Transfer of *Xanthomonas campestris* pv. *arecae* and *X. campestris* pv. *musacearum* to *X. vasicola* (Vauterin) as *X. vasicola* pv. *arecae* comb. nov. and *X. vasicola* pv. *musacearum* comb. nov. and Description of *X. vasicola* pv. *vasculorum* pv. nov.

David J. Studholme,1,4 Emmanuel Wicker,2 Sadik Muzemil Abrare,3 Andrew Aspin,4 Adam Bogdanove,5 Kirk Broders,6 Zoe Dubrow,5 Murray Grant,7 Jeffrey B. Jones,8 Georgina Karamura,9 Jillian Lang,10 Jan Leach,10 George Mahuku,11 Gloria Valentine Nakato,12 Teresa Coutinho,13 Julian Smith,4 and Carolee T. Bull14

1 Biosciences, University of Exeter, Exeter, U.K.
2 IPME, University of Montpellier, CIRAD, IRD, Montpellier, France
3 Southern Agricultural Research Institute (SARI), Areka Agricultural Research Center, Areka, Ethiopia
4 Fera Science Ltd., York, U.K.
5 Plant Pathology and Plant-Microbe Biology Section, School of Integrative Plant Science, Cornell University, 334 Plant Science Building, Ithaca, NY 14853, U.S.A.
6 Department of Biocultural Sciences and Pest Management, Colorado State University, Fort Collins, CO 80523, U.S.A.
7 School of Life Sciences, Gibbet Hill, University of Warwick, Coventry, CV4 7AL, U.K.
8 University of Florida, Plant Pathology Department, 1453 Fifield Hall, Gainesville, FL 32611, U.S.A.
9 Bioversity International, Uganda
10 Department of Biocultural Sciences and Pest Management, Colorado State University, Fort Collins, CO 80523, U.S.A.
11 International Institute of Tropical Agriculture (IITA), East Africa Hub, IITA-Tanzania, P.O. Box 34441, Dar es Salaam, Tanzania
12 International Institute of Tropical Agriculture (IITA), Plot 15B, Naguru East Road, Upper Naguru, P.O. Box 7878, Kampala, Uganda
13 Department of Microbiology and Plant Pathology, Centre for Microbial Ecology and Genomics (CMEG), Forestry and Agricultural Biotechnology Institute (FABI), University of Pretoria, Private Bag X28, Pretoria 0028, South Africa
14 Department of Plant Pathology and Environmental Microbiology, Penn State University, University Park, PA, U.S.A.

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ABSTRACT

We present an amended description of the bacterial species *Xanthomonas vasicola* to include the causative agent of banana *Xanthomonas* wilt, as well as strains that cause disease on *Areca* palm, *Tripsacum* grass, sugarcane, and maize. Genome-sequence data reveal that these strains all share more than 98% average nucleotide with each other and with the type strain. Our analyses and proposals should help to resolve the taxonomic confusion that surrounds some of these pathogens and help to prevent future use of invalid names.

The aim of this letter is to resolve the taxonomy of several bacterial lineages that phylogenetically fall within the species *Xanthomonas vasicola* Vauterin et al. 1995. These lineages include an economically important pathogen of banana and enset (*X. campestris* pv. *musacearum* Yirgou and Bradbury 1968), a pathogen of *Areca* palm (*X. campestris* pv. *arecae* Rao and Mohan 1970) and closely related bacteria isolated from *Tripsacum* grass. Also within scope is a subset of *X. campestris* pv. *vasculorum* (Cobb 1894) Dye 1978 from sugarcane and maize. Finally, it includes strains from maize assigned to a taxon with an invalid name, [*X. campestris* pv. *zeae*]. In this manuscript, pathovar names that have no standing in nomenclature are presented with square brackets ([]) as is standard (Bull et al. 2012).

