

# 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.

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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*, within the *gamma-Proteobacteria*, collectively cause disease on more than 400 plant species (Hayward 1993), though some members are apparently nonpathogenic (Garita-Cambronero 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 nomenespecies 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 nomenespecies 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; Rodriguez-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 reported for Ethiopia as early as the 1930s (Castellani 1939). However, only in the 21st century did the disease establish in the banana-growing areas of Burundi, Democratic Republic of Congo, Kenya, Rwanda, Tanzania, and Uganda (Biruma et al. 2007; Carter et al. 2010; Ndungo et al. 2006; Reeder et al. 2007; Tushemereirwe et al. 2004). In this region around the Great Lakes of eastern and central Africa, BXW disease severely challenges the livelihoods and food security of millions (Blomme et al. 2013, 2017; Biruma

et al. 2007; Nakato et al. 2018; Shimwela et al. 2016; Tinzaara et al. 2016). There is confusion in the literature about the taxonomy of this pathogen, with some authors adopting the invalid name [*X. vasicola* pv. *musacearum*]. The use of this name was motivated by studies suggesting a close relationship between *X. campestris* pv. *musacearum* (Yirgou and Bradbury 1968) Dye 1978b and *X. vasicola* pv. *holcicola* (Elliott 1930) Vauterin et al. 1995 based on fatty acid methyl ester (FAME) analysis, genomic fingerprinting using rep-PCR and partial nucleotide sequencing of the *gyrB* gene (Aritua et al. 2007; Parkinson et al. 2009). In this letter, we formally propose the name *X. vasicola* pv. *musacearum* as a comb. nov., according to the Standards for naming pathovars (Young et al. 2001).

The species *X. vasicola* Vauterin 1995 was created to encompass *X. campestris* pv. *holcicola* (Elliott 1930) Dye 1978 and a subset of strains of *X. campestris* pv. *vasculorum* (Cobb 1894) Dye 1978 (Vauterin et al. 1995; Young et al. 1978). *X. campestris* pv. *vasculorum* was split in two: the pathotype and some other strains were transferred to *X. axonopodis* pv. *vasculorum* (Cobb) Vauterin, Hoste, Kersters & Swings, while the remainder were transferred to the new species *X. vasicola*.

The background to this splitting of *X. campestris* pv. *vasculorum* is that taxonomic studies revealed phenotypic and genomic differences among *X. campestris* pv. *vasculorum* strains, despite their shared host ranges (Destéfano et al. 2003; Dookun et al. 2000; Péros et al. 1994; Stead 1989; Vauterin et al. 1992, 1995). Vauterin and colleagues distinguish type-A strains from type-B by sodium dodecyl sulfate-polyacrylamide gel electrophoresis (SDS-PAGE) of proteins, gas chromatography of fatty acid methyl esters and DNA-DNA hybridization (Yang et al. 1993). Type-A and type-B strains can also be distinguished by PCR-restriction fragment length polymorphism analysis (Destéfano et al. 2003). Table 1 lists examples of *X. campestris* pv. *vasculorum* (Cobb 1894) Dye 1978 strains that were classified in one or more of those studies. Vauterin and colleagues assigned type-A strains to *X. axonopodis* pv. *vasculorum* (Cobb) Vauterin, Hoste, Kersters & Swings and assigned type-B (Vauterin et al. 1995) to [*X. vasicola* pv. *vasculorum*]. The type strain of *X. campestris* pv. *vasculorum* (Cobb 1894) Dye 1978 was among those assigned to *X. axonopodis* pv. *vasculorum* (Cobb) Vauterin, Hoste, Kersters & Swings.

The names *X. vasicola* and *X. vasicola* pv. *holcicola* are listed in the Comprehensive List of Names of Plant Pathogenic Bacteria (Bull et al. 2010; Young et al. 1996). However, as pointed out in Bergey’s Manual (Brenner and Staley 2005), the name [*X. vasicola* pv. *vasculorum*] (Vauterin et al. 1995) was excluded from the Names of Plant Pathogenic Bacteria 1864–1995 (Young et al. 1996) on the grounds that it was defective in terms of the Standards (Young et al. 2001). Specifically, it lacked a modern description differentiating it from other pathovars (Young et al. 2004) and lacked designation of a pathotype strain (Young et al. 1996). This is understandable given that Vauterin and colleagues were primarily concerned with species-level reclassification of the genus rather than focusing on individual pathovars. Although the name [*X. vasicola* pv. *vasculorum*] (Vauterin et al. 1995) is invalid, this name has come to be understood by the community to represent a meaningful biological grouping; that is, a set of *X. campestris* pv. *vasculorum* strains that are biochemically and phylogenetically similar to *X. vasicola* and pathogenically distinct. Therefore, we propose a formal description of *X. vasicola* pv. *vasculorum* pv. nov. that adheres to the Standards (Young et al. 2001), to harmonize the formal nomenclature with that which is in common use.

