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Genome sequences of distinct genotypes of bacterial pathogen *Xanthomonas euvesicatoria* pv. *euvesicatoria* from pepper (*Capsicum annuum* L.) in Serbia
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CONFIDENTIAL

Genome sequences of distinct genotypes of bacterial pathogen *Xanthomonas euvesicatoria* pv. *euvesicatoria* from pepper (*Capsicum annuum* L.) in Serbia

1.1 Author names

Tatjana Popović Milovanović¹, Shannon F. Greer², Renata Ilić³, Aleksandra Jelušić⁴, Daisy Bown², Murray Grant², Joana G. Vicente⁵ and David J. Studholme^{6,*}

1.2 Affiliation(s)

¹ Institute for Plant Protection and Environment, Belgrade, Serbia.

² School of Life Sciences, University of Warwick, UK.

³ University of Novi Sad, Faculty of Agriculture, Serbia.

⁴ University of Belgrade, Institute for Multidisciplinary Research, Serbia.

⁵ Fera Science Ltd, York, UK.

⁶ Biosciences, University of Exeter, UK.

1.3 Corresponding author and email address

* Correspondence D.J.S. d.j.studholme@exeter.ac.uk

1.4 Keywords

Pepper; *Capsicum annuum* L.; Serbia; genome sequence; *Xanthomonas euvesicatoria* pv. *euvesicatoria*; *X. campestris* pv. *vesicatoria* group A; plasmid; Illumina sequencing; Unicycler assembly; pathogenicity.

2. Abstract

We present genome sequence data for three strains of the bacterial pathogen *Xanthomonas euvesicatoria* pv. *euvesicatoria* (*Xeu*) collected from pepper crops showing bacterial spot symptoms in 2016 at Irig, Serbia. We generated raw sequencing reads and annotated contig-level genome assemblies. We checked for the presence of sequences of known type-3 secretion system (T3SS) effector genes and plasmid-like sequences. All three strains fell in the same clade within *Xeu*. Strain X13 is most closely related to strain 66b, collected in Bulgaria in 2012. Strains X22 and X31 are most closely related to Tu-10 collected in the Southeastern Anatolia region of Türkiye in 2020. In common with other members of the clade, all three strains share a 75-kb plasmid that carries T3SS effector genes *avrBs3*, *xopBA*, *xopAQ* and *xopE*. Additionally, strain X13 shares extensive sequence similarity to the pXCV183 plasmid, including T3SS effector gene *xopAX*, and shares extensive sequence similarity with plasmid pXap41, including T3SS effector gene *xopE3*. This difference in plasmid content might contribute to the observed difference in virulence among the Serbian *Xeu* strains. The three Serbian strains lack the 31-kb plasmid pLMG730.4 that has been in several Vietnamese and Canadian strains within this clade of *Xeu*. The data presented will be a useful resource for future molecular epidemiology and genomic surveillance of this pathogen in the Balkan region, augmenting the previously available draft genome sequences of *Xeu* strains 66b (Bulgaria) and 83M (North Macedonia).

3. Data summary

Genome sequence data generated in this study is publicly available via BioProject: PRJNA985260 (<https://www.ncbi.nlm.nih.gov/bioproject/?term=PRJNA985260>).

The raw sequence reads are deposited in the Sequence Read Archive under accession SRP444629 (<https://trace.ncbi.nlm.nih.gov/Traces/?view=study&acc=SRP444629>).

All command line code is deposited in GitHub at <https://github.com/davidstudholme/xanthomonas-euvesicatoria-serbia>.

4. Introduction

Among European countries, Serbia is one of the leaders in production of vegetable peppers (*Capsicum annuum* L.). This encompasses diverse produce, including bell peppers and traditional varieties like Leskovac red pepper, Somborska Babura, Šorokšari, Palanačko čudo, Stržanka, Romana, Kurtovska kapija, Šilja and Slonovo uvo. Peppers are a staple in Serbian cuisine and used in a wide range of dishes, including the popular ajvar (a pepper-based relish), stuffed peppers, and various salads and stews. Serbia also exports peppers and pepper products, contributing to the country's export revenues [1]. Several diseases impact on pepper production, including bacterial spot, caused by four bacterial taxa that are associated with the disease: *Xanthomonas euvesicatoria* pv. *euvesicatoria* (Xeu), *Xanthomonas euvesicatoria* pv. *peppersans*, *Xanthomonas hortorum* pv. *gardneri*, *Xanthomonas vesicatoria* [2–6]. Xeu, previously known as *X. campestris* pv. *vesicatoria* group A [7, 8], is a seedborne pathogen that is listed as an A2 (high-risk) quarantine organism by the European and Mediterranean Plant Protection Organization (EPPO). Besides Serbia, the Xeu pathogen has also been reported in Bulgaria, Czechia, Greece, Montenegro, North Macedonia, and Türkiye [6, 9–11]. Recently, Xeu was detected on pepper leaves of the cultivar (cv.) Somborka, grown in commercial fields in Kosovo [12].

Infected seeds and planting material are the primary sources of inoculum, but pathogen also can survive in plant debris, soil, and the rhizosphere of non-hosts [6]. A severe outbreak of bacterial-spot disease on pepper (cv. Salcalik) in the eastern Mediterranean region of Turkey during 1999 - 2002 was due to the use of infected seeds for sowing, with the disease incidence ranging from 50% to 95% [9]. In the agroecological conditions of Serbia, Xeu is regularly present, with the severity of disease and the extent of economic damage strongly influenced by prevailing weather conditions [14]. Since the mid-1980s, the disease has been steadily spreading throughout the country and is considered one of the most economically important diseases of pepper. Particularly severe outbreaks were reported in 1987, causing substantial yield losses in the Srem and Bačka region (Vojvodina) [13, 14].

Xanthomonads grow optimally at temperatures between 25 and 30 °C, such that conditions in southern Europe are highly conducive to bacterial spot disease [6]. Bacteria infect host plants mainly through stomata and hydathodes but can also enter via wounds caused by mechanical damage, insect activity, or adverse weather conditions [6]. Bacterial-spot symptoms on pepper include angular lesions that later become brown and necrotic on the leaves, fruits, petioles and stems [6]. On leaves, small water-soaked lesions initially develop with a greasy appearance and irregular shape. Over time, the tissue in the center of these lesions turns brown. The spots enlarge, coalesce, and necrosis spreads over larger areas. Infected fruits develop small, greenish-brown spots that later

necrotize and crack, resulting in a blistered appearance. According to EFSA [15] although recent data on economic losses caused by bacterial spot of tomato and pepper in the EU are lacking, these pathogens are considered significant for both crops, with infections reported to cause yield losses of up to 30%.

Genomics has informed numerous research studies on *Xanthomonas* pathogens, including *X. euvesicatoria* [16–20]. For example, genome sequences have facilitated the cataloguing of virulence effectors [21–24], which the pathogen secretes and translocates into the host via the type-3 secretion system (T3SS). The specific repertoire of T3SS effectors influences the interactions between host and pathogen, for example determining host range [25, 26]. Genome sequences have also been crucial in developing tools for pathogen detection and for molecular epidemiology [27–30]. Although two strains of *Xeu* from neighbouring countries North Macedonia and Bulgaria have been sequenced [31], no genome sequence data was available for *Xeu* isolated in Serbia. Therefore, we performed genome sequencing on three strains from our collection, originating from pepper grown at the Irig locality in Serbia. The objectives were to ascertain the degree of genetic variation among the isolates and to identify which lineages of *Xeu* they belong to. Furthermore, we previously observed that isolate X13 was more virulent than strain X22 [32]; therefore, in the present study we generated genome sequences as a resource to investigate genetic differences among these strains might underlie this difference in virulence.

5. Materials and methods

We isolated three strains of *Xeu* from diseased pepper leaves (cv. Crveno Zlato) showing bacterial spot symptoms in 2016 at Irig, in the Srem region of Vojvodina, Serbia. Before isolation, the leaves were first rinsed under tap water and air-dried on filter paper. Small sections were then taken from the margins of necrotic and healthy tissue and macerated in sterile distilled water. Yeast extract-dextrose-calcium carbonate (YDC) agar was used for isolation and maintained of pure cultures. Bacterial strains develop characteristic pale yellowish, convex and mucoid bacterial colonies at 26 °C after 72 h. The strains were designated as X13 (WHRI 10185), X22 (WHRI 10186) and X31 (WHRI 10187) and confirmed to belong to *X. euvesicatoria* pv. *euvesicatoria* using two conventional duplex-PCRs, each including two primer combinations: Bs-XeF/Bs-XeR and Bs-XvF/Bs-XvR; Bs-XgF/Bs-XgR and Bs-XpF/Bs-XpR, as described by Koenraadt and colleagues [33].

Pepper plants were grown in the pots filled with a substrate composed of white and black peat mixed in a 1:1 ratio (by volume), with a particle size of <50 mm (Domoflor, Vilnius, Lithuania). The substrate's nutrient composition was NPK = 14:16:18, with a water-holding capacity of 300% – 700% and a pH range of 6±1. Each pot was filled to a final weight of 5 ± 0.5 kg and weighed daily. Pathogenicity tests were performed on young pepper plants in phase BBCH 29 (the first secondary apical lateral shoot was visible) grown under normal watering (every second day) and fertilization (1% solution of Solugal Universal fertilizer NPK 20:20:20 + MNE - Anorel NV, Belgium). Bacterial suspensions were prepared by suspending pure culture of strains grown on Yeast Dextrose Calcium-carbonate Agar for 48 hours in sterile distilled water at an approximately 10⁷ cfu mL⁻¹. Plants were spray-inoculated using a handheld sprayer and then covered with plastic bags to maintain high humidity for 48 hours after inoculation and maintained at temperature 25±2 °C for the subsequent ten days, after which the plants were transplanted into soil and maintained under field conditions (locality Belgrade). Pepper plants inoculated with sterile distilled water served as

121 **untreated controls**. Pathogenicity testing was performed with four independent replicates, with
122 each replicate containing three plants (i.e. a total of 12 plants per strain).

123 We evaluated appearance of symptoms in the form of spots/lesions with haloes above the leaf
124 surface during 21 days of post-inoculation period. Disease severity was rated 21 days after
125 inoculation, using a modified 0–4 rating scale (0: symptomless leaves; 1: limited number of lesions
126 affecting up to 10% of the leaf area; 2: leaves with 11–49% of their surface affected; 3: 50–80% of
127 the surface affected; 4: leaves with more than 80% of the surface covered by lesions or leaves
128 completely dead) [32]. Scores were used to calculate the disease severity index (DSI) [32], which was
129 subjected to analysis of variance (ANOVA) and compared by Fisher's LSD test, with $p < 0.01$
130 considered statistically significant (Statistica Inc. software, version 14.0.1.25). A box-plot analysis
131 was conducted to illustrate the variation in disease severity index among the strains.

132 Bacterial strains were grown in King's B liquid medium at 28 °C and DNA extracted as described
133 previously at protocols.io [34]. Genomic DNA was extracted from frozen bacterial pellets using the
134 protocol described at protocols.io [35] with the Qiagen 67563 MagAttract HMW DNA Kit.

135 Genomic DNA was checked by agarose gel electrophoresis and quantified using a Qubit fluorometer
136 (Life Technologies). Whole-genome shotgun sequencing was performed on the Illumina NovaSeq
137 6000 platform to generate pairs of 151-nucleotide sequence reads at the University of Exeter
138 Sequencing Facility using the NEBNext Ultra FS II DNA Library Preparation Kit for Illumina from New
139 England Biolabs.

140 All command lines and configuration files for the computational analyses in this study are available
141 in the GitHub repository at <https://github.com/davidjstudholme/xanthomonas-euvesicatoria-serbia>
142 [36].

143 Prior to assembly, we performed filtering and trimming of the sequence reads using Trim Galore [37]
144 version 0.6.7, which utilizes Cutadapt [38] version 3.5. The command line is provided in the GitHub
145 repository that accompanies this manuscript. We assembled the data de novo using SPAdes 4.0.0
146 [39] via the Snippy v. 0.5.1 wrapper script. The command lines are provided in the GitHub
147 repository. Genome assemblies were submitted to GenBank [40, 41] via the NCBI Submission Portal
148 [42], after which they were annotated via the NCBI Prokaryotic Genome Annotation Pipeline (PGAP)
149 version 6.5 [43]. Assembly quality was assessed using CheckM version 1.2.4 [44]. The command line
150 is provided in the GitHub repository.

151 We generated an approximate maximum likelihood phylogenomic tree from genome sequence
152 assemblies using PhaME [45] and FastTree 2 [46] as described in the protocol at protocols.io [47].
153 The genome sequences included in the analysis are listed in Supplementary Table S1. The resulting
154 phylogenetic tree was rendered as graphics using the web-based Interactive Tree of Life (iTOL) [48].

