Whole Genome Resources of 17 *Curtobacterium flaccumfaciens* Strains Including Pathotypes of *C. flaccumfaciens* pv. *betae*, *C. flaccumfaciens* pv. *oortii*, and *C. flaccumfaciens* pv. *poinsettiae*

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Curtobacterium flaccumfaciens complex species in the family *Microbacteriaceae* encompasses a group of plant-pathogenic actinobacterial strains affecting annual crops and ornamental plants. The species includes five pathovars, namely *C. flaccumfaciens* pv. *betae*, *C. flaccumfaciens* pv. *flaccumfaciens*, *C. flaccumfaciens* pv. *ilicis*, *C. flaccumfaciens* pv. *oortii*, and *C. flaccumfaciens* pv. *poinsettiae*. Despite the economic importance of *C. flaccumfaciens*, its members have rarely been investigated for their phylogenetic relationships, molecular characteristics, and virulence repertoires, due, in part, to the lack of whole-genome resources. Here, we present the whole-genome sequence of 17 *C. flaccumfaciens* strains representing members of four pathovars isolated from different plant species in a diverse geographical and temporal span. The genomic data presented in this study will pave the way for research on the comparative genomics, phylogenomics, and taxonomy of *C. flaccumfaciens* and extend our understanding of the virulence features of the species.

Gram-positive actinobacterial plant pathogens in the family *Microbacteriaceae* comprise a series of economically important agents infecting several annual crops, ornamental plants, and vegetables (Dye and Kemp 1977; Jacques et al. 2012). Plant-pathogenic members in this group include *Clavibacter* spp., *Rathayibacter* spp., *Leifsonia xyli*, and *Curtobacterium flaccumfaciens* (Vidaver and Davis 1988). The latter species is a complex taxon comprising several pathovars as well as nonpathogenic, environmental, and, in some cases, clinical species (Francis et al. 2011). Among the gram-positive bacterial plant pathogens, *C. flaccumfaciens* is the least-studied member in terms of genomic features and pathogenicity determinants (Chen et al. 2021; Thapa et al. 2019). Plant-pathogenic members of *C. flaccumfaciens* are subdivided into five pathovars based on their host of isolation, pathogenicity, and host range (Collins and Jones 1983; Davis and Vidaver 2001; Davis 1986, 2001). Pathovars of the species include *C. flaccumfaciens* pv. *flaccumfaciens*, causing bacterial wilt of dry beans (Hedges 1922), *C. flaccumfaciens* pv. *poinsettiae*,

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Keywords

actinobacteria, bacterial wilt of beans, coryneform bacteria, *Microbacteriaceae*, quarantine pathogen, bacterial pathogenesis

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Table 1. Source, place, and date of isolation, and genomic information of the *Curtobacterium flaccumfaciens* strains used in this study