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. *vasculorum*, *X. axonopodis* pv. *vasculorum* (to which the strain clearly does not belong), and [*X. vasicola* pv. *vasculorum*] (Lewis Ivey et al. 2010; Qhobela and Claflin 1992; Qhobela et al. 1990;

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

Strain <sup>z</sup>	Vauterin (Vauterin et al. 1992, 1995)	Dookun (Dookun et al. 2000)	Péros (Péros et al. 1994)	Current species assignment
NCPPB 186	Type A	Group A	n/a	<i>X. axonopodis</i>
NCPPB 891	Type A	Group A	G1	<i>X. axonopodis</i>
NCPPB 892	n/a	Group A	n/a	<i>X. axonopodis</i>
NCPPB 893	n/a	Group A	n/a	<i>X. axonopodis</i>
NCPPB 181	Type A	Group B	n/a	<i>X. axonopodis</i>
NCPPB 796 <sup>PT</sup>	Type A	Group B	n/a	<i>X. axonopodis</i>
NCPPB 899	n/a	Group D	n/a	<i>X. axonopodis</i>
NCPPB 900	n/a	Group D	n/a	<i>X. axonopodis</i>
NCPPB 795	Type B	Group C	n/a	<i>X. vasicola</i>
NCPPB 889	Type B	Group C	n/a	<i>X. vasicola</i>
NCPPB 206	n/a	Group C	n/a	<i>X. vasicola</i>
NCPPB 702	n/a	Group C	n/a	<i>X. vasicola</i>
NCPPB 795	n/a	Group C	n/a	<i>X. vasicola</i>
NCPPB 889	n/a	Group C	n/a	<i>X. vasicola</i>
NCPPB 890	n/a	Group C	n/a	<i>X. vasicola</i>
NCPPB 895	n/a	Group C	n/a	<i>X. vasicola</i>
NCPPB 1326	n/a	Group C	n/a	<i>X. vasicola</i>
NCPPB 1381	n/a	Group C	n/a	<i>X. vasicola</i>

<sup>z</sup> Superscript PT indicates the pathotype strain of *X. campestris* pv. *vasculorum*.

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 (Glaeser and Kämpfer 2015; Meier-Kolthoff et al. 2013, 2014; Richter and Rosselló-Móra 2009). We calculated pairwise average nucleotide identity (ANI) between representative *Xanthomonas* strains, including all available species type strains and relevant pathotype strains and tabulated these in Figure 1.

The pathotype strain (NCPPB 2005) of *X. campestris* pv. *musacearum* (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 >98.5% 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-Móra 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