155 We used two approaches to check for presence of reference genes and plasmids in our newly
156 sequenced genomes. One method was to perform BLASTN alignments against assembled genome
157 sequences from within the Proksee web application [49]. The other, complementary approach was
158 to align raw, unassembled genome sequencing reads against an assembled genome sequence using
159 BWA-mem [50] version 0.7.18 and default parameter values and options. Prior to BWA-mem
160 alignment, reads were first trimmed and filtered with TrimGalore as described in section 2.4. To
161 identify contigs that likely represent plasmid sequences, we additionally ran Platon 1.7 (in

162 “accuracy” mode) [51] against the Unicycler genome assemblies. Command lines and raw results are
163 in the GitHub repository.

164 To calculate ANI between assembled genome sequences, we used FastANI [52] version 1.1. The
165 command lines and raw results are provided in the GitHub repository.

166 We downloaded amino-acid sequences for predicted T3SS effectors on 13th June 2024 from the
167 EuroXanth DocuWiki [53]. We used TBLASTN to check for presence of each of the known T3SS
168 effector genes listed at the EuroXanth Docuwiki [53].

169 We identified single-nucleotide polymorphisms that distinguish between *Xeu* strains, from
170 fragments of genomic sequence reads versus the reference genome sequence of *Xeu* strain 85-10.
171 Alignment was performed using BWA-MEM 0.7.18 [50] with default settings, as described in the
172 GitHub repository [36]. This is a conservative approach that avoids false-positives SNPs arising from
173 errors in the de-novo assembly process. Custom scripts [36] identified SNPs across the genomes
174 where for all strains there is at least 10 x read coverage and at least 95 % consensus among the
175 aligned reads.

176 6. Results and discussion

177 6.1 Pathogenicity of the bacterial strains on pepper

178 All three tested strains (X13, X22 and X31) exhibited pathogenicity on inoculated pepper plants,
179 forming necrotic lesions with yellow halos ten days post-inoculation, which progressively spread
180 across existing and newly developed leaves over the following three weeks (Figure 1).

181 Strain X13 showed higher virulence than isolates X22 and X31, as evidenced by a statistically
182 significantly higher DSI (Figure 2). The DSI reached 29.83% for isolate X13, while it was 23.35% and
183 22.89% for isolates X22 and X31, respectively. Pepper plants inoculated with sterile distilled water
184 were symptomless.

185 Peppers in Serbia are predominantly cultivated from locally produced seeds, most of which belong
186 to autochthonous varieties that have been developed and maintained over generations.
187 Nevertheless, a smaller proportion of seeds and seedlings is imported, introducing potential
188 variability and, possibly, new sources of *Xeu*. Tomato, as another important host for xanthomonads
189 causing bacterial spot, relies mainly on imported seeds, which further complicates the tracing of
190 pathogen introduction routes. Due to these practices, combined with the wide distribution of the
191 pathogen in neighbouring countries such as Bulgaria, Montenegro, North Macedonia and Kosovo
192 [9, 10], it remains highly challenging to pinpoint the precise time or source of its introduction into
193 Serbian pepper and/or tomato crops. This situation highlights the need for continuous monitoring of
194 seed health and strict phytosanitary measures to limit the spread of bacterial spot pathogens.

195 6.2 Genome sequencing

196 We performed Illumina genome sequencing on the three *Xeu* strains X13, X22 and 31 and generated
197 contig-level genome assemblies of between 5.1 and 5.3 Mbp (see Table 1). The numbers of contigs
198 ranged from 76 to 98 and N_{50} was between 174.8 and 294.2 kbp. The G+C content was 64.5 %. We
199 assessed the genome assemblies using CheckM, which estimates completeness by checking for the
200 presence of single-copy marker genes that are expected to be universally present across
201 *Xanthomonas* genomes. Our genome assemblies contained 1159 of the 1163 markers as single

202 copies and one ¹ of the markers duplicated, with CheckM reporting a completeness score of 99.63 %
203 (see Table 1).

204 6.3 Serbian *X. euvesicatoria* strains are related to strains from Bulgaria and Türkiye

205 Phylogenomic analysis of currently available *Xeu* genome assemblies revealed six clades, each
206 containing four or more strains (Figure 3); additionally, the outlier strain XVP26 [54] fell outside the
207 six clades. Our tree is consistent with previously published phylogenies [55–58]. We are not aware of
208 any standard nomenclature for these clades and so have numbered them 1 through to 6, as
209 indicated in Figure 3. Clade 1 includes the type strain ATCC 11633 [12, 59] and the widely used
210 reference strain 85-10 [60].

211 Strains from the Balkan peninsula fall into two clades. Specifically, strain 83M from North Macedonia
212 [31] falls within Clade 2 along with strains from Canada, Türkiye and Vietnam. This North
213 Macedonian strain is particularly similar to strain DC 97 P2A [59] from Canada, possibly highlighting
214 the capacity for this pathogen to be disseminated over long distances.

215 Besides strain 83M in Clade 2, the other Balkan strains fall into Clade 6. Supplementary Figure S1
216 shows a phylogenomic tree for Clade 6 only, with other clades excluded to improve clarity. Figure 4
217 shows just those strains in Clade 6 for which genome sequence reads are publicly available. Clade 6
218 includes strain 66b isolated in Bulgaria [31] in 2012 as well as the three Serbian strains, plus strains
219 from Canada [59], Taiwan [54, 59], Türkiye [61], USA [54] and Vietnam [62]. Within this clade, the
220 Serbian strain X13 is nearly identical (99.8696 % ANI) to the Bulgarian strain 66b (Supplementary
221 Figure S1). Serbian strains X22 and X31 are nearly identical to each other (99.9983 % ANI) and are
222 located on a different sub-branch in Clade 6, nearly identical to strain Tu-10 isolated from the
223 Southeastern Anatolia region of Türkiye in 2020. This pattern suggests that there may have been at
224 least two introductions of the pathogen into the Srem region of Vojvodina (Irig), Serbia: one
225 introduction is represented by X13 and may be epidemiologically linked to neighbouring Bulgaria,
226 while X22 and X31 represent at least ⁴⁹ separate introduction that may be linked to Türkiye. Based
227 on the currently available strains and sequence data, it is not possible to determine the direction nor
228 the date of the pathogen's incursions.

229 We identified ⁵³ single-nucleotide polymorphisms (SNPs) in the core genome, using ⁷ alignments of
230 genomic sequence reads versus the 85-10 reference genome sequence; this approach avoids errors
231 introduced during the de-novo assembly process. The numbers of SNPs separating each strain are
232 summarised in the Supplementary Figure S2. Strains X22 and X31 are separated from each other by
233 22 SNPs, and they are separated from strain Tu-10 by 23 and 13 SNPs respectively. Strain X13 is
234 separated from strain 66b by 40 SNPs. These SNPs are listed in Supplementary Tables S2 - S5.

235 6.4 Comparison against *Xeu* 85-10 reference chromosome

236 We compared the genome sequence data from the three Serbian strains against the high-quality
237 sequence for the chromosome of the *Xeu* strain 85-10 [60] reference strain 85-10 (GenBank:
238 AM039952.1). Supplementary Figure S3 shows that most of this reference chromosome is conserved
239 in X13, X22 and X31. However, there are several regions of the 85-10 chromosome that are not
240 conserved in the Serbian strains.

241 The 25.2-kb chromosomal region spanning approximately positions 244 – 269 kb in the 85-10
242 chromosome is not conserved in the Serbian strains. This region includes loci XCV0209 - XCV0226.
243 Most of the predicted coding sequences in this region are of unknown function. However, it does

244 include putative transposase (XCV0214), IS 1477 transposase (XCV0222, XCV0223) and IS xac2
245 transposase (XCV0228, XCV0229), suggesting that it represents a mobile element.

246 The 85-10 chromosome contains a 14-kb region with homology to the filamentous phage phi-Lf at
247 approximately 2,784 kb to 2,798 kb [60] and likely represents a prophage that has integrated into
248 the bacterial genome. Part of this phage-like region of the 85-10 chromosome is missing from the
249 Serbian strains (see Supplementary Figure S3). Also in this vicinity is a large region of the 85-10
250 chromosome that is not conserved in the Serbian strains, nor in other strains belonging to *Xeu* Clade
251 6. This region contains numerous genes of unknown function. It also contains at least four copies of
252 insertion sequence IS 6100 and several genes whose functions are predicted (Figure 5). This includes
253 *gcvA*, *tniB*, *zitB*, *copA*, *strAB*, *qseBC* and *dsbG*.

254 Between the *tRNA-Thr* and *cyoA* genes in the 85-10 chromosome, are two IS 1477 insertion
255 sequences and an IS xac2 transposase gene adjacent to the *xopG* gene that encodes a type-three
256 secretion system effector, XopG. This *xopG* virulence effector gene is not conserved in the three
257 Serbian strains. This is consistent with previous studies that have shown that the chromosomal *xopG*
258 gene is somewhat unique to strain 85-10 [63].

259 6.5 Strain X13 (but not X22 and X31) contains plasmids similar to pXap41 and pXCV183

260 Having compared sequences against the reference strain 85-10 chromosome, we investigated
261 whether there was any evidence of plasmids in the sequencing data for Serbian strains X13, X22 and
262 X31. Platon identified nine contigs in X13, six contigs in X22 and five contigs X31 that likely represent
263 plasmid sequences; these contigs are listed in Table 2.

264 BLASTN searches confirmed that several of the contigs identified by Platon share similarity with
265 previously reported sequences of *Xanthomonas* plasmids; results are summarized in Figure 4. The
266 reference strain 85-10 contains a large plasmid pXCV183, which includes genes for the virulence
267 effector genes *xopH*, *avrBs1* and *xopAX*. BLASTN alignments of the X13 genome sequence against
268 pXCV183 revealed extensive sequence conservation of much of its length but not all (Figure 5). There
269 was no sequence similarity to *xopH* nor *avrBs1* but there was conservation of *xopAX*. The X13
270 genome gave complete coverage and 100% sequence identity against the pXCV183-like plasmid
271 pLMG930.2 in the genome of *X. euvesicatoria* pv. *euvesicatoria* strain LMG930 [64]. This suggests
272 that Serbian strain X13 harbours a pXCV183-like plasmid identical or nearly identical to pLMG930.2,
273 which includes the *xopAX* gene. The other two Serbian strains (X22 and X31) showed only very
274 limited sequence similarity to pLMG930.2, indicating that they do not share this pXCV183-like
275 plasmid (Supplementary Figure S4).

276 The Serbian strain X13 also shares extensive sequence conservation over most of the length of
277 plasmid pXap41 [65] from *Xanthomonas arboricola* pv. *pruni* strain CFBP 5530 (RefSeq:
278 NC_016053.1); see Figure 6. This sequence conservation includes the virulence effector gene *xopE*
279 (Supplementary Figure S5). This suggests that strain X13 contains a pXap41-like plasmid. Serbian
280 strains X22 and X31 contains sequences that match only about half of the pXap41 plasmid, including
281 the *xopE3* gene. This suggest that these strains might contain another distinct plasmid that shares
282 some limited similarity with pXap41; unfortunately, the assembly of only short sequence reads
283 precludes the complete assembly of plasmid sequences and resolution would require future
284 sequencing with long reads. It was previously reported that pXap41 was sufficiently unique to
285 *Xanthomonas arboricola* pv. *pruni* that it could be used for pathovar detection and identification
286 [65]. However, its presence in at least one *Xeu* strain calls its diagnostic usefulness into question.

287 **6.6 Strains X13, X22 and X31 have sequences matching 75- and 46-kbp plasmids from strain**
288 **Xe173**

289 All three Serbian strains (X13, X22 and X31) showed conservation of almost the entire length of a 75-
290 bp plasmid from Xe173, a *Xeu* strain of unknown origin, isolated from pepper and sequenced by at
291 the Chonnam National University, Korea (BioSample: SAMN42326212); see Supplementary Figure
292 S6. This plasmid harbours virulence effector genes *avrBs3*, *xopE3*, *xopAQ* and *xopBA*.

293 **6.7 Type-III secretion system effectors**

294 Genomes of strains X13, X22 and X31 contained genes for all of the previously defined [18] core
295 effectors found in xanthomonads that infect tomato or pepper; that is effectors *AvrBs2*, *XopD*,
296 *XopE2*, *XopF1*, *XopK*, *XopL*, *XopN*, *XopQ*, *XopR*, *XopX*, *XopZ1* and *XopAD*. Also present in all three
297 genomes were genes for *XopC1*, *XopE1*, *XopF2*, *XopI*, *XopJ1*, *XopJ3*, *XopO*, *XopP*, *XopAA*, *XopAI*,
298 *XopAK*, *XopAP*, all of which are commonly found in *X. euvesicatoria*. These genes, like the core
299 effector genes, are located on the chromosome of reference strain 85-10 [60]. Additionally, the
300 three Serbian strains all contain genes for *AvrBs3*, *XopE3* and *XopAQ* and *XopBA*, located on a 75-kbp
301 plasmid. They lack the chromosomal gene for *XopG*.

302 Despite sharing most of their effector repertoires in common, there are some differences between
303 Serbian strain X13 versus X22 and X31. Strain X13 contains a gene for *XopAX*, located on a pXCV183-
304 like plasmid that is not found in strains X22 and X31.

