10-1-2006

Emended classification of xanthomonad pathogens on citrus

Norman W. Schaad
USDA-ARS

Elena Postnikova
USDA-ARS

George Lacy
Virginia Polytechnic Institute and State University, Blacksburg, VA

Aaron Sechler
USDA-ARS

Irina V. Agarkova
University of Nebraska-Lincoln, iagarkova2@unl.edu

See next page for additional authors

Available online at www.sciencedirect.com
ScienceDirect
Systematic and Applied Microbiology 29 (2006) 690–695
SYSTEMATIC AND APPLIED MICROBIOLOGY
www.elsevier.de/syapm

ERRATUM

Emended classification of xanthomonad pathogens on citrus

Norman W. Schaad[a,*], Elena Postnikova[a], George Lacy[b], Aaron Sechler[a], Irina Agarkova[c], Paul E. Stromberg[a], Verlyn K. Stromberg[b], Anne K. Vidaver[c]

[a]*ARS-USDA, Foreign Disease-Weed Science Research Unit, 1301 Ditto Avenue, Ft. Detrick, MD 21702, USA*
[b]*Department of Plant Pathology, Physiology, and Weed Science, Virginia Polytechnic Institute and State University, Blacksburg, VA 24061, USA*
[c]*Department of Plant Pathology, University of Nebraska, Lincoln, NE 68588, USA*

In the paper by Schaad et al. [24] on reclassification of several xanthomonads, nomenclatural errors were made. The name *Xanthomonas smithii* subsp. *citri* proposed for the former taxon *X. campestris* pv. *citri* (= *X. axonopodis* pv. *citri*) is illegitimate. Following the reinstatement of *X. citri* (*ex* Hasse 1915) Gabriel et al. [9] as a validly published name, Young et al. [34] wrote that the reinstatement of this epithet was based on a description that was inadequate in terms of modern practice for the purpose of formal classification. This report was subsequently summarized by the International Committee on the Systematics of Bacteria (ICSB) Subcommittee on the Taxonomy of the Genus *Pseudomonas* and Related Organisms [32] as implying rejection of the epithet, which the Subcommittee itself appeared to endorse. As we now understand, in accord with the International Code of Nomenclature of Prokaryotes ('the Code'—hitherto the International Code of Nomenclature of Bacteria [14]) the Judicial Commission of the ICSP only may reject a name for precisely specified reasons (Rule 56a). We also misinterpreted the subsequent establishment of the pathovar "*citri*" within *Xanthomonas axonopodis* [29] as further evidence for rejection of reinstatement of *X. citri* [9]. Finally, believing that the epithet "*citri*" had been rejected, we followed rule 23a of the Code [14] and proposed an illegitimate specific epithet "*smithii*" (which also required establishing the subspecies epithet "*smithii*" replacing "*malvacearum*"; see rule 13a [14]). In fact, *X. citri* Gabriel et al. 1989 was a legitimate, validly published name that was allowed to fall into abeyance because of the inadequacies perceived in its description. Schaad et al. [24] indicated their support for the conclusions of Gabriel et al. [9] but included DNA–DNA reassociation data indicated as necessary by for modern classification [26,31]. One purpose of this note is to recognize by effective publication the species related to pathogenic xanthomonads of citrus. The second purpose is to avoid confusion in plant pathological literature by replacing the illegitimate subspecies name *X. smithii* subsp. "smithii" with *X. citri* subsp. "malvacearum". For that purpose, corrected protologues for those species and subspecies are reported here: *X. citri* subsp. *citri* and *X. citri* subsp. *malvacearum*; *X. fuscans* subsp. *fuscans* and *X. fuscans* subsp. *aurantifolii*; and *X. alfalfae* subsp. *alfalfae* and *X. alfalfae* subsp. *citrumelonis*.

We also present (Table 1) GenBank accession numbers for the intergeneric spacer (ITS) sequences for the type strains proposed in this note [24].

