	18	0	11	0	50	14	0	34	100	100	100	0
D12	γ -Hydroxybutyric acid	0	0	0	0	0	0	0	0	2	0	0	0	50	0	0	3	0	0	50	0
E1	<i>p</i> -Hydroxyphenylacetic acid	0	0	0	0	0	0	0	0	8	0	0	100	0	0	0	0	0	0	0	0
E2	Itaconic acid	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0
E3	α -Ketobutyric acid	0	34	0	58	60	100	50	0	66	0	11	100	100	71	63	3	0	0	100	0
E4	α -Ketoglutaric acid	50	100	50	100	100	100	100	100	93	100	100	100	100	100	100	91	100	100	100	60
E5	α -Ketovaleric acid	0	3	0	0	20	0	0	0	5	0	0	0	50	0	0	6	0	100	100	0
E6	D,L-Lactic acid	0	93	50	92	40	0	100	100	67	70	22	100	50	86	63	81	0	100	100	100
E7	Malonic acid	0	52	50	42	0	100	0	0	57	0	22	100	100	29	89	3	0	0	0	0
E8	Propionic acid	0	52	0	58	0	100	50	0	64	10	11	100	100	43	68	9	0	0	100	0
E9	Quinic acid	0	0	0	0	0	0	0	0	5	0	0	50	0	0	0	6	0	0	100	0
E10	D-Saccharic acid	50	0	0	0	40	100	0	20	23	0	11	100	100	29	89	0	0	0	50	0
E11	Sebacic acid	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
E12	Succinic acid	50	100	50	100	100	100	100	100	96	90	89	100	100	100	100	81	100	67	100	0
F1	Bromosuccinic acid	50	97	50	100	100	100	100	100	96	70	89	100	100	100	100	88	100	0	100	0
F2	Succinamic acid	50	93	0	100	100	100	100	20	93	30	89	100	100	100	74	47	100	33	100	0
F3	Glucuronamide	0	0	0	0	0	0	50	0	8	0	0	100	0	0	0	0	0	0	0	0
F4	Alaninamide	0	93	100	83	100	100	100	20	89	60	89	100	100	100	84	94	0	100	100	60

Continued on following page

TABLE 2—Continued

Carbon substrate		% of positive strains in DNA homology group:																			
Designation	Name	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
F5	D-Alanine	0	86	0	83	100	100	0	0	90	60	89	100	100	86	79	75	0	100	100	0
F6	L-Alanine	0	97	50	83	100	100	50	20	90	60	89	100	100	100	79	88	0	100	100	0
F7	L-Alanylglycine	0	93	50	75	100	100	100	20	90	50	89	100	100	86	74	97	0	100	100	20
F8	L-Asparagine	0	0	0	42	20	0	0	0	15	0	0	100	0	14	0	16	0	0	100	0
F9	L-Aspartic acid	0	48	0	58	60	50	100	20	60	0	33	100	50	43	16	56	80	67	100	0
F10	L-Glutamic acid	100	100	0	100	100	100	100	100	97	80	100	100	100	100	100	97	100	67	100	40
F11	Glycyl-L-aspartic acid	0	0	0	58	20	100	0	0	37	10	11	100	50	0	0	25	80	0	50	0
F12	Glycyl-L-glutamic acid	0	83	50	92	100	100	100	80	90	80	67	100	100	86	63	72	100	67	100	0
G1	L-Histidine	0	3	0	17	0	0	0	0	15	0	0	100	0	14	0	0	0	0	0	0
G2	Hydroxy-L-proline	0	24	0	58	80	100	0	0	63	0	89	50	100	29	42	50	20	100	100	0
G3	L-Leucine	0	0	0	33	0	50	0	0	12	0	11	50	100	29	5	3	0	0	100	0
G4	L-Ornithine	0	3	0	8	0	50	0	0	11	0	0	50	0	0	0	0	0	0	0	0
G5	L-Phenylalanine	0	0	0	0	0	50	0	0	5	0	0	100	0	14	0	0	0	0	100	0
G6	L-Proline	0	28	50	67	60	100	50	20	66	0	22	100	100	43	47	3	0	33	50	20
G7	L-Pyroglutamic acid	0	3	0	0	0	0	0	0	5	0	0	0	0	0	0	3	0	0	0	0
G8	D-Serine	0	0	0	8	0	0	0	0	3	0	0	0	0	14	0	0	0	0	0	0
G9	L-Serine	0	93	50	83	100	100	100	100	84	0	44	100	100	100	84	59	80	67	100	0
G10	L-Threonine	0	21	50	50	40	50	0	0	53	0	11	100	100	29	21	6	60	67	100	0
G11	DL-Carnitine	0	0	0	0	20	0	0	0	3	0	0	0	0	0	0	3	0	0	0	0
G12	γ -Aminobutyric acid	0	0	0	0	0	0	50	0	3	0	0	0	0	0	0	3	0	0	0	0
H1	Urocanic acid	0	3	0	17	0	0	0	0	19	10	0	100	0	14	0	0	20	0	0	0
H2	Inosine	0	7	0	42	60	0	50	0	52	0	0	100	0	14	21	0	20	33	50	0
H3	Uridine	0	7	0	42	80	0	0	0	49	0	0	100	50	14	5	12	40	67	50	0
H4	Thymidine	0	0	50	0	0	0	50	0	9	0	0	100	0	0	0	0	0	0	0	0
H5	Phenyl ethylamine	0	3	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0
H6	Putrescine	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0
H7	2-Aminoethanol	0	0	0	0	20	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
H8	2,3-Butanediol	0	0	0	0	0	0	0	0	4	0	0	0	50	14	0	3	0	33	50	0
H9	Glycerol	0	48	50	92	20	100	50	80	66	0	22	100	50	71	37	50	100	67	100	0
H10	DL- α -Glycerolphosphate	0	45	0	33	20	0	50	0	53	0	0	100	0	57	5	9	20	67	50	0
H11	Glucose 1-phosphate	0	34	0	17	20	0	50	0	51	0	0	100	0	14	26	25	100	67	0	0
H12	Glucose 6-phosphate	0	24	0	0	0	0	50	0	40	0	0	100	0	0	26	19	100	67	0	0

Group 12 (*X. campestris* pv. *pisi*) and group 20 (*X. albilineans*) were responsible for most of the atypical reactions within the genus.