305 Additionally, strain X13 shares extensive sequence similarity to the pXCV183 plasmid, including T3SS
306 effector gene *xopAX* and X13 shares extensive sequence similarity with plasmid pXap41, including
307 T3SS effector gene *xopE3*. None of the three Serbian strains share the 31-kb plasmid pLMG730.4
308 that is seen in several Vietnamese and Canadian strains within this clade of *Xeu*.

309 This protein, encoded by the *xopAX* gene, is one of four novel effectors discovered in strain 85-10 by
310 genome sequence analysis followed by a laboratory-based assay for translocation into host cells
311 [23]. The molecular function of *XopAX* is unknown; it has no clear homologues or known biochemical
312 activity. Being plasmid-encoded and patchily distributed among *Xeu* strains, *XopAX* is a candidate for
313 recent horizontal transfer and could contribute to strain-specific host interactions or virulence
314 differences [63]. Therefore, we hypothesise that the presence of *xopAX* gene in strain X13 might
315 contribute to its increased virulence.

316 **6.8 Conclusion**

317 These data will be a useful resource for future molecular epidemiology and genomic surveillance of
318 this pathogen in the Balkan region, augmenting the previously available draft genome sequences of
319 *Xeu* strains 66b (Bulgaria) and 83M (North Macedonia). The genome sequences reveal that Serbian
320 strains fall within the same clade as strain 66b and not the same clade as 83M. Although Serbian
321 strain X13 is genetically almost identical to Bulgarian strain 66b, there are genetic differences among
322 Serbian strains, notably in respect of plasmid-like sequences, and with strains X22 and X31 being
323 more distantly related. These differences, e.g. in the virulence effector *xopAX*, presumably
324 contribute to the observed difference in their virulence.

325 **7. Figures and tables**



326
327 **Figure 1. Representative examples of *Xanthomonas euvesicatoria* pv. *euvesicatoria* on pepper**
328 **plants. The** photographs show symptoms 10 days (A) and 21 days (B) post-inoculation with strain
329 X13.

330

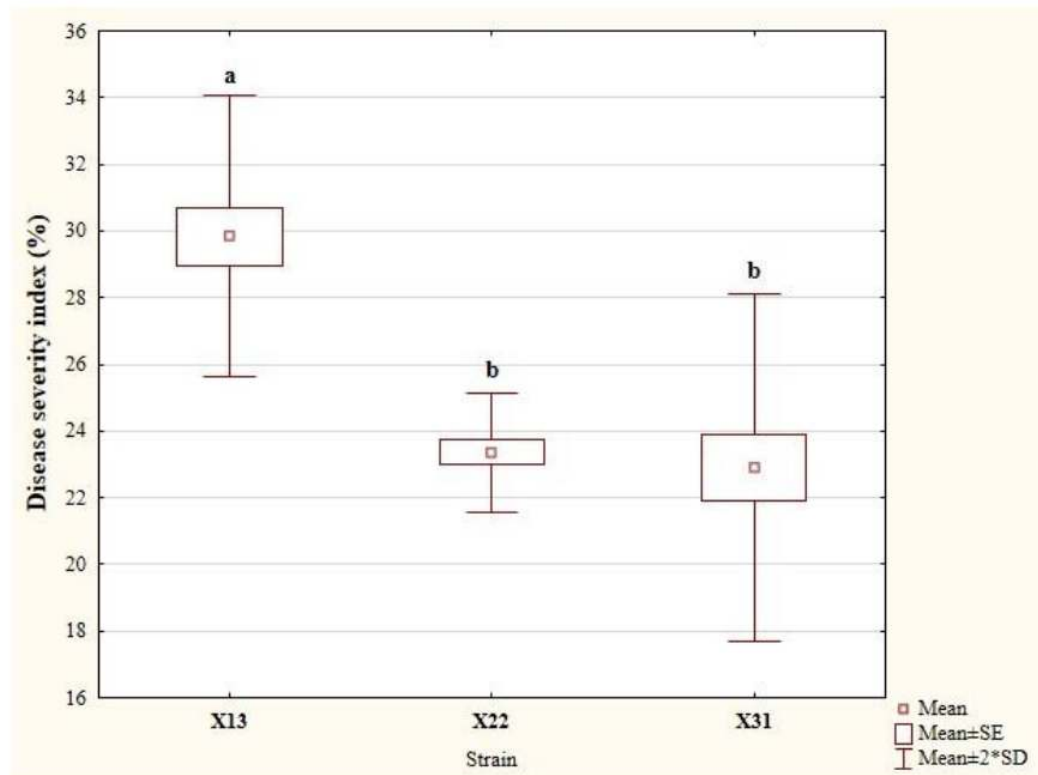
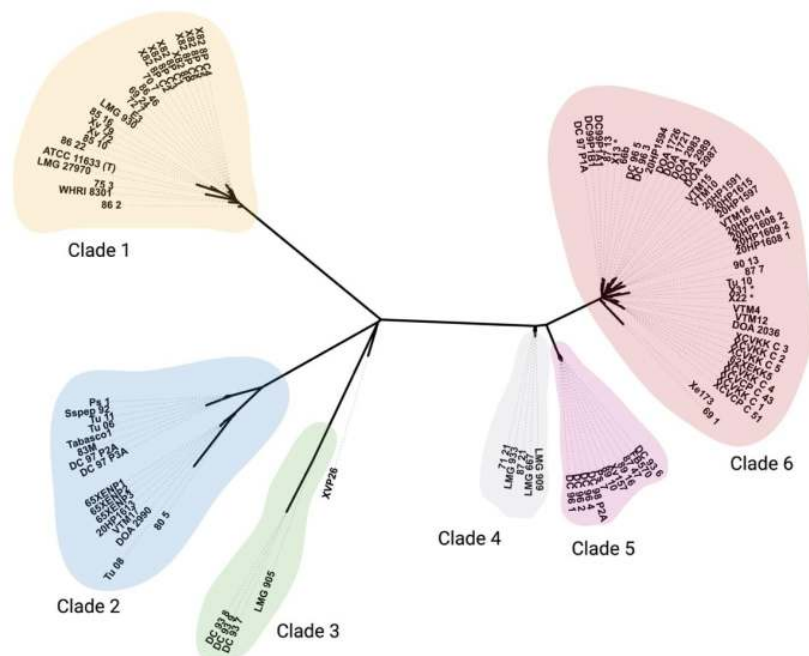


Figure 2. Disease severity index (DIS) values for *Xanthomonas euvesicatoria* pv. *euvesicatoria* strains X13, X22 and X31 on pepper plants. Significant differences are presented with a small letter above the bar.



338 **Figure 3. Phylogenetic placement of strains X13, X22, and X31 within *Xanthomonas euvesicatoria***
339 **pv. *euvesicatoria*.** The tree was inferred using an approximate maximum likelihood approach
340 implemented in FastTree 2 [46], based on the core genome alignment identified by PhaME [45]. The
341 visualization was rendered in the Interactive Tree of Life [48]. In addition to the three Serbian strains
342 sequenced in this study, the analysis includes previously published genomes listed in Supplementary
343 Table S1. The six major clades are shaded in different colours. Strain ATCC 11633, located in Clade 1,
344 is marked with “(T)” to indicate its designation as the pathotype and type strain. The three Serbian
345 strains are indicated with an asterisk (*) and are placed within Clade 6.

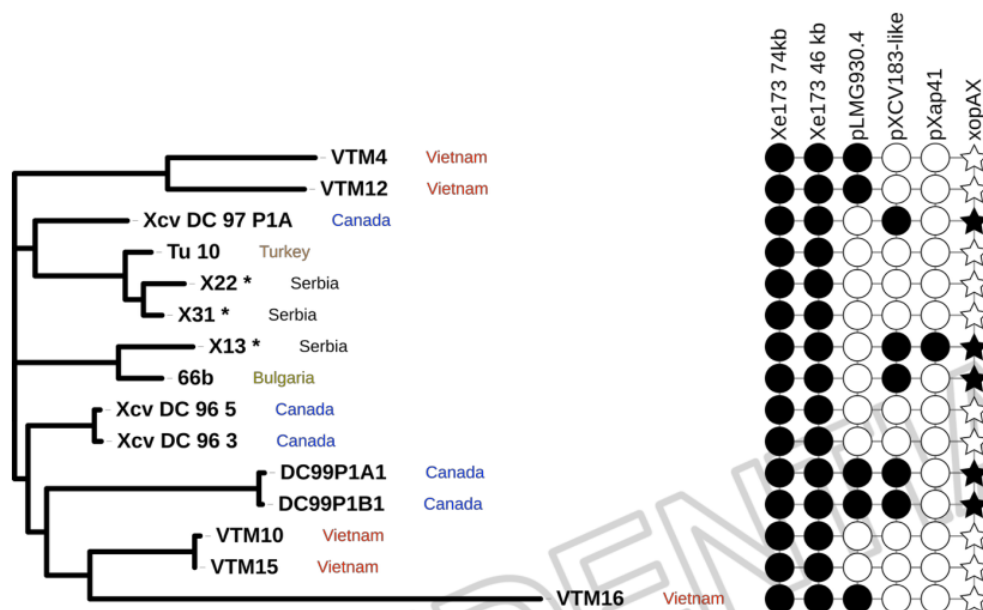


Figure 4. Phylogenetic position of strains X13, X22 and X31 within Clade 6. The approximate maximum likelihood tree is based on core genome sequences, generated using PhaME [45] and FastTree 2 [46]. In addition to the genomes of three Serbia strains, the tree also includes previously published genome sequences, which are listed in Supplementary Table S1. Presence and absence of plasmid sequences are indicated by black and white circles respectively. Presence and absence of the xopAX effector gene are indicated by black and white stars respectively. Presence and absence were inferred from BWA-mem alignments of sequence reads against the relevant reference sequences, as illustrated in Supplementary Figures S3 - S7. The tree was graphically rendered using the Interactive Tree of Life [48]. Each of the three Serbian strains sequenced in this study is marked with an asterisk (*).

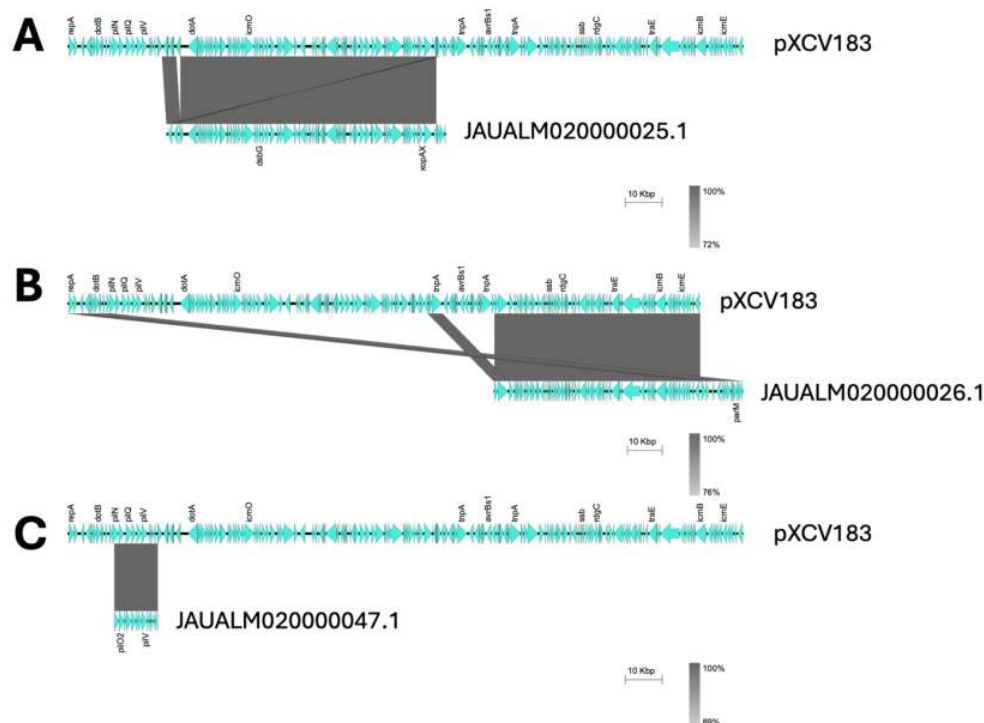


Figure 5. The genome of *Xeu* strain X13 contains sequences similar to plasmid pXCV183. Three contigs from the *Xeu* X13 genome assembly are aligned against the sequence of plasmid pXCV183 [60] using BLASTN within EasyFig [66]. The GenBank accession numbers of the contigs are indicated at the right side of each contig. Panels A, B and C each show pXCV183 aligned to one of the X13 genome contigs.

