



Comprehensive pangenomic, phylogenetic, and genome comparison analyses demonstrate that the causal agent of castor bean (*Ricinus communis* L.) bacterial blight is a pathovar of the *Xanthomonas euvesicatoria* species

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Received: 13 August 2025 / Accepted: 3 February 2026
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Abstract

Xanthomonas axonopodis pv. *ricini* is the major bacterial pathogen of castor bean (*Ricinus communis* L.), an important source for oil production in several countries; only castor bean has been reported as its natural host. Recently, its pathotype strain ICMP 5747 was shown to cause disease in eucalypt plants and to group with *Xanthomonas euvesicatoria* in a multi-locus sequence analysis (MLSA), raising doubts about its taxonomic position. The objective of this study was to assemble the genome sequence of strain ICMP 5747 and employ it in MLSA using Bayesian inference and maximum likelihood methods with four housekeeping genes, phylogenomics based on conserved homologous genes, and genome sequence comparisons against validly published or proposed *Xanthomonas* species to elucidate its taxonomic position. A 5.1 Mb draft genome sequence with a 65% GC content and 99.7% completeness was assembled. MLSA, phylogenomic reconstruction based on 368 conserved genes, and genome comparisons demonstrated that strain ICMP 5747 is more closely related to *X. euvesicatoria* strains than to the *X. axonopodis* type strain. Serendipitously, it was also found that the *X. axonopodis* pv. *commiphoreae* pathotype strain LMG 26789 is also more closely related to *X. euvesicatoria* strains. This study proposes the transfer of *X. axonopodis* pvs. *ricini* and *commiphoreae* to the *X. euvesicatoria* species, as *X. euvesicatoria* pv. *ricini* comb. nov. and *X. euvesicatoria* pv. *commiphoreae* comb. nov. to help establish the phylogenetic relationships among *Xanthomonas* species and determine the etiology of plant diseases.

Keywords Comparative genomics · MLSA · Phylogenomics · Pangenomics

Introduction

Xanthomonas axonopodis pv. *ricini* is a Gram-negative, strictly aerobic bacterium that was first described in Japan in 1928 by Yoshii and Takimoto (1928) as the causal agent of castor bean (*Ricinus communis* L.) bacterial leaf blight (BLB). Castor bean is a multipurpose inedible oilseed widely used in the pharmaceutical, cosmetic, biodiesel, and oil industries (ICOA 2018; Salihu et al. 2014). BLB is the only significant disease of bacterial etiology reported to date that threatens castor bean production (Dange et al. 2005). The bacterium causes circular or angular water-soaked lesions on castor bean leaves that progress to form necrotic lesions, which coalesce and result in blights surrounded by chlorotic haloes (Janse and Defrancq 1988). At advanced

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stages of infection, the disease causes premature senescence of the leaves (Yoshii and Takimoto 1928; Dange et al. 2005).

After its first report as *Bacterium ricinicola* (Yoshii and Takimoto 1928), this pathogen has been reclassified to *X. campestris* pv. *ricini* (Dye 1978), and *X. axonopodis* pv. *ricini* (Vauterin et al. 1995), which is the most accepted published name. However, its taxonomic position remains unclear. In a comprehensive study on *Xanthomonas*, two strains, ICMP 3031 and ICMP 7462, deposited in the International Collection of Microorganisms from Plants (ICMP) as belonging to the *ricini* pathovar clustered with *X. euvesicatoria* strains in a phylogenetic tree based on a multilocus sequence analysis (MLSA) using partial *dnaK* (chaperone Hsp70), *fyuA* (yersiniabactin ferric uptake receptor), *gyrB* (DNA gyrase B subunit), and *rpoD* (RNA polymerase sigma factor 70) gene sequences (Young et al. 2008). Nonetheless, the pathotype strain ICMP 5747 was not included in that study.

More recently, Ferraz et al. (2024), in a study aimed to determine the causal agents of eucalypt bacterial leaf blight in Brazil, noticed that the pathotype strain ICMP 5747 of *X. axonopodis* pv. *ricini* clustered with several pathovars of *X. euvesicatoria* in a phylogenetic tree based on partial sequences of the same four housekeeping genes used by Young et al. (2008). Even though in the study conducted by Ferraz et al. (2024), the authors carried out comprehensive genome comparisons among type strains of validly published *Xanthomonas* species, the lack of a reference genome for *X. axonopodis* pv. *ricini* hindered a conclusive definition of the taxonomic position of this pathovar. Interestingly, strain ICMP 5747 was able to cause severe leaf blight symptoms when artificially inoculated in a eucalypt hybrid clone (Ferraz et al. 2024), indicating that its host range is not restricted to castor bean.

According to the List of Prokaryotic Names with Standing Nomenclature (<https://lpsn.dsmz.de/>), the genus *Xanthomonas* currently consists of at least 35 validly published species, albeit some others have been proposed, many of which are responsible for causing severe diseases in crops of economic importance. In the past, a new *Xanthomonas* species was proposed for each new host species affected, leading to a proliferation of bacterial species without strong scientific support (Young et al. 1978). With the advent of more discriminatory experimental techniques, such as fatty acid methyl ester (FAME) profiling, some pathovars of *X. campestris* were transferred to new species, although the reclassification was inconclusive due to the lack of data on phenotypic characteristics and DNA-DNA hybridization, once considered the gold standard for species delineation (Vauterin et al. 1995). Parkinson et al. (2009) conducted comprehensive *gyrB* gene sequence comparisons among strains of the genus and found that some pathovars were highly divergent from the *X. campestris* type strain. Later,

based on MLSA, whole-genome sequencing, DNA-DNA hybridization, and phenotypic profiling, transfers of several pathovars into *X. axonopodis*, *X. citri*, *X. euvesicatoria*, *X. phaseoli*, and *X. vasicola* were proposed (Constantin et al. 2016; Bansal et al. 2022; Studholme et al. 2020). More recently, whole-genome sequencing and phylogenomic reconstruction were used to propose the transfer of 20 pathovars from *X. campestris* into *X. euvesicatoria* (Harrison et al. 2023). However, the taxonomic position of some *X. axonopodis* pathovars remains inconclusive.

Here, we describe the first draft genome sequence of the *X. axonopodis* pv. *ricini* pathotype strain ICMP 5747 (NCPBP 1063, B 651, ICMP 5747, LMG 861, and PDDCC 5747). MLSA, phylogenomic, and pangenomics analyses, as well as genome sequence comparisons of strain ICMP 5747 with those of validly published or proposed *Xanthomonas* species, were conducted to conclusively establish its taxonomic position. Inadvertently, the results also revealed the correct taxonomic positioning of the *X. axonopodis* pv. *comphoreae* pathotype strain.

Materials and methods

Bacterial growth and DNA extraction

The pathotype strain ICMP 5747 was grown on 523 agar medium (Kado and Heskett 1970) at 28 °C for 24 h. The genomic DNA was extracted using the Wizard® Genomic DNA Purification Kit (Promega, Madison, WI, USA) according to the manufacturer's instructions. The quality and quantity of the extracted DNA were assessed by electrophoresis in 1% agarose gel as well as using a NanoDrop 2000c spectrophotometer (Thermo Fisher Scientific) and a Qubit® 3.0 fluorometer (Thermo Fisher Scientific).

