Article

Phylogenomic Analysis Supports the Transfer of 20 Pathovars from *Xanthomonas campestris* into *Xanthomonas euvesicatoria*

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Abstract: The Gram-negative bacterial genus *Xanthomonas* includes numerous infra-specific taxa known as pathovars, which are defined primarily on host range and disease symptoms. With the advent of molecular sequence data, many pathovars have been transferred from *X. campestris* into other *Xanthomonas* species to better harmonise taxonomy and phylogeny. We performed whole-genome shotgun sequencing on pathotype strains of the following *X. campestris* pathovars: *blepharidis, carissae, clerodendri, convolvuli, coriandri, daturae, euphorbiae, fici, heliotropii, ionidii, lawsoniae, mirabilis, obscurae, paulliniae, pennamericanum, spermacoces, uppalii, vernoniae, viegasii* and *zingibericola*. These genomes showed more than 98% average nucleotide identity with the type-strain of *X. euvesicatoria* and less than 88% with the type-strain of *X. campestris*. We propose the transfer of these pathovars into *X. euvesicatoria* and present an emended species description for *X. euvesicatoria*.

Keywords: *Xanthomonas campestris*; pathovars; *Xanthomonas euvesicatoria*

1. Introduction

The genus *Xanthomonas* contains Gram-negative plant-associated bacteria, many of which are pathogens of crops, ornamentals, or other plants [1,2]. An important feature of *Xanthomonas* pathogen classification and nomenclature is the inclusion of infra-specific taxa known as pathovars, defined primarily on their host range. The taxonomy of pathovars is governed by the International Standards for Naming Pathovars of Phytopathogenic Bacteria [3]. These standards are devised by the Committee on the Taxonomy of Plant Pathogenic Bacteria under the auspices of the International Society for Plant Pathology.

Recently, there have been significant efforts to reconcile the taxonomy of *Xanthomonas* with phylogenetic relationships inferred from molecular sequence data as well as biochemical traits. Nevertheless, the taxonomic positions of some taxa are incongruent with their apparent evolutionary relationships. This is the case for more than 20 infra-specific taxa (i.e., pathovars) that are classified within the species *X. campestris*, yet appear to be only distantly related to the typestrain of this species, according to preliminary phylogenetic analysis based on the *gyrB* genetic locus [4]. In the present study, we perform a more robust phylogenetic analysis based on whole-genome sequencing rather than just that single locus. Thereby, we clarify the phylogeny and propose taxonomic revisions to reflect this.

The current inconsistencies between phylogeny and taxonomy can be explained by the historical context. Collectively, *Xanthomonas* bacteria cause disease in hundreds of plant species. However, most of these bacterial strains each causes disease on a narrow range of hosts, often a single plant genus or species. Before the advent of molecular methods, *Xanthomonas* pathogens were difficult to distinguish phenotypically other than by their host ranges and disease symptoms. Historically, the commonly accepted approach to taxonomy was to propose a new *Xanthomonas* species for each new host. This led to a proliferation of

Xanthomonas species, with over 100 being listed in the 1951 edition of Elliott's *Manual of Bacterial Plant Pathogens* [5]. Many of these species were subsequently lumped together as pathovars within a single species, *X. campestris*, in the 1974 edition of *Bergey's Manual of Determinative Bacteriology* [6] and a 1978 proposal on nomenclature and classification for plant pathogenic bacteria [7].

After the lumping together of diverse pathogens into *X. campestris*, there followed a period of splitting. Based on DNA—DNA hybridisation studies, a major revision of *Xanthomonas* taxonomy created several new *Xanthomonas* species. Some pathovars were transferred out of *X. campestris* into these new species [8]. In that study, 66 pathovars were also identified as being 'formerly' within *X. campestris* but not yet transferred to any of the new species. The authors recommended referring to these as "*Xanthomonas* species", without using a species name [8]. Although these authors generated fatty acid methyl ester (FAME) profiles for most of those 66 pathovars [9], they did not include these pathovars in their DNA—DNA hybridisation experiments nor their phenotypic analysis using the Biolog GN microplate system [8]. Therefore, this 1995 major update of *Xanthomonas* taxonomy did not assign these 66 pathovars to species [8].

Parkinson and colleagues furthered the case for additional *Xanthomonas* species in 2009. They performed an extensive survey of partial *gyrB* gene sequences across the genus [4]. This identified a number of *X. campestris* pathovars whose *gyrB* sequences were highly divergent from the *X. campestris* type strain. Many of these appeared to belong to what Parkinson called the "*X. euvesicatoria* species complex". However, phylogenetic analysis based on a single genetic locus can be unrepresentative of the wider genome. Therefore, Constantin and colleagues subjected pathotype strains to multi-locus sequence analysis (MLSA), whole-genome sequencing, DNA—DNA hybridisation and phenotypic profiling [10]. This polyphasic study proposed the transfer of several *X. campestris* pathovars into *X. euvesicatoria*, *X. citri*, *X. axonopodis*, and *X. phaseoli* [10]. Recent studies formally proposed transfer of a further 20 *X. campestris* pathovars to *X. citri* [11] and two to *X. vasicola* [12].

Despite previous progress in resolving taxonomy of *X. campestris* pathovars, there remain many whose position is yet to be addressed, perhaps because of the limited genetic data available for these. In the present study, we perform whole-genome sequencing and phylogenetic analysis to argue that pathovars *uppalii, lawsoniae, clerodendri, zingibericola, viegasii, pennamericanum, mirabilis, obscurae, paulliniae, daturae, convolvuli, carissae, fici, heliotropii, euphorbiae, vernoniae, spermacoces, coriandri, blepharidis, ionidii* should be transferred from *X. campestris* into *X. euvesicatoria*. Furthermore, we confirm that pathovars *aberrans, armoraciae, barbaraeae, incanae, papavericola, plantaginis*, and *raphani* are phylogenetically close to the type-strain of *X. campestris* and so do not require transfer.