Protologues

Abbreviations for culture collections in which type strains are on deposit: ATCC = American Type Culture Collection, Manassas, VA, USA; CFBP = Collection Francaise de Bacteries Phytopathogenes, Angers, France; ICMP = International Collection of Microorganisms from Plants, Auckland, New Zealand; ICPB = International Collection of Phytopathogenic

DOI of original article: 10.1016/j.syapm.2005.03.017
*Corresponding author.
E-mail address: norman.schaad@ars.usda.gov (N.W. Schaad).

doi:10.1016/j.syapm.2006.08.001

Table 1. 16S-23S Ribosomal intergeneric spacer sequences for type strains [24]

Proposed name	Strain designation	GenBank accession
Xanthomonas citri		
X. citri subsp. *citri*	ATCC 49118	DQ660898
X. citri subsp. *malvacearum*	ATCC 9924	DQ660901
Xanthomonas fuscans		
X. fuscans subsp. *fuscans*	ATCC 19315	DQ660900
X. fuscans subsp. *aurantifolii*	NCPPB 3236	DQ660897
Xanthomonas alfalfae		
X. alfalfae subsp. *alfalfae*	ATCC 11765	DQ660896
X. alfalfae subsp. *citrumelonis*	ATCC 49120	DQ660899

Bacteria, USDA, Ft. Detrick, MD, USA; LMG = Laboratorium Microbiologie Gent, Gent, Belgium; NCPPB = National Collection of Plant Pathogenic Bacteria, York, England.

Xanthomonas citri (*ex* Hasse 1915) Gabriel et al. [9] emend.

Etymology: ci'tri. N.L. gen. n. *citri* of citrus.

Description: The description of the species *X. citri* is encompassed within the description of the genus *Xanthomonas* Dowson, 1939 [25] emend. Vauterin et al. [29] and within the description provided by Gabriel et al. [9]. *X. citri* subsp. *citri* causes bacterial canker on *Citrus* spp. and *X. citri* subsp. *malvacearum* causes angular leaf spot and black arm of cotton (*Gossypium* spp.) whereas *X. campestris* and *X. axonopodis* do not affect either host [24]. *X. citri* does not produce a brown water soluble pigment on common media as does *X. fuscans* and *X. campestris* pv. *vignicola* [24]. *X. citri* is differentiated from all other xanthomonads, except *X. campestris* pv. *melonis* and *X. campestris* pv. *viticola,* by fatty acid profiles [33]. Additionally, *X. citri* differs from *X. campestris* and most other pathovars, subspecies, and species of *Xanthomonas* by serology [1,28], SDS-PAGE analysis of membrane proteins [28,30], isozyme analysis [13], DNA-DNA reassociation assays [8,24,29], ITS sequencing [24], RFLP [9,15], and rep-PCR profiles [20].

Type strain: ICPB 10518 = ATCC 49118 = LMG 9322.

Xanthomonas citri* subsp. *citri (*ex* Hasse 1915) Gabriel et al. 1989, subsp. nov.

Etymology: ci'tri. N.L. gen. n. *citri* of citrus.

Description: *X. citri* subsp. *citri* causes bacterial canker of citrus whereas *X. citri* subsp. *malvacearum* does not [24]. *X. citri* subsp. *citri* may be distinguished from *X. campestris* and most other *Xanthomonas* pathovars, subspecies, and species by DNA-DNA reassociation assays [8,24,29], ITS sequencing [24], rep-PCR profiles [20], and phenotypic traits [24]. Strains of *X. citri* subsp. *citri* produce single colonies on YDC and FS agars [23] after 40–44 and 56–60 h, respectively at 28–30 °C [24]. In contrast, *X. fuscans* subsp. *fuscans* and *X. fuscans* subsp. *aurantifolii* produce single colonies in 56–60 and 70–76 h, respectively, and *X. alfalfae* subsp. *alfalfae* and *X. alfalfae* subsp. *citrumelonis* grow in 30–34 and 40–44 h, respectively [24]. *X. citri* subsp. *citri* utilizes arabinose and lactose and hydrolyzes pectate whereas *X. citri* subsp. *malvacearum* does not [24]. *X. citri* subsp. *citri* reduces aspartic acid whereas *X. campestris* pv. *campestris* does not [24]. The latter utilizes raffinose and reduces saccharic acid whereas the former does not [24]. Both bacteria are differentiated by host pathogenicity assays and by serology [1–3,5,28] and membrane protein analysis [16,28,30]. Serology differentiates *X. citri* subsp. *citri* from *X. fuscans* subsp. *aurantifolii* [10,11,19]. Strains of *X. citri* subsp. *citri* are susceptible to bacteriophage CP1 and CP2 whereas those of *X. fuscans* subsp. *aurantifolii* are not [18]. *X. citri* subsp. *citri* is differentiated from *X. alfalfae* subsp. *citrumelonis* by isozyme analysis [13]. *X. citri* subsp. *citri* grows on FS and mSX agars, utilizes arabinose, maltose, lactose, mannitol, cellobiose, and asparatic acid; hydrolyzes pectate, liquifies gelatin, and results in an alkaline hydrolysis of litmus milk [24].