Bacterial genome sequencing, assembly, and annotation

The genomic DNA of strain ICMP 5747 was sequenced using the Illumina NovaSeq 6000 platform with 2 × 150-pb paired-end reads by GeneOne Biotechnology (Bangu, RJ, Brazil), and the quality assessment was carried out using FastQC v. 0.11.5 (Babraham Bioinformatics and Andrews 2010). Adapter sequences were removed using TrimGalore v. 0.6.6 (<https://github.com/FelixKrueger/TrimGalore>), and the reads were trimmed for quality and filtered for length using Trimmomatic v. 0.39 (Bolger et al. 2014) with the parameters HEADCROP: 15, CROP: 130, SLIDINGWINDOW: 4:20, and MINLEN: 130. The *ab initio* assembly of the genome sequence was performed using SPAdes v. 3.15.3 (Bankevich et al. 2012), selecting all odd k-mers from 21 to 127. An additional scaffolding step was performed

using RagTag v. 2.1.0 (Alonge et al. 2022) and selecting the complete genome of *X. euvesicatoria* pv. *alfalfae* CFBP 3836 (GenBank accession NZ_CP072268.1) as reference. Then, the scaffolds were corrected and polished using Pilon (Walker et al. 2014). Prokka v1.14.5 (Seemann 2014) was used for gene prediction and functional annotation, and the Proksee server (<https://proksee.ca/>) was used for genome visualization. To gain insights into the biological subsystems encoded in the draft genome, the annotated sequence was submitted to analysis by the Classic RAST algorithm at the Rapid Annotation using Subsystem Technology (RAST) server (Aziz et al. 2008). Completeness of the genome was assessed by BUSCO v. 5.4.6 (Simão et al. 2015) employing the Xanthomonadales lineage.

Multi-locus sequence analysis

RaxML-HP v. 8.2.12 (Stamatakis 2014) using the maximum likelihood (ML) method and MrBayes 3.2.7 (Ronquist et al. 2012) by Bayesian inference were utilized for phylogenetic reconstruction based on MLSA. Partial sequences of the housekeeping genes *dnaK*, *fyuA*, *gyrB*, and *rpoD* were used as suitable molecular markers (Ferraz et al. 2024; Young et al. 2008). The housekeeping gene sequences were obtained by blastN searching the genome sequence of each *Xanthomonas* strain retrieved from the National Center for Biotechnology Information (NCBI; www.ncbi.nlm.nih.gov/assembly/) and included in the analyses, using the *X. axonopodis* pv. *ricini* strain ICMP 3031 gene sequences (Ferraz et al. 2024) as queries. The DNA sequences of the loci to be compared were combined into multi-fasta files and were aligned using the Muscle tool (Edgar 2004) implemented in MEGA 11 (Tamura et al. 2021). The resulting Nexus files of each locus were then concatenated using Sequence Matrix v. 1.9 (Vaidya et al. 2011). For Bayesian inference, the nucleotide substitution models were defined using the Akaike Information Criterion (AIC) with MrModeltest2 v. 2.3 (Nylander 2004) and Paup* 4.0 v. 4.0b10 (Swofford 2002). The output files were submitted to both MrBayes v. 3.2.7 (Ronquist et al. 2012) and RaxML v. 8 (Stamatakis 2014) for the construction of phylogenetic trees. For all phylogenetic analyses, gene sequences from all *Xanthomonas* species that have been validly published or proposed, and from *Xylella fastidiosa* subsp. *fastidiosa* Temecula 1 (as an outgroup) were included. Figtree (<http://tree.bio.ed.ac.uk/software/figtree/>) and Inkscape v. 1.2.1 were used for visualizing and editing the trees, respectively.

Phylogenomic analysis

To generate a phylogenomic tree by the ML method, the genome sequences of 40 type or representative strains of validly published or proposed *Xanthomonas* species, and

the genome sequence of *X. fastidiosa* subsp. *fastidiosa* Temecula 1, as an outgroup, were downloaded from NCBI, their quality assessed by BUSCO (Simão et al. 2015), and submitted, along with the ICMP 5747 genome sequence, to the Cognac package (Crawford and Snitkin 2021) for R v.4.1.2 (R Development Core Team 2021) to identify conserved homologous genes and to obtain the alignment of their nucleotide sequences, which was submitted to FastTree v2.1.10 (Price et al. 2010). Then, the tree was visualized and edited as previously.

Pangenomic analysis

Complete genome sequences of *X. euvesicatoria* and *X. axonopodis* strains available at NCBI were retrieved and used to compare them with the draft genome sequences of *X. euvesicatoria* ATCC 11633 and *X. axonopodis* DSM 3585 type strains, as well as with the *X. axonopodis* pv. *ricini* ICMP 5747 pathotype strain through pangenomic analysis. Complete genome sequences of strains deposited at NCBI as *X. perforans* (Jones et al. 2004) were also included. First, the genomes were annotated with Prokka v. 1.14.6 (Seemann 2014) and then subjected to pangenomic analysis with Roary v.3.13.0. (Page et al. 2015) implemented in Galaxy Australia (<https://usegalaxy.org.au/>), setting the minimum percent identity for blastp to 95 and the percentage of isolates a gene must be in to be core to 100. The alignment and core gene output files were submitted to Gubbins v. 3.2.1 (Croucher et al. 2015), setting the number of iterations to 5 and using the Weighted Robinson Foulds model to obtain the tree file, which, together with the gene presence/absence file, was uploaded to Phandango (<https://jameshadfield.github.io/phandango/#/>) to generate a dendrogram.

Genome comparisons

The average nucleotide identity (ANIb) and the digital DNA-DNA hybridization (dDDH) indices were calculated to determine the similarity of the *X. axonopodis* pv. *ricini* ICMP 5747 and *X. axonopodis* pv. *commiphorae* LMG 26789 genome sequences with those of validly published and proposed *Xanthomonas* species. ANIb was calculated using the JSpeciesWS web server (<https://jspecies.ribohost.com/jspeciesws/>), and dDDH calculations were performed employing the Genome-to-Genome Distance Calculator 3.0 (GGDC) (<http://ggdc.dsmz.de>). In addition, to gain a better understanding of the genome sequence similarity of the ICMP 5747 and LMG 26789 pathotype strains with those of the *X. axonopodis* DSM 3585 and *X. euvesicatoria* ATCC 11633 type strains, Mauve v. 2.4.0 was used (Rissman et al. 2009). First, the contigs of the draft genome sequences were ordered with respect to their nearest relatives whose genome sequences were complete, according to the results

of pangenomic analysis. Then, the ordered contigs of the genomes of *X. axonopodis* pv. *ricini* ICMP 5747 and the complete genome sequence of *X. axonopodis* pv. *commiphorae* LMG 26789 were aligned with the ordered contigs of the *X. axonopodis* DSM 3585 and *X. euvesicatoria* ATCC 11633 type strains using Mauve v. 2.4.0 (Rissman et al. 2009) to identify local colinear blocks (LCBs), genome rearrangements, and syntenic regions.