100.00	99.03	98.03	98.61	98.41	98.48	98.62	98.82	98.87	98.87	98.63	98.39	87.06	89.59	90.03	90.19	90.11	90.09	90.55	90.56	90.69	90.63	91.34	91.24	<i>Xanthomonas</i> sp. NCPPB 1394
99.03	100.00	98.43	98.60	98.55	98.50	98.73	98.92	98.84	98.81	98.90	98.54	87.35	89.97	90.40	90.50	90.43	90.42	90.91	90.89	90.96	90.95	91.77	91.64	<i>X. vasicola</i> pv. <i>holcicola</i> NCPPB 2417 (T)
98.33	98.43	100.00	98.93	98.81	98.84	99.05	99.04	99.03	99.03	99.06	99.07	87.27	89.98	90.43	90.58	90.49	90.49	90.99	90.96	91.02	91.01	91.79	91.66	<i>X. campestris</i> pv. <i>musacearum</i> NCPPB 2005 (PT)
98.61	98.60	98.93	100.00	99.13	99.19	99.39	99.40	99.40	99.39	99.39	99.39	87.22	89.87	90.27	90.40	90.34	90.33	90.74	90.74	90.89	90.85	91.65	91.55	<i>X. campestris</i> pv. <i>arecae</i> NCPPB 2649 (PT)
98.41	98.55	98.81	99.13	100.00	99.30	99.31	99.43	99.41	99.41	99.47	99.42	87.22	89.87	90.31	90.44	90.36	90.39	90.76	90.73	90.89	90.84	91.69	91.56	<i>X. campestris</i> pv. <i>vasculorum</i> NCPPB 1326
98.48	98.60	98.64	99.19	99.50	100.00	99.38	99.48	99.47	99.47	99.50	99.47	87.22	89.91	90.34	90.45	90.37	90.40	90.76	90.75	90.91	90.86	91.70	91.66	<i>X. campestris</i> pv. <i>vasculorum</i> NCPPB 702
98.62	98.73	99.05	99.39	99.31	99.38	100.00	99.80	99.81	99.81	99.80	99.80	87.34	89.97	90.38	90.51	90.43	90.42	90.85	90.81	90.96	90.94	91.74	91.65	<i>X. campestris</i> pv. <i>vasculorum</i> NCPPB 206
98.65	98.82	98.84	99.40	99.43	99.48	99.60	100.00	99.98	99.97	99.87	99.84	87.36	90.02	90.39	90.53	90.47	90.45	90.85	90.83	91.00	90.94	91.85	91.72	[ <i>X. campestris</i> pv. <i>zeae</i> ] XGP
98.67	98.84	99.03	99.40	99.41	99.47	99.61	99.98	100.00	99.98	99.87	99.84	87.31	89.95	90.37	90.50	90.44	90.43	90.84	90.82	90.96	90.92	91.77	91.65	<i>X. campestris</i> pv. <i>vasculorum</i> NE744
98.67	98.81	99.03	99.39	99.41	99.47	99.61	99.97	99.98	100.00	99.98	99.85	87.32	89.95	90.37	90.49	90.43	90.42	90.84	90.82	90.96	90.92	91.77	91.66	[ <i>X. campestris</i> pv. <i>zeae</i> ] NCPPB 4614 (*)
98.63	98.80	99.05	99.38	99.47	99.50	99.63	99.87	99.87	99.98	100.00	99.99	87.46	90.04	90.42	90.56	90.49	90.47	90.85	90.83	90.99	90.96	91.86	91.74	[ <i>X. campestris</i> pv. <i>zeae</i> ] X45
98.50	98.84	99.07	99.36	99.42	99.47	99.58	99.84	99.84	99.95	99.99	100.00	87.42	90.04	90.44	90.54	90.47	90.46	90.83	90.82	90.99	90.95	91.86	91.71	[ <i>X. campestris</i> pv. <i>zeae</i> ] X29
87.06	87.35	87.27	87.22	87.22	87.34	87.36	87.31	87.32	87.46	87.42	100.00	87.79	87.79	87.46	87.44	87.35	87.35	87.53	87.55	87.59	87.42	87.28	87.43	<i>X. campestris</i> pv. <i>campestris</i> ATCC 33913 (T)
89.59	89.97	89.98	89.87	89.87	89.91	89.97	90.02	89.95	89.95	90.04	90.04	87.79	100.00	89.97	89.93	89.86	89.86	90.02	90.02	90.19	90.03	89.88	90.02	<i>X. nasturtii</i> WHRI 8853 (T)
90.03	90.40	90.43	90.27	90.31	90.34	90.38	90.39	90.37	90.37	90.42	90.44	87.46	89.97	100.00	90.36	90.32	90.31	90.32	90.30	90.45	90.38	90.35	90.53	<i>X. bromi</i> CFBP 1976 (T)
90.19	90.50	90.58	90.40	90.44	90.45	90.51	90.53	90.50	90.49	90.56	90.54	87.44	89.93	90.36	100.00	98.12	98.08	93.41	93.40	93.45	93.44	90.52	90.47	<i>X. axonopodis</i> pv. <i>axonopodis</i> LMG 982 (T)
90.11	90.43	90.49	90.34	90.36	90.37	90.43	90.47	90.44	90.43	90.49	90.47	87.35	89.86	90.32	98.12	100.00	98.64	93.25	93.24	93.33	93.25	90.40	90.40	<i>X. axonopodis</i> pv. <i>vasculorum</i> NCPPB 900
90.09	90.42	90.49	90.33	90.39	90.40	90.42	90.45	90.43	90.42	90.47	90.46	87.35	89.86	90.31	98.08	98.64	100.00	93.25	93.23	93.33	93.25	90.40	90.40	<i>X. axonopodis</i> pv. <i>vasculorum</i> CFBP 5823 (PT)
90.55	90.91	90.99	90.74	90.76	90.76	90.85	90.85	90.84	90.84	90.85	90.83	87.53	90.02	90.32	93.41	93.25	93.25	100.00	98.78	94.19	94.30	90.86	90.72	<i>X. perforans</i> 91-118 (T)
90.56	90.89	90.96	90.74	90.73	90.75	90.81	90.83	90.82	90.82	90.83	90.82	87.55	90.02	90.30	93.40	93.24	93.23	98.78	100.00	94.21	94.30	90.87	90.72	<i>X. alfalfae</i> subsp. <i>alfalfae</i> CFBP 3836 (T)
90.69	90.96	91.02	90.89	90.89	90.91	90.96	91.00	90.96	90.96	90.99	90.99	87.59	90.19	90.45	93.45	93.33	93.33	94.19	94.21	100.00	96.39	90.89	90.89	<i>X. fusans</i> pv. <i>fusans</i> LMG 826 (T)
90.63	90.95	91.01	90.85	90.84	90.86	90.94	90.94	90.92	90.92	90.96	90.95	87.42	90.03	90.38	93.44	93.25	93.25	94.30	94.30	96.39	100.00	90.82	90.75	<i>X. citri</i> pv. <i>citri</i> LMG 9322 (T)
91.34	91.77	91.79	91.65	91.69	91.70	91.74	91.85	91.77	91.77	91.86	91.86	87.28	89.88	90.35	90.52	90.40	90.40	90.86	90.87	90.89	90.82	100.00	91.71	<i>X. oryzae</i> pv. <i>oryzae</i> ATCC 35933 (T)
91.24	91.64	91.66	91.55	91.56	91.58	91.65	91.72	91.65	91.66	91.74	91.75	87.43	90.02	90.35	90.47	90.40	90.40	90.72	90.72	90.81	90.75	91.71	100.00	<i>X. prunicola</i> CFBP 8353 (T)