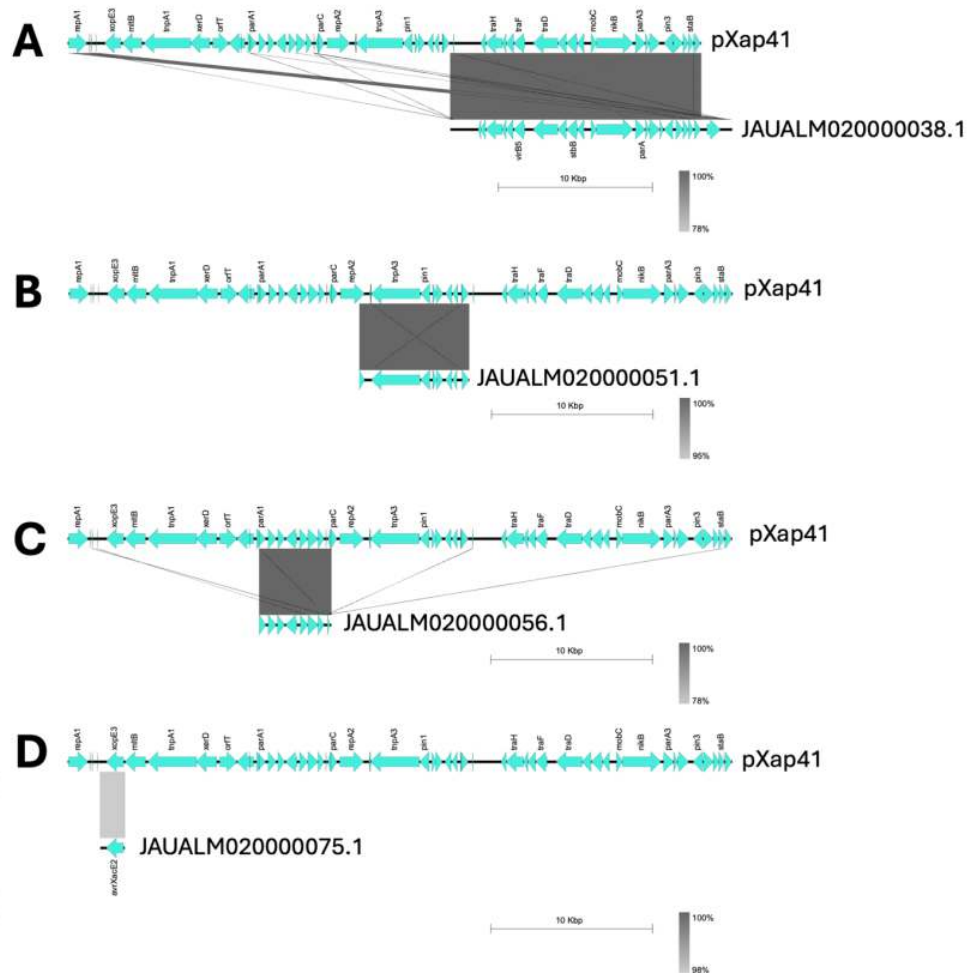


Figure 6. The genome of *Xeu* strain X13 contains sequences similar to plasmid pXap41. Four contigs from the *Xeu* X13 genome assembly are each aligned against the sequence of plasmid pXap41 [65] using BLASTN within EasyFig [66]. The GenBank accession numbers of the contigs are indicated at the right side of each contig. The gene names are directly taken from the annotation in the GenBank database; note that the *avrXacE2* is a previous name for effector gene whose standardised name is *xopE2*. Panels A, B, C and D each show pXap41 aligned to one of the X13 genome contigs.

Table 1. Summary of genome sequence assembly results. Completeness and contamination were estimated using CheckM [44]. Other metrics were calculated using QUAST [67]. All genome assemblies and raw sequence data are available via BioProject PRJNA985260.

Strain name	CheckM contamination score (%) *	Number of contigs	Total length of assembly (Mbp)	N ₅₀ length (kbp)	L ₅₀ count	Assembly accession number
X13 (= WHRI10185)	0.49	98	5.3	174.8	9	GCA_030345975.2
X22 (= WHRI10186)	0.03	76	5.1	294.2	6	GCA_030345985.2
X31 (= WHRI10187)	0.03	76	5.1	244.3	7	GCA_030345955.2

* All three genome assemblies had a CheckM completeness score of 99.63 % for the 1163 *Xanthomonas* marker set.

379

380 **Table 2. Platon identifies contigs potentially representing plasmid sequences.** Genome sequence
381 assemblies of strains X13, X22 and X31 were searched for likely plasmid sequences using Platon [51]
382 in the default “accuracy” mode.

Strain X13					
Accession number	Length (bp)	BLASTN match description	BLASTN match accession number	Nucleotide sequence identity (%)	
JAUALM020000026.1	72,015	pXCV183	AM039951.1	99.98	
JAUALM020000047.1	11,728	pXCV183	AM039951.1	99.88	
JAUALM020000038.1	18,296	pXap41	FR875157.1	99.98	
JAUALM020000032.1	30,942	Xe173 46-kbp	CP170255.1	100	
JAUALM020000035.1	24,998	Xe173 75-kbp	CP170255.1	100	
JAUALM020000044.1	12,819	Xe173 75-kbp	CP170255.1	99.85	
JAUALM020000055.1	4575	Xe173 75-kbp	CP170255.1	100	
JAUALM020000067.1	1798	Xe173 75-kbp	CP170255.1	100	
JAUALM020000069.1	1692	Xe173 75-kbp	CP170255.1	100	
Strain X22					
Accession number	Length (bp)	BLASTN match	BLASTN match accession number	Nucleotide sequence identity (%)	
JAUAL020000023.1	30,942	Xe173 46-kbp	CP170255.1	100	
JAUAL020000027.1	21,713	Xe173 75-kbp	CP170254.1	100	
JAUAL020000035.1	10,600	Xe173 75-kbp	CP170254.1	100	
JAUAL020000037.1	10,214	Xe173 75-kbp	CP170254.1	99.81	
JAUAL020000042.1	6087	Xe173 75-kbp	CP170254.1	100	
JAUAL020000048.1	2494	Xe173 75-kbp	CP170254.1	100	
Strain X31					

Accession number	Length (bp)	BLASTN match	BLASTN match accession number	Nucleotide sequence identity (%)	
JAUALK020000025.1	32,629	Xe173 46-kbp	CP170255.1	100	
JAUALK020000029.1	21,710	Xe173 75-kbp	CP170254.1	100	
JAUALK020000036.1	12,880	Xe173 75-kbp	CP170254.1	99.85	
JAUALK020000038.1	10,803	Xe173 75-kbp	CP170254.1	100	
JAUALK020000044.1	6087	Xe173 75-kbp	CP170254.1	100	

8. Author statements

8.1 Author contributions

Author Contributions: Conceptualization: T.P.M. and D.J.S; Investigation: T.P.M., S.G., R.I., A.J., D.B., J.V.; Resources: T.P.M., R.I., A.J.; Data curation, D.J.S.; Writing—original draft preparation, D.J.S and T.P.M.; Writing—review and editing: S.F.G., J.V., T.P.M. and D.J.S.; Supervision, M.G.; Funding acquisition, T.P.M., M.G., J.V., D.J.S.

8.2 Conflicts of interest

The authors declare that there are no conflicts of interest.

8.3 Funding information

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9. References

1. Petrović M, Savić B, Cvijanović V. Financial aspects of pepper (*Capsicum annuum* L) production on family farms in Serbia. *Ekonomika Poljopr* 2021;68:1015–1028.

- 411 2. **Abrahamian P, Klein-Gordon JM, Jones JB, Vallad GE.** Epidemiology, diversity, and management
412 of bacterial spot of tomato caused by *Xanthomonas perforans*. *Appl Microbiol Biotechnol*
413 2021;105:6143–6158.
- 414 3. **Obradovic A, Mavridis A, Rudolph K, Arsenijevic M, Mijatovic M.** Bacterial Diseases of Pepper
415 in Yugoslavia. In: De Boer SH (editor). *Plant Pathogenic Bacteria*. Dordrecht: Springer
416 Netherlands. pp. 255–258.
- 417 4. **Obradović A, Mavridis A, Rudolph K, Arsenijević M.** Bacterial spot of capsicum and tomato in
418 Yugoslavia. *EPPO Bull* 2000;30:333–336.
- 419 5. **Potnis N, Timilsina S, Strayer A, Shantharaj D, Barak JD, et al.** Bacterial spot of tomato and
420 pepper: diverse *Xanthomonas* species with a wide variety of virulence factors posing a
421 worldwide challenge. *Mol Plant Pathol* 2015;16:907–920.
- 422 6. *Xanthomonas euvesicatoria* pv. *euvesicatoria* (XANTEU). <https://gd.eppo.int/taxon/XANTEU>
423 (accessed 29 September 2025).
- 424 7. **Jones JB, Lacy GH, Bouzar H, Stall RE, Schaad NW.** Reclassification of the *Xanthomonads*
425 Associated with Bacterial Spot Disease of Tomato and Pepper. *Syst Appl Microbiol* 2004;27:755–
426 762.
- 427 8. **Jones JB, Stall RE, Bouzar H.** Diversity among *xanthomonads* pathogenic on pepper and tomato.
428 *Annu Rev Phytopathol* 1998;36:41–58.
- 429 9. **Aysan Y, Sahin F.** Occurrence of bacterial spot disease, caused by *Xanthomonas axonopodis* pv.
430 *vesicatoria*, on pepper in the eastern Mediterranean region of Turkey. *Plant Pathol*
431 2003;52:781–781.
- 432 10. **Popović T, Menković J, Pantelić M, Obradović A.** First Report of *Xanthomonas euvesicatoria*
433 Causing Bacterial Leaf Spot of Pepper (*Capsicum annuum*) in Montenegro. *Plant Dis*
434 2022;106:1514.
- 435 11. **Vancheva T, Bogatzevska N, Moncheva P, Mitrev S, Vernière C, et al.** Molecular Epidemiology
436 of *Xanthomonas euvesicatoria* Strains from the Balkan Peninsula Revealed by a New Multiple-
437 Locus Variable-Number Tandem-Repeat Analysis Scheme. *Microorganisms* 2021;9:536.
- 438 12. **Xhemali B, Bellameche F, Gjinojci G, Modica F, Biondi E, et al.** First report of *Xanthomonas*
439 *euvesicatoria* pv. *euvesicatoria* causing bacterial leaf spot of pepper in Kosovo. *J Plant Pathol*
440 2024;107:779–780.
- 441 13. **Arsenijević M.** *Bakterioze biljaka*. Naučna knjiga; 1988.
- 442 14. **Balaž J.** Pegavost lišća paprike prouzrokovana bakterijom *Xanthomonas campestris* pv.
443 *vesicatoria*. *Savrem Poljopr Vanred Broj* 1994;42:341–345.
- 444 15. **EFSA Panel on Plant Health (PLH).** Scientific Opinion on the pest categorisation of *Xanthomonas*
445 *campestris* pv. *vesicatoria* (Doidge) Dye. *EFSA J*;12. Epub ahead of print June 2014. DOI:
446 10.2903/j.efsa.2014.3720.

- 447 16. Bianco MI, Ponso MA, Garita-Cambronero J, Conforte VP, Galván TE, *et al.* Genomic and
448 phenotypic insight into *Xanthomonas vesicatoria* strains with different aggressiveness on
449 tomato. *Front Microbiol* 2023;14:1185368.
- 450 17. Jones JB, Bouzar H, Stall RE, Almira EC, Roberts PD, *et al.* Systematic analysis of xanthomonads
451 (*Xanthomonas* spp.) associated with pepper and tomato lesions. *Int J Syst Evol Microbiol*
452 2000;50:1211–1219.
- 453 18. Potnis N, Krasileva K, Chow V, Almeida NF, Patil PB, *et al.* Comparative genomics reveals
454 diversity among xanthomonads infecting tomato and pepper. *BMC Genomics* 2011;12:146.
- 455 19. Preangtong Y, Patarapuwadol S, Phiriyangkul P, Kanhayart T, Kositcharoenkul N, *et al.*
456 Characterisation and Genomic Diversity of *Xanthomonas* Species Causing Bacterial Spot Disease
457 of Tomato and Pepper in Thailand. *Plant Pathol* 2025;74:1315–1334.
- 458 20. Subedi A, Barrera LBT de la, Lewis Ivey M, Egel D, Kebede M, *et al.* Population genomics reveals
459 an emerging lineage of *Xanthomonas* perforans on pepper. *Phytopathology*. Epub ahead of print
460 11 July 2023. DOI: 10.1094/PHYTO-04-23-0128-R.
- 461 21. Popov G, Fraiture M, Brunner F, Sessa G. Multiple *Xanthomonas euvesicatoria* Type III Effectors
462 Inhibit flg22-Triggered Immunity. *Mol Plant-Microbe Interactions*® 2016;29:651–660.
- 463 22. Roden JA, Belt B, Ross JB, Tachibana T, Vargas J, *et al.* A genetic screen to isolate type III
464 effectors translocated into pepper cells during *Xanthomonas* infection. *Proc Natl Acad Sci*
465 2004;101:16624–16629.
- 466 23. Teper D, Burstein D, Salomon D, Gershovitz M, Pupko T, *et al.* Identification of novel
467 *Xanthomonas euvesicatoria* type III effector proteins by a machine-learning approach. *Mol Plant*
468 *Pathol* 2016;17:398–411.
- 469 24. Thieme F, Szczesny R, Urban A, Kirchner O, Hause G, *et al.* New type III effectors from
470 *Xanthomonas campestris* pv. *vesicatoria* trigger plant reactions dependent on a conserved N-
471 myristoylation motif. *Mol Plant-Microbe Interact MPMI* 2007;20:1250–1261.
- 472 25. Galán JE, Lara-Tejero M, Marlovits TC, Wagner S. Bacterial Type III Secretion Systems:
473 Specialized Nanomachines for Protein Delivery into Target Cells. *Annu Rev Microbiol*
474 2014;68:415–438.
- 475 26. Schreiber KJ, Chau-Ly IJ, Lewis JD. What the Wild Things Do: Mechanisms of Plant Host
476 Manipulation by Bacterial Type III-Secreted Effector Proteins. *Microorganisms* 2021;9:1029.
- 477 27. An S-Q, Potnis N, Dow M, Vorhölter F-J, He Y-Q, *et al.* Mechanistic insights into host adaptation,
478 virulence and epidemiology of the phytopathogen *Xanthomonas*. *FEMS Microbiol Rev* 2019;1–
479 32.
- 480 28. Catara V, Cubero J, Pothier JF, Bosis E, Bragard C, *et al.* Trends in Molecular Diagnosis and
481 Diversity Studies for Phytosanitary Regulated *Xanthomonas*. *Microorganisms* 2021;9:862.
- 482 29. Jacques M-A, Arlat M, Boulanger A, Boureau T, Carrère S, *et al.* Using Ecology, Physiology, and
483 Genomics to Understand Host Specificity in *Xanthomonas*. *Annu Rev Phytopathol* 2016;54:163–
484 187.