Results

Characteristics of the ICMP 5747 pathotype genome sequence

The ICMP 5747 genome assembly comprises 5.1 Mb distributed among 33 contigs with sizes between 1,075 and 4,930,012 nucleotides with a 251.9X sequencing depth and a mean GC content of 65.0%. The largest contig of the assembly (4.9 Mb) comprises 96% of the draft genome sequence, and its size represents the N50. A total of 4,201 coding DNA sequences (CDS) and 65 RNA genes (five rRNA, fifty-nine tRNA, and one tmRNA) were predicted (Fig. 1a). BUSCO assessed the completeness of the final assembly as 99.7%,

with 1,147 complete and single-copy, one complete and duplicated, one fragmented, and three missing genes (Supplementary Table 1).

Among the proteins encoded by the predicted CDS, 2,359 received known functional assignments by Prokka, whereas the remaining were annotated as hypothetical proteins. The RAST analysis revealed that 47% of the genes code for subsystems related to bacterial biological functions. These genes were allocated by homology into 26 subsystem categories. The categories with the highest CDS abundance were amino acids and derivatives (374 genes); carbohydrates (366); protein metabolism (298); and cofactors, vitamins, prosthetic groups, and pigments (259) (Figure 1b). The joint analysis of Prokka and RAST annotation showed the presence of genes coding for type II, III, and VI secretion systems, antibiotics, multidrug resistance, copper tolerance, as well as for toxin production and tolerance (data not shown).

MLSA groups the ICMP 5747 strain with the *X. euvesicatoria* type strain

A Bayesian tree was constructed with the partial *dnaK*, *fyuA*, *gyrB* and *rpoD* gene sequences using GTR+I+G as the best-fit evolutionary model predicted by the IAC with MrModel

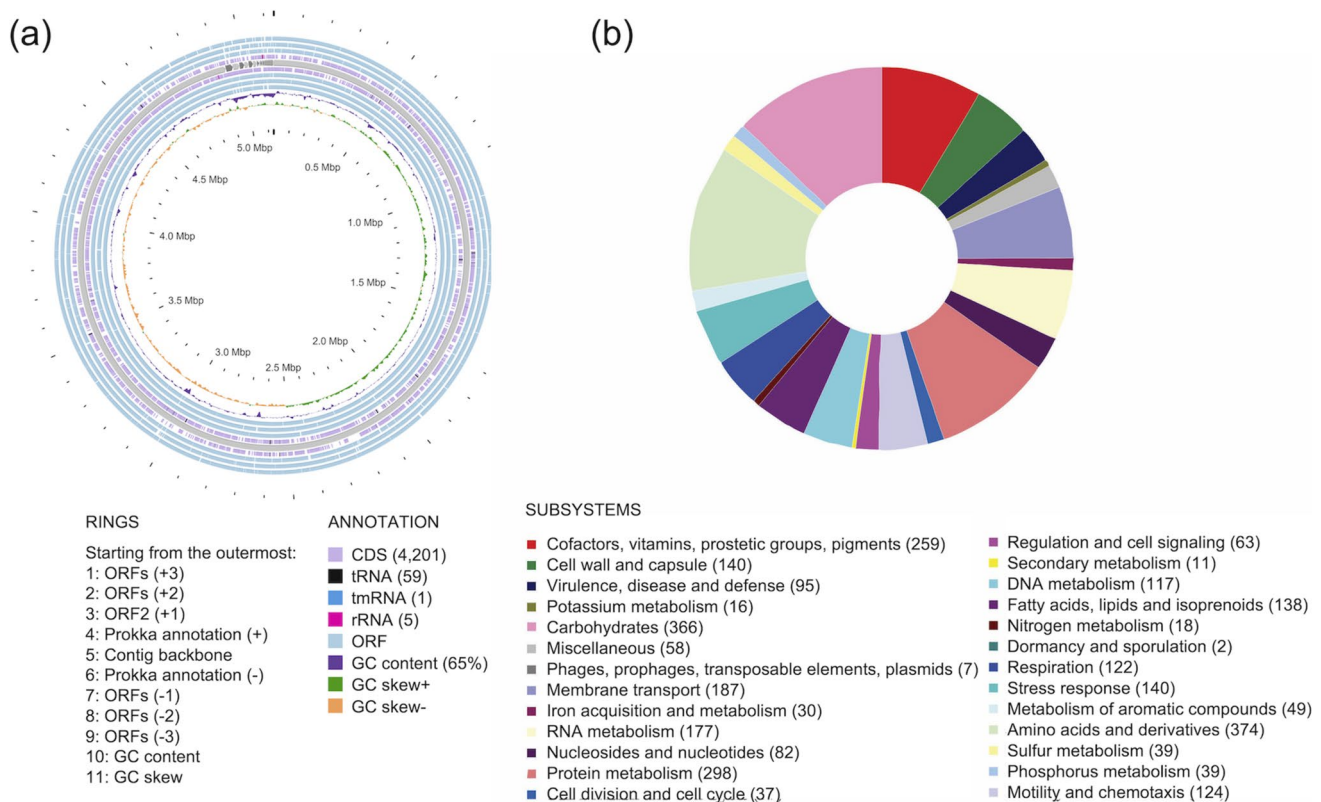
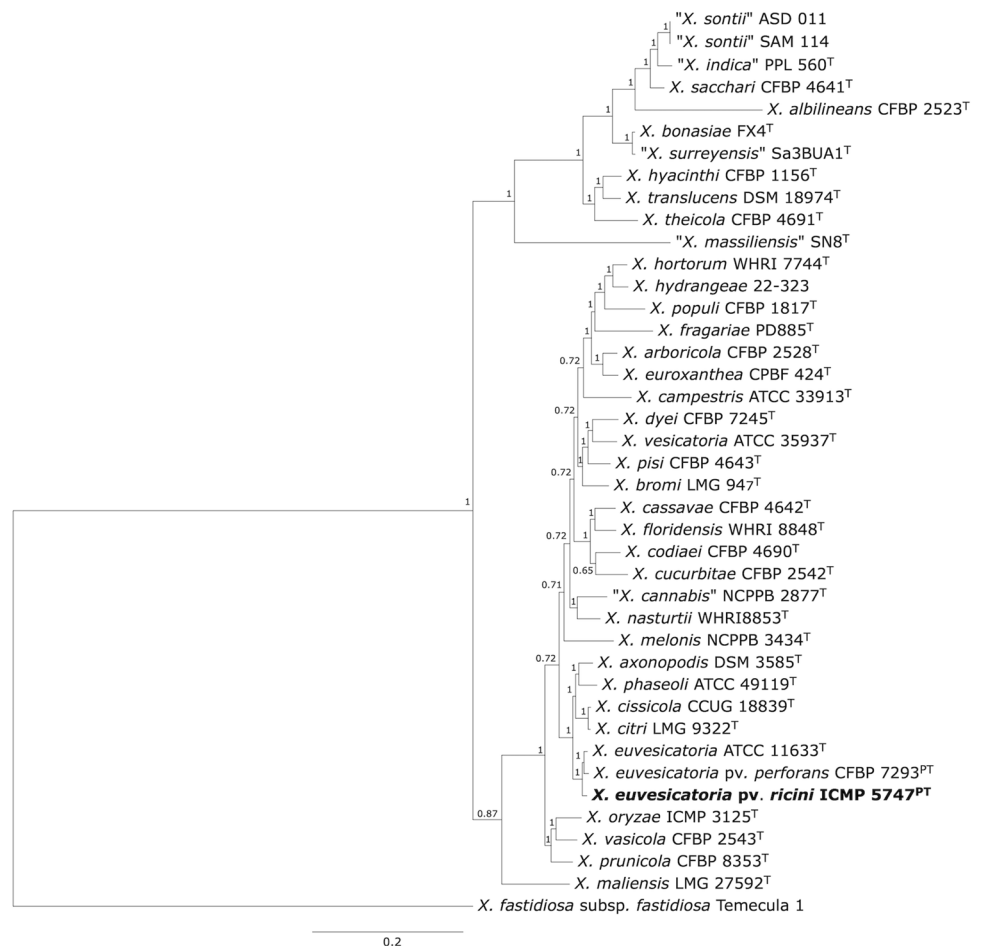