There is confusion surrounding the taxonomy of some of these lineages, not least around the previous splitting of *Xanthomonas campestris* pv. *vasculorum* into two new taxa: *X. axonopodis* pv. *vasculorum* and [*X. vasicola* pv. *vasculorum*] (Vauterin et al. 1995). The latter name currently has no standing in the nomenclature, yet has nevertheless been widely adopted. Our first objective is to formally transfer these lineages into the species *X. vasicola*. A second objective is to formally propose *X. vasicola* pv. *vasculorum* according to the International Standards for Naming Pathovars of Phytopathogenic Bacteria (Young et al. 2001), which hereafter we call the Standards. Our description of this pathovar corresponds to the previous proposal (Vauterin et al. 1995) but also incorporates [*X. campestris* pv. *zeae*] and agrees closely with the adopted usage of this name by the community. Despite a previous proposal (Vauterin et al. 1995), the name [*X. vasicola* pv. *vasculorum*] was excluded from the Names of Plant Pathogenic Bacteria (Young et al. 1996) due to the lack of a pathotype with an adherent description for the pathovar. Therefore, the name [*X. vasicola* pv. *vasculorum*] currently has no standing in the nomenclature and needs to be proposed as a pv. nov. Only a subset of *X. campestris* pv. *vasculorum* strains fall within *X. vasicola* (while others fall within *X. axonopodis*, including the pathotype strain). Therefore, the problem cannot be solved by transferring *X. campestris* pv. *vasculorum* into *X. vasicola* as a comb. nov. because no name-bearing strain is being transferred into *X. vasicola*.

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Members of the genus *Xanthomonas*, collectively cause disease on more than 400 plant species (Hayward 1993), though some members are apparently nonpathogenic (Garita-Cambroner et al. 2016; Vauterin et al. 1996; Vicente et al. 2017) and some have been isolated from clinical samples such as skin microbiota (Seité et al. 2017). Historically, taxonomy of *Xanthomonas* was tied to the host of isolation (Starr 1981; Wernham 1948), with the genus being split into large numbers of species, each defined by this single phenotypic feature (Dye 1962). Subsequently, most of the species were transferred (i.e., “lumped”) into a single species, *X. campestris*, and designated as nosenspecies because the organisms could not be distinguished from one another by phenotypic and physiological tests (Dye and Lelliott 1974; Lapage et al. 1992). As a temporary solution, and to help to maintain a connection with the historical and plant-pathological literature, these nosenspecies were designated as pathovars within *X. campestris*, each defined by host range or disease syndrome (Dye et al. 1980). More recently, DNA sequence comparisons and biochemical approaches revealed that in *X. campestris*, pathovar designation does not always correlate with phylogeny (Parkinson et al. 2007, 2009; Rodríguez-R et al. 2012). There have been heroic advances to improve the taxonomy of the genus as a whole (Rademaker et al. 2005; Vauterin et al. 1990, 1995, 2000) and of individual taxa (Constantin et al. 2016; da Gama et al. 2018; Jones et al. 2004; Timilsina et al. 2019; Trébaol et al. 2000), based on phenotypic, chemotaxonomic, and genotypic analyses. But in a number of taxa there remain unresolved issues.

The bacterial pathogen *X. campestris pv. musacearum* (Yirgou and Bradbury 1968) Dye 1978 presents a major threat to cultivation of banana and enset crops in central and eastern Africa, where it causes banana Xanthomonas wilt (BXW) and enset Xanthomonas wilt (EXW). Originally described as *X. musacearum* (Yirgou and Bradbury 1968), this pathogen was first isolated in Ethiopia from enset and banana in the 1960s and early 1970s, respectively (Yirgou and Bradbury 1968, 1974). Symptoms consistent with EXW were described as XW in the pathological literature. For example, various authors proposed a formal description of *X. musacearum* (Yirgou and Bradbury 1968) that adheres to the Standards (Young et al. 2001), to harmonize the formal nomenclature with that which is in common use.

| Strain | Vauterin (1992, 1995) | Doorkun (2000) | Péros (1994) | Current species assignment |
|-------|----------------------|---------------|--------------|---------------------------|
| NCPPB 186 | Type A | Group A | n/a | X. axonopodis |
| NCPPB 891 | Type A | Group A | G1 | X. axonopodis |
| NCPPB 892 | n/a | Group A | n/a | X. axonopodis |
| NCPPB 893 | n/a | Group A | n/a | X. axonopodis |
| NCPPB 181 | Type A | Group B | n/a | X. axonopodis |
| NCPPB 796pt | Type A | Group B | n/a | X. axonopodis |
| NCPPB 890 | n/a | Group D | n/a | X. axonopodis |
| NCPPB 795 | Type B | Group C | n/a | X. vasicola |
| NCPPB 889 | Type B | Group C | n/a | X. vasicola |
| NCPPB 206 | n/a | Group C | n/a | X. vasicola |
| NCPPB 702 | n/a | Group C | n/a | X. vasicola |
| NCPPB 795 | n/a | Group C | n/a | X. vasicola |
| NCPPB 889 | n/a | Group C | n/a | X. vasicola |
| NCPPB 890 | n/a | Group C | n/a | X. vasicola |
| NCPPB 895 | n/a | Group C | n/a | X. vasicola |
| NCPPB 1326 | n/a | Group C | n/a | X. vasicola |
| NCPPB 1381 | n/a | Group C | n/a | X. vasicola |