Proposal for a new classification. By synthesizing data derived from comparative protein electrophoresis and FAME analyses in previous studies (48, 51, 52, 60) and the DNA hybridization data reported in this study, we obtained a new picture of the internal relationships of the genus *Xanthomonas*. On the basis of the DNA homology matrix data, the *X. campestris* pathogens do not belong to a single species, but belong to 15 genotypic groups. Since DNA hybridization experiments measure levels of total genomic homology, this technique is the most reliable substitute for DNA sequence comparison and has been recommended as the standard criterion for designating species (29, 38, 56); levels of DNA homology of 60 to 70% are considered the minimum levels for strains belonging to the same species. Sufficient evidence is now available to classify each of the DNA homology groups as a separate species of the genus *Xanthomonas*.

The revised classification described below is based on genomic relatedness data rather than phenotypic and phytopathogenic specialization data. Such a classification should allow avirulent xanthomonads, which are regarded increasingly as important from an ecological point of view, to be identified on the basis of genotypic relatedness data. In addition, previously undetected relationships should become evident. Obvious examples are found in group 15, which harbors the pathogens isolated from crucifers, and group 16, which contains most

TABLE 3. Phenotypic significance of the *Xanthomonas* DNA homology groups based on Biolog GN microplate assay data

DNA homology group	No. of strains tested	Relative homogeneity value ^a	No. of groups differentiated
1	2	0.89	18
2	29	0.79	15
3	2	0.73	19
4	12	0.77	15
5	5	0.81	15
6	2	0.89	19
7	2	0.68	19
8	5	0.92	17
9	99	0.67	10
10	10	0.84	16
11	9	0.83	12
12	2	0.95	19
13	2	0.85	18
14	7	0.79	14
15	19	0.81	18
16	32	0.77	14
17	5	0.92	19
18	13	0.82	19
19	2	0.84	19
20	5	0.95	19

^a See text.

FIG. 3. Average reactions of members of the genus *Xanthomonas* with 95 carbon compounds in the GN microplate assay, with the characteristic compounds indicated. The names of the carbon compounds used, as defined by letters (rows) and numbers (columns), are given in Table 2.

of the pathovars isolated from members of the Poaceae. Knowledge concerning the relationships among these pathogens can help us understand their mechanism of infection.

In the revised classification described below, the previously described species *X. albilineans*, *X. fragariae*, *X. oryzae*, and *X. populi* are not affected. The type species, *X. campestris* (Pammel 1895) Dowson 1939, is emended to include only DNA homology group 15 (i.e., the pathovars obtained from crucifers). *X. axonopodis* Starr and Garces 1950 is emended to include all of the former *X. campestris* group 9 pathovars. We propose the following species names for the other *Xanthomonas* DNA homology groups (Table 1): *Xanthomonas hortorum* for group 2; *Xanthomonas arboricola* for group 4; *Xanthomonas cassavae* for group 5; *Xanthomonas codiae* for group 6; *Xanthomonas bromi* for group 7; *Xanthomonas cucurbitae* for group 8; *Xanthomonas vasicola* for group 11; *Xanthomonas pisi* for group 12; *Xanthomonas melonis* for group 13; *Xanthomonas vesicatoria* for group 14; *Xanthomonas translucens* for group 16; *Xanthomonas hyacinthi* for group 17; *Xanthomonas theicola* for group 18; and *Xanthomonas sacchari* for group 19.

The elevation of pathovars to species rank falls outside the nomenclatural statements concerning the international standards for naming pathovars of phytopathogenic bacteria (18), but is subject to the rules of the *International Code of Nomenclature of Bacteria* (31a). For all nomenclatural changes we have taken a rather conservative viewpoint, respecting as much as possible phytopathological relevance. We have applied the rules of the *International Code of Nomenclature of Bacteria* in assigning the species name *X. campestris* to group 15, which contains type strain LMG 568 (= NCPPB 528), and the name *X. axonopodis* to group 9. Rather than adopting the name of the oldest described pathovar as the species epithet, we preferred to use a more general name in those cases where pathovars from diverse host plants constitute a new species (e.g., *X.*

arboricola for pathogens of trees). New names were also proposed when the new species does not include the pathovar reference strain of the former *X. campestris* pathovar (*X. codiae* for former *X. campestris* pv. poinsetticola type B strains; *X. bromi* for strains obtained from brome grass; *X. sacchari* for strains obtained from Guadeloupe and received as *X. albilineans*).

Since the relevance of the host specificity of most of the pathovars has not been determined and for phytopathological reasons we retained the pathovar designations as infrasubspecific epithets within the new species.

Description of the genus *Xanthomonas* Dowson 1939. The description below is based on the phenotypic description of Bradbury (7), as revised by Van den Mooter and Swings (46) and Palleroni and Bradbury (36), as well as the results of Yang et al. (58, 60), Auling et al. (2), and this study. G+C content data were obtained from the studies of De Vos and De Ley (14), Vera Cruz et al. (53), Van den Mooter et al. (44, 45), and Vauterin et al. (50; this study).

Xanthomonads are plant pathogens or are associated with plants. Most *xanthomonad* strains form yellow mucoid smooth colonies. The yellow pigments are mono- or dibromo arylpolyenes called xanthomonadins (1), which are characteristic of the genus. The exopolysaccharide xanthan, which is responsible for the mucoid or viscous cultures, is typical of the genus.

The cells are gram-negative rods which are 0.4 to 0.6 by 1.0 to 2.9 μ m. They occur mostly alone or in pairs, but chains occur as well. Filamentous cells are occasionally seen. Cells are usually motile by means of one polar flagellum.