Fig. 1 Characteristics of the *Xanthomonas euvesicatoria* pv. *ricini* ICMP 5747 genome. **(a)** Genomic map indicating annotation features. **(b)** Predicted subsystems of the annotated genome according to the classic RAST pipeline

Fig. 2 Phylogenetic relationship of *Xanthomonas euvesicatoria* pv. *ricini* ICMP 5747 with validly published or proposed *Xanthomonas* species based on partial *dnaK*, *fyuA*, *gyrB*, and *rpoD* gene sequences. *Xylella fastidiosa* subsp. *fastidiosa* Temecula 1 was used as an outgroup. The phylogenetic tree was constructed by Bayesian inference with MrBayes and visualized and edited with FigTree and Inkscape, respectively. Numbers on the nodes indicate Bayesian posterior probabilities. T, PT, and quotation marks indicate type strains, pathotype strains, and proposed but not validly published species, respectively. Scale bar indicates the number of nucleotide substitutions per site



test for all four genes. In the tree built with gene sequences from type or reference strains of validly published or proposed *Xanthomonas* species and *X. fastidiosa* subsp. *fastidiosa* Temecula 1 (as an outgroup), strain ICMP 5747 grouped with *X. euvesicatoria*, including the pathotype strain for *X. euvesicatoria* pv. *perforans* (Figure 2). *X. axonopodis* was placed in a divergent clade that also included *X. phaseoli*. Despite little differences in the tree topologies, phylogenetic reconstruction using ML with RaxML (substitution model: GTR+CAT for all gene sequences) confirmed the placement of the ICMP 5747 strain in the *X. euvesicatoria* clade (Supplementary Figure 1). In all phylogenetic analyses, tree branching was well supported.

Phylogenomics allocates strain ICMP 5747 to the *X. euvesicatoria* species

In order to confirm the taxonomic position of the ICMP 5747 strain, a phylogenomic reconstruction was conducted with conserved homologous genes present in the genomes of validly published or proposed *Xanthomonas* species. BUSCO indicated that the genome sequences included in the analysis show at least 96.6% completeness, 1,108 complete and

single-copy, a maximum of 5 complete and duplicated, 14 fragmented, and 32 missing genes. The only exception was the genome sequence of the *X. phaseoli* type strain, which showed 84.7% completeness with 973 complete and single-copy, 2 complete and duplicated, 100 fragmented, and 68 missing genes (Supplementary Table 1). These results indicated that the genome sequences were suitable for genome comparisons. Cognac identified 368 gene homologs conserved among the 41 *Xanthomonas* and *X. fastidiosa* (as an outgroup) genomes that were employed to build a phylogenomic tree using the ML method. This analysis also placed the ICMP 5747 strain in the same clade with the *X. euvesicatoria* type strain. In this case, the *X. axonopodis* type strain was placed in a monophyletic and divergent clade distant from the ICMP 5747 strain (Fig. 3).

The genome sequence of strain ICMP 5747 is more similar to that of *X. euvesicatoria*

Genome sequence comparisons were conducted using the similarity indices ANIb and dDDH to aid in the determination of the taxonomic position of the ICMP 5747 strain. When compared with the genome sequences of validly

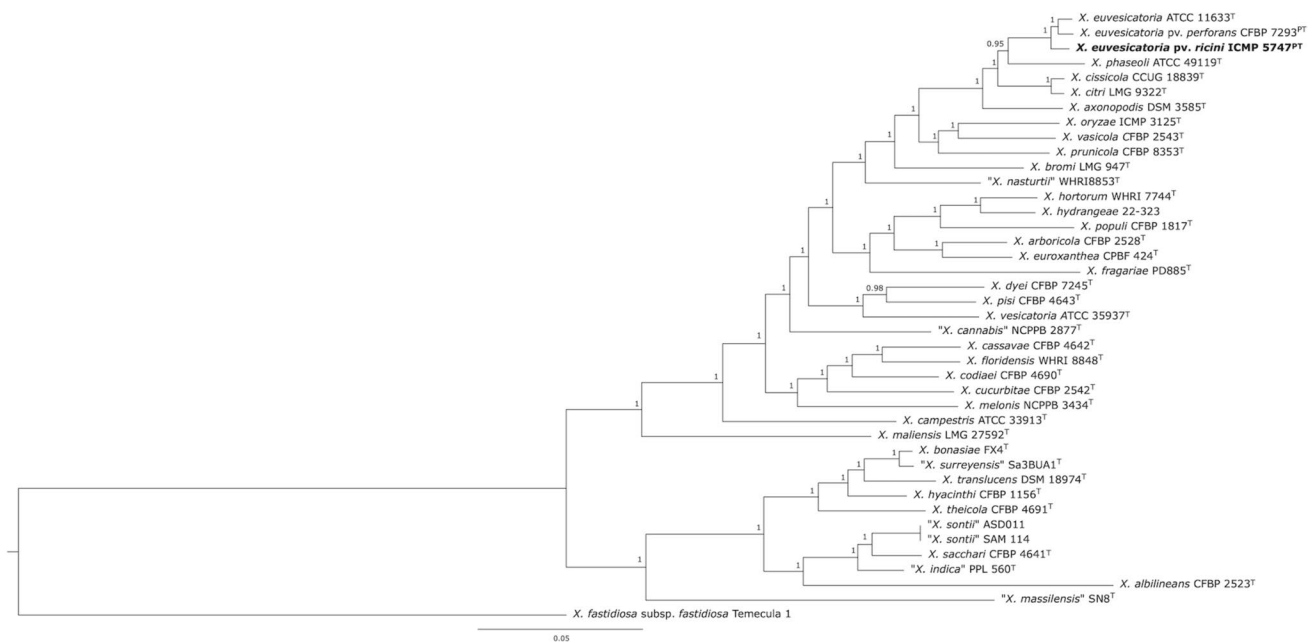


Fig. 3 Phylogenomic relationship of *Xanthomonas euvesicatoria* pv. *ricini* ICMP 5747 with validly published or proposed *Xanthomonas* species, based on the sequences of 368 gene homologs identified by Cognac to be conserved among all strains included in the analysis. The tree was constructed using the Maximum Likelihood method employing *Xylella fastidiosa* subsp. *fastidiosa* Temecula 1 as an out-