2. Materials and Methods

The bacterial strains used in this study are listed in Table 1 and were purchased from the National Collection of Plant Pathogens (NCPPB), York, United Kingdom. For the preparation of genomic DNA, bacteria were grown in plates with King's B agar medium [13] at 28 °C for 48 h. Single colonies were picked and transferred to Universals with 10 mL King's B broth medium and incubated overnight at 28 °C at 220 rpm. Next, 1.8 mL of culture was transferred to a 2 mL Eppendorf tube and centrifuged at 5000× *g* for 10 min. The supernatant was discarded, and another 1.8 mL of culture was added to this pellet, and tubes were centrifuged for 2 min at 5000× *g*. The pellets were used for DNA extraction immediately or flash-frozen in liquid nitrogen and stored at −20 °C until extraction. This procedure for bacterial growth is documented in protocols.io at https://dx.doi.org/10.17504/protocols.io.ewov1nr92gr2/v1 (accessed on 19 November 2022).

Table 1. Bacterial pathotype strains used in this study. Fatty acid methyl ester (FAME) clusters are shown according to their designation in the study by Yang and colleagues [9]. Those that belong to Yang's FAME clusters 1 and 14 are indicated with those respective numbers. (1) Strains are related (>0.4 similarity index) to FAME cluster 1. Strains are remotely related (0.2–0.4 similarity index) to FAME cluster 1 [1].

Pathovar	Strain NCPPB Number	Host	FAME Cluster	References
Controls: *X. campestris*				
aberrans	2986	*Brassica oleracea* var. *capitata*	2	[14]
armoraciae	347	*Iberis* sp.	1	[15–17]
barbareae	983	*Barbarea vulgaris*	7	[18]
incanae	937	*Matthiola* sp.	2	[19]
papavericola	2970	*Papaver rhoeas*	2	[20]
plantaginis	1061	*Plantago lanceolata*	3	[21]
raphani	1946	*Raphanus sativus*	2	[22]
Controls: *X. euvesicatoria*				
alangii	1336	*Alangium lamarckii*	1	[10,23]
physalidis	1756	*Physalis minima*	1	[10,24]
Controls: *X. citri*				
merremiae	3114	*Merremia gangetica*	1	[11,25]
trichodesmae	585	*Trichodesma zeylanicum*	1	[11,26]
Control: *X. phaseoli*				
passiflorae	2346	*Passiflora edulis*	1	[27]
Transfer to *Xanthomonas euvesicatoria*				
blepharidis	1757	*Blepharis boarhaavifolia*	1	[28]
carissae	2373	*Carissa carandas*	1	[29]
clerodendri	575	*Clerodendron* sp.	1	[30]
convolvuli	2498	*Convolvulus arvensis*	(1)	[31]
coriandri	1758	*Coriandrum sativum*	1	[32]
daturae	2932	*Datura metel*	N.d.	[33]
euphorbiae	1828	*Euphorbia acalyphoides*	1	[34]
fici	2372	*Ficus religiosa*	(1)	[35]
heliotropii	2057	*Heliotropium sudanicum*	[1]	[34]
ionidii	1334	*Ionidium heterophyllum*	1	[36]
lawsoniae	579	*Lawsonia inermis*	[1]	[37]
mirabilis	4348	*Mirabilis jalapa*	N.d.	[38]
obscurae	3759	*Ipomea obscura*	N.d.	[39]
paulliniae	3079	*Paullinia cupana*	(1)	[40]
pennamericanum	4349	*Pennisetum americanum*	N.d.	[41]
spermacoces	1760	*Spermacoce hispida*	14	[28]
uppalii	586	*Ipomoea muricata*	(1)	[42]
vernoniae	1787	*Vernonia cinerea*	(1)	[43]
viegasii	4351	*Pachystachys lutea*	N.d.	[44]
zingibericola	4352	*Zingiber officinale*	(1)	[45]

Genomic DNA was extracted using the Qiagen MagAttract HMW DNA kit following the manufacturer's instructions with some modifications. This modified procedure for DNA extraction is documented in protocols.io at https://dx.doi.org/10.17504/protocols.io.5jyl89428v2w/v1 (accessed on 19 November 2022).

Sequencing libraries were prepared using the NEBNext® Ultra™ II FS DNA Library Prep kit (New England Biolabs) according to the manufacturer's instructions. Libraries were sequenced at the University of Exeter's DNA sequencing facility on the Illumina NovaSeq 6000 platform to generate paired 150-bp reads.

Sequence reads were assembled de novo using SPAdes version 3.15.1 [46] as described in protocols.io at https://dx.doi.org/10.17504/protocols.io.kxygxzrqzv8j/v1 (accessed on 19 November 2022). The resulting genome assemblies were annotated by the NCBI Prokaryotic Genome Annotation Pipeline (PGAP) [47]. Assembly quality was assessed using CheckM version 1.2.2 [48], selecting its markers for genus *Xanthomonas*. Pairwise average nucleotide identities (ANI) between genome assemblies were calculated using FastANI [49]. Phylogenomic analysis used PhaME [50] and FastTree [51] as described in the protocol at https://dx.doi.org/10.17504/protocols.io.261geny57g47/v1 (accessed on19 November 2022). The resulting phylogenetic tree was visualised using the Interactive Tree of Life [52].

3. Results

3.1. Genome Sequencing and Assembly

We sequenced the genomes of the pathotype strains for each of 32 pathovars of *X. campestris*, which are listed in Table 1. These sequenced strains included 20 pathovars whose *gyrB* sequences suggested a closer relationship to *X. euvesicatoria* rather than to *X. campestris* [4]. It also includes, as controls, strains that have recently been transferred from *X. campestris* into *X. euvesicatoria* [10] or *X. citri* [11]. A further set of controls comprised seven pathovars that are closely related to the type strain of *X. campestris* [4]. Finally, we include the pathotype strain of *X. axonopodis* pv. *passiflorae* [53], synonymous with *X. campestris* pv. *passiflorae*, which has been mentioned in the literature as "*X. phaseoli* pv. *passiflorae*" [54].

The raw sequencing reads and draft-quality genome assemblies are available in the Sequence Read Archive [55,56] via BioProject accessions PRJNA742925 and PRJNA774128. Summary statistics for the genome assemblies are provided in Table 2. Assemblies consisted of between 18 and 136 contigs with N_{50} lengths ranging between 93 and 996 kb. CheckM reported each assembly as more than 99.6% complete and no more than 1.71% contamination (see Table A2 in Appendix B).