Type strain: ICPB 10518 = ATCC 49118 = LMG 9322.

Xanthomonas citri* subsp. *malvacearum (*ex* Smith 1901) subsp. nov., nom. rev.

Etymology: mal.va.ce.a'rum. N.L. pl. gen. n. malvacearum, of *Malvaceae* (of malvaceous plants of the family *Malvaceae*).

Description: *X. citri* subsp. *malvacearum* causes angular leaf spot and black arm of cotton (*Gossypium hirsutum*) whereas *X. citri* subsp. *citri* does not [24]. *X. citri* subsp. *malvacearum* is differentiated from *X. campestris* pv. *campestris* and most other *Xanthomonas* pathovars, subspecies, and species by DNA-DNA reassociation assays [8,24,29], rep-PCR profiles [20], by serology [3], and SDS-PAGE patterns of membrane proteins [30], ITS sequencing [24], and phenotypic characters [24]. Strains of *X. citri* subsp. *malvacearum* produce single colonies on YDC and FS agars [23] after 40–44 and 56–60 h, respectively, at 28–30 °C [24]. In contrast, *X. fuscans* subsp. *fuscans* and *X. fuscans* subsp.

aurantifolii produce single colonies in 56–60 and 70–76 h, respectively, and *X. alfalfae* subsp. *alfalfae* and *X. alfalfae* subsp. *citrumelonis* grow in 30–34 and 40–44 h, respectively [24]. Further, RFLP profiles differentiate *X. citri* subsp. *malvacearum* from *X. fuscans* subsp. *fuscans*, and *X. alfalfae* subsp. *alfalfae* [15]. *X. campestris* pv. *campestris* utilizes melizitose and hydrolyzes pectate whereas *X. citri* subsp. *malvacearum* does not [24]. *X. citri* subsp. *malvacearum* produces an alkaline reaction without hydrolysis in litmus milk whereas *X. citri* subsp. *citri* causes an alkaline reaction with hydrolysis [24]. *X. citri* subsp. *malvacearum* grows on FS and mSX agars [23], liquifies gelatin, and most strains (60%) utilize maltose [24].

Type strain: ICPB 10528 = ATCC 9924 = ICMP 217 = LMG 785.

The type strain designated here, although identical in pathogenicity [24], is different from strain ICMP 5739 = LMG 761 = NCPPB 633, indicated as the type strain for *X. campestris* pv. *malvacearum* (*X. axonopodis* pv. *malvacearum*) [7,29].

Xanthomonas fuscans sp. nov.

Etymology: fus'cans. L. part. adj. *fuscans* browning/darkening.

Description: The description of the species *X. fuscans* is encompassed within the description of the genus *Xanthomonas* Dowson 1939 (Approved Lists 1980 [25]) emend. Vauterin et al., 1995 [29]. *X. fuscans* subsp. *fuscans*, causes blight of beans (*Phaseolus vulgaris*) and *X. fuscans* subsp. *aurantifolii* causes cankers on *Citrus* spp. whereas *X. campestris* and *X. axonopodis* do not affect either host [24]. *X. fuscans* is differentiated from all other xanthomonads, except *X. campestris* pv. *vignicola,* by production of a water soluble brown pigment on several common agar media including YDC [4,17,22–24]. Additionally, *X. fuscans* is differentiated from most other *Xanthomonas* pathovars and species by DNA–DNA reassociation assays [8,24,29], ITS sequencing [24], and rep-PCR profiles [20].

Type strain: ICPB 10520 = ATCC 19315 = ICMP 239 = LMG 826 = NCPPB 381.

Xanthomonas fuscans* subsp. *fuscans subsp. nov.

Etymology: fus'cans. L. part. adj. *fuscans* browning/darkening.