- 485 30. **Timilsina S, Potnis N, Newberry EA, Liyanapathirana P, Iruegas-Bocardo F, et al.**
486 Xanthomonas diversity, virulence and plant–pathogen interactions. *Nat Rev Microbiol*
487 2020;18:415–427.
- 488 31. **Vancheva T, Lefeuvre P, Bogatzewska N, Moncheva P, Biology F, et al.** Draft Genome Sequences
489 of Two Xanthomonas euvesicatoria Strains from the Balkan Peninsula. 2015;3:6–7.
- 490 32. **Milovanović TP, Jelušić A, Iličić R, Trkulja N, Damjanović J, et al.** Biocontrol potential of
491 indigenous pepper seed *Bacillus* strains against *Xanthomonas euvesicatoria*. *Pest Manag Sci*
492 2025;81:4875–4885.
- 493 33. **Koenraadt H, Van Betteray B, Germain R, Hiddink G, Jones JB, et al.** Development of specific
494 primers for the molecular detection of bacterial spot of pepper and tomato. *Acta Horti*
495 2009;99–102.
- 496 34. **Grant M, Greer, Vicente V Joana.** Culturing Xanthomonas v1. Epub ahead of print 3 August
497 2022. DOI: 10.17504/protocols.io.ewov1nr92gr2/v1.
- 498 35. **Grant M, Greer S, Vicente J.** DNA extraction using the Qiagen 67563 MagAttract HMW DNA Kit
499 (48) v1. Epub ahead of print 3 August 2022. DOI: 10.17504/protocols.io.5jyl89428v2w/v1.
- 500 36. **Studholme DJ.** davidstudholme/xanthomonas-euvesicatoria-serbia: v1.0r. Epub ahead of print
501 24 September 2025. DOI: 10.5281/ZENODO.17194556.
- 502 37. **Krueger F.** Babraham Bioinformatics - Trim Galore!
503 http://www.bioinformatics.babraham.ac.uk/projects/trim_galore/ (accessed 14 July 2020).
- 504 38. **Martin M.** Cutadapt removes adapter sequences from high-throughput sequencing reads.
505 *EMBnet.journal* 2011;17:10–12.
- 506 39. **Bankevich A, Nurk S, Antipov D, Gurevich A a, Dvorkin M, et al.** SPAdes: a new genome
507 assembly algorithm and its applications to single-cell sequencing. *J Comput Biol J Comput Mol*
508 *Cell Biol* 2012;19:455–77.
- 509 40. **Benson DA.** GenBank. *Nucleic Acids Res* 2004;33:D34–D38.
- 510 41. **Wick RR, Judd LM, Gorrie CL, Holt KE.** Unicycler: Resolving bacterial genome assemblies from
511 short and long sequencing reads. *PLOS Comput Biol* 2017;13:e1005595.
- 512 42. **Sayers EW, Bolton EE, Brister JR, Canese K, Chan J, et al.** Database resources of the national
513 center for biotechnology information. *Nucleic Acids Res* 2022;50:D20–D26.
- 514 43. **Tatusova T, DiCuccio M, Badretdin A, Chetvernin V, Nawrocki EP, et al.** NCBI prokaryotic
515 genome annotation pipeline. *Nucleic Acids Res* 2016;44:6614–24.
- 516 44. **Chklovski A, Parks DH, Woodcroft BJ, Tyson GW.** CheckM2: a rapid, scalable and accurate tool
517 for assessing microbial genome quality using machine learning. *Nat Methods* 2023;20:1203–
518 1212.

- 519 45. **Shakya M, Ahmed SA, Davenport KW, Flynn MC, Lo C-C, et al.** Standardized phylogenetic and
520 molecular evolutionary analysis applied to species across the microbial tree of life. *Sci Rep*
521 2020;10:1723.
- 522 46. **Price MN, Dehal PS, Arkin AP.** FastTree 2 – Approximately Maximum-Likelihood Trees for Large
523 Alignments. *PLoS ONE* 2010;5:e9490.
- 524 47. **Studholme DJ.** Phylogenomic analysis of *Xanthomonas* v1. Epub ahead of print 3 August 2022.
525 DOI: 10.17504/protocols.io.261geny57g47/v1.
- 526 48. **Letunic I, Bork P.** Interactive Tree Of Life (iTOL) v5: an online tool for phylogenetic tree display
527 and annotation. *Nucleic Acids Res* 2021;49:W293–W296.
- 528 49. **Grant JR, Enns E, Marinier E, Mandal A, Herman EK, et al.** Proksee: in-depth characterization
529 and visualization of bacterial genomes. *Nucleic Acids Res* 2023;51:W484–W492.
- 530 50. **Li H.** Aligning sequence reads, clone sequences and assembly contigs with BWA-MEM. 2013;3.
- 531 51. **Schwengers O, Barth P, Falgenhauer L, Hain T, Chakraborty T, et al.** Platon: identification and
532 characterization of bacterial plasmid contigs in short-read draft assemblies exploiting protein
533 sequence-based replicon distribution scores. *Microb Genomics* 2020;6:e000398.
- 534 52. **Jain C, Rodriguez-R LM, Phillippy AM, Konstantinidis KT, Aluru S.** High throughput ANI analysis
535 of 90K prokaryotic genomes reveals clear species boundaries. *Nat Commun* 2018;9:5114.
- 536 53. **Costa J, Pothier JF, Bosis E, Boch J, Kölliker R, et al.** A Community-Curated DokuWiki Resource
537 on Diagnostics, Diversity, Pathogenicity, and Genetic Control of *Xanthomonas*. *Mol Plant-*
538 *Microbe Interactions*® 2024;37:347–353.
- 539 54. **Kaur A, Minsavage GV, Potnis N, Jones JB, Goss EM.** Evolution of copper resistance in
540 *Xanthomonas euvesicatoria* pv. *perforans* population. *mSystems* 2024;e01427-24.
- 541 55. **Dhakal U, Dobhal S, Alvarez AM, Arif M.** Phylogenetic Analyses of *Xanthomonas* Causing
542 Bacterial Leaf Spot of Tomato and Pepper: *Xanthomonas euvesicatoria* Revealed Homologous
543 Populations Despite Distant Geographical Distribution. *Microorganisms* 2019;7:462.
- 544 56. **Jibrin MO, Potnis N, Timilsina S, Minsavage GV, Vallad GE, et al.** Genomic Inference of
545 Recombination-Mediated Evolution in *Xanthomonas euvesicatoria* and *X. perforans*. *Appl*
546 *Environ Microbiol* 2018;84:e00136-18.
- 547 57. **Roach R, Mann R, Gambley CG, Chapman T, Shivas RG, et al.** Genomic sequence analysis
548 reveals diversity of Australian *Xanthomonas* species associated with bacterial leaf spot of
549 tomato, capsicum and chilli. *BMC Genomics* 2019;20:310.
- 550 58. **Subedi A, Iruegas-Bocardo F, Luo L, Minsavage GV, Roberts PD, et al.** Amylase-associated
551 genetic pattern in *Xanthomonas euvesicatoria* on pepper. *Appl Environ Microbiol* 2024;e01313-
552 24.
- 553 59. **Tambong JT, Xu R, Cuppels D, Chapados J, Gerdis S, et al.** Whole-Genome Resources and
554 Species-Level Taxonomic Validation of 89 Plant-Pathogenic *Xanthomonas* Strains Isolated from
555 Various Host Plants. *Plant Dis* 2022;106:1558–1565.

- 556 60. **Thieme F, Koebnik R, Bekel T, Berger C, Boch J, et al.** Insights into genome plasticity and
557 pathogenicity of the plant pathogenic bacterium *Xanthomonas campestris* pv. *vesicatoria*
558 revealed by the complete genome sequence. *J Bacteriol* 2005;187:7254–66.
- 559 61. **Subedi A, Kara S, Aysan Y, Minsavage GV, Timilsina S, et al.** Draft genome sequences of 11
560 *Xanthomonas* strains associated with bacterial spot disease in Turkey. *Access Microbiol*
561 2023;5:acmi000586.v3.
- 562 62. **Subedi A, Nga NTT, Tien DTK, Minsavage GV, Roberts PD, et al.** Draft genomes announcement
563 of Vietnamese *Xanthomonas euvesicatoria* strains causing bacterial spot on pepper. *Access*
564 *Microbiol* 2024;6:000741.v3.
- 565 63. **Barak JD, Vancheva T, Lefeuvre P, Jones JB, Timilsina S, et al.** Whole-Genome Sequences of
566 *Xanthomonas euvesicatoria* Strains Clarify Taxonomy and Reveal a Stepwise Erosion of Type 3
567 Effectors. *Front Plant Sci*;7. Epub ahead of print 2016. DOI: 10.3389/fpls.2016.01805.
- 568 64. **Richard D, Boyer C, Lefeuvre P, Canteros BI, Beni-Madhu S, et al.** Complete Genome Sequences
569 of Six Copper-Resistant *Xanthomonas* Strains Causing Bacterial Spot of Solaneous Plants,
570 Belonging to *X. gardneri*, *X. euvesicatoria*, and *X. vesicatoria*, Using Long-Read Technology.
571 *Genome Announc*;5. Epub ahead of print 23 February 2017. DOI: 10.1128/genomeA.01693-16.
- 572 65. **Pothier JF, Vorhölter F-J, Blom J, Goesmann A, Pühler A, et al.** The ubiquitous plasmid pXap41
573 in the invasive phytopathogen *Xanthomonas arboricola* pv. *pruni*: complete sequence and
574 comparative genomic analysis. *FEMS Microbiol Lett* 2011;323:52–60.
- 575 66. **Sullivan MJ, Petty NK, Beatson SA.** Easyfig: a genome comparison visualizer. *Bioinforma Oxf*
576 *Engl* 2011;27:1009–10.
- 577 67. **Gurevich A, Saveliev V, Vyahhi N, Tesler G.** QUAST: quality assessment tool for genome
578 assemblies. *Bioinforma Oxf Engl* 2013;29:1072–5.
- 579

Supplementary information

Table S1. Genome sequence assemblies used in this study.