Table 2. Summary statistics for genome sequence assemblies. All data can be accessed via Bio-Projects PRJNA742925 and PRJNA774128. All sequences strains are the pathotype strains for their respective pathovars.

Assembly Accession	Strain (NCPPB Number)	Length (b.p.)	Number of Contigs	N_{50} Length (b.p.)
GCA_020813115.1	*aberrans* 2986	5,136,506	75	145,536
GCA_020731405.1	*armoraciae* 347	5,063,577	72	149,552
GCA_020813315.1	*barbareae* 983	4,982,365	62	208,499
GCA_020813295.1	*incanae* 937	4,916,318	50	191,313
GCA_020813015.1	*papavericola* 2970	5,509,044	46	220,536
GCA_020813005.1	*plantaginis* 1061	5,214,263	76	153,285
GCA_020813075.1	*raphani* 1946	4,898,270	53	196,893
GCA_019193005.1	*alangii* 1336	4,984,130	20	399,322
GCA_019192985.1	*physalidis* 1756	5,125,394	37	354,850
GCA_019201545.1	*merremiae* 3114	5,092,415	53	310,143
GCA_019201525.1	*trichodesmae* 585	5,572,310	82	194,166
GCA_019201075.1	*passiflorae* 2346	5,022,320	68	164,613

Table 2. *Cont.*

Assembly Accession	Strain (NCPPB Number)	Length (b.p.)	Number of Contigs	N$_{50}$ Length (b.p.)
GCA_019201485.1	*blepharidis* 1757	4,969,587	58	167,765
GCA_019201365.1	*carissae* 2373	5,089,141	136	93,135
GCA_019201225.1	*clerodendri* 575	5,097,109	39	312,137
GCA_019201245.1	*convolvuli* 2498	4,982,289	54	201,220
GCA_019201305.1	*coriandri* 1758	5,049,250	34	522,126
GCA_019201325.1	*daturae* 2932	5,173,277	46	333,897
GCA_019201425.1	*euphorbiae* 1828	4,926,792	26	995,918
GCA_019201375.1	*fici* 2372	4,880,201	87	109,976
GCA_019201405.1	*heliotropii* 2057	5,161,499	120	107,075
GCA_019201465.1	*ionidii* 1334	4,974,037	50	264,595
GCA_019201185.1	*lawsoniae* 579	5,050,397	112	114,657
GCA_019201145.1	*mirabilis* 4348	5,091,739	25	745,972
GCA_019201105.1	*obscurae* 3759	5,007,609	61	242,019
GCA_019201285.1	*paulliniae* 3079	4,806,543	18	540,544
GCA_019201165.1	*pennamericanum* 4349	5,014,174	87	133,002
GCA_019201445.1	*spermacoces* 1760	5,070,626	45	344,807
GCA_019201115.1	*uppalii* 586	4,954,104	37	305,235
GCA_019201345.1	*vernoniae* 1787	4,961,493	98	150,860
GCA_019201265.1	*viegasii* 4351 [PT]	5,007,865	38	232,093
GCA_019201205.1	*zingibericola* 4352	4,926,474	31	267,819