Description: *X. fuscans* subsp. *fuscans*, originally described as *Phytomonas phaseoli* var. fuscans by Burkholder [4], causes fuscous blight of beans (*Phaseolus vulgaris*) whereas *X. fuscans* subsp. *aurantifolii* does not [24]. Fuscous blight may resemble common blight, caused by *X. campestri* pv. *phaseoli. X. fuscans* subsp. *fuscans* is differentiated from *X. campestris* pv. *campestris* by serology [27] and membrane protein analysis [16,28]. *X. fuscans* subsp. *fuscans* is differentiated from most other *Xanthomonas* pathovars, subspecies, and species by DNA–DNA reassociation assays [24,29], ITS sequences [24], rep-PCR profiles [20], RFLP profiles [15], and phenotypic traits [24]. Strains of *X. fuscans* subsp. *fuscans* produce single colonies on YDC and FS agar after 56–60 and 70–76 h, respectively, at 28–30 °C [24]. In contrast, *X. citri* subsp. *citri* and *X. citri* subsp. *malvcearum* produce single colonies in 40–44 and 56–60 h, respectively, and *X. alfalfae* subsp. *alfalfae* and *X. alfalfae* subsp. *citrumelonis* grow in 30–34 and 40–44 h, respectively [24]. Strains of *X. fuscans* subsp. *fuscans* grow on FS and mSX agars [23], utilize maltose, hydrolyze pectin, and produce an alkaline hydrolysis of litmus milk [24]. *X. fuscans* subsp. *fuscans* produces a water soluble brown pigment on several common agar media including YDC [4,17,22–24]. Except for *X. fuscans* subsp. *aurantifolii* and *X. campestris* pv. *vignicola*, no other xanthomonad produces this brown pigment [24].

Type strain: ICPB 10520 = ATCC 19315 = ICMP 239 = LMG 826 = NCPPB 381.

Xanthomonas fuscans* subsp. *aurantifolii subsp. nov.

Etymology: au.ran.ti.fol'i.i. N.L. n. *Aurantium*, a genus of citrus plants; N.L. gen. n. *folii* of/from a leaf; N.L. gen. n. *aurantifolli* of/from a citrus leaf.

Description: *X. fuscans* subsp. *aurantifolii*, originally described as a pathovar of *X. campestris* [9], causes cankers on Mexican lime (*Citrus aurantifolia*) [18] and occasionally on lemon (*C. limon*), orange (*C. sinensis*), and grapefruit (*C. paradisi*) whereas *X. fuscans* subsp. *fuscans* does not affect citrus [24]. *X. fuscans* subsp. *aurantifolii* is differentiated from most other *Xanthomonas* pathovars, subspecies, and species by DNA–DNA reassociation assays [8,24,29], rep-PCR profiles [20], ITS sequences [24], and phenotypic traits [24]. Strains of *X. fuscans* subsp. *aurantifolii* produce single colonies on YDC and FS agars [23] after 56–60 and 70–76 h, respectively, at 28–30 °C [24]. In contrast, *X. citri* subsp. *citri* and *X. citri* subsp. *malvacearum* produce single colonies in 40–44 and 56–60 h, respectively, and *X. alfalfae* subsp. *alfalfae* and *X. alfalfae* subsp. *citrumellonis* grow in 30–34 and 40–44 h, respectively [24]. *X. fuscans* subsp. *aurantifolii* is distinguished from *X. citri* subsp. *citri* and *X. alfalfae* subsp. *citrumelonis* as it precipitates litmus milk and hydrolyses gelatin. *X. fuscans* subsp. *aurantifolii* does not utilize maltose or hydrolyze pectate whereas *X. citri* subsp. *citri* and *X. fuscans* subsp. *fuscans* do [24]. *X. fuscans* subsp. *aurantifolii* precipitates litmus milk, whereas *X. fuscans* subsp. *fuscans* does not [24]. *X. fuscans* subsp. *fuscans* is distinguished from *X. citri* subsp. *citri* and *X. campestris* pv. *campestris* by failing to utilize arabinose and lactose [24]. Serology differentiates *X. citri* subsp. *citri* from *X. fuscans* subsp. *aurantifolii* [10,11,19]. Strains of *X. citri* subsp. *citri* are susceptible to bacteriophage CP1 and CP2 whereas those of *X. fuscans* subsp. *aurantifolii* are not [18]. Strains of *X. fuscans* subsp. *aurantifolii* utilize lactose, mannitol, and cellobiose and precipitate litmus milk [24]. Strains of *X. fuscans* subsp. *aurantifolii*

produce a water-soluble brown pigment on several common agar media including YDC [6,22,24]. Except for *X. fuscans* subsp. *fuscans* and *X. campestris* pv. *vignicola*, no other xanthomonad produces this brown pigment [24].

Type strain: ICPB 10470 = NCPPB 3236 = CFBP 2901.