Accession number	Strain	Geographical location	Reference
GCA_020880045.1	87-47	Australia	[1]
GCA_020880235.1	Xv157	Australia	[1]
GCA_001401555.1	LMG 27970	Belgium: Merelbeke	-
GCA_001691375.1	LMG 933	Brazil	[2]
GCA_000802325.1	66b	Bulgaria: Pavlikeni, Veliko Tarnovo	[3]
GCA_020879135.1	Ps-7	Canada: Ontario	[1]
GCA_020879635.1	Xcv DC 93-9	Canada: Ontario	[1]
GCA_020879655.1	Xcv DC 97 P1A	Canada: Ontario	[1]
GCA_020879745.1	Xcv DC 96-3	Canada: Ontario	[1]
GCA_020879775.1	Xcv DC 96-1	Canada: Ontario	[1]
GCA_020879795.1	DC99P1B1	Canada: Ontario	[1]
GCA_020879815.1	Xcv DC 98 P2A	Canada: Ontario	[1]
GCA_020879825.1	Xcv DC 93-6	Canada: Ontario	[1]
GCA_020879845.1	Xcv DC 96-5	Canada: Ontario	[1]
GCA_020879875.1	Xcv DC 96-4	Canada: Ontario	[1]
GCA_020880275.1	Ps-1	Canada: Ontario	[1]
GCA_020880315.1	Xcv DC 93-8	Canada: Ontario	[1]
GCA_020880395.1	Xcv Sspep 92	Canada: Ontario	[1]
GCA_020880575.1	Xcv DC 96-2	Canada: Ontario	[1]
GCA_020880635.1	Xcv DC 97 P2A	Canada: Ontario	[1]
GCA_020880835.1	Xcv DC 93-7	Canada: Ontario	[1]
GCA_020880855.1	DC99P1A1	Canada: Ontario	[1]
GCA_020880895.1	Xcv DC 97 P3A	Canada: Ontario	[1]
GCA_001691325.1	LMG 905	India	[2]
GCA_001691345.1	LMG 909	Ivory Coast	[2]
GCA_000802345.1	83M	Macedonia: Strumitsa	[3]
GCA_030345955.2	X31	Serbia: Irig	This study
GCA_030345975.2	X13	Serbia: Irig	This study
GCA_030345985.2	X22	Serbia: Irig	This study
GCA_020880135.1	87-21	Taiwan	[1]
GCA_040091395.1	XVP26	Taiwan	[4]

GCA_020880015.1	89-10	Thailand	[1]
GCA_048855765.1	65XENP3	Thailand	[5]11/5/25 10:10:00 AM
GCA_048855785.1	65XENP1	Thailand	[5]
GCA_048855825.1	65XENP2	Thailand	[5]
GCA_048855905.1	20HP1615	Thailand	[5]
GCA_048855925.1	20HP1614	Thailand	[5]
GCA_048855965.1	20HP1613	Thailand	[5]
GCA_048855985.1	20HP1608-2	Thailand	[5]
GCA_048856005.1	20HP1609-2	Thailand	[5]
GCA_048856105.1	20HP1608-1	Thailand	[5]
GCA_048856135.1	20HP1597	Thailand	[5]
GCA_048856265.1	20HP1594	Thailand	[5]
GCA_048856285.1	62XEKK5	Thailand	[5]
GCA_048856305.1	20HP1591	Thailand	[5]
GCA_048856325.1	XCVCP-C-51	Thailand	[5]
GCA_048856365.1	XCVCP-C-43	Thailand	[5]
GCA_048856465.1	XCVKK-C-4	Thailand	[5]
GCA_048856485.1	XCVKK-C-5	Thailand	[5]
GCA_048856505.1	XCVKK-C-3	Thailand	[5]
GCA_048856545.1	XCVKK-C-2	Thailand	[5]
GCA_048856565.1	XCVKK-C-1	Thailand	[5]
GCA_048856605.1	DOA-2987	Thailand	[5]
GCA_048856625.1	DOA-2990	Thailand	[5]
GCA_048856645.1	DOA-2989	Thailand	[5]
GCA_048856725.1	DOA-2983	Thailand	[5]
GCA_048856805.1	DOA-1721	Thailand	[5]
GCA_048856825.1	DOA-2036	Thailand	[5]
GCA_048856865.1	DOA-1726	Thailand	[5]
GCA_028598835.1	Tu-08	Turkey	[6]
GCA_028598895.1	Tu-06	Turkey	[6]
GCA_028599415.1	Tu-11	Turkey	[6]
GCA_028599425.1	Tu-10	Turkey	[6]
GCA_000009165.1	85-10	Unknown	[7]
GCA_001691315.1	LMG 667 (= ICMP 4799)	Tonga	[2]
GCA_020879415.1	FB570	Unknown	[1]
GCA_042448555.1	Xe173	Unknown	[4]
GCA_001908795.1	LMG 930	USA	[8]

GCA_040091415.1	X82-8P_C6	USA	29 [4]
GCA_040091435.1	X82-8P_C5	USA	[4]
GCA_040091455.1	X82-8P_C4	USA	[4]
GCA_040091475.1	X82-8P_C3	USA	[4]
GCA_040091495.1	X82-8P_C2	USA	[4]
GCA_040091515.1	X82-8P_C1	USA	[4]
GCA_040091535.1	X82-8P	USA	[4]
GCA_040202735.2	WHRI 8301 (= 75-3)	USA	[1]
GCA_045763815.1	Tabasco1	USA	[4]
GCA_045763835.1	90-13	USA	[4]
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GCA_045763865.1	89-16	USA	[4]
GCA_045763895.1	87-13	USA	[4]
GCA_045763915.1	80-5	USA	[4]
GCA_045763955.1	72-7	USA	[4]
GCA_045763975.1	71-21	USA	[4]
GCA_045764005.1	70-7	USA	[4]
GCA_045764015.1	69-1	USA	[4]
GCA_045764025.1	69-24	USA	[4]
GCA_020879155.1	Xv 79	USA: Florida	[1]
GCA_020879265.1	Xv 72	USA: Florida	[1]
GCA_020879485.1	E3	USA: Florida	[1]
GCA_020880035.1	86-46	USA: Florida	[1]
GCA_020880115.1	86-22	USA: Florida	[1]
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GCA_020880345.1	71-21	USA: Florida	[1]
GCA_020880375.1	85-16	USA: Florida	[1]
GCA_020880435.1	75-3	USA: Florida	[1]
GCA_020880415.1	ATCC 11633	USA: New Jersey	[1]
GCA_033548465.1	VTM16	Vietnam	[9]
GCA_033548475.1	VTM15	Vietnam	[9]
GCA_033548515.1	VTM17	Vietnam	[9]
GCA_033548535.1	VTM10	Vietnam	[9]
GCA_033548565.1	VTM4	Vietnam	[9]
GCA_033548575.1	VTM12	Vietnam	[9]

Table S2. Single-nucleotide polymorphisms that distinguish strain X31 from strain Tu-10.

Position on GenBank: AM039952.1	Reference allele	Alternative allele	66b	Tu-10	X13	X22	X31
109416	a	g		x			
690978	a	g		x			
816441	g	t		x			
861129	a	c					x
991500	t	c		x			
1788346	t	g					x
1805242	t	c					x
2169416	a	g					x
2537946	g	a		x			
2934251	c	g					x
3205571	g	a					x
3839830	t	c		x			
4054862	t	c		x			

Table S3. Single-nucleotide polymorphisms that distinguish strain X22 from strain Tu-10.

Position on GenBank: AM039952.1	Reference allele	Alternative allele	66b	Tu-10	X13	X22	X31
74213	t	c				x	
109416	a	g		x			
512211	a	g				x	
690978	a	g		x			
809587	a	g				x	
816441	t	t		x			
991500	t	c		x			
995341	t	c				x	
1018308	g	c				x	
1961368	g	a				x	
2172890	a	t				x	
2387221	a	g				x	
2537946	g	a		x			
2545054	c	t				x	
2842022	c	t				x	
2949554	a	g				x	
3221165	a	g				x	
3839830	t	c		x			
4054862	t	c		x			
4778002	t	c				x	
4798644	a	c				x	
5100000	c	t				x	
5165931	g	c				x	

Table S4. Single-nucleotide polymorphisms that distinguish strain X13 from strain 66b.

Position on GenBank: AM039952.1	Reference allele	Alternative allele	66b	Tu-10	X13	X22	X31
8597	g	t			x		
76591	c	g			x		
394769	t	c	x				
649516	a	c	x				
876873	c	a	x				
893962	g	c			x		
928172	t	c			x		
980425	a	g			x		
1227342	t	g	x				
1281625	t	a			x		
1297319	g	a	x				
1384282	a	c			x		
1442912	g	a	x				
1505099	g	a	x				
1590365	c	t			x		
1600893	g	t	x				
1860694	t	g	x				
1937698	t	g			x		
2169318	a	c			x		
2371313	g	t	x				
2827142	g	a			x		
2827143	c	g			x		
2888596	t	c			x		
2894479	c	a	x				
2929910	g	a			x		
2966894	c	g			x		
3025998	t	a	x				
3623235	t	c	x				
3626498	t	c	x				
3770912	g	a	x				
4278932	g	t	x				
4278933	t	g	x				
4375039	c	t	x				
4426191	t	c	x				
4673860	c	t	x				
4761790	c	g	x				
4810267	g	t	x				
5030625	g	a	x				

5054504	c	t	x				
5157251	t	c			x		

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Table S5. Single-nucleotide polymorphisms that distinguish strain X22 from strain X31.

Position on GenBank: AM039952.1	Reference allele	Alternative allele	66b	Tu-10	X13	X22	X31
74213	t	c				x	
512211	a	e				x	
809587	a	g				x	
861129	a	c					x
995341	t	c				x	
1018308	g	c				x	
1788346	t	g					x
1805242	t	c					x
1961368	g	a				x	
2169416	a	g					x
2172890	a	t				x	
2387221	a	g				x	
2545054	c	t				x	
2842022	c	t				x	
2934251	c	g					x
2949554	a	g				x	
3205571	g	a					x
3221165	a	g				x	
4778002	t	c				x	
4798644	a	c				x	
5100000	c	t				x	
5165931	g	c				x	

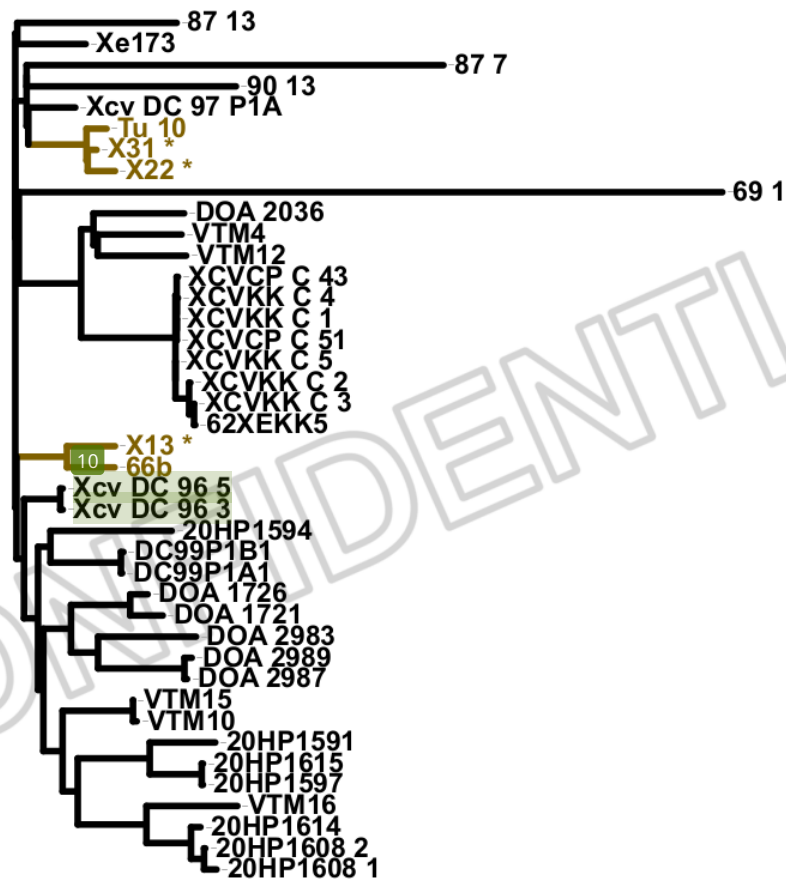


Figure S1. Phylogenetic position of strains X13, X22 and X31 within Clade 6 of *X. euvesicatoria* pv. *euvesicatoria*. The tree is based on core genome sequences, generated using PhaME [10] and FastTree 2 [11]. In addition to the genomes of three Serbia strains, the tree also includes previously published genome sequences, whose accession numbers are listed in Supplementary Table S1. The tree was graphically rendered using the Interactive Tree of Life [12].