3.2. Phylogenomic Reconstruction

The phylogenetic positions of many of these pathovars had previously been inferred on the basis of partial sequences of the *gyrB* locus. Therefore, we used our newly generated genome assemblies to explore the levels of genomic similarity, going beyond that single locus. We used PhaME [50] to infer the phylogeny based on whole-genome sequence data (Figure 1). The resulting tree included a clade that includes the type-strain of *X. euvesicatoria* together with the pathotype strains of *X. euvesicatoria* pathovars *perforans*, *alangii*, *allii*, *raphani* and *physalidis* (Figure 1). Into this clade also fell pathovars *blepharidis*, *carissae*, *clerodendri*, *convolvuli*, *coriandri*, *daturae*, *euphorbiae*, *fici*, *heliotropii*, *ionidii*, *lawsoniae*, *mirabilis*, *obscurae*, *paulliniae*, *pennamericanum*, *spermacoces*, *uppalii*, *vernoniae*, *viegasii* and *zingibericola*, suggesting that these 20 pathovars phylogenetically fall within the species *X. euvesicatoria*. Consistent with previous studies [4,11], pathovars *merremiae* and *trichodesmae* showed phylogenetic proximity to *X. citri*. Pathovars *aberrans*, *armoraciae*, *barbaraeae*, *incanae*, *papavericola*, *plantaginis* and *raphani* all fall close to the type-strain of *X. campestris*, as expected. Pathovar *passiflorae* falls closer to the type-strain of *X. phaseoli* than to *X. axonopodis*.
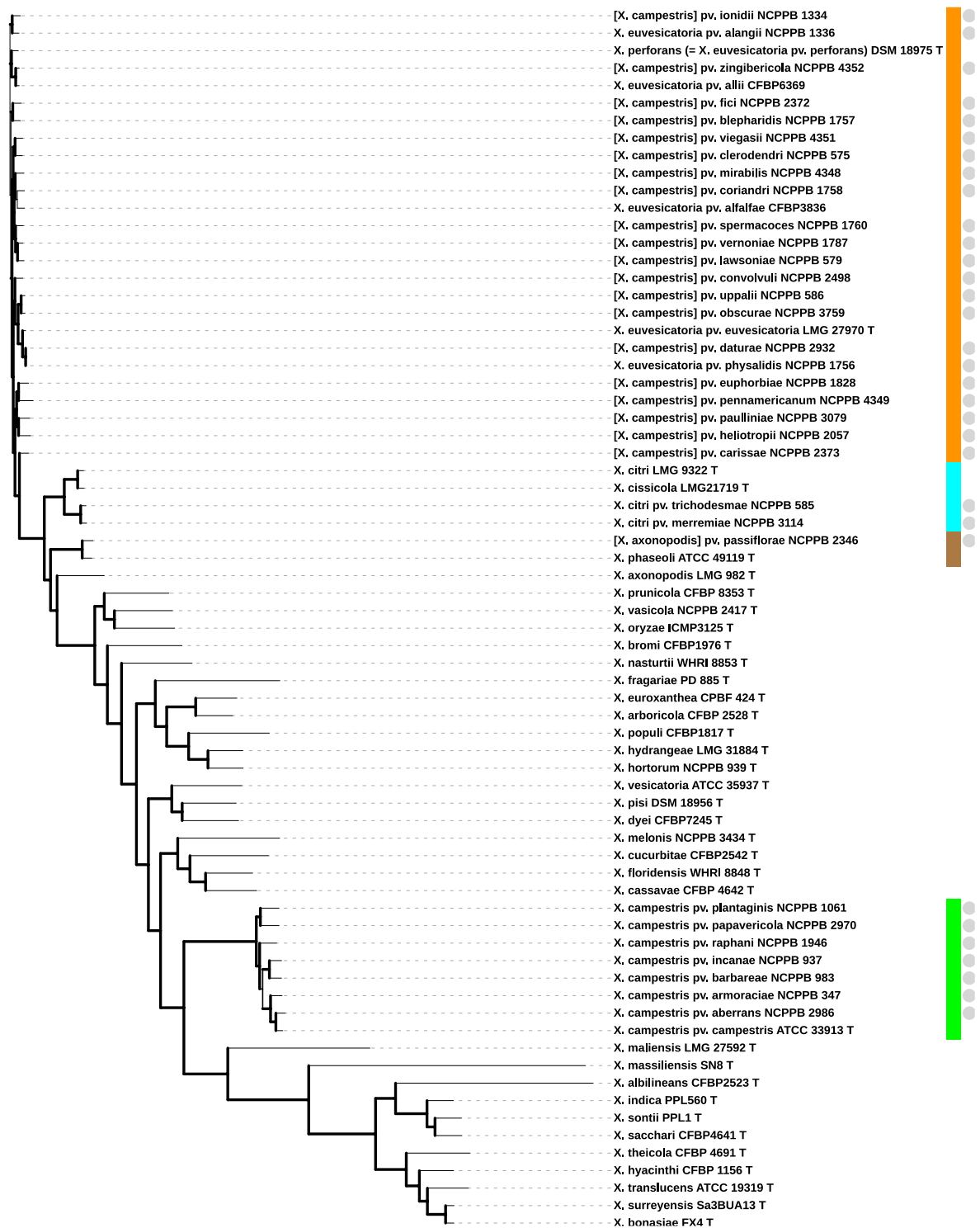
Figure 1. Phylogenetic tree, based on core genome sequences, for the newly sequenced strains, species type strains and relevant pathovar pathotype strains of *Xanthomonas*, generated using PhaME [50] and FastTree [51]. The tree was graphically rendered using the Interactive Tree of Life [52]. Configuration and tree files are available from https://github.com/davidjstudholme/phylogenomics-Xanthomonas-2 (accessed on 19 November 2022). Grey circles indicate genomes sequenced in the present study. Clades corresponding to *X. euvesicatoria*, *X. citri*, *X. phaseoli* and *X. campestris* are indicated by strips of orange, cyan, brown and green, respectively. A list of accession numbers and references for the genome sequences is provided in Appendix A as Table A1.

3.3. Species Delineation Based on Average Nucleotide Identity

The results of the genome-based phylogenetic analysis supported the proposition that 20 pathovars are evolutionarily much closer to *X. euvesicatoria* than to *X. campestris* (Figure 1). However, to delineate the bounds of bacterial species, the standard approach is to use genome-wide average nucleotide identity (ANI). Therefore, we calculated pairwise ANI between each of the pathotype strains and type strains of relevant *Xanthomonas* species. These ANI values are summarised in Table 3.

Pathovars *blepharidis, carissae, clerodendri, convolvuli, coriandri, daturae, euphorbiae, fici, heliotropii, ionidii, lawsoniae, mirabilis, obscurae, paulliniae, pennamericanum, spermacoces, uppalii, vernoniae, viegasii* and *zingibericola* each share more than 97% ANI with the type-strain of *X. euvesicatoria*. This is above widely accepted thresholds for delineating species boundaries at 94–96% [57–61]. On the other hand, these pathovars showed less than 86% ANI with the X. campestris type strain, well below the threshold for inclusion. This supports the transfer of these 20 pathovars from *X. campestris* into *X. euvesicatoria*.

Consistent with phylogeny, pathovars *aberrans, armoraciae, barbaraeae, incanae, papavericola, plantaginis* and *raphani* show high levels of ANI with the *X. campestris* type strain. These ANI values are all above 96%, supporting their current taxonomic position with this species. As expected, *X. citri* pv. *merremiae, X. citri*, pv. *trichodesmae, X. euvesicatoria* pv. *alangii* and *X. euvesicatoria* pv. *physalidis* each had >96% ANI to their respective species type-strains. Pathovar *passiflorae* showed 98.16% ANI with *X. phaseoli* but only 93.42% with *X. axonopodis* LMG 982[T]. This supports the transfer of this pathovar from *X. axonopodis* to *X. phaseoli*.

Table 3. Percentage average nucleotide identities (ANI) between genomes of the newly sequenced *X. campestris* pathotype strains versus genomes of type strains of *X. campestris, X. citri* and *X. euvesicatoria* [10,62,63]. Values of ANI exceeding 96% are highlighted in bold.