TABLE 1. Classification of strains previously assigned to *Xanthomonas campestris pv. musacearum*

Adoption of competing classifications and invalid names has led to the potentially confusing use of three different valid species names (*X. campestris, X. axonopodis, and X. vasicola*) to describe this group of bacteria in the literature. For example, various authors have referred to the strain NCPPB 1326 as *X. campestris pv. musacearum, X. axonopodis pv. musacearum* (to which the strain clearly does not belong), and *X. vasicola pv. musacearum* (Lewis Ivey et al. 2010; Qhobela and Claflin 1992; Qhobela et al. 1990;
Wasukira et al. 2014). Type-B strains NCPPB 1326, NCPPB 702, and NCPPB 206 were erroneously described as X. axonopodis pv. vasculorum (Lewis Ivey et al. 2010) though they are clearly members of X. vasicola. We acknowledge that our taxonomic proposals will likely not eliminate mistakes such as these.

A further source of confusion is the status of strains isolated from maize for which some authors use the invalid name [X. campestris pv. zeae] (Coutinho and Wallis 1991; Qhobela et al. 1990). A useful nomenclature for this group has become more pressing since the recent outbreak of leaf streak on corn in the United States, caused by bacteria very closely related to strains previously described as [X. campestris pv. zeae]. One of these strains, NCPPB 4614 (=SAM119), was suggested to be the eventual pathotype strain of X. vasicola pv. vasculorum though no formal proposal and description was made (Korus et al. 2017; Lang et al. 2017). We concur with the previous suggestion (Lang et al. 2017) that strains classified to [X. vasicola pv. vasculorum] and [X. campestris pv. zeae] (Vauterin et al. 1995) are insufficiently distinct to warrant separate pathovars and therefore strains previously named [X. campestris pv. zeae] are assigned into the newly described X. vasicola pv. vasculorum pv. nov.

Draft or complete sequence assemblies are now available for more than a thousand Xanthomonas genomes, including those of type strains for most species and pathotypes for most pathovars. Genomic sequences can offer some advantages for phylogeny and taxonomy, such as generally applicable threshold values for species delineation (Glæser and Kämpfer 2015; Meier-Kolthoff et al. 2013, 2014; Richter and Rosselló-Mora 2009). We calculated pairwise average nucleotide identity (ANI) between representative X. vasicola pv. vasculorum and [X. campestris pv. zeae] (Lang et al. 2017; Potnis et al. 2011; Sanko et al. 2011; Sanko and Rosselló-Mora 2009; Vauterin et al. 2014). Type-B strains NCPPB 1326, NCPPB 702, and NCPPB 206 were erroneously described as X. axonopodis pv. vasculorum (Yirgou and Bradbury 1968) Dye 1978b shares 98.43% ANI with the type strain of X. vasicola (NCPPB 2417) but only 87.27% with the type strain of X. campestris (ATCC 33913). Strains of X. campestris pv. vasculorum called [X. vasicola pv. vasculorum] share >95.8% ANI with the type strain of X. vasicola, as do strains of [X. campestris pv. zeae], including SAM119 (=NCPPB 4614), which we propose as the pathotype strain of X. vasicola pv. vasculorum pv. nov. Furthermore, unclassified strains NCPPB 902, NCPPB 1394, NCPPB 1395, and NCPPB 1396, from Tripsacum laxum (Mulder 1961), and the pathotype strain of X. campestris pv. arecae (Rao and Mohan 1970) Dye 1978 (NCPPB 2649) all share more than 98% ANI with the type strain of X. vasicola, which places them unambiguously within X. vasicola. We note that former X. campestris pv. vasculorum strains NCPPB 900 and CFBP 5823 share much higher ANI with the type strain of X. axonopodis (98.08 to 98.12%) than with the type strain of X. vasicola (90.43%), which is consistent with their assignment to X. axonopodis pv. vasculorum (Cobb) Vauterin, Hoste, Kersters & Swings.