Catalase is present, but urease and indole are not produced. Nitrate is not reduced to nitrite. Oxidase is absent or only weakly reactive. Acetoin is not formed. Litmus milk is not acidified. There is no growth at pH 4.5 or at 4 or 37°C. Growth is inhibited by 6% NaCl, 30% glucose, 0.01% methyl green,

0.01% thionin, 0.01% lead acetate, or 0.1% triphenyl tetrazoliumchloride. Strains are usually susceptible to erythromycin and tetracycline. Small amounts of acid are produced from many carbohydrates but not from L-rhamnose, adonitol, sorbose, D-sorbitol, *meso*-erythritol, or *meso*-inositol. Glycine, L-glutamine, and L-asparagine are not utilized as sole carbon and nitrogen sources. *Xanthomonas* strains are chemoorganotrophic. One or more growth factors may be required.

Xanthomonas strains contain the following nine fatty acids: 11:0 iso, 11:0 iso 3OH, 12:0 3OH, 13:0 iso 3OH, 15:0 iso, 16:1 *cis*-9, 16:0, 17:1 iso F, and 17:0 iso. Among these fatty acids, 11:0 iso, 11:0 iso 3OH, and 13:0 iso 3OH are characteristic of the genus and are useful criteria for differentiating *Xanthomonas* strains from other bacteria.

Xanthomonas strains contain spermidine as the major polyamine. Spermine is usually present in detectable amounts, whereas 2-hydroxyputrescine, 1,3-diaminopropane, and putrescine are never present. Some strains contain cadaverine.

As determined by the Biolog GN microplate test, the following carbon compounds are oxidized by at least 94% of the strains (and thus these reactions are characteristic of the genus): D-fructose, α -D-glucose, D-mannose, methylpyruvate, and α -ketoglutaric acid. The following carbon compounds are not oxidized by more than 94% of the strains: α -cyclodextrin, adonitol, D-arabitol, *meso*-erythritol, *meso*-inositol, xylitol, D-glucosaminic acid, γ -hydroxybutyric acid, itaconic acid, sebacic acid, L-ornithine, L-pyrogutamic acid, D-serine, DL-carnitine, γ -aminobutyric acid, phenyl ethylamine, putrescine, 2-aminoethanol, and 2,3 butanediol.

The G+C contents of members of the genus range from 63.3 to 69.7 mol%. The type species is *Xanthomonas campestris*.

Description of *Xanthomonas campestris* (Pammel 1895) Dowson 1939 emend. The description of *X. campestris* is the same as that of the genus. Strains of this species cause disease in various crucifers (members of the Brassicaceae). This species can be subdivided into the following pathovars on the basis of isolation from certain hosts: *X. campestris* pv. *aberrans*, *X. campestris* pv. *armoraciae*, *X. campestris* pv. *barbareae*, *X. campestris* pv. *campestris*, *X. campestris* pv. *incanae*, *X. campestris* pv. *raphani* and (based on work by Palleroni et al. [37]) *X. campestris* pv. *plantaginis*. Strains of *X. campestris* pv. *aberrans* and *X. campestris* pv. *raphani* have been found to induce disease symptoms in cabbage and radish similar to the disease symptoms induced by *X. campestris* pv. *campestris* (50a), and hence the relevance of these two pathovars can be questioned.

X. campestris can be distinguished from other *Xanthomonas* species by the presence of metabolic activity on the carbon substrates dextrin, glycogen, *N*-acetyl-D-glucosamine, cellobiose, L-fucose, D-galactose, gentiobiose, lactulose, maltose, D-melibiose, D-psicose, D-trehalose, monomethylsuccinate, malonic acid, D-saccharic acid, succinic acid, bromosuccinic acid, and L-glutamic acid and by a lack of metabolic activity on the carbon substrates *N*-acetyl-D-galactosamine, L-arabinose, α -D-lactose, D-mannitol, β -methyl-D-glucoside, L-rhamnose, D-sorbitol, formic acid, D-galactonic acid lactone, D-galacturonic acid, D-gluconic acid, D-glucuronic acid, β -hydroxybutyric acid, *p*-hydroxyphenylacetic acid, α -ketovaleric acid, quinic acid, glucuronamide, L-asparagine, glycyl-L-aspartic acid, L-histidine, L-leucine, L-phenylalanine, urocanic acid, uridine, thymidine, and DL- α -glycerolphosphate.

X. campestris is the type species of the genus, and its G+C content is 65.8 to 66.6 mol% (68.0 to 68.3 mol% for *X. campestris* pv. *incanae*). The type strain is LMG 568 (= NCPPB 528 = ICMP 13 = ATCC 33913 = DSM 3586).

Description of *Xanthomonas arboricola* sp. nov. *Xanthomonas arboricola* (ar.bo.ri'co.la L. fem. n. *arbor*, tree; L. v. *colere*,

to inhabit; L. adj. *arboricola*, living in trees). The description of *X. arboricola* is the same as that of the genus. The following pathovars are distinguished on the basis of phytopathogenic specialization: *X. arboricola* pv. *corylina*, *X. arboricola* pv. *juglandis*, *X. arboricola* pv. *poinsettiicola*, *X. arboricola* pv. *populi*, *X. arboricola* pv. *pruni*, and (based on work by Palleroni et al. [37]) *X. arboricola* pv. *celebensis*. *X. arboricola* pv. *poinsettiicola* includes the type C strains of the former taxon *X. campestris* pv. *poinsettiicola*.