Xanthomonas alfalfae (*ex* Riker et al. 1935) sp. nov., nom. rev.

Etymology: al.fal'fae. N.L. gen. n. *alfalfae* from alfalfa (*Medicago sativa*).

Description: The description of the species *X. alfalfae* is encompassed within the description of the genus *Xanthomonas* Dowson 1939 (Approved Lists 1980 [25]) emend. Vauterin et al. 1995 [29]. Strains of *X. alfalfae* subsp. *alfalfae* cause leaf spots on alfalfa (*Medicago sativa*) and strains of *X. alfalfae* subsp. *citrumelonis* cause leaf spots on seedlings of *Citrus* spp. whereas other strains of *X. campestris*, *X. axonopodis*, and any other xanthomonads do not [24]. *X. alfalfae* is differentiated from other *Xanthomonas* pathovars, subspecies, and species by DNA–DNA reassociation assays [8,24,29], rep-PCR profiles [20], RFLP profiles [15], ITS sequences [24] and phenotypic traits [24]. *X. alfalfae* does not produce a brown water soluble pigment on common media as does *X. fuscans* and *X. campestris* pv. *vignicola* [24]. Strains of *X. alfalfae* grow much faster than other xanthomonads on SX and FS agars [23] and utilize a broader range of carbon sources [24]. *X. alfalfae*, and its subspecies, utilize arabinose, maltose, lactose, mannitol, and cellobiose; liquify gelatin; and produce an alkaline hydrolysis of litmus milk whereas *X. axonopodis* does not [24].

Type strain: ICPB 10701 = ATCC 11765 = LMG 495.

Xanthomonas alfalfae **subsp. *alfalfae*** (*ex* Riker et al., 1935) subsp. nov.

Etymology: al.fal'fae. N.L. gen. n. *alfalfae* from alfalfa (*Medicago sativa*).

Description: *X. alfalfae* subsp. *alfalfae* causes leaf spot of alfalfa [21] whereas *X. alfalfae* subsp. *citrumelonis* does not [24]. *X. alfalfae* subsp. *alfalfae* is distinguished from *X. campestris* pv. *campestris* and most other *Xanthomonas* pathovars, subspecies, and species by DNA–DNA reassociation assays [8,24,29], RFLP profiles [15], rep-PCR profiles [20], and ITS sequences [24]. Strains of *X. alfalfae* subsp. *alfalfae* produce single colonies on YDC and FS agarss [23] after 30–34 and 40–44 h, respectively, at 28–30 °C [24]. In contrast, *X. citri* subsp. *citri* and *X. citri* subsp. *malvcearum* produce single colonies in 40–44 and 56–60 h, respectively, and *X. fuscans* subsp. *fuscans* and *X. fuscans* subsp *aurantifolii* grow in 56–60 and 70–76 h, respectively [24]. *X. alfalfae* subsp. *alfalfae* produces acid from most carbon sources whereas *X. campestris* pv. *campestris* does not [24]. *X. campestris* pv. *campestris* utilizes raffinose whereas *X. alfalfae* subsp. *alfalfae* does not [24]. *X. alfalfae* subsp. *alfalfae* grows faster on YDC agar than do most other xanthomonads [24]. Strains of *X. alfalfae* subsp. *alfalfae* produce an alkaline reaction on saccharic acid whereas strains of *X. alfalfae* subsp. *citrumelonis* do not [24]. *X. alfalfae* subsp. *alfalfae* utilizes arabinose, maltose, lactose, mannitol, melizitose, and cellobiose, liquifies gelatin, and produces an alkaline hydrolysis of litmus milk [24].

Type strain: ICPB 10701 = ATCC 11765 = LMG 495.

Xanthomonas alfalfae **subsp. *citrumelonis*** subsp. nov.

Etymology: ci.tru.me'lo.nis. N.L. gen. n. *citrumelonis* of citrumelo (*Citroncirus* sp.; hybrid of *Citrus paradisi* x *Poncirus trifoliata*).