The high ANI levels (Fig. 1) clearly delineate a species that includes the type strain of X. vasicola (i.e., NCPPB 2417). It has been proposed that the boundary of a prokaryotic species can be delimited by 95 to 96% ANI (Richter and Rosselló-Mora 2009). By this criterion, X. campestris pv. arecae, X. campestris pv. musacearum, and [X. vasicola pv. zeae] clearly fall within X. vasicola and outside X. campestris. The next-nearest species to X. vasicola is X. oryzae; ANI between the respective type strains of these two species is 91.7%.

Despite the usefulness of ANI for delimiting species boundaries, it does not include any model of molecular evolution and thus is unsuited for phylogenetic reconstruction. Therefore, we used 3

![Fig. 1. Average nucleotide identity (ANI) with type strains of Xanthomonas species.](image-url)
This indicates that natural infection of maize by *X. vasicola* except for NCPPB 2005, which was isolated from enset (*Ensete ventricosum*). The cartoon images denote typical host plants from which each clade of bacteria PRJNA163305, PRJNA163307, PRJNA31213, PRJNA374510, PRJNA439013, PRJNA439327, PRJNA439328, PRJNA439329, and PRJNA449864 (Lang et al. 2017; Sanko et al. 2018; Wasukira et al. 2014, 2012). Whole-genome shotgun sequence reads were obtained from the Sequence Read Archive (Leinonen et al. 2011) via BioProjects PRJNA73853, PRJNA163305, PRJNA163307, PRJNA31213, PRJNA374510, PRJNA439013, PRJNA439327, PRJNA439328, PRJNA439329, and PRJNA449864 (Lang et al. 2017; Sanko et al. 2018; Wasukira et al. 2014, 2012). The cartoon images denote typical host plants from which each clade of bacteria.

Strain NCPPB 206 of *X. campestris pv. pseudogibsonii* isolated from maize. in contrast to most strains of this pathovar being isolated from sugarcane. On the basis of phylogenetic analysis of DNA sequence, this strain clearly falls within *X. vasicola* (Wasukira et al. 2014) and has the fatty-acid type characteristic of *X. vasicola* (Dookun et al. 2000). However, it is phylogenetically distinct from the strains of *X. campestris pv. zea*, as illustrated in Figures 1 and 2. Indicates that natural infection of maize by *X. vasicola* is not restricted to strains of *X. campestris pv. zea*.

Overall, our molecular sequence analyses strongly point to the existence of a phylogenetically coherent species, *X. vasicola* Vauterin 1995, that includes strains previously assigned to *X. campestris* pathovars *musaearum* and *arecae*, some strains of *X. campestris* pv. *vasculorum*, and strains collected from corn and *Tripsacum laxum* grass that have not been previously assigned to species nor pathovar. Here we propose that the pathovar *X. vasicola* pv. *vasculorum* nov. includes strains formerly classified as *X. campestris* pv. *vasculorum* but distinguishable from *X. axonopodis* pv. *vasculorum* (Cobb) Vauterin, Hoste, Kersters & Swings by protein SDS-PAGE, FAME analysis, and DNA hybridization (Vauterin et al. 1992, 1995; Yang et al. 1993). Our analyses also support the transfer of *X. campestris pv. arecae* (Rao and Mohan 1970) Dye 1978 to *X. vasicola*. Although only a single genome of this pathovar has been sequenced, fortunately that genome belongs to the pathotype strain of the pathovar (Bull et al. 2010; Rao and Mohan 1970). Our results are consistent with previous evidence for similarity between *X. campestris pv. musaeareum* and strains of *X. vasicola*, based on FAME, genomic fingerprinting with rep-PCR, and *gyrB* sequencing (Aritua et al. 2007; Parkinson et al. 2007). The formal species description for *X. vasicola* Vauterin 1995 states that this species can be clearly distinguished by its FAME profiles (Vauterin et al. 1995). Pathogenicity studies demonstrated phenotypic distinctiveness of *X. campestris pv. musaeareum* (Yirgou and Bradbury 1968) Dye 1978 on banana; *X. campestris pv. musaeareum* produces severe disease on this host, whereas *X. vasicola pv. holcicola* NCPPB 2417 and *X. campestris pv. pseudogibsonii* NCPPB 702 (which belongs to *X. vasicola*) induced no symptoms (Aritua et al. 2007). The species description (Vauterin et al. 1995) also states that *X. vasicola* is characterized by metabolic activity on the carbon substrates d-psicose and l-glutamic acid, and by a lack of metabolic activity on a range of carbon substrates (further detailed in the emended description). We are not aware that these metabolic activities have been tested for *X. campestris pv. arecae*, *X. campestris pv. musaeareum*, and *X. campestris pv. zea*; it is possible that the species description may need to be amended to...
accommodate any deviation from this definition among the repositioned pathovars.