**Fig. 1.** Average nucleotide identity (ANI) with type strains of *Xanthomonas* species. Genome sequence assemblies were obtained from GenBank and aligned against each other and ANI was calculated using the *dnadiff* function in MUMmer version 4 (Marçais et al. 2018). Accession numbers of the genome assemblies: GCA\_000774005.1, GCA\_000772705.1, GCA\_000277875.1, GCA\_000770355.1, GCA\_000277995.1, GCA\_000159795.2, GCA\_000278035.1, GCA\_003111865.1, GCA\_002191965.1, GCA\_002191955.1, GCA\_003111905.1, GCA\_003111825.1, GCA\_000007145.1, GCA\_001660815.1, GCA\_002939755.1, GCA\_001401595.1, GCA\_002939725.1, GCA\_000724905.2, GCA\_000192045.3, GCA\_000488955.1, GCA\_001401605.1, GCA\_002018575.1, GCA\_000482445.1, and GCA\_002846205.1 (da Silva et al. 2002; Harrison and Studholme 2014; Jacques et al. 2013; Lang et al. 2017; Potnis et al. 2011; Sanko et al. 2018; Studholme et al. 2010; Vicente et al. 2017; Wasukira et al. 2014, 2012). Type strains are indicated by T. Pathotype strains that are not also type strains are indicated by PT. Strain NCPPB 4614 (=SAM119) was previously proposed as a member of [*X. campestris* pv. *zeae*] and is also the pathotype for [*X. vasicola* pv. *vasculorum*] and is indicated with an asterisk.

RaxML via the RealPhy pipeline (Bertels et al. 2014; Stamatakis et al. 2005) to elucidate phylogenetic relationships, using a maximum-likelihood method based on genome-wide sequencing data. This approach has the additional advantage of being based on sequence reads rather than on genome assemblies, where the latter may be of variable quality and completeness (Bertels et al. 2014).