Description: *X. alfalfae* subsp. *citrumelonis*, originally described as pathovar "*citrumelo*" of *X. campestris* [9], causes citrus bacterial spot [12]; *X. alfalfae* subsp *alfalfae* does not [24]. *X. alfalfae* subsp *citrumelonis* is distinguished from *X. campestris* pv. *campestris* and other *Xanthomonas* pathovars, subspecies, and species by DNA-DNA reassociation assays [8,24,29], rep-PCR profiles [20], ITS sequences [24], and phenotypic traits [24]. Strains of *X. alfalfae* subsp. *citrumelonis* produce single colonies on YDC and FS agars [23] after 30–34 and 40–44 h, respectively, at 28–30 °C [24]. In contrast, *X. citri* subsp. *citri* and *X. citri* subsp. *malvacearum* produce single colonies in 40–44 and 56–60 h, respectively, and *X. fuscans* subsp. *fuscans* and *X. fuscans* subsp. *aurantifolii* grow in 56–60 and 70–76 h, respectively [24]. *X. alfalfae* subsp. *citrumelonis* strains are differentiated from *X. citri* subsp. *citri* and *X. citri* subsp. *malvacearum* and *X. fuscans* subsp. *aurantifolii* by serological assays [2,12,19]. *X. alfalfae* subsp. *citrumelonis* utilizes raffinose whereas *X. alfalfae* subsp. *alfalfae*, *X. citri* subsp. *citri*, and *X. citri* subsp. *malvacearum* strains do not [24]. *X. alfalfae* subsp. *alfalfae* and *X. alfalfae* subsp. *citrumelonis* can be differentiated from *X. fuscans* subsp. *aurantifolii* on their more rapid growth on agar media, liquefaction of gelatin, and utilization of maltose [24]. *X. alfalfae* subsp. *citrumelonis* is distinguished from *X. citri* subsp. *citri* by utilizing raffinose, producing acid from cellobiose and mannitol, and growing faster on YDC and FS agars [24]. All strains of *X. alfalfae* subsp. *citrumelonis* utilize mannitol and raffinose whereas strains of *X. citri* subsp. *malvacearum* do not [24].

Type strain: ICPB 10483 = ATCC 49120 = LMG 9325.

Acknowledgements

We thank Dr. J.P. Euzeby for proof reading our protologues and Dr. B.J. Tindall and Dr. J.M. Young for reviewing our nomenclature.

References

[1] A.M. Alvarez, A.A. Benedict, C.Y. Mizumoto, Identification of xanthomonads and grouping of strains of *Xanthomonas campestris* pv. *campestris* with monoclonal antibodies, Phytopathology 75 (1985) 722–728.

[2] A.M. Alvarez, A.A. Benedict, C.Y. Mizumoto, L.W. Pollard, E.L. Civerolo, Analysis of *Xanthomonas campestris* pv. *citri* and *Xanthomonas campestris* pv. *citrumelo* with monoclonal antibodies, Phytopathology 81 (1991) 857–865.

[3] R.H. Brlansky, R.F. Lee, E.L. Civerolo, Detection of *Xanthomonas campestris* pv. *citrumelo* and *X. citri* from citrus using membrane entrapment immuno-fluorescence, Plant Dis. 74 (1990) 863–868.

[4] W.H. Burkholder, The bacterial diseases of bean. A comparative study. Memiors of the Cornell Agricultural Research Station No. 127, 1930.

[5] E.L. Civerolo, F. Fan, *Xanthomonas campestris* pv. *citri* detection and identification by enzyme-linked immunosorbent assay, Plant Dis. 66 (1982) 231–236.

[6] S.A.L. Destefano, N.J. Rodrigues, Characterization of pigment producer strains of *Xanthomonas axonopodis* pv. *aurantifolii* (C Type), Summa Phytopathol. 27 (2002) 287–291.

[7] D.W. Dye, J.F. Bradbury, M. Goto, A.C. Hayward, R.A. Lelliot, M.N. Schroth, International standards for naming pathovars of phytopathogenic bacteria and a list of pathovar names and pathotype strains, Rev. Plant Pathol. 59 (1980) 153–168.

[8] D.S. Egel, J.H. Graham, R.E. Stall, Genomic relatedness of *Xanthomonas campestris* strains causing diseases of citrus, Appl. Environ. Microbiol. 57 (1991) 2724–2730.

[9] D.W. Gabriel, M.T. Kingsley, J.E. Hunter, T. Gottwald, Reinstatement of *Xanthomonas citri* (*ex* Hasse) and *X. phaseoli* (*ex* Smith) to species and reclassification of all *X. campestris* pv. *citri* strains, Int. J. Syst. Bacteriol. 39 (1989) 14–22.

[10] M. Goto, Citrus canker, in: J. Kumar, H.S. Choube, U.S. Sing, A.N. Mukhopadhay (Eds.), Plant Diseases of International Importance, Vol. III. Diseases of Fruit Crops, Prentince-Hall, Englewood Cliffs, 1992, pp. 170–208.