Overall, it seems that the species *X. vasicola* (including *X. vasicola* pv. *holcicola*, *X. campestris* pv. *vasculorum* type-B strains, *X. campestris* pv. *zeae* strains, *X. campestris* pv. *arecae*, and some strains isolated from *T. laxum*) is almost exclusively associated with monocot plants of the families Palmae and Gramineae. In this respect, it is similar to its closest sibling species *X. oryzae*, whose host range is limited to Gramineae (Bradbury 1986). The exception is a report of leaf blight and dieback in *X. campestris* (Coutinho et al. 2015), remarkable given the phylogenetic distance between this dicot plant and *X. vasicola*. The host range of *X. vasicola* is most appropriate to indicate this relationship. The natural host for *X. vasicola* pv. *holcicola* (LMG 736, NCPPB 2417, ICMP 3103, and CFBP 2543) as the type strain of *X. vasicola*, although they did not use the pathovar epithet for the specific epithet of the species as is most appropriate to indicate this relationship. The natural host range of *X. vasicola* pv. *holcicola* includes the cereal crops millet and sorghum on which it causes bacterial leaf streak (Table 2) as well as wild grass belonging to the genus *Holcus*. The host range of the strains that Vauterin et al. (1995) called [X. vasicola pv. *holcicola* (Elliott 1930) Vauterin et al. 1995 (synonym *X. vasicola* pv. *holcicola*)] is less well defined because in most of the relevant pre-1995 literature it is impossible to distinguish between type-A and type-B of *X. campestris* pv. *vasculorum* and therefore between *X. axonopodis* pv. *vasculorum* and strains belonging to *X. vasicola*. However, *X. campestris* pv. *vasculorum* type-B strains (that is, members of *X. vasicola*) have been isolated from sugarcane and maize and shown to infect these hosts on artificial inoculation (Karamura et al. 2015; Vauterin et al. 1995).

In conclusion, analysis of available genome sequence data, combined with published pathogenicity and biochemical data, strongly supports the transfer of the *X. campestris* pathovars *musacearum* and *arecae* to the species *X. vasicola* as, respectively, (i) *X. vasicola* pv. *musacearum* comb. nov. with NCPPB 2005 as the pathotype strain (being the type strain of *X. vasicola* Yirgou & Bradbury and pathotype strain of *X. campestris* pv. *musacearum*) and (ii) *X. vasicola* pv. *arecae* comb. nov. with NCPPB 2649 as the pathotype strain (being the type strain of *X. arecae* Rao & Mohan and pathotype strain of *X. campestris* pv. *arecae*). Strains NCPPB 206, NCPPB 702, NCPPB 795, NCPPB 890, NCPPB 895, NCPPB 1326, NCPPB 1381, and NCPPB 4614 form a phylogenetically and phenotypically coherent group with a distinctive host range causing symptoms on maize and sugarcane but not on banana (Aritua et al. 2007; Karamura et al. 2015) that falls within *X. vasicola* pv. *vasculorum* pv. nov. The strains isolated from *T. laxum* are also clearly within the phylogenetic bounds of *X. vasicola* and form a distinct clade but cannot be assigned to any pathovar. The previous proposal of [X. vasicola pv. *vasculorum*] was invalid due in part to the lack of a designated pathotype strain (Vauterin et al. 1995). We designate NCPPB 4614 as the pathotype strain for this pathovar, following the previous suggestion by Lang et al. (2017). This strain was previously proposed as the pathotype of *X. vasicola pv. vasculorum* (Lang et al. 2017) and causes disease symptoms on maize and sugarcane (Lang et al. 2017) but not on banana.