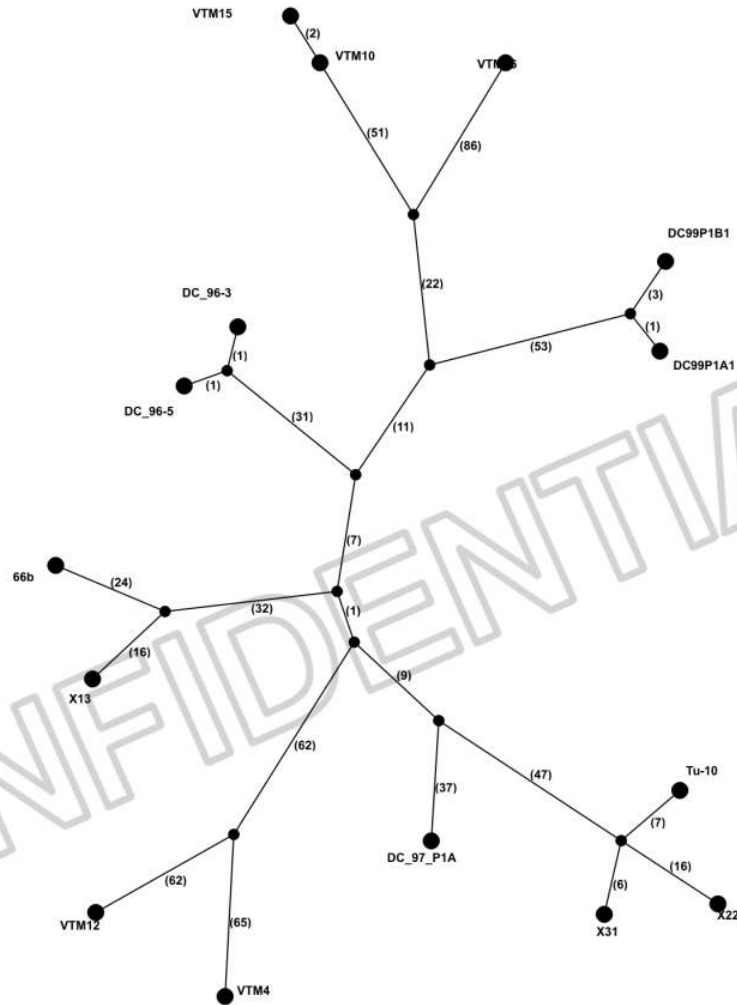
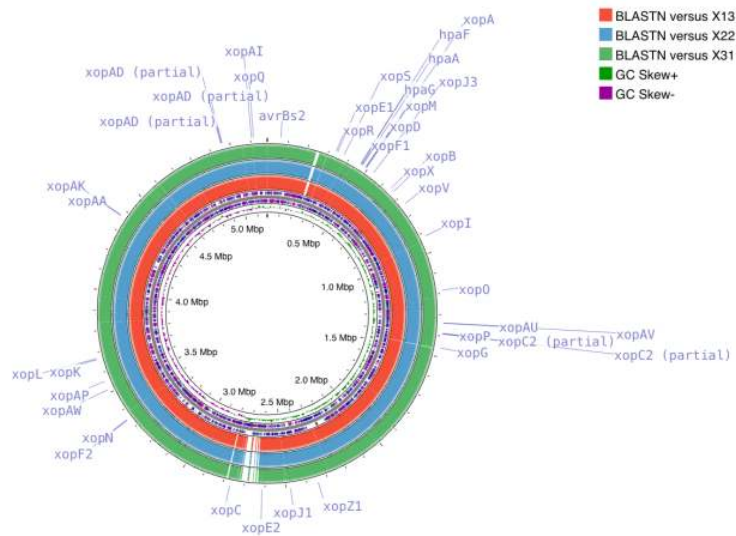


Figure S2. TCS network, created with PopArt for *X. euvesicatoria* pv. *euvesicatoria* strains in Clade 6. The numbers of single-nucleotide polymorphisms (SNPs) separating each node are indicated on the edges. The network is based on SNPs called against the 85-10 reference genome sequence.

A



B

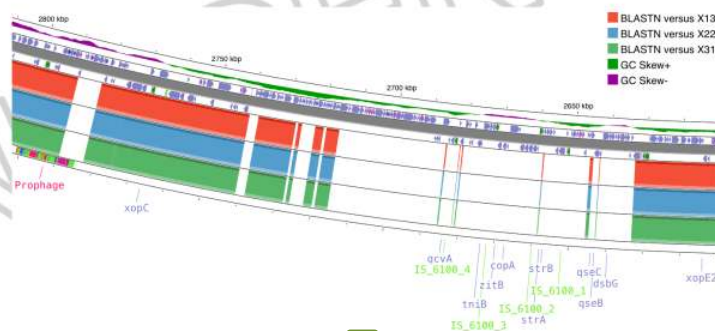
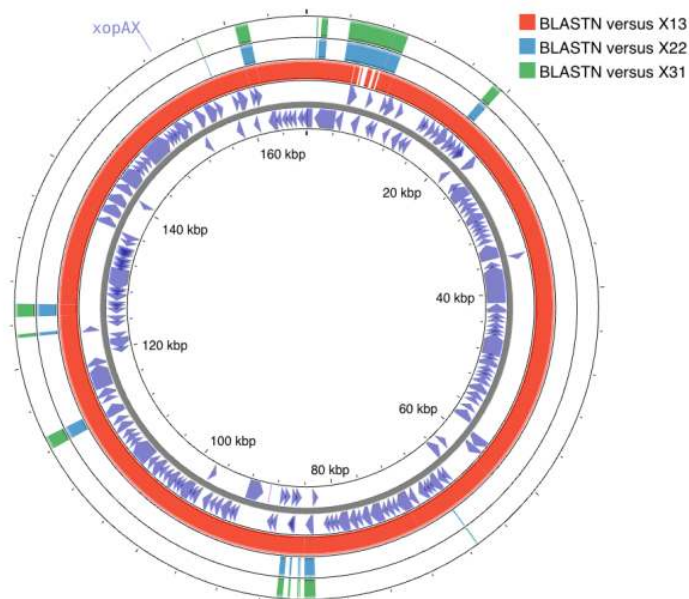


Figure S3. Comparison of Serbian *X. euvesicatoria* pv. *euvesicatoria* strains against the chromosome of reference strain 85-10. In Panel A the sequence of the 85-10 chromosome (GenBank: [AY1039952.1](#)) is represented as a circle. Sequence similarity to X13, X22 and X31 genome sequences, identified through BLASTN searches, is indicated by the colouring of concentric circular tracks. The BLASTN searches were performed and visualised using Proksee web server [13]. Panel B is zoomed in to the region around the *xopC* and *xopE* genes, to more clearly illustrate the regions of the *Xeu* 85-10 chromosome that are absent from the Serbian *Xeu* strains.

A



B

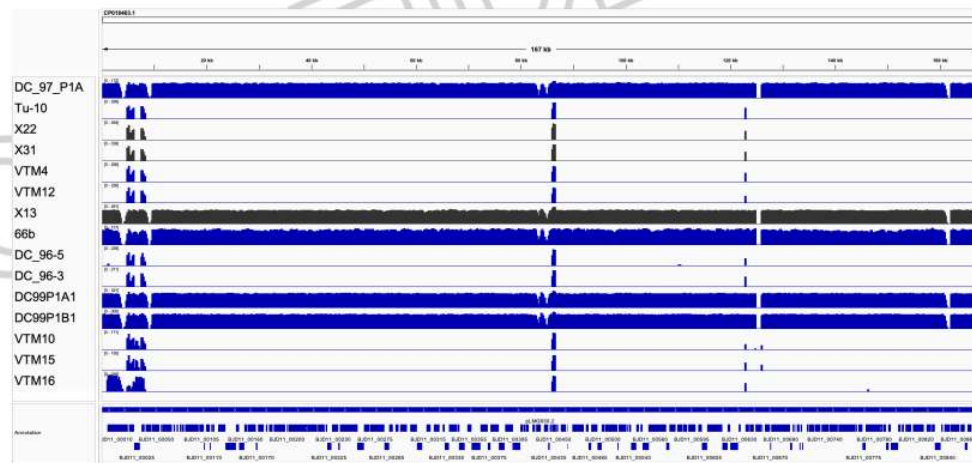
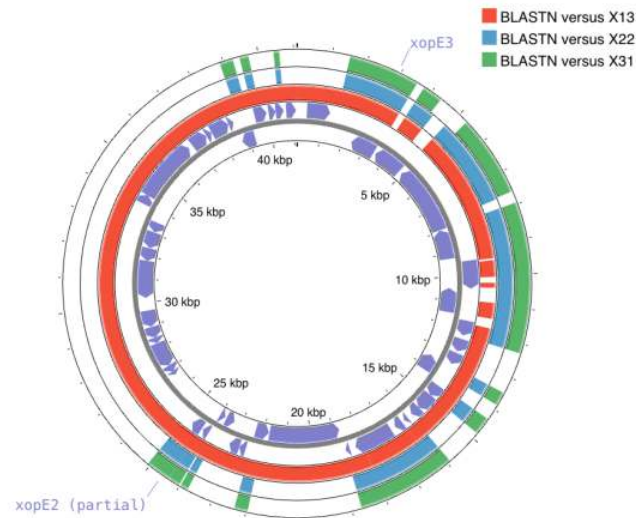


Figure S4. Strain X13 shares extensive sequence similarity with pXCV183-like plasmid pLMG930.2. Panel A: The sequence of the plasmid pLMG930.2 (GenBank: CP018463.1) is represented as a circle. Sequence similarity to *Xeu* genome sequences, identified through BLASTN searches, is indicated by the colouring of concentric circular tracks. The BLASTN searches were performed and visualised using Proksee web server [13]. Panel B: An alignment of genomic sequence reads from the 15 *Xeu* strains of Clade 6 versus plasmid pLMG930.2. The alignment was performed using BWA-mem [14] and a plot of coverage was visualized with the Integrative Genome Viewer (IGV) [15].

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A



B

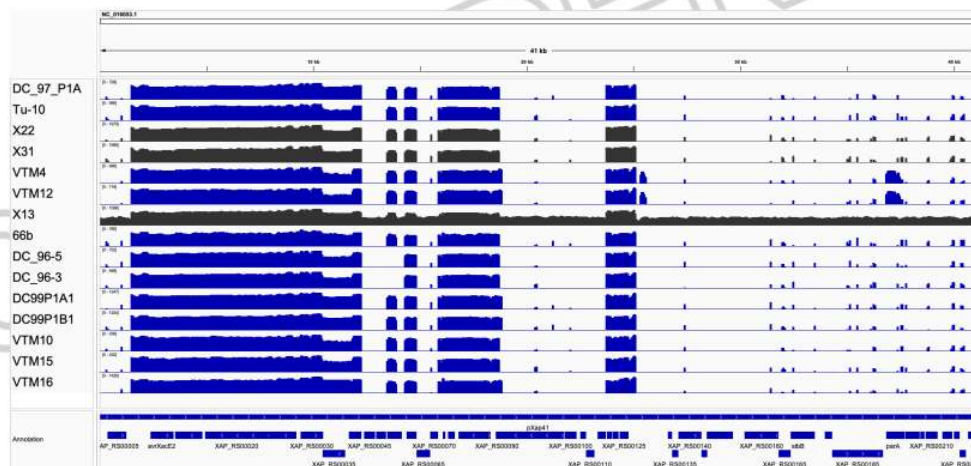


Figure S5. Strain X13 shares extensive sequence similarity with plasmid pXap41. The sequence of the *Xanthomonas arboricola* pv. *pruni* CFBP 5530 plasmid pXap41 (RefSeq: NC_016053.1) is represented as a circle. Sequence similarity to *Xeu* genome sequences, identified through BLASTN searches, is indicated by the colouring of concentric circular tracks. The BLASTN searches were performed and visualised using Proksee web server [13]. Panel B: An alignment of genomic sequence reads from the 15 *Xeu* strains of Clade 6 versus plasmid pXap41. The alignment was performed using BWA-mem [14] and a plot of coverage was visualized with the Integrative Genome Viewer (IGV) [15].

■ BLASTN versus X13
 ■ BLASTN versus X22
 ■ BLASTN versus X31

avrBs3
 xopA
 xopE3
 xopBA

70 kbp
 60 kbp
 50 kbp
 40 kbp
 30 kbp
 20 kbp
 10 kbp

CP170064.1

10 kb 20 kb 30 kb 40 kb 50 kb 60 kb 70 kb

DC_97_P1A

Tu-10

X22

X31

VTM4

VTM12

X13

66b

DC_96-5

DC_96-3

DC99P1A1

DC99P1B1

VTM10

VTM15

VTM16

Annotations

12_04503 ABCD12_04501 ABCD12_04506 ABCD12_04512 ABCD12_04516 ABCD12_04528 ABCD12_04536 ABCD12_04541 ABCD12_04549 ABCD12_04556 ABCD12_04563 ABCD12_04567 ABCD12_04570 ABCD12_04574

ABCD12_04531 ABCD12_04537 ABCD12_04513 ABCD12_04523 ABCD12_04535 ABCD12_04540 ABCD12_04546 ABCD12_04552 ABCD12_04566 ABCD12_04573

S6. Strains X13, X22 and X31 share extensive sequence similarity with a 75-kbp plasmid from strain Xe173. The sequence of the plasmid (GenBank: CP170254.1) is represented as a circle. Sequence similarity to *Xeu* genome sequences, identified through BLASTN searches, is indicated by the colouring of concentric circular tracks. The BLASTN searches were performed and visualised using Proksee web server [13]. **Panel B:** An alignment of genomic sequence reads from the 15 *Xeu* strains of Clade 6 versus the 75-kb plasmid. The alignment was performed using BWA-mem [14] and a plot of coverage was visualized with the Integrative Genome Viewer (IGV) [15].