[11] M. Goto, A. Toyoshima, M.A. Messina, A comparative study of the strains of *Xanthomonas campestris* pv. *citri* isolated from citrus canker in Japan and cancrosis B in Argentina, Ann. Phytopathol. Soc. Jpn 46 (1980) 329–338.

[12] T.R. Gottwald, A.M. Alvarez, J.S. Hartung, A.A. Benedict, Diversity of *Xanthomonas campestris* pv. *citrumelo* strains associated with epidemics of citrus bacterial spot in Florida citrus nurseries: correlation of detached leaf, monoclonal antibody, and restriction fragment length polymorphism assays, Phytopathology 81 (1991) 749–753.

[13] Q.B. Kubicek, E.L. Civerolo, M.R. Bonde, J.S. Hartung, G.L. Peterson, Isozyme analysis of Xanthomonas campestris pv. *citri*, Phytopathology 79 (1989) 297–300.

[14] S.P. Lapage, P.H.A. Sneath, E.F. Lessel, V.B.D. Skerman, H.P.R. Seeliger, W.A. Clark (Eds.), International Code of Nomenclature of Bacteria (1976 Revision). Bacteriological Code, American Society for Microbiology, Washington, DC, 1976.

[15] G.R. Lazo, R. Roffey, D.W. Gabriel, Pathovars of *Xanthomonas campestris* are distinguished by restriction fragment length polymorphisms, Int. J. Syst. Bacteriol. 37 (1987) 214–221.

[16] G.V. Minsavage, N.W. Schaad, Characterization of membrane proteins of *Xanthomonas campestris* pv. *campestris*, Phytopathology 73 (1983) 747–755.

[17] A.B.C. Mkandawire, R.B. Mabagala, P. Guzman, P. Gepts, R.L. Gilbertson, Genetic diversity and pathogenic variation of common bacterial blight bacteria (*Xanthomonas campestris* pv. *phaseoli* and *X. campestris* pv. *phaseoli* var. *fuscans*) suggests pathogenic coevolution with the common bean, Phytopathology 94 (2004) 593–603.

[18] T. Namekata, Estudos Comparativos Entre *Xanthomonas citri* [Hasse] Dow., Agente Causal do Cancro Citrico e *Xanthomonas Citri* [Hasse] Dow, N.F.SP. *aurantifolia*, Agente Causal da Cancrose do limoeiro Galego. 65f. Tese (Doutoramento) – Escola Superior de Agricultura ''Luiz de Queiroz'', Universidade de Sao Paulo, Piracicaba, 1971.

[19] T. Namekata, A.R. de Oliveira, Comparative serological studies between *Xanthomonas citri* and a bacterium causing canker on Mexican lime, in: Proceedings of International Conference on Plant Pathogenic Bacteria, Wageningen, The Netherlands, 1972, pp. 151–152 (365pp).

[20] J.L.W. Rademaker, F.J. Louws, M.H. Schultz, U. Rossbach, L. Vauterin, J. Swings, F.J. de Bruijn, A comprehensive species to strain taxonomic framework for *Xanthomonas*, Phytopathology 95 (2005) 1098–1111.

[21] A.J. Riker, F.R. Jones, M.C. Davis, Bacterial leaf spot of alfalfa, J. Agric. Res. 51 (1935) 177–182.

[22] N.W. Schaad, Initial identification of common genera, in: N.W. Schaad, J.B. Jones, W. Chun (Eds.), Laboratory Guide for Identification of Plant Pathogenic Bacteria, third ed, APS Press, St. Paul, MN, 2001, pp. 1–16 (373pp).

[23] N.W. Schaad, J.B. Jones, G.H. Lacy, *Xanthomonas*, in: N.W. Schaad, J.B. Jones, W. Chun (Eds.), Laboratory Guide for Identification of Plant Pathogenic Bacteria, third ed, APS Press, St. Paul, MN, 2001, pp. 175–200 (373pp).