| Current taxon | Proposed taxon | Pathotype or type strains | Additional strains in NCPPB known to be part of the newly proposed taxon | Natural hosts | Hosts by inoculation |
|---------------|----------------|----------------------------|-----------------------------------------------|--------------|----------------------|
| *X. campestris* pv. *arecae* (Rao and Mohan 1970) Dye 1978 | *X. vasicola* pv. *arecae* pv. nov. | NCPPB 2649 = ICMP 5719 = LMG 533 | None | Areca catechu | (Bradbury 1986; Kumar 1993, 1983) |
| *X. campestris* pv. *musacearum* (Yirgou and Bradbury 1968) Dye 1978 | *X. vasicola* pv. *musacearum* pv. nov. | NCPPB 2005 = ATCC 49084 = CFBP 7123 = ICMP 2870 = LMG 785 | NCPPB 2251; NCPPB 4378; NCPPB 4379; NCPPB 4380; NCPPB 4381; NCPPB 4383; NCPPB 4384; NCPPB 4386; NCPPB 4387; NCPPB 4388; NCPPB 4389; NCPPB 4390; NCPPB 4391; NCPPB 4392; NCPPB 4393; NCPPB 4394; NCPPB 4395; NCPPB 4433; NCPPB 4434 | Ensete ventricosum, Musa sp. | (Bradbury 1986), Tripsacum sp. (E. Wicker, unpublished observation) |
| [X. vasicola pv. *zeae* Coutinho and Wallis 1991] | *X. vasicola* pv. *zeae* pv. *vagans* nov. | NCPPB 4614 = SAM119 | None | Zea mays (Coutinho and Wallis 1991) | Sorghum sp. | (Lang et al. 2017) |
| [X. vasicola pv. *zeae* Qhobela et al. 1990] | *X. vasicola* pv. *zeae* pv. *vagans* nov. | NCPPB 4614 = SAM119 | | None | Zea mays (Coutinho and Wallis 1991) | Sorghum sp. | (Lang et al. 2017) |
| *X. campestris* pv. *holcicola* (Elliott 1930) Vauterin et al. 1995 (synonym of *X. campestris* pv. *holcicola*) | *X. vasicola* pv. *holcicola* Elliott 1930 | NCPPB 2417 = CFBP 2543 = ICMP 3103 = LMG 736 | | None | Echinocloa frumentacea, Pennisetum typhoides, Setaria italic, Panicum miliaceum, Sorghum spp., Zea mays | (Bradbury 1896) |
| *X. campestris* pv. *vasculorum* type B = [X. vasicola pv. *vasculorum* (Vauterin et al. 1995)] | *X. vasicola* pv. *vasculorum* pv. nov. | NCPPB 4614 = SAM119 | NCPPB 989; NCPPB 1060; NCPPB 1241; NCPPB 2417; NCPPB 2930; NCPPB 3162 | None | Saccharum spp., Zea mays, *Eucalyptus grandis* (Coutinho et al. 2015, Bradbury 1986), Vetiveria zizanoides (Kumar 1983, 1993) |
| Xanthomonas sp. | *X. vasicola* Vauterin et al. 1995 | Not applicable | NCPPB 1394; NCPPB 1395; NCPPB 1396; NCPPB 902 | |}

TABLE 2. Host ranges of the taxa discussed in this letter

5
EMENDED DESCRIPTION OF X. VASICOLA VAUTERIN ET AL. 1995

The characteristics are as described for the genus and the species (Vauterin et al. 1995) extended with phylogenetic data from this study. The species can be clearly distinguished from other xanthomonads by multilocus sequence analysis (MLSA) and whole genome sequence analysis with members having more than 98% ANI with the type strain. SDS-PAGE protein and FAME profiles have been shown to be distinguishing for some pathovars (Arita et al. 2007; Vauterin et al. 1992; Yang et al. 1993) by the presence of metabolic activity on the carbon substrates P-d-psicose and L-glutamic acid, and by a lack of metabolic activity on the carbon substrates N-acetyl-D-galactosamine, L-arabinose, D-a-D-lactose, D-melibiose, P-methyl-D-glucoside, L-rhamnose, D-sorbitol, formic acid, D-galactonic acid lactone, D-galacturonic acid, D-glucuronic acid, D-glucuronic acid, P-hydroxyphenylacetic acid, a-ketocarboxylic acid, quinic acid, glucuronamide, L-asparagine, L-histidine, L-phenylalanine, uracil, inosine, uridine, thymidine, D,L-a-glycerol phosphate, glucose 1-phosphate, and glucose 6-phosphate. The G+C content is between 63.1 and 63.6 mol% as calculated from whole-genome sequence data. The type strain is X. vasicola pv. holcicola LMG 736 (= CFPB 2543 = ICMP 3103 = NCPPB 2417).