Pathovar and NCPPB Number	*X. euvesicatoria* LMG 27970 [T]	*X. campestris* ATCC 33913	*X. citri* LMG 9322	*X. phaseoli* 49119
X. campestris pv. *aberrans* 2986	85.80	**98.66**	85.65	85.88
X. campestris pv. *armoraciae* 347	85.74	**98.16**	85.79	85.88
X. campestris pv. *barbareae* 983	85.79	**97.31**	85.84	85.95
X. campestris pv. *incanae* 937	85.78	**97.29**	85.79	85.89
X. campestris pv. *papavericola* 2970	85.66	**96.49**	85.60	85.78
X. campestris pv. *plantaginis* 1061	85.88	**96.45**	85.78	85.79
X. campestris pv. *raphani* 1946	85.83	**97.23**	85.72	85.80
X. phaseoli pv. *passiflorae* 2346	93.86	85.96	93.65	**98.16**
X. citri pv. *merremiae* 3114	93.85	85.81	**96.20**	93.91
X. citri pv. *trichodesmae* 585	93.77	85.83	**96.16**	93.82
X. euvesicatoria pv. *alangii* 1336	**98.01**	85.86	94.33	94.18
[*X. campestris*] pv. *blepharidis* 1757	**97.90**	85.86	94.45	94.11
[*X. campestris*] pv. *carissae* 2373	**97.54**	85.80	94.73	94.12
[*X. campestris*] pv. *clerodendri* 575	**97.98**	85.85	94.31	94.08
[*X. campestris*] pv. *convolvuli* 2498	**98.13**	85.93	94.50	94.14
[*X. campestris*] pv. *coriandri* 1758	**97.98**	85.89	94.47	94.10
[*X. campestris*] pv. *daturae* 2932	**98.73**	85.85	94.27	94.01
[*X. campestris*] pv. *euphorbiae* 1828	**97.57**	85.91	94.41	94.10
[*X. campestris*] pv. *fici* 2372	**98.00**	85.91	94.40	94.19
[*X. campestris*] pv. *heliotropii* 2057	**97.53**	85.97	94.31	94.06
[*X. campestris*] pv. *ionidii* 1334	**97.92**	85.88	94.38	94.08
[*X. campestris*] pv. *lawsoniae* 579	**98.04**	85.90	94.45	94.12

Table 3. *Cont.*

Pathovar and NCPPB Number	*X. euvesicatoria* LMG 27970 [T]	*X. campestris* ATCC 33913	*X. citri* LMG 9322	*X. phaseoli* 49119
[*X. campestris*] pv. *mirabilis* 4348	**98.00**	85.84	94.36	94.17
[*X. campestris*] pv. *obscurae* 3759	**98.42**	85.93	94.37	94.11
[*X. campestris*] pv. *paulliniae* 3079	**97.69**	85.85	94.36	94.37
[*X. campestris*] pv. *pennamericanum* 4349	**97.45**	85.80	94.27	94.04
X. euvesicatoria pv. *physalidis* 1756	**98.74**	85.92	94.31	94.10
[*X. campestris*] pv. *spermacoces* 1760	**97.83**	85.86	94.50	94.10
[*X. campestris*] pv. *uppalii* 586	**98.38**	85.95	94.37	94.09
[*X. campestris*] pv. *vernoniae* 1787	**98.10**	85.95	94.41	94.18
[*X. campestris*] pv. *viegasii* 4351	**98.05**	85.94	94.31	94.18
[*X. campestris*] pv. *zingibericola* 4352	**98.10**	85.88	94.47	94.23

4. Discussion

The species *Xanthomonas campestris* has encompassed numerous pathovars, which are assemblages of strains sharing similar host ranges and pathology. With the advent of cheap and easy molecular sequencing, it has become apparent that there is great genetic heterogeneity among strains classified as *X. campestris* and at least 38 species have been described for this genus [64]. Previous studies [4,8,10,12,65] have highlighted that many pathovars classified within *X. campestris* are more closely related to other *Xanthomonas* species than to the type strain of *X. campestris*. Consequently, recent taxonomic revisions have transferred many *X. campestris* pathovars into different species [10–12,66]. Nevertheless, there remain *X. campestris* pathovars whose taxonomy remains to be resolved in the light of genetic and genomic evidence.

Here, the results of our genome sequencing and phylogenomic analysis are consistent with recently published taxonomic revisions that place pathovars *merremiae* and *trichodesmae* within *X. citri* and pathovars *alangii* and *physalidis* in *X. euvesicatoria* [10]. These results further support the transfer of pathovar *passiflorae* within *X. phaseoli* and a further 20 pathovars into *X. euvesicatoria*.

We also sequenced type strains of pathovars *aberrans*, *armoraciae*, *barbaraeae*, *campestris*, *incanae*, *papavericola*, *plantaginis*, and *raphani* and investigated their evolutionary relationships. Consistent with previous studies that were limited to sequencing a single genetic locus [4], we find that these are closely related to the type strain of *X. campestris* and fall within the boundaries of this species as delineated by ANI [67]. Therefore, we do not here propose any changes to the taxonomy of these pathovars. However, we previously noted [68] confusion and redundancy in the nomenclature for *X. campestris* isolates that cause nonvascular leaf spot disease on *Brassica* spp. We reiterate the previous proposal that such isolates should be classified as *X. campestris* pv. *raphani* rather than *armoraceae* [68].

In summary, 20 *X. campestris* pathovars examined in the current study have not been previously transferred from *X. campestris*, though analysis of limited available DNA sequence suggested that phylogenetically there would be a case for doing so [4]. Here, we present draft genome assemblies for the pathotype strains of these 20 pathovars for the purpose of assigning them to species. All of these could thereby be unambiguously assigned to either *X. euvesicatoria* on the basis of a 96% threshold for genome-wide ANI. Below, we present emended taxonomic descriptions to implement the proposed taxonomic transfers.

Emended description *of X. euvesicatoria* Jones et al., 2006 [69,70] emend. Constantin et al., 2016 [10].

The characteristics of the genus and species of *X. euvesicatoria* are as previously described (Ah-You et al. [71], Constantin et al. [10], Vauterin et al. [8]). In addition to the pathovars described in Constantin et al. [10], we provide phylogenomic evidence for additional pathovars to constitute *X. euvesicatoria*.

Emended description of *X. euvesicatoria* pv. *blepharidis* (Srinivasan and Patel 1956 [28], Dye 1978 [7]) comb. nov.

=*X. campestris* pv. *blepharidis* (Srinivasan and Patel 1956 [28]) Dye 1978 [7]

Description as provided by Srinivasan and Patel [28], Bradbury [72] and phylogenomic comparisons in the present study. Pathotype strain: NCPPB 1757, ATCC 17995, ICMP 5722, LMG 557.

Emended description of *X. euvesicatoria* pv. *carissae* (Moniz et al., 1964 [29], Dye 1978 [7]) comb. nov.

=*X. campestris* pv. *carissae* (Moniz et al., 1964 [29]) Dye 1978 [7]

Description as provided by Moniz et al. [29], Bradbury [72] and phylogenomic comparisons in the present study. Pathotype strain: NCPPB 2373, ICMP 3034, LMG 669.