[24] N.W. Schaad, E. Postnikova, G.H. Lacy, A. Sechler, I. Agarkova, P.E. Stromberg, V.K. Stromberg, A.K. Vidaver, Reclassification of *Xanthomonas campestris* pv. *citri* (*ex* Hasse 1915) Dye 1978 forms A, B/C/D, and E as *X. smithii* subsp. *citri* (*ex* Hasse) sp. nov. nom. rev. comb. nov., *X. fuscans* subsp. *aurantifolii* (*ex* Gabriel 1989) sp. nov. nom. rev. comb. nov., and *X. alfalfae* subsp. *citrumelo* (*ex* Riker and Jones) Gabriel *et al.*, 1989 sp. nov. nom. rev. comb. nov.; *X. campestris* pv. *Malvacearum* (*ex* Smith 1901) Dye 1978 as *X. smithii* subsp. *smithii* nov. comb. nov. nom. nov.; *X. campestris* pv. *alfalfae* (*ex* Riker and Jones, 1935) Dye 1978 as *X. alfalfae* subsp. *alfalfae* (*ex* Riker *et al.*, 1935) sp. nov. nom. rev.; and ''var. fuscans'' of *X. campestris* pv. *phaseoli* (*ex* Smith,

1987) Dye 1978 as *X. fuscans* subsp. *fuscans* sp. nov, Syst. Appl. Microbiol. 28 (2005) 494–518.

[25] V.B.D. Skerman, V. McGowan, P.H.A. Sneath (Eds.), Approved lists of bacterial names, Int. J. Syst. Bacteriol. 30 (1980) 225–420.

[26] E. Stackebrandt, W. Frederiksen, G.M. Garrity, P.A.D. Grimont, P. Kampfer, M.C.L. Maiden, X. Nesme, R. Rossello-Mora, J. Swings, H.G. Truper, L. Vauterin, A.C. Ward, W.B. Whitman, Report of the *ad hoc* committee for the re-evaluation of the species definition in bacteriology, Int. J. Syst. Evol. Microbiol. 52 (2002) 1043–1047.

[27] X. Sun, R.E. Stall, J.B. Jones, J. Cubero, T.W. Gottwald, J.H. Graham, W.N. Dixon, T.S. Schubert, P.H. Chaloux, V.K. Stromberg, G.H. Lacy, B.D. Sutton, Detection and characterization of a new strain of citrus canker bacteria from Key/Mexican lime and alemow in South Florida, Plant Dis. 88 (2004) 1179–1188.

[28] N. Thaveechai, N.W. Schaad, Serological and electrophoretic analysis of a membrane protein of *Xanthomonas campestris* pv. *campestris* from Thailand, Phytopathology 76 (1986) 139–147.

[29] L. Vauterin, B. Hoste, K. Kersters, J. Swings, Reclassification of *Xanthomonas*, Int. J. Syst. Bacteriol. 45 (1995) 472–489.

[30] L. Vauterin, P. Yang, B. Hoste, M. Vancanneyt, E.L. Civerolo, J. Swings, K. Kersters, Differentiation of *Xanthomonas campestris* pv. *citri* strains by sodium dodecyl sulfate-polyacrylamide gel electrophoresis of proteins, fatty acid analysis, and DNA-DNA hybridization, Int. J. Syst. Bacteriol. 41 (1991) 535–542.

[31] L.G. Wayne, D.J. Brenner, R.R. Colwell, P.A.D. Grimont, O. Kandler, M.I. Krichevsky, L.H. Moore, W.E.C. Moore, R.G.E. Murray, E. Stackebrandt, M.P. Starr, H.G. Trüpper, Report of the *ad hoc* committee on the reconciliation of approaches to bacterial systematics, Int. J. Syst. Bacteriol. 37 (1987) 463–464.

[32] E. Yabuuchi, P. De Vos, Minutes of the meetings of the international committee of systematic bacteriology subcommittee on the taxonomy of the genus *Pseudomonas* and related organisms (17 and 20 September 1990, Japan), Int. J. Syst. Bacteriol. 45 (1995) 877–878.

[33] P. Yang, L. Vauterin, M. Vancanneyt, J. Swings, K. Kersters, Application of fatty acid methyl esters for taxonomic analysis of the genus *Xanthomonas*, Syst. Appl. Microbiol. 16 (1993) 47–71.

[34] J.M. Young, J.F. Bradbury, L. Gardan, R.I. Gvozdyak, D.E. Stead, Y. Takikawa, A.K. Vidaver, Comment on the reinstatement of *Xanthomonas citri* (*ex* Hasse 1915) Gabriel *et al*. 1989 and *X. phaseoli* (*ex* Smith 1897) Gabriel *et al*. 1989. Indication of the need for minimal standards for the genus *Xanthomonas*, Int. J. Syst. Bacteriol. 41 (1991) 172–177.