group, visualized and edited with FigTree and Inkscape, respectively. Numbers on the nodes indicate bootstrap values. T, PT, and quotation marks indicate type strains, pathotype strains, and proposed but not validly published species, respectively. Scale bar indicates the number of nucleotide substitutions per site

published or proposed *Xanthomonas* species, the ICMP 5747 strain showed ANIb values above 97% with coverage above 86% with those of *X. euvesicatoria* pathovars *euvesicatoria* and *perforans*. ANIb values were below 94% for all the other paired genome comparisons, including a 92.41% value for *X. axonopodis*. As for dDDH, the only comparisons that resulted in values above 77% were with the two *X. euvesicatoria* pathovars abovementioned. All other comparisons resulted in dDDH values below 58%. The dDDH value for the paired comparison with the *X. axonopodis* type strain was only 52.0% (Table 1).

The genome of the *X. axonopodis* pathovar *ricini* is more similar to that of the *X. euvesicatoria* type strain

Since no complete genome sequences of the *X. axonopodis* DSM 3585 and *X. euvesicatoria* ATCC 11633 type strains were available, pangenomic analysis was employed to identify the *X. axonopodis* and *X. euvesicatoria* complete genome sequences whose gene content was most similar to their draft genome sequences. In the pangenomic dendrogram, the genome sequence of ICMP 5747 clustered with those of *X. euvesicatoria* strains. The complete genome sequence of *X. axonopodis* pv. *vasculorum* strain NCPPB 796 was the most similar to the draft genome

sequence of the *X. axonopodis* DSM 3585 type strain, the complete genome sequence of *X. euvesicatoria* pv. *vesicatoria* 85-10 was the most similar to the draft genome sequence of the *X. euvesicatoria* ATCC 11633 type strain, and the complete genome sequence of *X. euvesicatoria* pv. *perforans* TC2-1 was the most similar to the draft genome sequence of the *X. euvesicatoria* pv. *ricini* ICMP 5747 pathotype strain (Fig. 4). Therefore, these complete genome sequences were used to order the contigs of the draft genomes of the type strains. The ICMP 5747 genome sequence and those of all *X. euvesicatoria* strains analyzed formed a cluster separate from that of the *X. axonopodis* strains (Fig. 4).

In this analysis, it was noticed that the genome sequence of the *X. axonopodis* pv. *commiphorae* LMG 26789 pathotype strain also clustered with all *X. euvesicatoria* genomes included, distant from the *X. axonopodis* clade (Fig. 4), suggesting it was not correctly allocated at the species level. Consistently, comparisons of the LMG 26789 genome sequence with those of validly published or proposed *Xanthomonas* species revealed ANIb and dDDH values above 98 (with >85% sequence coverage) and 88%, respectively, for paired comparisons with *X. euvesicatoria* strains (Table 1). Comparisons with other validly published or proposed *Xanthomonas* species resulted in ANIb and dDDH values lower than 94% and 60%, respectively.

Table 1 Average Nucleotide Identity (ANIb) and digital DNA-DNA hybridization (dDDH) values for genome comparisons between *Xanthomonas euvesicatoria* pv. *ricini* ICMP 5747 and *X. euvesicatoria* pv. *commiphoreae* LMG 26789 with validly published and proposed *Xanthomonas* species

Species/pathovar	Strain ¹	ICMP 5747		LMG 26789	
		ANIb % (coverage)	dDDH (%)	ANIb % (coverage)	dDDH (%)
<i>X. albilineans</i>	CFBP 2523 ^T	76.16 (51.40)	24.3	76.30 (50.80)	22.00
<i>X. arboricola</i>	CFBP 2528 ^T	85.35 (68.54)	35.2	86.42 (67.83)	32.60
<i>X. axonopodis</i>	DSM 3585 ^T	92.41 (84.51)	52.0	92.54 (84.04)	49.80
<i>X. bonasiae</i>	FX4 ^T	78.67 (47.64)	25.7	78.77 (46.87)	23.30
<i>X. bromi</i>	LMG 947 ^T	88.65 (74.32)	39.5	88.66 (73.89)	37.00
<i>X. campestris</i>	ATCC 33913 ^T	84.47 (67.29)	32.1	84.51 (66.32)	29.70
“ <i>X. cannabis</i> ”	NCPPB 2877 ^T	86.73 (74.11)	35.9	86.70 (72.45)	33.20
<i>X. cassavae</i>	CFBP 4642 ^T	86.31 (65.94)	35.3	86.44 (63.89)	32.70
<i>X. cissicola</i>	CCUG 18839 ^T	93.51 (79.42)	57.1	93.78 (78.02)	55.50
<i>X. citri</i>	LMG 9322 ^T	93.47 (82.05)	57.1	93.76 (80.35)	55.30
<i>X. codiae</i>	CFBP 4690	85.97 (70.07)	34.4	85.93 (68.61)	31.90
<i>X. cucurbitae</i>	CFBP 2542 ^T	85.24 (71.66)	33.3	85.39 (69.96)	31.00
<i>X. dyei</i>	CFBP 7245 ^T	85.47 (67.90)	34.0	85.63 (67.02)	31.40
<i>X. euroxanthea</i>	CPBF 424 ^T	86.35 (69.94)	35.1	86.44 (68.83)	32.60
<i>X. euvesicatoria</i> pv. <i>euvesicatoria</i>	ATCC 11633 ^T	97.54 (86.81)	85.0	98.34 (85.63)	88.70
<i>X. euvesicatoria</i> pv. <i>perforans</i>	CFBP 7293 ^{PT}	97.95 (90.89)	86.1	98.62 (90.13)	89.60
<i>X. floridensis</i>	WHRI 8848 ^T	85.97 (67.89)	34.5	86.03 (66.71)	31.90
<i>X. fragariae</i>	PD885 ^T	85.47 (64.07)	33.8	85.53 (60.32)	31.20
<i>X. hortorum</i>	WHRI 7744 ^T	85.78 (62.83)	34.3	85.82 (61.97)	31.90
<i>X. hyacinthi</i>	CFBP 1156 ^T	78.77 (45.20)	25.7	78.98 (44.80)	23.30
<i>X. hydrangeae</i>	22–323	85.85 (66.79)	34.3	86.00 (65.34)	31.90
“ <i>X. indica</i> ”	PPL 560 ^T	78.56 (49.89)	25.5	78.62 (49.53)	22.90
<i>X. maliensis</i>	LMG 27592 ^T	81.95 (62.76)	28.9	81.98 (62.68)	26.50
“ <i>X. massiliensis</i> ”	SN8 ^T	77.20 (41.46)	24.2	77.26 (41.63)	21.80
<i>X. melonis</i>	NCPPB 3434 ^T	88.28 (73.02)	33.1	85.59 (69.96)	30.70
<i>X. nasturii</i>	WHRI 8853 ^T	89.12 (68.88)	38.9	88.37 (71.99)	36.40
<i>X. oryzae</i>	ICPM 3125 ^T	89.12 (68.88)	41.7	89.18 (67.85)	39.40
<i>X. phaseoli</i>	ATCC 49119 ^T	93.46 (81.66)	56.0	93.40 (80.69)	54.00
<i>X. pisi</i>	CFBP 4643 ^T	85.98 (66.65)	34.5	86.07 (66.31)	32.00
<i>X. populi</i>	CFBP 1817 ^T	85.55 (67.66)	33.7	85.54 (66.84)	31.10
<i>X. prunicola</i>	CFBP 8353 ^T	88.99 (73.63)	40.8	89.10 (73.01)	38.40
<i>X. sacchari</i>	CFBP 4641 ^T	78.46 (49.23)	25.4	78.45 (48.82)	22.80
“ <i>X. sontii</i> ”	ASD 011	78.60 (48.07)	25.5	78.57 (47.78)	22.90
“ <i>X. sontii</i> ”	SAM 114	78.62 (48.50)	25.5	78.59 (48.14)	22.90
“ <i>X. surreyensis</i> ”	Sa3BUA1 ^T	78.95 (47.18)	25.7	78.88 (46.22)	23.10
<i>X. theicola</i>	CFBP 4691 ^T	78.81 (43.84)	25.7	78.91 (42.44)	23.50
<i>X. translucens</i>	DSM 18974 ^T	78.54 (49.76)	25.7	78.58 (49.37)	23.30
<i>X. vasicola</i>	CFBP 2543 ^T	89.46 (77.64)	41.5	89.57 (76.98)	39.10
<i>X. vesicatoria</i>	ATCC 35937 ^T	85.49 (67.67)	33.7	85.55 (66.27)	31.20