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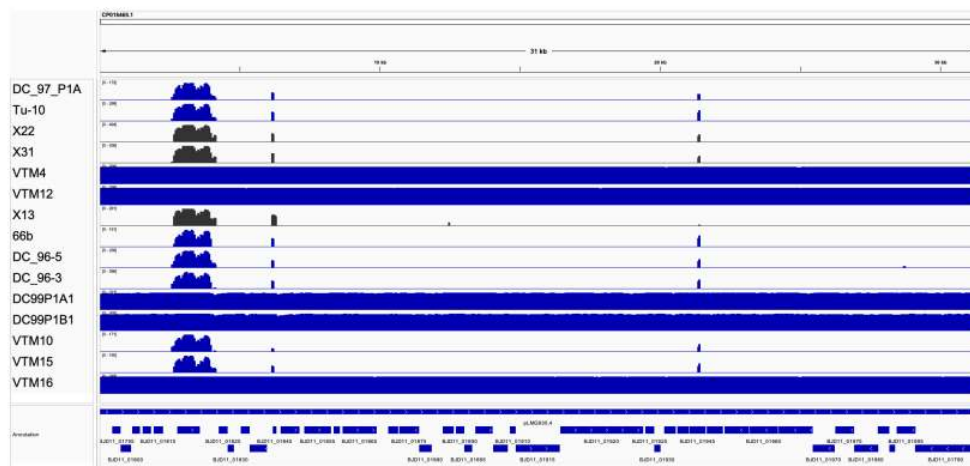


Figure S7. Strains X13, X22 and X31 do not share extensive sequence similarity with 31-kb plasmid pLMG930.4. An alignment of genomic sequence reads from the 15 *Xeu* strains of Clade 6 versus plasmid pLMG930.4 (GenBank: CP018465.1). The alignment was performed using BWA-mem [14] and a plot of coverage was visualized with the Integrative Genome Viewer (IGV) [15].

References

1. Tambong, J.T.; Xu, R.; Cuppels, D.; Chapados, J.; Gerdis, S.; Eyres, J.; Koziol, A.; Dettman, J. Whole-Genome Resources and Species-Level Taxonomic Validation of 89 Plant-Pathogenic *Xanthomonas* Strains Isolated from Various Host Plants. *Plant Disease* **2022**, *106*, 1558–1565, doi:10.1094/PDIS-11-21-2498-SC.
2. Barak, J.D.; Vancheva, T.; Lefeuvre, P.; Jones, J.B.; Timilsina, S.; Minsavage, G.V.; Vallad, G.E.; Koebnik, R. Whole-Genome Sequences of *Xanthomonas Euvesicatoria* Strains Clarify Taxonomy and Reveal a Stepwise Erosion of Type 3 Effectors. *Frontiers in Plant Science* **2016**, *7*, doi:10.3389/fpls.2016.01805.
3. Vancheva, T.; Lefeuvre, P.; Bogatzevska, N.; Moncheva, P.; Biology, F.; Kliment, S.; Montpellier, U.M.R.I. Draft Genome Sequences of Two *Xanthomonas Euvesicatoria* Strains from the Balkan Peninsula. **2015**, *3*, 6–7, doi:10.1128/genomeA.01528-14.
4. Kaur, A.; Minsavage, G.V.; Potnis, N.; Jones, J.B.; Goss, E.M. Evolution of Copper Resistance in *Xanthomonas Euvesicatoria* Pv. *Perforans* Population. *mSystems* **2024**, e01427-24, doi:10.1128/msystems.01427-24.
5. Preangtong, Y.; Patarapuwadol, S.; Phiriyangkul, P.; Kanhayart, T.; Kositcharoenkul, N.; Kositratana, W.; Watcharachaiyakup, J. Characterisation and Genomic Diversity of *Xanthomonas* Species Causing Bacterial Spot Disease of Tomato and Pepper in Thailand. *Plant Pathology* **2025**, *74*, 1315–1334, doi:10.1111/ppa.14094.
6. Subedi, A.; Kara, S.; Aysan, Y.; Minsavage, G.V.; Timilsina, S.; Roberts, P.D.; Goss, E.M.; Jones, J.B. Draft Genome Sequences of 11 *Xanthomonas* Strains Associated with Bacterial Spot Disease in Turkey. *Access Microbiol* **2023**, *5*, acmi000586.v3, doi:10.1099/acmi.0.000586.v3.

7. Thieme, F.; Koebnik, R.; Bekel, T.; Berger, C.; Boch, J.; Büttner, D.; Caldana, C.; Gaigalat, L.; Goesmann, A.; Kay, S.; et al. Insights into Genome Plasticity and Pathogenicity of the Plant Pathogenic Bacterium *Xanthomonas Campestris* Pv. *Vesicatoria* Revealed by the Complete Genome Sequence. *Journal of bacteriology* **2005**, *187*, 7254–7266, doi:10.1128/JB.187.21.7254-7266.2005.
8. Richard, D.; Boyer, C.; Lefeuvre, P.; Canteros, B.I.; Beni-Madhu, S.; Portier, P.; Pruvost, O. Complete Genome Sequences of Six Copper-Resistant *Xanthomonas* Strains Causing Bacterial Spot of Solaneous Plants, Belonging to *X. Gardneri*, *X. Euvesicatoria*, and *X. Vesicatoria*, Using Long-Read Technology. *Genome announcements* **2017**, *5*, doi:10.1128/genomeA.01693-16.
9. Subedi, A.; Nga, N.T.T.; Tien, D.T.K.; Minsavage, G.V.; Roberts, P.D.; Goss, E.M.; Jones, J.B. Draft Genomes Announcement of Vietnamese *Xanthomonas Euvesicatoria* Strains Causing Bacterial Spot on Pepper. *Access Microbiol* **2024**, *6*, 000741.v3, doi:10.1099/acmi.0.000741.v3.
10. Shakya, M.; Ahmed, S.A.; Davenport, K.W.; Flynn, M.C.; Lo, C.-C.; Chain, P.S.G. Standardized Phylogenetic and Molecular Evolutionary Analysis Applied to Species across the Microbial Tree of Life. *Scientific reports* **2020**, *10*, 1723, doi:10.1038/s41598-020-58356-1.
11. Price, M.N.; Dehal, P.S.; Arkin, A.P. FastTree 2 - Approximately Maximum-Likelihood Trees for Large Alignments. *PLoS ONE* **2010**, *5*, doi:10.1371/journal.pone.0009490.
12. Letunic, I.; Bork, P. Interactive Tree Of Life (iTOL) v5: An Online Tool for Phylogenetic Tree Display and Annotation. *Nucleic Acids Research* **2021**, *49*, W293–W296, doi:10.1093/nar/gkab301.
13. Grant, J.R.; Enns, E.; Marinier, E.; Mandal, A.; Herman, E.K.; Chen, C.-Y.; Graham, M.; Van Domselaar, G.; Stothard, P. Proksee: In-Depth Characterization and Visualization of Bacterial Genomes. *Nucleic Acids Res* **2023**, *51*, W484–W492, doi:10.1093/nar/gkad326.
14. Li, H. Aligning Sequence Reads, Clone Sequences and Assembly Contigs with BWA-MEM. **2013**, *3*.
15. Robinson, J.T.; Thorvaldsdóttir, H.; Winckler, W.; Guttman, M.; Lander, E.S.; Getz, G.; Mesirov, J.P. Integrative Genomics Viewer. *Nature biotechnology* **2011**, *29*, 24–26, doi:10.1038/nbt.1754.

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-
- 29 Renqiao Wen, Hongcheng Wei, Tiejun Zhang, Peng Ma, Qin Wang, Chao Li, Zhonghan Li, Changwei Lei, Hongning Wang. "Epidemiological Characterisation of blaNDM-Positive Enterobacterales from Food-Producing Animal Farms in Southwest China", Microorganisms, 2023 14 words — < 1%
Crossref
-
- 30 Jamie Harrison, Rana M. F. Hussain, Andrew Aspin, Murray R. Grant, Joana G. Vicente, David J. Studholme. "Phylogenomic Analysis Supports the Transfer of 20 Pathovars from Xanthomonas campestris into Xanthomonas euvesicatoria", Taxonomy, 2023 13 words — < 1%
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- 31 modis.marine.usf.edu 13 words — < 1%
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34 Desi Utami, Sarah Jade Meale, Anthony Joseph Young. " Bacterial Leaf Spot Susceptibility Screening of Chili Pepper Cultivars Using qPCR Determination of pv. titers ", *Phytopathology®*, 2023 12 words — < 1%
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35 bmcgenomics.biomedcentral.com 12 words — < 1%
Internet

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37 Yuhong Huang, Yang Liu, Chang Liu, Congyang Yi, Jinsheng Lai, Hongqing Ling, Handong Su, Fangpu Han. "Distinct evolutionary trajectories of subgenomic centromeres in polyploid wheat", *Genome Biology*, 2025 11 words — < 1%
Crossref

38 Christine M. Vogel, Daniel B. Potthoff, Martin Schäfer, Niculò Barandun, Julia A. Vorholt. "Protective role of the Arabidopsis leaf microbiota against a bacterial pathogen", *Nature Microbiology*, 2021 10 words — < 1%
Crossref

39 Joël F. Pothier, Frank-Jörg Vorhölter, Jochen Blom, Alexander Goesmann, Alfred Pühler, Theo H.M. Smits, Brion Duffy. "The ubiquitous plasmid pXap41 in the invasive phytopathogen *Xanthomonas arboricola* pv. *pruni*: complete sequence and comparative genomic analysis", *FEMS Microbiology Letters*, 2011 10 words — < 1%
Crossref

40 Julissa Enciso-Ibarra, Ana Roque, Carmen Bolán-Mejia, Karen Enciso-Ibarra, Adrián González-Castillo, Bruno Gomez-Gil. "Vibrio eleionomae sp. nov., isolated from shrimp (*Penaeus vannamei*) pond water", *International Journal of Systematic and Evolutionary Microbiology*, 2023 10 words — < 1%
Crossref

41 M. Šević, K. Gašić, M. Đorđević, M. Ignjatov, M. Mijatović, B. Zečević, A. Obradović. "Efficacy of biocontrol agents and bactericides in control of pepper bacterial spot", Acta Horticulturae, 2016

Crossref

10 words — < 1%

42 assets.researchsquare.com

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43 pure.umcutrecht.nl

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10 words — < 1%

44 "Biotic and Abiotic Stress Tolerance in Plants", Springer Science and Business Media LLC, 2018

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45 M. Soliman. "Xanthomonas euvesicatoria Associated with Bacterial Spot on Pepper Fruits in Egypt", Journal of Plant Protection and Pathology, 2022

Crossref

9 words — < 1%

46 Peter Abrahamian, Sujan Timilsina, Gerald V. Minsavage, Neha Potnis, Jeffrey B. Jones, Erica M. Goss, Gary E. Vallad. " Molecular Epidemiology of Outbreaks in Tomato Plants from Transplant to Field as Determined by Single-Nucleotide Polymorphism Analysis ", Applied and Environmental Microbiology, 2019

Crossref

9 words — < 1%

47 Qiongying Shen, Dehou Deng, Guangliang Li, Jia Yin Ruan et al. "Electroacupuncture Frequency for Chemotherapy-Induced Neuropathy in Breast Cancer: A Randomized Controlled Trial", The Oncologist, 2025

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49	Internet	9 words — < 1%
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53	new.esp.org Internet	8 words — < 1%
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55	www.zjujournals.com Internet	8 words — < 1%
56	www1.up.poznan.pl Internet	8 words — < 1%
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59 "Integrated Pest and Disease Management in Greenhouse Crops", Springer Science and Business Media LLC, 2020

Crossref

6 words — < 1%

60 Chengchao Wu, Tianshu Zhou, Wenfu Ke, Wei Xiong et al. "Deciphering Haploid Chromosome Conformation Alternation in Down Syndrome by Multiple Haploid Omics Analysis", Genomics, Proteomics & Bioinformatics, 2025

Crossref

6 words — < 1%

61 F. Thieme, R. Koebnik, T. Bekel, C. Berger et al. "Insights into Genome Plasticity and Pathogenicity of the Plant Pathogenic Bacterium *Xanthomonas campestris* pv. *vesicatoria* Revealed by the Complete Genome Sequence", *Journal of Bacteriology*, 2005

Crossref

6 words — < 1%

62 Ghosoun Habib Sabri Al-Rubaie, Saba Abd Al-Hadi Kadhim Al-Falooji. "Chemical and Molecular Detection of New Strains of *Xanthomonas Campestris* pv. *Vesicatoria* and *Pseudomonas putida* Associated with Tomato Crop", *IOP Conference Series: Earth and Environmental Science*, 2023

Crossref

6 words — < 1%

63 Gundry, M., W. Li, S. B. Maqbool, and J. Vijg. "Direct, genome-wide assessment of DNA mutations in single cells", *Nucleic Acids Research*, 2012.

Crossref

6 words — < 1%

64 Manoj Choudhary, Gerald V. Minsavage, Erica M. Goss, Sujan Timilsina et al. " Whole genome sequence-based classification of *Xanthomonas euvesicatoria* pv. and computational analysis of type III secretion system ", *Phytopathology®*, 2023

6 words — < 1%

65 Manoj Choudhary, Gerald V. Minsavage, Erica M. Goss, Sujan Timilsina et al. " Whole-Genome-Sequence-Based Classification of pv. and Computational Analysis of the Type III Secretion System ", *Phytopathology*®, 2024 6 words — < 1%

Crossref

66 Neha Potnis. "Harnessing Eco-Evolutionary Dynamics of Xanthomonads on Tomato and Pepper to Tackle New Problems of an Old Disease", *Annual Review of Phytopathology*, 2021 6 words — < 1%

Crossref

67 Tatyana Ponomarenko, Marina Nevskaya, Oksana Marinina. "An Assessment of the Applicability of Sustainability Measurement Tools to Resource-Based Economies of the Commonwealth of Independent States", *Sustainability*, 2020 6 words — < 1%

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