X. arboricola can be distinguished from other *Xanthomonas* species by the presence of metabolic activity on the carbon substrates dextrin, glycogen, Tween 80, *N*-acetyl-D-glucosamine, cellobiose, L-fucose, D-galactose, gentiobiose, maltose, D-psicose, D-trehalose, monomethylsuccinate, acetic acid, DL-lactic acid, succinic acid, bromosuccinic acid, succinamic acid, L-glutamic acid, glycyl-L-glutamic acid, and glycerol and by a lack of metabolic activity on the carbon substrates *N*-acetyl-D-galactosamine, L-arabinose, D-mannitol, β -methyl-D-glucoside, D-raffinose, L-rhamnose, formic acid, D-galactonic acid lactone, D-galacturonic acid, D-gluconic acid, D-glucuronic acid, *p*-hydroxyphenylacetic acid, α -ketovaleric acid, quinic acid, D-saccharic acid, glucuronamide, L-phenylalanine, thymidine, and glucose 6-phosphate.

The G+C content is 66.0 to 67.0 mol%. The type strain is *X. arboricola* pv. *juglandis* LMG 747 (= NCPPB 411 = ICMP 35).

Description of *Xanthomonas axonopodis* Starr and Garces 1950 emend. The description of *X. axonopodis* is the same as that of the genus. The following pathovars are distinguished on the basis of phytopathogenic specialization on a wide variety of host plants: *X. axonopodis* pv. *axonopodis*, *X. axonopodis* pv. *alfalfae*, *X. axonopodis* pv. *bauhiniae*, *X. axonopodis* pv. *begoniae*, *X. axonopodis* pv. *cajani*, *X. axonopodis* pv. *cassavae*, *X. axonopodis* pv. *cassiae*, *X. axonopodis* pv. *citri* (formerly *X. campestris* pv. *citri* group A strains [24]), *X. axonopodis* pv. *aurantifolii* (formerly *X. campestris* pv. *citri* group B, C, and D strains; reclassified as *X. campestris* pv. *aurantifolii* by Gabriel et al. [22]), *X. axonopodis* pv. *citrumelo* (formerly *X. campestris* pv. *citri* group E strains; reclassified as *X. campestris* pv. *citrumelo* by Gabriel et al. [22]), *X. axonopodis* pv. *clitoriae*, *X. axonopodis* pv. *coracanae*, *X. axonopodis* pv. *cyamopsidis*, *X. axonopodis* pv. *desmodii*, *X. axonopodis* pv. *desmodiigangetici*, *X. axonopodis* pv. *desmodiilaxiflori*, *X. axonopodis* pv. *desmodirotundifolii*, *X. axonopodis* pv. *dieffenbachiae*, *X. axonopodis* pv. *erythrinae*, *X. axonopodis* pv. *glycines*, *X. axonopodis* pv. *lespedezae*, *X. axonopodis* pv. *malvacearum*, *X. axonopodis* pv. *manihotis*, *X. axonopodis* pv. *patelii*, *X. axonopodis* pv. *phaseoli*, *X. axonopodis* pv. *phaseoli-fuscans*, *X. axonopodis* pv. *phyllanthi*, *X. axonopodis* pv. *poinsettiicola*, *X. axonopodis* pv. *rhynchosiae*, *X. axonopodis* pv. *ricini*, *X. axonopodis* pv. *sesbaniae*, *X. axonopodis* pv. *tamarindi*, *X. axonopodis* pv. *vasculorum*, *X. axonopodis* pv. *vesicatoria*, *X. axonopodis* pv. *vignaeradiatae*, *X. axonopodis* pv. *vignicola*, and *X. axonopodis* pv. *vitians*, as well as (based on work by Palleroni et al. [37]) *X. axonopodis* pv. *betlicola*, *X. axonopodis* pv. *biophyti*, *X. axonopodis* pv. *fascicularis*, *X. axonopodis* pv. *khayae*, *X. axonopodis* pv. *maculifoliigardeniae*, *X. axonopodis* pv. *martyiicola*, *X. axonopodis* pv. *melhusii*, *X. axonopodis* pv. *nakataecorchori*, *X. axonopodis* pv. *pedalii*, *X. axonopodis* pv. *physalidicola*, and *X. axonopodis* pv. *punicae*. The following pathovars include the type A strains of the corresponding former *X. campestris* pathovars: *X. axonopodis* pv. *poinsettiicola*, *X. axonopodis* pv. *vasculorum*, *X. axonopodis* pv. *vesicatoria*, and *X. axonopodis* pv. *vitians*. *X. axonopodis* pv. *cassavae* includes the type B strains of the former taxon *X. campestris* pv. *cassavae*.

X. axonopodis can be distinguished from other *Xanthomonas* species by the presence of metabolic activity on the carbon

substrates dextrin, cellobiose, gentiobiose, maltose, D-psicose, D-trehalose, monomethylsuccinate, succinic acid, bromosuccinic acid, succinamic acid, D-alanine, L-alanine, L-alanylglycine, L-glutamic acid, and glycyl-L-glutamic acid and by a lack of metabolic activity on the carbon substrates β -methyl-D-glucoside, L-rhamnose, formic acid, D-galactonic acid lactone, D-galacturonic acid, D-glucuronic acid, *p*-hydroxyphenylacetic acid, α -ketovaleric acid, quinic acid, glucuronamide, L-phenylalanine, and thymidine.

The G+C content is 65.0 to 67.6 mol%. The type strain is LMG 538 (= NCPPB 457 = ATCC 19312 = ICMP 50 = DSM 3585).

Description of *Xanthomonas bromi* sp. nov. *Xanthomonas bromi* (bro'mi. L. masc. gen. n. *bromi*, from bromegrass). The description of *X. bromi* is the same as that of the genus. Strains of this species cause wilting disease on bromegrass (*Bromus* spp.).