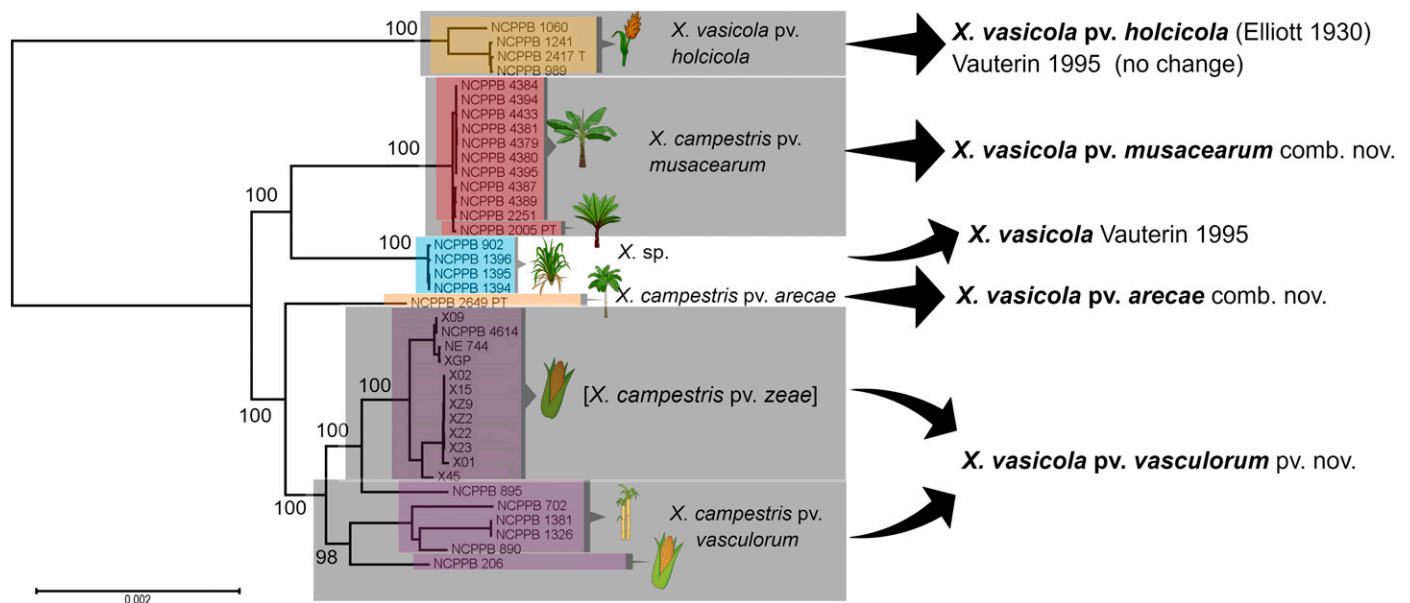
Figure 2 depicts the phylogeny of *X. vasicola* based on RealPhy analysis of genome-wide sequence data. Pathovars *X. vasicola* pv. *holcicola* and *X. campestris* pv. *musacearum* are monophyletic, comprising well supported clades within the *X. vasicola* species. A third well supported clade includes the four *Xanthomonas* strains originating from the grass *Tripsacum laxum*. A fourth clade consists of mostly *X. campestris* pv. *vasculorum* strains isolated from sugarcane but also includes *X. campestris* pv. *vasculorum* strain NCPPB 206 isolated from maize and several strains from maize attributed previously named [*X. campestris* pv. *zeae*]. The sequenced strains of [*X. campestris* pv. *zeae*] from corn (Coutinho and Wallis 1991; Lang et al. 2017; Qhobela et al. 1990; Sanko et al. 2018) are monophyletic and fall within the clade containing type-B strains of *X. campestris* pv. *vasculorum* (Fig. 2). The single sequenced strain of *X. campestris* pv. *arecae* is the pathotype and it falls immediately adjacent to the *X. vasicola* clade containing strains from corn and *X. campestris* pv. *vasculorum* type-B strains (Fig. 2).

Strain NCPPB 206 of *X. campestris* pv. *vasculorum* was 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. *zeae*], as illustrated in Figures 1 and 2. This indicates that natural infection of maize by *X. vasicola* is not restricted to strains of [*X. campestris* pv. *zeae*].