Emended description of *X. euvesicatoria* pv. *clerodendri* (Patel et al., 1952 [30], Dye 1978 [7]) comb. nov.

=*X. campestris* pv. *clerodendri* (Patel et al., 1952 [30]) Dye 1978 [7]

Description as provided by Patel et al. [30], Bradbury [72] and phylogenomic comparisons in the present study. Pathotype strain: NCPPB 575, ATCC 11676, ICMP 445, CIP 106789, LMG 684, DSMZ 13067, CCUG 43811.

Emended description of *X. euvesicatoria* pv. *convolvuli* (Nagarkoti et al., 1973, Dye 1978) comb. nov.

=*X. campestris* pv. *convolvuli* (Nagarkoti et al., 1973 [31]) Dye 1978 [7]

Description as provided by Nagarkoti et al. [31], Bradbury [72] and phylogenomic comparisons in the present study. Pathotype strain: NCPPB 2498, ICMP 5380, LMG 685.

Emended description of *X. euvesicatoria* pv. *coriandri* (Srinivasan et al., 1961 [32], Dye 1978 [7]) comb. nov.

=*X. campestris* pv. *coriandri* (Srinivasan et al., 1961 [32]) Dye 1978 [7]

Description as provided by Srinivasan et al., 1961 [32], Bradbury [72] and phylogenomic comparisons in the present study. Pathotype strain: NCPPB 1758, ATCC 17996, ICMP 5725, LMG 867.

Emended description of *X. euvesicatoria* pv. *daturae* (Jain et al., (1975) [33], Bradbury 1986) comb. nov.

=*X. campestris* pv. *daturae* (Jain et al., 1975) [33] Bradbury 1986 [72]

Description as provided by *X. campestris* f.sp. *daturi* Jain et al. [33], Bradbury [72] and phylogenomic comparisons in the present study. The original description of *X. campestris* pv. *Daturae* [72] used the epiphet "*daturi*". However, the correct genitive singular form is *daturae* since *Datura* is feminine [73]. We note that *daturae* (rather than "*daturi*") is the name adopted by other authors [4,8,74,75] and by the NCBI Taxonomy database [73] txid487861. Pathotype strain: NCPPB 2932.

Emended description of *X. euvesicatoria* pv. *Euphorbiae* (Sabet et al., 1969 [34], Dye [7] 1978) comb. nov.

=X. *campestris* pv. *Euphorbiae* (Sabet et al., 1969 [34]) Dye 1978 [7]

Description as provided by Sabet et al. [34], Bradbury [72] and phylogenomic comparisons in the present study. Pathotype strain: NCPPB 1828, ICMP 5730, LMG 863.

Emended description of *X. euvesicatoria* pv. *Fici* (Cavara 1905 [35], Dye 1978 [7]) comb. nov.

=*X. campestris* pv. *fici* (Cavara 1905 [35]) Dye 1978 [7]

Description as provided by Cavara [35], Duff [76], Jindal and Patel [77], Bradbury [72] and phylogenomic comparisons in the present study. Pathotype strain: NCPPB 2372, ICMP 3036, LMG 701.

Emended description of *X. euvesicatoria* pv. *heliotropii* (Sabet et al., 1969 [34], Dye 1978 [7]) comb. nov.

=*X. campestris* pv. *heliotropii* (Sabet et al., 1969 [34]) Dye 1978 [7]

Description as provided by Sabet et al. [34], Bradbury [72] and phylogenomic comparisons in the present study. Bradbury [72] notes that gelatin is hydrolysed, but not starch. Pathotype strain: NCPPB 2057, ICMP 5778, LMG 73.

Emended description of *X. euvesicatoria* pv. *ionidii* (Padhya and Patel 1963 [36] Dye 1978 [7]) comb. nov.

=*X. campestris* pv. *ionidii* (Padhya and Patel 1963 [36]) Dye 1978 [7]

Description as provided by Padhya and Patel 1963 [36], Bradbury [72] and phylogenomic comparisons in the present study. Pathotype strain: NCPPB 1755, ATCC 17993.

Emended description of *X. euvesicatoria* pv. *Lawsoniae* (Patel et al., 1951 [37], Dye 1978 [7]) comb. nov.

=*X. campestris* pv. *lawsoniae* (Patel et al., 1951 [37]) Dye 1978 [7]

Description as provided by Patel et al. [37], Bradbury [72] and phylogenomic comparisons in the present study. Pathotype strain: NCPPB 579, ATCC 11674, ICMP 319, LMG 756.

Emended description of *X. euvesicatoria* pv. *mirabilis* (ex Durgapal and Trivedi 1976 [38], Dye et al., 1991 [38]) comb. nov.

=*X. campestris* pv. *mirabilis* (ex Durgapal and Trivedi 1976 [38]) Dye et al., 1991 [78]

Description as provided by Durgapal and Trivedi [38]) Dye et al. [78], and phylogenomic comparisons in the present study. Pathotype strain: NCPPB 4348, ICMP 8949.

Emended description of *X. euvesicatoria* pv. *obscurae* (Chand and Singh 1994 [39]) comb. nov.

=*X. campestris* pv. *obscurae* Chand and Singh 1994 [39]

Description as provided by Chand and Singh [39] and phylogenomic comparisons in the present study. Pathotype strain: NCPPB 3759 (incorrectly reported as NCPPB 3359 in Chand and Singh [39]), ICMP 12547.

Emended description of *X. euvesicatoria* pv. *paulliniae* (Robbs et al., 1982 [40]) comb. nov.
=*X. campestris* pv. *Paulliniae* Robbs et al. 1982 [40]

Description as provided by Robbs et al. [40] and phylogenomic comparisons in the present study. Pathotype strain (holotype): NCPPB 3079, ICMP 8919, LMG 9053.

Emended description of *X. euvesicatoria* pv. *Pennamericanum* (Qhobela and Claflin 1988 [41]) comb. nov.

=*X. campestris* pv. *Pennamericanum* Qhobela and Claflin 1988 [41]

Description as provided by Qhobela and Claflin [41] and phylogenomic comparisons in the present study. Pathotype strain: NCPPB 4349, ICMP 9627, ATCC 49152.