X. bromi can be distinguished from other xanthomonads by its SDS-PAGE protein patterns and FAME profiles (51), by the presence of metabolic activity on the carbon substrates dextrin, *N*-acetyl-D-glucosamine, cellobiose, D-galactose, gentiobiose, maltose, D-psicose, sucrose, D-trehalose, turanose, monomethylsuccinate, D-glucuronic acid, DL-lactic acid, succinic acid, bromosuccinic acid, succinamic acid, alaninamide, L-alanylglycine, L-aspartic acid, L-glutamic acid, glycyl-L-glutamic acid, and L-serine, and by a lack of metabolic activity on the carbon substrates *N*-acetyl-D-galactosamine, D-raffinose, *cis*-aconitic acid, formic acid, D-galactonic acid lactone, D-galacturonic acid, α -hydroxybutyric acid, *p*-hydroxyphenylacetic acid, α -ketovaleric acid, malonic acid, quinic acid, D-saccharic acid, D-alanine, L-asparagine, glycyl-L-aspartic acid, L-histidine, hydroxy-L-proline, L-leucine, L-phenylalanine, L-threonine, urocanic acid, and uridine.

The G+C content is 65.6 mol%. The type strain is LMG 947 (= CFBP 1976).

Description of *Xanthomonas cassavae* (ex Wiehe and Dowson 1953) sp. nov., nom. rev. Strains of this species are pathogenic for *Manihot* spp. (Euphorbiaceae). The description of *X. cassavae* is the same as that of the genus. *X. cassavae* includes the type A strains of the former taxon *X. campestris* pv. *cassavae*.

X. cassavae can be distinguished from the other *Xanthomonas* species on the basis of SDS-PAGE protein patterns and FAME profiles (48, 60). *X. cassavae* can also be distinguished from other *Xanthomonas* species by the presence of metabolic activity on the carbon substrates L-fucose, gentiobiose, maltose, D-melibiose, D-trehalose, monomethylsuccinate, succinic acid, bromosuccinic acid, succinamic acid, alaninamide, D-alanine, L-alanine, L-alanylglycine, L-glutamic acid, glycyl-L-glutamic acid, and L-serine and by a lack of metabolic activity on the carbon substrates α -D-lactose, D-mannitol, β -methyl-D-glucoside, D-raffinose, L-rhamnose, D-sorbitol, formic acid, D-galactonic acid lactone, D-galacturonic acid, D-gluconic acid, D-glucuronic acid, α -hydroxybutyric acid, β -hydroxybutyric acid, *p*-hydroxyphenylacetic acid, malonic acid, propionic acid, quinic acid, glucuronamide, L-histidine, L-leucine, L-phenylalanine, urocanic acid, thymidine, and glucose 6-phosphate.

The G+C content is 64.2 to 66.1 mol%. The type strain is LMG 673 (= NCPPB 101 = ICMP 204).

Description of *Xanthomonas codiae* sp. nov. *Xanthomonas codiae* (co.di.æ'i. L. neut. gen. n. *codiae*, from croton). The description of *X. codiae* is the same as that of the genus. Strains of this species cause wilting disease on *Codiaeum variegatum*. *X. codiae* includes the type B strains of the former taxon *X. campestris* pv. *poinsetticola*.

X. codiae can be distinguished from other *Xanthomonas* species by its SDS-PAGE protein patterns (48), by the pres-

ence of metabolic activity on the carbon substrates dextrin, glycogen, Tween 40, Tween 80, *N*-acetyl-D-glucosamine, cellobiose, D-galactose, gentiobiose, α -D-lactose, lactulose, maltose, D-melibiose, β -methyl-D-glucoside, D-psicose, sucrose, D-trehalose, turanose, monomethylsuccinate, acetic acid, *cis*-aconitic acid, citric acid, α -ketobutyric acid, malonic acid, propionic acid, D-saccharic acid, succinic acid, bromosuccinic acid, succinamic acid, alaninamide, D-alanine, L-alanine, L-alanylglycine, L-glutamic acid, glycyl-L-aspartic acid, glycyl-L-glutamic acid, hydroxy-L-proline, L-proline, L-serine, and glycerol, and by a lack of metabolic activity on the carbon substrates *N*-acetyl-D-galactosamine, L-arabinose, L-fucose, L-rhamnose, formic acid, D-galactonic acid lactone, D-galacturonic acid, D-gluconic acid, D-glucuronic acid, *p*-hydroxyphenylacetic acid, α -ketovaleric acid, DL-lactic acid, quinic acid, glucuronamide, L-asparagine, L-histidine, urocanic acid, inosine, uridine, thymidine, DL- α -glycerolphosphate, glucose 1-phosphate, and glucose 6-phosphate.

The G+C content is 66.3 mol%. The type strain is LMG 8678 (= ICMP 9513).

Description of *Xanthomonas cucurbitae* (ex Bryan 1926) sp. nov., nom. rev. The description of *X. cucurbitae* is the same as that of the genus. Strains of this species are isolated from diseased *Citrullus vulgaris*, *Cucumis sativus*, and *Cucurbita* spp. (Cucurbitaceae).

X. cucurbitae can be distinguished from other *Xanthomonas* species on the basis of its SDS-PAGE protein patterns (48), by the presence of metabolic activity on the carbon substrates dextrin, glycogen, cellobiose, maltose, D-psicose, D-trehalose, monomethylsuccinate, DL-lactic acid, succinic acid, bromosuccinic acid, L-glutamic acid, and L-serine, and by a lack of metabolic activity on the carbon substrates *N*-acetyl-D-galactosamine, L-arabinose, gentiobiose, α -D-lactose, lactulose, D-mannitol, β -methyl-D-glucoside, D-raffinose, L-rhamnose, D-sorbitol, sucrose, turanose, acetic acid, *cis*-aconitic acid, citric acid, formic acid, D-galactonic acid lactone, D-galacturonic acid, D-gluconic acid, D-glucuronic acid, β -hydroxybutyric acid, *p*-hydroxyphenylacetic acid, α -ketobutyric acid, α -ketovaleric acid, malonic acid, propionic acid, quinic acid, glucuronamide, D-alanine, L-asparagine, glycyl-L-aspartic acid, L-histidine, hydroxy-L-proline, L-leucine, L-phenylalanine, L-threonine, urocanic acid, inosine, uridine, thymidine, DL- α -glycerolphosphate, glucose 1-phosphate, and glucose 6-phosphate.