¹ Quotation marks indicate proposed but not validly published species² PT, pathotype strain; T, type strain

When the ordered draft genome sequence of the ICMP 5747 pathotype and the complete genome sequence of the LMG 26789 pathotype were aligned with those of the *X.*

euvesicatoria and *X. axonopodis* type strains, more and larger LCBs, as well as fewer genome rearrangements (inversions and transpositions) were observed for the alignment

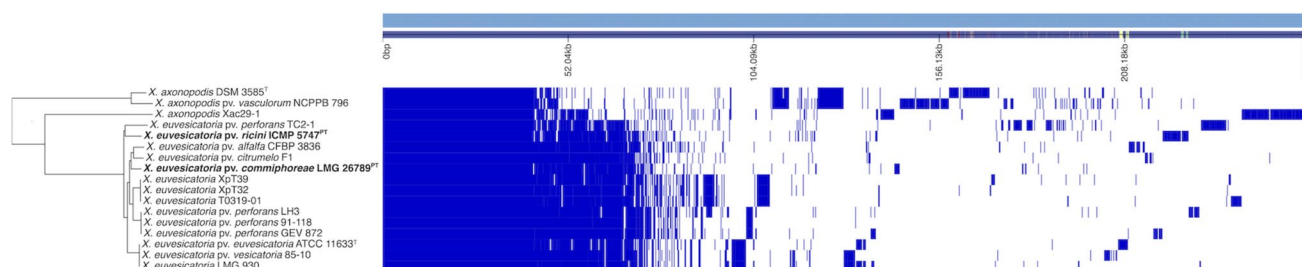


Fig. 4 Gene-content-based relationship of the draft genome sequences of *X. euvesicatoria* pv. *ricini* ICMP 5747 and *X. euvesicatoria* pv. *commiphoreae* LMG 26789 pathotype strains (in boldface) with complete genome sequences of *X. euvesicatoria* and *X. axonopodis* strains. The dendrogram depicts genome similarity based on core

genes, and blue/white bars indicate the presence/absence of genes. The *X. axonopodis* DSM 3585 and *X. euvesicatoria* ATCC 11633 type strains are also shown in boldface. Pangenomics was conducted with Roary and visualized with Phandango.

with the *X. euvesicatoria* type strain than with the *X. axonopodis* type strain (Fig. 5). Despite a few rearrangements, the genomes of strains ICMP 5747 and LMG 26789 showed higher levels of synteny with the ATCC 11633 type strain genome, indicating higher genomic conservation with respect to the *X. euvesicatoria* species.

Discussion

Motivated by the observation that the strain ICMP 5747, the pathotype of *X. axonopodis* pv. *ricini*, caused bacterial leaf blight in eucalypt plants and grouped with several pathovars of *X. euvesicatoria* in an MLSA employing partial sequences of the housekeeping genes *dnaK*, *fyuA*, *gyrB*, and *rpoD* (Ferraz et al. 2024), this study set out to clarify its taxonomic position. Until the publication of the study by Ferraz et al. (2024), the only host that had been reported for *X. axonopodis* pv. *ricini* was castor bean, on which it causes the only bacterial disease of economic importance, reported in Russia, Japan, Korea, Uganda, India, and Brazil (Khanam et al. 2025; Massola Jr. et al. 2016). The genome of the ICMP 5747 strain was sequenced and compared to those of *Xanthomonas* species validly published or proposed.

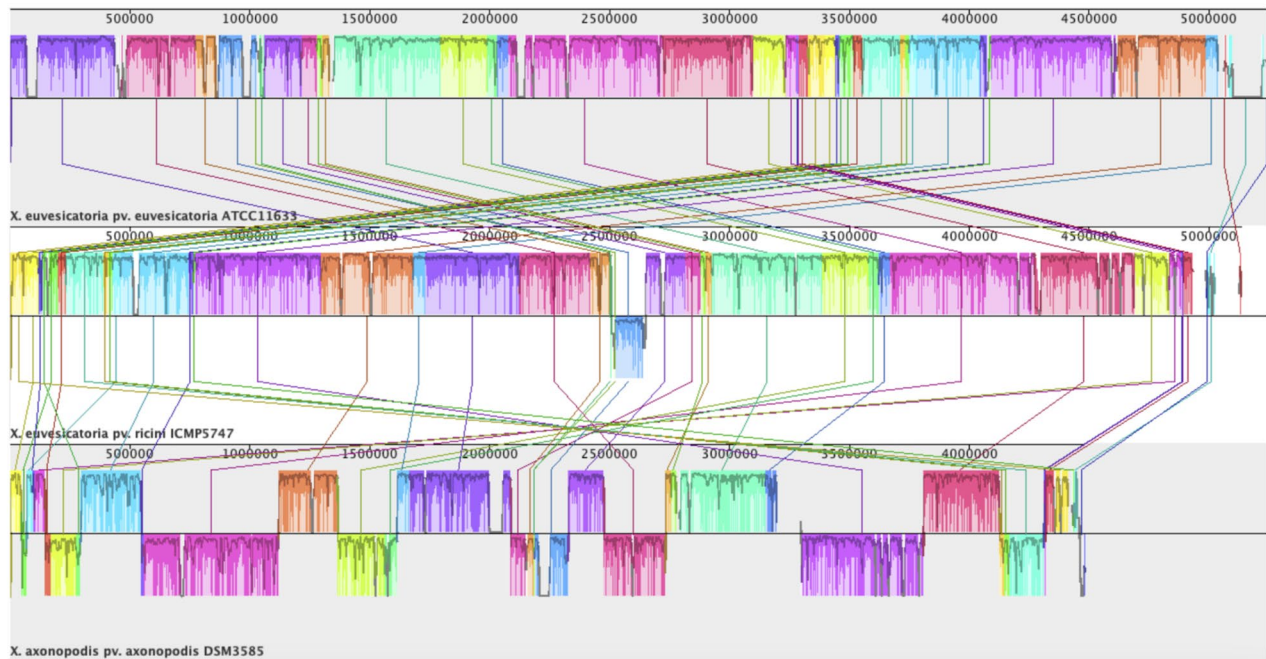
The genome size of strain ICMP 5747 was more similar to those of sequenced *X. euvesicatoria* strains than to those of sequenced *X. axonopodis* strains. A comprehensive approach was employed to conclusively establish the taxonomic position of the strain ICMP 5747. First, MLSA using Bayesian inference with MrBayes as well as ML analysis with RaxML placed the ICMP 5747 strain together with *X. euvesicatoria* in a group that diverged from *X. axonopodis*, confirming the results previously obtained by Ferraz et al. (2024). These observations are supported by early findings indicating that other strains deposited in the ICMP culture collection as *X. axonopodis* pv. *ricini* clustered with *X. euvesicatoria* in an MLSA (Young et al. 2008), indicating that they are taxonomically misclassified.