Emended description of *X. euvesicatoria* pv. *Spermacoces* (Srinivasan and Patel 1956 [28], Dye 1978 [7]) comb. nov.

=*X. campestris* pv. *Spermacoces* (Srinivasan & Patel 1956 [28]) Dye 1978 [7]

Description as provided by Srinivasan & Patel [28], Bradbury [72] and phylogenomic comparisons in the present study. Pathotype strain: NCPPB 1760, ATCC 17998, ICMP 5751, LMG 868.

Emended description of *X. euvesicatoria* pv. *Uppalii* (Patel 1948 [42], Dye 1978 [7]) comb. nov.

=*X. campestris* pv. *uppalii* (Patel 1948 [42]) Dye 1978 [7]

Description as provided by Patel [42], Bradbury [72] and phylogenomic comparisons in the present study. Pathotype strain: NCPPB 586, ATCC 11641, ICMP 5756, LMG 893.

Emended description of *X. euvesicatoria* pv. *vernoniae* (Patel et al., 1968 [43], Dye 1978 [7]) comb. nov.

=*X. campestris* pv. *vernoniae* (Patel et al., 1968 [43]) Dye 1978 [7]

Description as provided by Patel et al. [43], Bradbury [72] and phylogenomic comparisons in the present study. Pathotype strain: NCPPB 1787, ICMP 5758, LMG 9058.

Emended description of *X. euvesicatoria* pv. *viegasii* (Robbs et al., 1989 [44]) comb. nov.

=*X. campestris* pv. *viegasii* Robbs et al., 1989 [44]

Description as provided by Robbs et al. [44], and phylogenomic comparisons in the present study. Pathotype strain: NCPPB 4351, ICMP 9261, IBSF 575.

Emended description of *X. euvesicatoria* pv. *zingibericola* (Ren and Fang 1981 [45], Bradbury 1986 [72]) comb. nov.

=*X. campestris* pv. *zingibericola* (Ren and Fang 1981 [45]) Bradbury 1986 [72]

Description as provided by Ren and Fang 1981 [45], Bradbury [72] and phylogenomic comparisons in the present study. Pathotype strain: NCPPB 4352, ICMP 8787, LMG 9060.

Emended description *of X. phaseoli* (ex Smith 1897 [79]) Gabriel et al., 1989 [80] emend. Constantin et al., 2016 [10]

The characteristics of the genus and species of *X. phaseoli* are as previously described (Ah-You et al. [71], Constantin et al. [10], Vauterin et al. [8], Smith 1897 [79]) Gabriel et al., 1989 [80]). In addition to the pathovars described in Constantin et al. [10], we provide phylogenomic evidence for an additional pathovar to constitute *X. phaseoli*.

Emended description of *X. phaseoli* pv. *passiflorae* (Pereira 1969 [27], Dye 1978 [7], Goncalves and Rosato 2000 [53]) comb. nov.

=*X. axonopodis* pv. *Passiflorae* (Pereira 1969 [27], Dye 1978 [7]) Goncalves and Rosato 2000 [53]

Description as provided by Pereira [27], Bradbury [72], Goncalves and Rosato [53] and phylogenomic comparisons in the present study. Pathotype strain: NCPPB 2346, ICMP 3151, LMG 810.

Appendix A

Table A1. Genome sequences used in phylogenomic analysis.

GenBank Accession	Taxon	Reference
GCA_019201075.1	[*X. axonopodis*] pv. *passiflorae* NCPPB 2346	This study
GCA_019201485.1	[*X. campestris*] pv. *blepharidis* NCPPB 1757	This study
GCA_019201365.1	[*X. campestris*] pv. *carissae* NCPPB 2373	This study
GCA_019201225.1	[*X. campestris*] pv. *clerodendri* NCPPB 575	This study

Table A1. *Cont.*

GenBank Accession	Taxon	Reference
GCA_019201245.1	[*X. campestris*] pv. *convolvuli* NCPPB 2498	This study
GCA_019201305.1	[*X. campestris*] pv. *coriandri* NCPPB 1758	This study
GCA_019201325.1	[*X. campestris*] pv. *daturae* NCPPB 2932	This study
GCA_019201425.1	[*X. campestris*] pv. *euphorbiae* NCPPB 1828	This study
GCA_019201375.1	[*X. campestris*] pv. *fici* NCPPB 2372	This study
GCA_019201405.1	[*X. campestris*] pv. *heliotropii* NCPPB 2057	This study
GCA_019201465.1	[*X. campestris*] pv. *ionidii* NCPPB 1334	This study
GCA_019201185.1	[*X. campestris*] pv. *lawsoniae* NCPPB 579	This study
GCA_019201545.1	[*X. campestris*] pv. *merremiae* NCPPB 3114	This study
GCA_019201145.1	[*X. campestris*] pv. *mirabilis* NCPPB 4348	This study
GCA_019201105.1	[*X. campestris*] pv. *obscurae* NCPPB 3759	This study
GCA_019201285.1	[*X. campestris*] pv. *paulliniae* NCPPB 3079	This study
GCA_019201165.1	[*X. campestris*] pv. *pennamericanum* NCPPB 4349	This study
GCA_019201445.1	[*X. campestris*] pv. *spermacoces* NCPPB 1760	This study
GCA_019201525.1	[*X. campestris*] pv. *trichodesmae* NCPPB 585	This study
GCA_019201115.1	[*X. campestris*] pv. *uppalii* NCPPB 586	This study
GCA_019201345.1	[*X. campestris*] pv. *vernoniae* NCPPB 1787	This study
GCA_019201265.1	[*X. campestris*] pv. *viegasii* NCPPB 4351	This study
GCA_019201205.1	[*X. campestris*] pv. *zingibericola* NCPPB 4352	This study
GCA_002939705.1	*X. albilineans* CFBP 2523 [T]	-
GCA_001013475.1	*X. arboricola* CFBP 2528 [T]	[81]
GCA_001401595.1	*X. axonopodis* LMG 982 [T]	-
GCA_017163705.1	*X. bonasiae* FX4 [T]	[82]
GCA_002939755.1	*X. bromi* CFBP 1976 [T]	[83]
GCA_020813115.1	*X. campestris* pv. *aberrans* NCPPB 2986	This study
GCA_020731405.1	*X. campestris* pv. *armoraciae* NCPPB 347	This study
GCA_020813315.1	*X. campestris* pv. *barbareae* NCPPB 983	This study
GCA_000007145.1	*X. campestris* pv. *campestris* ATCC 33913 [T]	[62]
GCA_020813295.1	*X. campestris* pv. *incanae* NCPPB 937	This study
GCA_020813015.1	*X. campestris* pv. *papavericola* NCPPB 2970	This study
GCA_020813005.1	*X. campestris* pv. *plantaginis* NCPPB 1061	This study
GCA_020813075.1	*X. campestris* pv. *raphani* NCPPB 1946	This study
GCA_000454545.1	*X. cassavae* CFBP 4642 [T]	[84]
GCA_002019225.1	*X. cissicola* LMG 21719 [T]	[11]
GCA_002018575.1	*X. citri* LMG 9322 [T]	[85]
GCA_002939885.1	*X. cucurbitae* CFBP 2542 [T]	-
GCA_002939865.1	*X. dyei* CFBP 7245 [T]	-
GCA_900476395.1	*X. euroxanthea* CPBF 424 [T]	[86]
GCA_019193005.1	*X. euvesicatoria* pv. *alangii* NCPPB 1336	This study
GCA_017724035.1	*X. euvesicatoria* pv. *alfalfae* CFBP3836	[87]
GCA_000730305.1	*X. euvesicatoria* pv. *allii* CFBP6369	[88]
GCA_001401555.1	*X. euvesicatoria* pv. *euvesicatoria* LMG 27970 [T]	-
GCA_019192985.1	*X. euvesicatoria* pv. *physalidis* NCPPB1756	This study
GCA_001642575.1	*X. floridensis* WHRI 8848 [T]	[89]
GCA_900380235.1	*X. fragariae* PD 885 [T]	[90]