The G+C content is 66.1 to 66.8 mol%. The type strain is LMG 690 (= NCPPB 2597 = ICMP 2299).

Description of *Xanthomonas hortorum* sp. nov. *Xanthomonas hortorum* (hor.to'rum. L. masc. gen. n. *hortorum*, from gardens). The description of *X. hortorum* is the same as that of the genus. The following pathovars are distinguished on the basis of phytopathogenic specialization: *X. hortorum* pv. *hederae*, *X. hortorum* pv. *pelargonii*, and *X. hortorum* pv. *vitians*. *X. hortorum* pv. *carotae* and *X. hortorum* pv. *taraxaci* have been distinguished on the basis of hybridization data by Palleroni et al. (37).

X. hortorum pv. *hederae* and *X. hortorum* pv. *vitians* together can be distinguished as a separate group from other xanthomonads on the basis of the results of SDS-PAGE of proteins, whereas *X. hortorum* pv. *pelargonii* constitutes a separate group (48). On the basis of FAME analysis data, *X. hortorum* pv. *pelargonii* and *X. hortorum* pv. *hederae* together form a distinct group (60). *X. hortorum* can be distinguished from other *Xanthomonas* species by the presence of metabolic activity on the carbon substrates cellobiose, gentiobiose, maltose, D-melibiose, D-psicose, D-trehalose, monomethylsuccinate, DL-lactic acid, succinic acid, bromosuccinic acid, succinamic acid, alaninamide, L-alanine, L-alanylglycine, L-glutamic acid, and

L-serine and by a lack of metabolic activity on the carbon substrates *N*-acetyl-D-galactosamine, L-arabinose, α -D-lactose, D-mannitol, β -methyl-D-glucoside, L-rhamnose, D-sorbitol, formic acid, D-galactonic acid lactone, D-galacturonic acid, D-gluconic acid, D-glucuronic acid, β -hydroxybutyric acid, *p*-hydroxyphenylacetic acid, α -ketovaleric acid, quinic acid, D-saccharic acid, glucuronamide, L-asparagine, glycyl-L-aspartic acid, L-histidine, L-leucine, L-phenylalanine, urocanic acid, inosine, uridine, and thymidine.

The G+C content is 63.6 to 65.1 mol%. The type strain is *X. hortorum* pv. *hederae* LMG 733 (= NCPPB 939 = ICMP 453).

Description of *Xanthomonas hyacinthi* (ex Wakker 1883) sp. nov., nom. rev. The description of *X. hyacinthi* is the same as that of the genus. Strains of this species cause wilting disease in *Hyacinthus orientalis*.

X. hyacinthi strains have very distinct SDS-PAGE protein and FAME profiles (48, 60). This species can be distinguished from other *Xanthomonas* species by the presence of metabolic activity on the carbon substrates dextrin, glycogen, cellobiose, D-galactose, gentiobiose, maltose, D-psicose, sucrose, D-trehalose, monomethylsuccinate, β -hydroxybutyric acid, succinic acid, bromosuccinic acid, succinamic acid, L-glutamic acid, glycyl-L-glutamic acid, glycerol, glucose 1-phosphate, and glucose 6-phosphate and by a lack of metabolic activity on the carbon substrates *N*-acetyl-D-galactosamine, L-fucose, α -D-lactose, lactulose, D-mannitol, D-melibiose, D-raffinose, L-rhamnose, D-sorbitol, acetic acid, *cis*-aconitic acid, citric acid, formic acid, D-galactonic acid lactone, D-galacturonic acid, D-gluconic acid, D-glucuronic acid, α -hydroxybutyric acid, *p*-hydroxyphenylacetic acid, α -ketobutyric acid, α -ketovaleric acid, DL-lactic acid, malonic acid, propionic acid, quinic acid, D-saccharic acid, glucuronamide, alaninamide, D-alanine, L-alanine, L-alanylglycine, L-asparagine, L-histidine, L-leucine, L-phenylalanine, L-proline, and thymidine.

The G+C content is 69.2 to 69.3 mol%. The type strain is LMG 739 (= NCPPB 599 = ICMP 189 = ATCC 19314 = CFBP 1156).

Description of *Xanthomonas melonis* sp. nov. *Xanthomonas melonis* (me.lo'nis. L. fem. gen. n. *melonis*, from melon). The description of *X. melonis* is the same as that of the genus. The strains of this species are isolated from diseased melons (*Cucumis melo*).

X. melonis can be distinguished from other *Xanthomonas* species by the presence of metabolic activity on the carbon substrates dextrin, glycogen, Tween 40, Tween 80, *N*-acetyl-D-glucosamine, cellobiose, L-fucose, D-galactose, gentiobiose, lactulose, maltose, D-melibiose, D-psicose, sucrose, D-trehalose, monomethylsuccinate, acetic acid, *cis*-aconitic acid, citric acid, α -ketobutyric acid, malonic acid, propionic acid, D-saccharic acid, succinic acid, bromosuccinic acid, succinamic acid, alaninamide, D-alanine, L-alanine, L-alanylglycine, L-glutamic acid, glycyl-L-glutamic acid, hydroxy-L-proline, L-leucine, L-proline, L-serine, and L-threonine and by a lack of metabolic activity on the carbon substrates *N*-acetyl-D-galactosamine, L-arabinose, D-mannitol, L-rhamnose, D-sorbitol, formic acid, D-galactonic acid lactone, D-galacturonic acid, D-gluconic acid, D-glucuronic acid, *p*-hydroxyphenylacetic acid, quinic acid, glucuronamide, L-asparagine, L-histidine, L-phenylalanine, urocanic acid, inosine, thymidine, DL- α -glycerolphosphate, glucose 1-phosphate, and glucose 6-phosphate.

The G+C content is 66.1 mol%. The type strain is LMG 8670 (= ICMP 8682).