To further support the taxonomic position of strain ICMP 5747, an ML-based phylogenomic tree was built using 368 homologous genes conserved among validly published or proposed *Xanthomonas* species identified with Cognac. This tree confirmed the placement of the ICMP 5747 strain in the *X. euvesicatoria* clade, which diverged from a monophyletic *X. axonopodis* clade. In addition, ANIb values above 95% and dDDH values above 70% (accepted cut-off values for species separation) (Richter and Rosselló-Móra 2009; Meier-Kolthoff et al. 2013) were obtained only when the ICMP 5747 strain genome sequence was compared with those of *X. euvesicatoria* strains, but not with those of any other *Xanthomonas* species validly published or proposed. This taxonomic allocation of the ICMP 5747 strain is consistent with the observation that its genome shares more homologous genes, carries more LCBs, fewer rearrangements, and is more syntenic with that of the *X. euvesicatoria* type strain than with that of the *X. axonopodis* type strain, as indicated by pangenomic and sequence alignment analyses.

Serendipitously, it was found that the genome of the pathotype strain of *X. axonopodis* pv. *commiphoreae* is more similar to those of *X. euvesicatoria* strains based on pangenomic analysis, which was supported by ANIb and dDDH values, as well as by similarities in genome organization detected by sequence alignments. These results agree with those of an MLSA study using the four housekeeping genes *dnaK*, *fyuA*, *gyrB*, and *rpoD*, indicating that this pathovar clustered with *X. euvesicatoria*, *X. perforans*, and *X. alfalfa* (Samantha et al. 2013), being the latter two species currently recognized as distinct *X. euvesicatoria* pathovars. More recently, a study suggested that the LMG 26789 pathotype strain should be allocated to the *X. euvesicatoria* species based on index similarity calculations (Bansal et al. 2018), but this transfer to *X. euvesicatoria* has not been formally proposed.

Altogether, the results of MLSA, phylogenomics, pangenomics, and genome comparisons strongly support that the pathotype strain ICMP 5747 of the bacterial

(a)



(b)

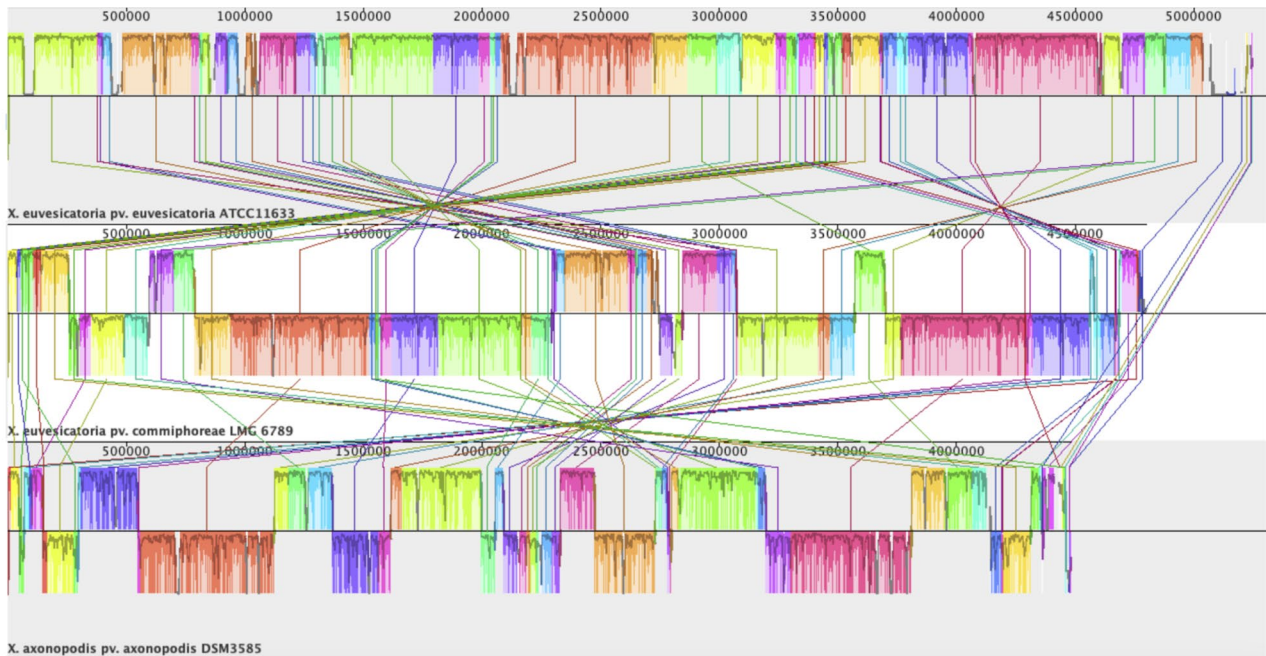


Fig. 5 Genome sequence alignment of (a) *Xanthomonas euvesicatoria* pv. *ricini* ICMP 5747 and (b) *X. euvesicatoria* pv. *commiphoreae* LMG 26789 pathotype strains with *X. axonopodis* DSM 3585 and *X. euvesicatoria* ATCC 11633 type strains using progressive Mauve. First, the contigs of the draft genome sequence of the DSM 3585 type strain were ordered against the complete genome sequence of *X. axonopodis* pv. *vasculorum* NCPB 796, the contigs of the draft genome sequence of the ATCC 11633 type strain were ordered against the *X. euvesicatoria* pv. *vesicatoria* 85-10 complete genome sequence, and

the contigs of the draft genome sequence of the ICMP 5747 pathotype strain were ordered against the complete genome sequence of *X. euvesicatoria* pv. *perforans* TC2-1. Then, the ordered genomes were aligned among themselves. Local colinear blocks (LCBs) are connected by a line identified by a unique colour and indicate genomic rearrangements. LCBs below the horizontal line of each strain indicate inverted regions. Numbers above the bars indicate the positions in the genome sequences

pathogen that causes BLB in castor bean plants, and likely other strains currently classified as *X. axonopodis* pv. *ricini* (Young et al. 2008) are indeed members of the *X. euvesicatoria* species. Based on results of MLSA (Samantha et al. 2013), clustering in a pangenomics analysis, calculation of genome similarity indices (this study; Bansal et al. 2018), and comparisons of genome sequence organization, it is also demonstrated that the pathotype strain of *X. axonopodis* pv. *commiphoreae* is a member of the *X. euvesicatoria* species as well. These findings demonstrate that, despite the recent transfers among *Xanthomonas* species, further scrutiny is required to clarify the taxonomic position of some plant pathogens of economic importance.