X. vasicola pv. holcicola Vauterin et al. 1995. =X. campestris pv. holcicola (Elliott) Dye 1978. Description as presented by Vauterin et al. (1995). The pathovar is distinguished on the basis of phytopathogenic specialization. As shown here and elsewhere (Lang et al. 2017), the pathovar is distinct from other pathovars by its gyrB gene sequence (Parkinson et al. 2009) and genome-wide sequence analysis. Gelatin slowly liquefied, starch not hydrolyzed. Growth quite rapid and very mucoid when cultured on yeast-peptone-sucrose agar based media for 48 h at 28°C. According to Bradbury (1986), the natural hosts include Ensete ventricosum (enset) and Musa spp. (banana). Additional hosts by inoculation: Saccharum sp. (sugarcane) and Zea mays (maize) and disease is exhibited as a bacterial wilt where leaves wilt and wither; yellowish bacterial masses are found in vascular tissue and parenchyma. It is not known if the strains being transferred to this taxon conform to the species description for metabolic activity.

Pathotype strain: NCPPB 2005 (= CFPB 7123 = DSM 24447 = ICMP 2870 = ICMP XM130 = PDDCC 2870).

LITERATURE CITED

Arita, V., Parkinson, N., Thwaites, R., Heeney, J. V., Jones, D. R., Tushemereire, W., et al. 2007. Characterization of the Xanthomonas sp. causing wilt of enset and banana and its proposed reclassification as a strain of X. vasicola. Plant Pathol. 56:170-177.

Bertels, F., Silander, O. K., Pachkov, M., Rainey, P. B., and van Nimwegen, E. 2014. Automated reconstruction of whole-genome phylogenies from short-sequence reads. Mol. Biol. Evol. 31:1077-1088.

Biruma, M., Pillay, M., Tripathi, L., Blomme, G., Abele, S., Mwangi, M., et al. 2007. Banana Xanthomonas wilt: A review of the disease, management strategies and future research directions. Afr. J. Biotechnol. 6:953-962.

Blomme, G., Dita, M., Jacobsen, K., Pérez-Vicente, L., Molina, A., Ocimati, W., et al. 2017. Bacterial diseases of bananas and enset: Current state of knowledge and integrated approaches towards sustainable management. Front. Plant Sci. 8:1290.

Blomme, G., Ploetz, R., Jones, D., De Langhe, E., Price, N., Gold, C., et al. 2013. A historical overview of the appearance and spread of Musa pests and pathogens on the African continent: Highlighting the importance of clean Musa planting materials and quarantine measures. Ann. Appl. Biol. 162:4-26.

Bradbury, J. F. 1986. Guide to Plant Pathogenic Bacteria. CAB International, Wallingford, U.K.

Brenner, D. J., and Shaley, J. T. 2005. Bergey’s Manual of Systematic Bacteriology. Vol. 2. The Proteobacteria. Part B, the Gammaproteobacteria. Springer-Verlag, New York.

Bull, C. T., De Boer, S. H., Denny, T. P., Firrao, G., Fischer-Le Saux, M., Saddler, G. S., et al. 2012. List of new names of plant pathogenic bacteria. Springer-Verlag, New York.

Constantin, E. C., Cleenwerck, I., Maes, M., Baeyen, S., Van Malderghem, C., De Vos, P., et al. 2016. Genetic characterization of strains named as Xanthomonas axonopodis pv. dieffenbachiae leads to a taxonomic revision of the X. axonopodis species complex. Plant Pathol. 65:792-806.

Coutinho, T. A., and Wallis, F. 1993. Bacterial streak disease of maize (Zea mays L.) in South Africa. J. Phytopathol. 133:112.

Coutinho, T. A., and Wallis, F. 1994. Bacterial streak disease of maize (Zea mays L.) in South Africa. J. Phytopathol. 133:112.

Coutinho, T. A., and Wallis, F. 1994. Bacterial streak disease of maize (Zea mays L.) in South Africa. J. Phytopathol. 133:112.
sp. nov., a new species that causes bacterial bract spot of artichoke (Cynara scolymus L.). Int. J. Syst. Evol. Microbiol. 50:1471-1478.