Description of *Xanthomonas pisi* (ex Goto and Okabe 1958) sp. nov., nom. rev. The description of *X. pisi* is the same as that of the genus. Isolated from diseased *Pisum sativum* (Fabaceae).

X. pisi has a distinct SDS-PAGE protein profile (48). It can

be distinguished from other *Xanthomonas* species by the presence of metabolic activity on the carbon substrates dextrin, glycogen, Tween 40, Tween 80, *N*-acetyl-D-galactosamine, *N*-acetyl-D-glucosamine, L-arabinose, cellobiose, L-fucose, D-galactose, gentiobiose, α -D-lactose, lactulose, maltose, D-mannitol, D-melibiose, β -methyl-D-glucoside, D-psicose, D-raffinose, L-rhamnose, D-sorbitol, sucrose, D-trehalose, turanose, monomethylsuccinate, *cis*-aconitic acid, citric acid, formic acid, D-galactonic acid lactone, D-galacturonic acid, D-gluconic acid, D-glucuronic acid, α -hydroxybutyric acid, *p*-hydroxyphenylacetic acid, α -ketobutyric acid, DL-lactic acid, malonic acid, propionic acid, D-saccharic acid, succinic acid, bromosuccinic acid, succinamic acid, glucuronamide, alaninamide, D-alanine, L-alanine, L-alanylglycine, L-asparagine, L-aspartic acid, L-glutamic acid, glycyl-L-aspartic acid, glycyl-L-glutamic acid, L-histidine, L-phenylalanine, L-proline, L-serine, L-threonine, urocanic acid, inosine, uridine, thymidine, glycerol, DL- α -glycerolphosphate, glucose 1-phosphate, and glucose 6-phosphate and by a lack of metabolic activity on the carbon substrates acetic acid, β -hydroxybutyric acid, and α -ketovaleric acid.

The G+C content is 64.6 mol%. The type strain is LMG 847 (= NCPPB 762 = ICMP 570).

Description of *Xanthomonas sacchari* sp. nov. *Xanthomonas sacchari* (sac'cha.ri. L. masc. gen. n., *sacchari*, from sugar). The description of *X. sacchari* is the same as that of the genus. The strains of this species are isolated from diseased sugarcane (*Saccharum officinarum*).

X. sacchari strains have very distinct SDS-PAGE protein and FAME profiles (51, 60) and can be distinguished from other *Xanthomonas* species by the presence of metabolic activity on the carbon substrates dextrin, glycogen, Tween 40, Tween 80, *N*-acetyl-D-glucosamine, L-arabinose, cellobiose, L-fucose, D-galactose, gentiobiose, α -D-lactose, lactulose, maltose, D-melibiose, β -methyl-D-glucoside, D-psicose, sucrose, D-trehalose, turanose, monomethylsuccinate, acetic acid, *cis*-aconitic acid, citric acid, α -hydroxybutyric acid, β -hydroxybutyric acid, α -ketobutyric acid, α -ketovaleric acid, DL-lactic acid, propionic acid, quinic acid, succinic acid, bromosuccinic acid, succinamic acid, alaninamide, D-alanine, L-alanine, L-alanylglycine, L-asparagine, L-aspartic acid, L-glutamic acid, glycyl-L-glutamic acid, hydroxy-L-proline, L-leucine, L-phenylalanine, L-serine, L-threonine, and glycerol and by a lack of metabolic activity on the carbon substrates *N*-acetyl-D-galactosamine, D-raffinose, L-rhamnose, D-sorbitol, *p*-hydroxyphenylacetic acid, malonic acid, glucuronamide, L-histidine, urocanic acid, thymidine, glucose 1-phosphate, and glucose-6-phosphate.

The G+C content is 68.5 mol%. The type strain is LMG 471.

Description of *Xanthomonas theicola* sp. nov. *Xanthomonas theicola* (the.i'co.la. L. fem. gen. n. *theae*, from tea; L. v. *colere*, to inhabit; L. adj. *theicola*, living in tea). The description of *X. theicola* is the same as that of the genus. The strains of this species cause disease in tea plants (*Camellia sinensis*).

X. theicola strains have very distinct SDS-PAGE protein and FAME profiles (48, 60) and can be distinguished from other *Xanthomonas* species by the presence of metabolic activity on the carbon substrates dextrin, glycogen, Tween 40, Tween 80, cellobiose, L-fucose, D-galactose, gentiobiose, maltose, D-psicose, β -hydroxybutyric acid, α -ketovaleric acid, DL-lactic acid, alaninamide, D-alanine, L-alanine, L-alanylglycine, and hydroxy-L-proline and by a lack of metabolic activity on the carbon substrates *N*-acetyl-D-galactosamine, *N*-acetyl-D-glucosamine, α -D-lactose, lactulose, D-mannitol, D-melibiose, β -methyl-D-glucoside, D-raffinose, sucrose, *cis*-aconitic acid, citric acid, formic acid, D-galactonic acid lactone, D-galacturonic acid, D-gluconic acid, D-glucuronic acid, *p*-hydroxyphenylacetic acid, α -ketobutyric acid, malonic acid, propionic acid,

quinic acid, D-saccharic acid, bromosuccinic acid, glucuronamide, L-asparagine, glycyl-L-aspartic acid, L-histidine, L-leucine, L-phenylalanine, urocanic acid, and thymidine.

The G+C content is 69.2 mol%. The type strain is LMG 8684 (= ICMP 6774).

Description of *Xanthomonas translucens* (ex Jones, Johnson, and Reddy 1917) sp. nov., nom. rev. The description of *X. translucens* is the same as that of the genus. The strains of this species cause diseases in various members of the Poaceae. On the basis of phytopathogenic specialization or differences in virulence (3, 11), the following pathovars can be distinguished: *X. translucens* pv. arrhenatheri, *X. translucens* pv. cerealis, *X. translucens* pv. graminis, *X. translucens* pv. hordei, *X. translucens* pv. phlei, *X. translucens* pv. phleipratensis, *X. translucens* pv. poae, *X. translucens* pv. secalis, *X. translucens* pv. translucens, and *X. translucens* pv. undulosa.