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 *musacearum* 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* pv. 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. *musacearum* 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. *musacearum* (Yirgou and Bradbury 1968) Dye 1978 on banana; *X. campestris* pv. *musacearum* produces severe disease on this host, whereas *X. vasicola* pv. *holcicola* NCPPB 2417 and *X. campestris* pv. *vasculorum* 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. *musacearum*, and [*X. campestris* pv. *zeae*]; it is possible that the species description may need to be amended to



**Fig. 2.** Maximum-likelihood phylogenetic tree based on genomic sequencing reads. The maximum likelihood tree was generated using RealPhy (Bertels et al. 2014) and RaxML (Stamatakis et al. 2005). Bootstrap values are expressed as percentages of 500 trials. Type and pathotype strains are indicated by T and PT, respectively. Whole-genome shotgun sequence reads were obtained from the Sequence Read Archive (Leinonen et al. 2011) via BioProjects PRJNA73853, PRJNA163305, PRJNA163307, PRJNA31213, PRJNA374510, PRJNA374557, 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 have been typically isolated. *Xanthomonas vasicola* pv. *holcicola* strain NCPPB 989 was isolated from velvet grass (*Holcus* sp.), while strains NCPPB 1060, NCPPB 1241, and NCPPB 2417 were isolated from sorghum (*Sorghum vulgare*). Strains of *X. campestris* pv. *musacearum* were isolated from banana (*Musa* spp.) except for NCPPB 2005, which was isolated from enset (*Ensete ventricosum*). Strains of *X. campestris* pv. *zeae* were isolated from maize (*Zea mays*), as was *X. campestris* pv. *vasculorum* NCPPB 206. The remaining *X. campestris* pv. *vasculorum* strains were isolated from sugarcane (*Saccharum* spp.). The pathotype strain of *X. campestris* pv. *arecae*, namely NCPPB 2649, was isolated from betel palm (*Areca catechu*).

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 *Eucalyptus* caused by *X. vasicola* (Coutinho et al. 2015), remarkable given the phylogenetic distance between this dicot plant and the usual monocot hosts of *X. vasicola*; the infected South African plantation was in an area where sugarcane is grown.

Vauterin et al. (1995) designated the pathotype strain of *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. *vasculorum*] 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. musacearum* 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

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

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
<i>X. campestris</i> pv. <i>arecae</i> (Rao and Mohan 1970) Dye 1978	<i>X. vasicola</i> pv. <i>arecae</i> pv. nov.	NCPPB 2649 = ICMP 5719 = LMG 533	None	<i>Areca catechu</i> (Bradbury 1986; Kumar 1993, 1983)	<i>Cocos nucifera</i> , <i>Saccharum</i> sp. (Bradbury 1986)
<i>X. campestris</i> pv. <i>musacearum</i> (Yirgou and Bradbury 1968) Dye 1978	<i>X. vasicola</i> pv. <i>musacearum</i> 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	<i>Ensete ventricosum</i> , <i>Musa</i> sp. (Bradbury 1986), <i>Tripsacum</i> sp. (E. Wicker, unpublished observation)	<i>Saccharum</i> sp. (Karamura et al. 2015), <i>Zea mays</i> (Karamura et al. 2015; Aritua et al. 2007)
[ <i>X. vasicola</i> pv. <i>zeae</i> Coutinho and Wallis 1991] [ <i>X. vasicola</i> pv. <i>zeae</i> Qhobela et al. 1990]	<i>X. vasicola</i> pv. <i>vasculorum</i> pv. nov.	NCPPB 4614 = SAM119	None	<i>Zea mays</i> (Coutinho and Wallis 1991)	<i>Sorghum</i> sp. (Lang et al. 2017)
<i>X. vasicola</i> pv. <i>holcicola</i> (Elliott 1930) Vauterin et al. 1995 (synonym of <i>X. campestris</i> pv. <i>holcicola</i> )	<i>X. vasicola</i> pv. <i>holcicola</i> (Elliott 1930) Vauterin et al. 1995	NCPPB 2417 = CFBP 2543 = ICMP 3103 = LMG 736	NCPPB 989; NCPPB 1060; NCPPB 1241; NCPPB 2417; NCPPB 2930; NCPPB 3162	<i>Panicum miliaceum</i> , <i>Sorghum</i> spp., <i>Zea mays</i> (Bradbury 1986)	<i>Echinochloa frumentacea</i> , <i>Pennisetum typhoides</i> , <i>Setaria italica</i> (Bradbury 1986)
<i>X. campestris</i> pv. <i>vasculorum</i> type B = [ <i>X. vasicola</i> pv. <i>vasculorum</i> (Vauterin et al. 1995)]	<i>X. vasicola</i> pv. <i>vasculorum</i> pv. nov.	NCPPB 4614 = SAM119	NCPPB 206; NCPPB 702; NCPPB 795; NCPPB 889; NCPPB 890; NCPPB 895; NCPPB 1326; NCPPB 1381; NCPPB 4614	<i>Saccharum</i> spp., <i>Zea mays</i> , <i>Eucalyptus grandis</i> (Coutinho et al. 2015; Bradbury 1986; Vauterin et al. 1995)	<i>Saccharum</i> spp., <i>Zea mays</i> (Karamura et al. 2015)
<i>Xanthomonas</i> sp.	<i>X. vasicola</i> Vauterin et al. 1995	Not applicable	NCPPB 1394; NCPPB 1395; NCPPB 1396; NCPPB 902	<i>Tripsacum laxum</i> (Mulder 1961), <i>Vetiveria zizanioides</i> (Kumar 1983, 1993)	Not known