Table A1. *Cont.*

GenBank Accession	Taxon	Reference
GCA_003064105.1	*X. hortorum* NCPPB 939 [T]	[91]
GCA_009769165.1	*X. hyacinthi* CFBP 1156 [T]	[92]
GCA_905142475.1	*X. hydrangeae* LMG 31884 [T]	[93]
GCA_022669045.1	*X. indica* PPL560 [T]	[94]
GCA_009192945.1	*X. maliensis* LMG 27592 [T]	[95]
GCA_900018785.1	*X. massiliensis* SN8 [T]	[96]
GCA_020783655.1	*X. melonis* NCPPB 3434 [T]	-
GCA_001660815.1	*X. nasturtii* WHRI 8853 [T]	[89]
GCA_004136375.1	*X. oryzae* ICMP 3125 [T]	[97]
GCA_013112235.1	*X. perforans* DSM 18975 [T]	-
GCA_022749655.1	*X. phaseoli* ATCC 49119 [T]	-
GCA_001010415.1	*X. pisi* DSM 18956 [T]	[98]
GCA_002940065.1	*X. populi* CFBP 1817 [T]	-
GCA_002846205.1	*X. prunicola* CFBP 8353 [T]	[99]
GCA_002940085.1	*X. sacchari* CFBP 4641 [T]	-
GCA_008119715.1	*X. sontii* PPL1 [T]	[100]
GCA_014836395.1	*X. surreyensis* Sa3BUA13 [T]	[101]
GCA_014236795.1	*X. theicola* CFBP 4691 [T]	[102]
GCA_020880735.1	*X. translucens* ATCC 19319 [T]	[103]
GCA_000772705.2	*X. vasicola* NCPPB 2417 [T]	[12]
GCA_001908725.1	*X. vesicatoria* ATCC 35937 [T]	[104]

Appendix B

Table A2. Assessment of completeness and contamination using CheckM.

GenBank Accession	Pathovar	Completeness (%)	Contamination (%)
GCA_020813115.1	*aberrans*	99.89	0.03
GCA_019193005.1	*alangii*	99.94	0.61
GCA_020731405.1	*armoraciae*	99.89	0.03
GCA_020813315.1	*barbareae*	99.85	0.03
GCA_019201485.1	*blepharidis*	99.89	0.03
GCA_020813135.1	*campestris*	99.77	0
GCA_019201365.1	*carissae*	99.94	0.41
GCA_019201225.1	*clerodendri*	99.94	0.36
GCA_019201245.1	*convolvuli*	99.94	0.03
GCA_019201305.1	*coriandri*	99.89	0.3
GCA_019201325.1	*daturae*	99.87	0.53
GCA_019201425.1	*euphorbiae*	99.89	0.03
GCA_019201375.1	*fici*	99.94	0.68
GCA_019201405.1	*heliotropii*	99.82	0.32
GCA_020813295.1	*incanae*	99.64	0.53
GCA_019201465.1	*ionidii*	99.89	0.15
GCA_019201185.1	*lawsoniae*	99.64	0.03
GCA_019201545.1	*merremiae*	99.81	0.34
GCA_019201145.1	*mirabilis*	99.94	0.22

Table A2. *Cont.*

GenBank Accession	Pathovar	Completeness (%)	Contamination (%)
GCA_019201105.1	*obscurae*	99.94	0.07
GCA_020813015.1	*papavericola*	99.89	1.71
GCA_019201075.1	*passiflorae*	99.89	0.42
GCA_019201285.1	*paulliniae*	99.89	0.03
GCA_019201165.1	*pennamericanum*	99.89	0
GCA_019192985.1	*physalidis*	99.94	0.03
GCA_020813005.1	*plantaginis*	99.89	0.53
GCA_020813075.1	*raphani*	99.89	0.11
GCA_019201445.1	*spermacoces*	99.89	0.03
GCA_019201525.1	*trichodesmae*	99.76	0.93
GCA_019201115.1	*uppalii*	99.62	0.25
GCA_019201345.1	*veroniae*	99.89	0.37
GCA_019201265.1	*viegasii*	99.94	0.03
GCA_019201205.1	*zingibericola*	99.89	0.18

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