X. translucens strains can be distinguished from other xanthomonads by their SDS-PAGE protein patterns and FAME profiles (51, 60), by the presence of metabolic activity on the carbon substrates dextrin, maltose, D-psicose, D-trehalose, alaninamide, L-alanylglycine, and L-glutamic acid, and by a lack of metabolic activity on the carbon substrates *N*-acetyl-D-galactosamine, α -D-lactose, D-mannitol, D-melibiose, β -methyl-D-glucoside, D-raffinose, L-rhamnose, D-sorbitol, acetic acid, *cis*-aconitic acid, formic acid, D-galactonic acid lactone, D-galacturonic acid, D-gluconic acid, D-glucuronic acid, *p*-hydroxyphenylacetic acid, α -ketobutyric acid, α -ketovaleric acid, malonic acid, propionic acid, quinic acid, D-saccharic acid, glucuronamide, L-histidine, L-leucine, L-phenylalanine, L-proline, L-threonine, urocanic acid, inosine, thymidine, and DL- α -glycerolphosphate.

The G+C content is 69.1 to 69.7 mol%. The type strain is *X. translucens* pv. translucens LMG 876 (= NCPPB 973 = ATCC 19319 = ICMP 5752).

Description of *Xanthomonas vasicola* sp. nov. *Xanthomonas vasicola* (vas.i'co.la. L. neut. n. vas, vascular bundle; L. v. colere, to inhabit; L. adj. vasicola, living in vascular bundles). The description of *X. vasicola* is the same as that of the genus. The following pathovars are distinguished on the basis of phytopathogenic specialization: *X. vasicola* pv. holcicola and *X. vasicola* pv. vasculorum. The latter pathovar includes the strains of the former taxon *X. campestris* pv. vasculorum type B.

The species can be clearly distinguished from other xanthomonads by its SDS-PAGE protein and FAME profiles (51, 60), by the presence of metabolic activity on the carbon substrates D-psicose and L-glutamic acid, and by a lack of metabolic activity on the carbon substrates *N*-acetyl-D-galactosamine, L-arabinose, α -D-lactose, D-melibiose, β -methyl-D-glucoside, L-rhamnose, D-sorbitol, formic acid, D-galactonic acid lactone, D-galacturonic acid, D-gluconic acid, D-glucuronic acid, *p*-hydroxyphenylacetic acid, α -ketovaleric acid, quinic acid, glucuronamide, L-asparagine, L-histidine, L-phenylalanine, urocanic acid, inosine, uridine, thymidine, DL- α -glycerolphosphate, glucose 1-phosphate, and glucose 6-phosphate.

The G+C content is 64.2 mol%. The type strain is *X. vasicola* pv. holcicola LMG 736 (= NCPPB 2417 = ICMP 3103 = CFBP 2543).

Description of *Xanthomonas vesicatoria* (ex Doidge 1920) sp. nov., nom. rev. *X. vesicatoria* includes the strains of the former taxon *X. campestris* pv. vesicatoria type B. The description of *X. vesicatoria* is the same as that of the genus. The strains are isolated from diseased pepper plants (*Capsicum* spp.) and tomato plants (*Lycopersicon* spp.), as well as a number of other, mainly solanaceous hosts.

The species can be distinguished from other xanthomonads on the basis of its SDS-PAGE protein patterns (48), by the

presence of metabolic activity on the carbon substrates dextrin, Tween 80, L-fucose, gentiobiose, maltose, D-psicose, D-trehalose, monomethylsuccinate, succinic acid, bromosuccinic acid, succinamic acid, alaninamide, L-alanine, L-glutamic acid, and L-serine, and by a lack of metabolic activity on the carbon substrates L-arabinose, D-galactose, α -D-lactose, β -methyl-D-glucoside, D-raffinose, *cis*-aconitic acid, formic acid, D-galactonic acid lactone, D-gluconic acid, D-glucuronic acid, *p*-hydroxyphenylacetic acid, α -ketovaleric acid, quinic acid, glucuronamide, glycyl-L-aspartic acid, thymidine, and glucose 6-phosphate.

The G+C content is 65.6 mol%. The type strain is LMG 911 (= NCPPB 422 = ICMP 63).

***Xanthomonas* sp.** A total of 66 former *X. campestris* pathovars have not been placed in any *Xanthomonas* species yet. These include pathovars alangii, amaranthicola, amorphophalli, aracearum, arecae, argemones, arracaciae, azadirachtae, badrii, betae, bilvae, blepharidis, boerhaaviae, brunneivaginae, cannabis, cannae, carissae, centellae, clerodendri, convolvuli, coriandri, daturae, durantae, esculenti, eucalypti, euphorbiae, fici, guizotiae, gummisudans, heliotropii, ionidii, lantanae, laureliae, lawsoniae, leeana, leersiae, mangiferaeindicae, merremiae, mirabilis, musacearum, nigromaculans, olitorii, papavericola, passiflorae, paullinae, pennamericanum, phormiicola, physalidis, plantaginis, sesami, spermacoces, syngonii, tardicrescens, thespesiae, thirumalacharii, tribuli, trichodesmae, uppalii, vernoniae, viticola, vitiscarnosae, vitistrifoliae, vitiswoodrowii, zantedeschiae, zingibericola, and zinniae.

Although protein and FAME profiles of almost all of these pathovars have been determined, it would be premature to classify them in the current species on the basis of these data alone. Rather than maintaining them as pathovars of *X. campestris*, we propose that they should be considered *Xanthomonas* sp. until they are properly allocated in the new *Xanthomonas* classification. In order to preserve the pathovar designations which they currently have, plant pathologists might use a nomenclature such as *Xanthomonas* sp. followed by the appropriate pathovar epithet.

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