Tushemereirwe, W., Kangire, A., Ssekiwoko, F., Offord, L. C., Crozier, J., Boa, E., et al. 2004. First report of Xanthomonas campestris pv. musacearum on banana in Uganda. Plant Pathol. 53:802.

Vauterin, L., Hoste, B., Kersters, K., and Swings, J. 1995. Reclassification of Xanthomonas. Int. J. Syst. Bacteriol. 45:472-489.

Vauterin, L., Rademaker, J., and Swings, J. 2000. Synopsis on the taxonomy of the genus Xanthomonas. Phytopathology 90:677-682.

Vauterin, L., Swings, J., Kersters, K., Gillis, M., Mew, T. W., Schroth, M. N., et al. 1990. Towards an improved taxonomy of Xanthomonas. Int. J. Syst. Bacteriol. 40:312-316.

Vauterin, L., Yang, P., Alvarez, A., Takikawa, Y., Roth, D. A., Vidaver, A. K., et al. 1996. Identification of non-pathogenic Xanthomonas strains associated with plants. Syst. Appl. Microbiol. 19:96-105.

Vauterin, L., Yang, P., Hoste, B., Pot, B., Swings, J., and Kersters, K. 1992. Taxonomy of xanthomonads from cereals and grasses based on SDS-PAGE of proteins, fatty acid analysis and DNA hybridization. J. Gen. Microbiol. 138:1467-1477.

Vicente, J. G., Rothwell, S., Holub, E. B., and Studholme, D. J. 2017. Pathogenic, phenotypic and molecular characterisation of Xanthomonas nasturtii sp. nov. and Xanthomonas floridensis sp. nov., new species of Xanthomonas associated with watercress production in Florida. Int. J. Syst. Evol. Microbiol. 67:3645-3654.

Wasukira, A., Coulter, M., Al-Sowayeh, N., Thwaites, R., Paszkiewicz, K., Kubiriba, J., et al. 2014. Genome sequencing of Xanthomonas vasicola pathovar vasculorum reveals variation in plasmids and genes encoding lipopolysaccharide synthesis, type-IV pilus and type-III secretion effectors. Pathogens 3:211-237.

Wasukira, A., Tayebwa, J., Thwaites, R., Paszkiewicz, K., Aritua, V., Kubiriba, J., et al. 2012. Genome-wide sequencing reveals two major sub-lineages in the genetically monomorphic pathogen Xanthomonas campestris pathovar musacearum. Genes (Basel) 3:361-377.

Wernham, C. C. 1948. The species value of pathogenicity in the genus Xanthomonas. Phytopathology 38:283-291.

Yang, P., Vauterin, L., Vancanneyt, M., Swings, J., and Kersters, K. 1993. Application of fatty acid methyl esters for the taxonomic analysis of the genus Xanthomonas. Syst. Appl. Microbiol. 16:47-71.

Yirgou, D., and Bradbury, J. F. 1974. A note on wilt of banana caused by the enset wilt organism Xanthomonas musacearum. East Afr. Agric. For. J. 40:111-114.

Yirgou, D., and Bradbury, J. F. 1968. Bacterial wilt of enset (Ensete ventricosum) incited by Xanthomonas musacearum sp. Phytopathology 58:111-112.

Young, J. M., Bull, C. T., De Boer, S. H., Firrao, G., Gardan, L., Saddler, G. E., et al. 2001. International Standards for Naming Pathovars of Phytopathogenic Bacteria. International Society for Plant Pathology. https://www.isppweb.org/about_tppb_naming.asp

Young, J. M., Bull, C. T., De Boer, S. H., Firrao, G., Saddler, G. E., Stead, D. E., et al. 2004. Names of plant pathogenic bacteria, 1864–2004. Rev. Plant Pathol. 75:721-763.

Young, J. M., Dye, D. W., Bradbury, J. F., Panagopoulos, C. G., and Robbs, C. F. 1978. A proposed nomenclature and classification for plant pathogenic bacteria. N.Z. J. Agric. Res. 21:153-177.

Young, J. M., Saddler, G. S., Takikawa, Y., de Boer, S. H., Vauterin, L., Gardan, L., et al. 1996. Names of plant pathogenic bacteria 1864–1995. Rev. Plant Pathol. 75:721-763.