(Supplementary Fig. S1). Furthermore, given that strains from corn formerly described by the invalid name [*X. campestris* pv. *zeae*] are members of *X. vasicola* and have host ranges that cannot be distinguished from the pathotype strain of *X. vasicola* pv. *vasculorum* pv. nov., we propose that these strains are members of this pathovar. Phylogenetic data support this as the corn strains represent a subclade within strains of *X. campestris* pv. *vasculorum* that fall within the emended *X. vasicola*.

#### 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 (Aritua et al. 2007; Vauterin et al. 1992; Yang et al. 1993) 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, *P*-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-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 (= CFBP 2543 = ICMP 3103 = NCPPB 2417).

***X. vasicola* pv. *holcicola* Vauterin et al. 1995.** =*X. campestris* pv. *holcicola* (Elliott) Dye 1978. Description is 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 MLSA and genome-wide sequence analysis. According to Bradbury (1986), gelatin and starch are hydrolyzed by most isolates examined. The natural host range includes: *Panicum miliaceum*, *Sorghum* spp., *S. alnum*, *S. bicolor* (*S. vulgare*), *S. caffrorum*, *S. durra*, *S. halepense*, *S. sudanense*, *S. technicum* (*S. bicolor* var. *technicus*), and *Zea mays*. The artificial host range (by inoculation) includes *Echinochloa frumentacea*, *Pennisetum typhoides*, and *Setaria italica*.

Pathotype strain: CFBP 2543 (= ICMP 3103 = LMG 736 = NCPPB 2417 = PDDCC 3103).

***X. vasicola* pv. *vasculorum* pv. nov.** Description as for the species and this pathovar is distinguished on the basis of phytopathogenic specialization and includes the strains of the former taxon *X. campestris* pv. *vasculorum* type B and pathogens from corn. The pathovar is identified to species and distinguished from other pathovars by its *gyrB* gene sequence (Parkinson et al. 2009) and genome-wide sequence analysis. It is not known whether the strains being transferred to this taxon conform to the species description for metabolic activity. According to previously published work (Aritua et al. 2007; Coutinho et al. 2015; Hayward 1962; Karamura et al. 2015), the natural host range includes *Saccharum* spp., *Zea mays*, and *Eucalyptus grandis* and does not cause symptoms on banana.

Pathotype strain: NCPPB 4614 (= CFBP 8549 = SAM119).

***X. vasicola* pv. *arecae* (Rao & Mohan) Dye 1978 comb. nov.** =*X. campestris* pv. *arecae* (Rao & Mohan) Dye 1978. Description as for the species and this pathovar is distinguished on the basis of phytopathogenic specialization. The pathovar is identified to species and distinguished from other pathovars by its *gyrB* gene sequence (Parkinson et al. 2009) and by genome-wide sequence analysis. According to Bradbury (1986), the natural host

range includes *Areca catechu* (areca nut). Bradbury (1986) reports the artificial host range to include *Cocos nucifera* (coconut). Needle prick into sugar cane produced limited streaks, but the bacteria did multiply to some extent and could be reisolated. Disease: leaf stripe. Long, narrow water-soaked lesions, becoming dark brown or black with age. It is not known if the strains being transferred to this taxon conform to the species description for metabolic activity.

Pathotype strain: LMG 533 (= ICMP 5719 = NCPPB 2649 = PDDCC 5791).

***X. vasicola* pv. *musacearum* (Yirgou & Bradbury) Dye 1978 comb. nov.** =*X. campestris* pv. *musacearum* (Yirgou & Bradbury) Dye 1978. Description as for the species and this pathovar is identified to species and distinguished on the basis of phytopathogenic specialization and 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 (= CFBP 7123 = DSM 24447 = ICMP 2870 = ICPB XM130 = PDDCC 2870).

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