These taxonomic revisions are important since the host range of plant pathogens could be broader than previously suspected. As for *X. euvesicatoria* pv. *ricini*, it has recently been demonstrated that it also causes disease in eucalypt plants (Ferraz et al. 2024), at least upon artificial inoculation. However, the host range of *X. euvesicatoria* pv. *ricini* is currently unknown and is subject of investigation by our research group, considering its possible implication for agriculture production. Although Castor bean is an important source to produce oil in several countries (ICOA 2018), it also grows as an invasive plant in the tropics around the world and could serve as a reservoir for *X. euvesicatoria* pv. *ricini*, threatening the production not only of eucalypt in commercial plantations but also some other crops of economic importance. In addition, methods for specific detection of the pathogen have not been developed. Further genome comparisons aimed at identifying pathovar-specific DNA sequence could aid in the development of molecular detection methods. For now, although epidemiological studies remain to be conducted, it is advisable to establish methods to prevent the association of *X. euvesicatoria* pv. *ricini* with eucalypt plants by eradicating castor bean plants from production areas. Sources of castor bean resistance to *X. euvesicatoria* pv. *ricini* remain to be identified. With respect to *X. euvesicatoria* pv. *commiphoreae* LMG 26789, it was isolated from Guggal (*Commiphora wightii* (Arnott) Bhandari with gum oozing symptoms (Samantha et al. 2013). Guggal is a small tree used to extract a golden yellow to brown gum resin used in India to treat diverse human diseases. Among 123 plant species inoculated with the pathogen, only *Commiphora caudata*, *C. myrrha*, *C. stocksiana*, and *C. wightii* were found susceptible (Samantha et al. 2013).

The present study makes a valuable contribution to the understanding of the phylogenetic relationships among strains of the genus *Xanthomonas*, which will also facilitate elucidation of the etiological, biological, and molecular aspects of the interaction between *Xanthomonas* and their host plants. Based on the conclusive evidence provided in this study, the transfer of *X. axonopodis* pv. *ricini* and *X.*

axonopodis pv. *commiphoreae* to *X. euvesicatoria* emend. as *X. euvesicatoria* pv. *ricini* comb. nov. and *X. euvesicatoria* pv. *commiphoreae* comb. nov., respectively, is proposed.

Taxonomy

Emended description of *Xanthomonas euvesicatoria* (Jones et al. 2004) emend. (Constantin et al. 2016)

Genus and species characteristics as previously described by Jones et al. (2004) and Constantin et al. (2016), amended by genome comparison evidence provided in this study.

***X. euvesicatoria* pv. *ricini* (Yoshii and Takimoto 1928) Badel et al., 2026 comb. nov.**

= *X. axonopodis* pv. *ricini* (Yoshii and Takimoto 1928) Vauterin et al. 1995.

The description is the same as for the species, extended by information published by Vauterin et al. (1995) and by genome-based evidence from this study. The pathotype strain *X. axonopodis* pv. *ricini* ICMP 5747 is a member of this taxon (this study).

Hosts: *Ricinus communis* L. (fam. Euphorbiaceae) (Yoshii and Takimoto 1928), *Eucalyptus urophylla* × *E. globulus* (fam. Myrtaceae) (Ferraz et al. 2024).

Pathotype strain: ATCC 19317 = ICMP 5747 = LMG 861 = NCPPB 1063.

***X. euvesicatoria* pv. *commiphoreae* (Samantha et al. 2013) Badel et al., 2026 comb. nov.**

= *X. axonopodis* pv. *commiphoreae* (Samantha et al. 2013).

The description is the same as for the species, extended by information published by Vauterin et al. (1995), Samantha et al. (2013), and by genome-based evidence from this study. The pathotype strain *X. axonopodis* pv. *commiphoreae* LMG 26789 is a member of this taxon (Samantha et al. 2013; this study).

Hosts: Guggal (*Commiphora wightii* (Arn.) Bhandari); hill mango (*C. caudata* (Wight & Arn.) Engl.), common mirrh (*C. myrrha* (Nees) Engl.), Bayisa guggal (*C. stocksiana* (Engl.) Engl.) (fam. Burseraceae).

Pathotype strain: LMG 26789 = CFBP 7580 = DXA 01.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s40858-026-00789-6>.

Acknowledgments The authors thank Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) – Brazil, for providing doctoral scholarships to YFN, DCLS, and AAS. Thanks also to the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) – Brazil, for providing a doctoral scholarship to AAS and for partly funding this study - Finance Code 001. The authors also thank the Núcleo de Análise de Biomoléculas (NuBioMol) for support in genome sequence assembly. NuBioMol is financially supported

by the following Brazilian agencies: Fundação de Amparo à Pesquisa do Estado de Minas Gerais (Fapemig), CAPES, CNPq, Financiadora de Estudos e Projetos (Finep), and Sistema Nacional de Laboratórios em Nanotecnologias (SisNANO)/Ministério da Ciência, Tecnologia e Informação (MCTI). This research was partly developed with the support of the Universidade Federal de Viçosa (UFV) Cluster.

Authors' contribution Conceptualization: Jorge L. Badel; Methodology: Jorge L. Badel, Pedro M. P. Vidigal; Formal analysis and investigation: Jorge L. Badel; Debora C. L. Santos, Yane F. Neves, Adryelle A. Sousa; Writing - original draft preparation: Debora C. L. Santos, Yane F. Neves; Writing - review and editing: Jorge L. Badel, Rafael F. Alfenas, Acelino C. Alfenas; Funding acquisition: Jorge L. Badel; Resources: Jorge L. Badel; Supervision: Jorge L. Badel, Rafael F. Alfenas, Acelino C. Alfenas.

Funding The Article Processing Charge (APC) for the publication of this research was funded by the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior - Brasil (CAPES) (ROR identifier: 00x0ma614). This study was partly funded by Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) – Brazil, Finance Code 001, and Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) – Brazil.

Data availability The shotgun genome sequencing project of the ICMP 5747 strain has been deposited at DDBJ/ENA/GenBank under the accession number PRJNA814626. The version described in this paper was the first genome sequence for the strain deposited at GenBank. Additional data is available upon reasonable request from the corresponding author.

Declarations

Conflict of interest The authors declare no conflict of interest associated with this publication.

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