Strain	Other names	Taxon	Host	Year	Country	Colony color (pigmentation)	Genome size (bp)
CFBP 2402 ^{PT}	ICMP 2594 ^{PT} , LMG 3596 ^{PT} , NCPPB 374 ^{PT}	<i>C. flaccumfaciens</i> pv. <i>betae</i>	<i>Beta vulgaris</i>	1955	U.K.	Yellow-Dry	3,768,077
CFBP 1384 ^{PT}	NCPPB 2113 ^{PT} , ATCC 25283 ^{PT} , ICMP 2632 ^{PT} , LMG 3702 ^{PT}	<i>C. flaccumfaciens</i> pv. <i>oortii</i>	<i>Tulipa gesneriana</i>	1967	Netherlands	Yellow-Fluidal	4,024,422
CFBP 2403 ^{PT}	ICMP 2566 ^{PT} , ATCC 9682 ^{PT} , NCPPB 854 ^{PT}	<i>C. flaccumfaciens</i> pv. <i>poinsettiae</i>	<i>Euphorbia pulcherrima</i>	Missing	U.S.A.	Orange-Dry	3,616,077
CFBP 3400	PD 1751	<i>C. flaccumfaciens</i> pv. <i>oortii</i>	<i>Zantedeschia aethiopica</i>	1990	Netherlands	Yellow-Dry	3,773,592
CFBP 3423	NCPPB 2344, ATCC 23827	<i>C. flaccumfaciens</i> pv. <i>flaccumfaciens</i>	<i>Phaseolus vulgaris</i>	1957	U.S.A.	Yellow-Fluidal	3,906,894
CFBP 3422	NCPPB 2343, ATCC 12813	<i>C. flaccumfaciens</i> pv. <i>flaccumfaciens</i>	<i>Phaseolus vulgaris</i>	1956	U.S.A.	Orange-Dry	3,587,123
CFBP 3417	NCPPB 558	<i>C. flaccumfaciens</i> pv. <i>flaccumfaciens</i>	<i>Phaseolus vulgaris</i>	1958	U.S.A.	Orange-Fluidal	3,731,936
CFBP 3401	LMG 7238, PDDCC 4735	<i>C. flaccumfaciens</i> pv. <i>betae</i>	<i>Beta vulgaris</i>	Missing	U.K.	Yellow-Dry	3,771,893
CFBP 3415	LMG 7321	<i>C. flaccumfaciens</i> pv. <i>poinsettiae</i>	<i>Euphorbia pulcherrima</i>	Missing	U.S.A.	Orange-Fluidal	3,693,818
CFBP 8818	Tom50, ICMP 22062	<i>C. flaccumfaciens</i> pv. <i>flaccumfaciens</i>	<i>Solanum lycopersicum</i>	2015	Iran	Red-Dry	3,718,276
CFBP 8819	50R, ICMP 22071	<i>C. flaccumfaciens</i> pv. <i>flaccumfaciens</i>	<i>Phaseolus vulgaris</i>	2014	Iran	Red-Fluidal	3,722,562
CFBP 8820	P990, ICMP 22053	<i>C. flaccumfaciens</i> pv. <i>flaccumfaciens</i>	<i>Capsicum annuum</i>	2015	Iran	Yellow-Fluidal	3,841,555
CFBP 8821	Cmmeg20, ICMP 22056	<i>C. flaccumfaciens</i>	<i>Solanum melongena</i>	2014	Iran	Yellow-Fluidal	3,667,557
CFBP 8822	Xeu15, ICMP 21400	<i>C. flaccumfaciens</i>	<i>Capsicum annuum</i>	2013	Iran	Yellow-Fluidal	3,715,976
CFBP 8823	Cff156	<i>C. flaccumfaciens</i> pv. <i>flaccumfaciens</i>	<i>Phaseolus vulgaris</i>	2015	Iran	Orange-Fluidal	3,749,403
CFBP 8824	G105, ICMP 22064	<i>C. flaccumfaciens</i>	<i>Solanum lycopersicum</i>	2015	Iran	Red-Fluidal	3,603,541
CFBP 8825	Tom827, ICMP 22084	<i>C. flaccumfaciens</i>	<i>Solanum lycopersicum</i>	2015	Iran	Yellow-Fluidal	3,707,673

(Continued on next page)

^a CDS = coding sequences.^b Presence of plasmids was evaluated using both PlasmidFinder and SourceFinder services, while the presence of phages was evaluated using SourceFinder. ND = Not detected.^c The numbers indicate the contig number in the FASTA files (in the GenBank database) in which the corresponding sequence was detected.

causing bacterial canker of poinsettia (Pirone and Bender 1941), *C. flaccumfaciens* pv. *betae*, the agent of silvering disease of red beet (Keyworth et al. 1956), *C. flaccumfaciens* pv. *ilicis*, causing bacterial blight of American holly (Mandel et al. 1961; Young et al. 2004), and *C. flaccumfaciens* pv. *oortii*, the agent of bacterial wilt and spot of tulip (Saaltink and Maas Geesteranus 1969). Two additional pathovars including '*C. flaccumfaciens* pv. *basellae*', the causal agent of bacterial leaf spot of malabar spinach (*Basella alba* or *B. rubra*) (Chen et al. 2000), and '*C. flaccumfaciens* pv. *beticola*', the causal agent of bacterial leaf spot of sugar beet (Chen et al. 2007) were also proposed. However, the Committee on the Taxonomy of Plant Pathogenic bacteria (Bull et al. 2010) has not accepted them to date as valid taxa.

Among these pathovars, bacterial wilt of dry beans caused by *C. flaccumfaciens* pv. *flaccumfaciens* and bacterial canker of poinsettia caused by *C. flaccumfaciens* pv. *poinsettiae* are economically important, the former one being included as a quarantine pathogen in the Annex II part A of European Regulation 2019/2072 and in the A2 list of the European and Mediterranean Plant Protection Organization and the latter one being included in the alert lists of EPPO (EPPO 2011; Osdaghi et al. 2020a). While molecular diagnostic tests are available to detect and identify *C. flaccumfaciens* pv. *flaccumfaciens*

Table 1. (Continued from previous page)

					Plasmid/phage ^b			GenBank accession number
No. of			G+C% content	Coverage x	Plasmid Finder	SourceFinder		
CDSs ^a	Genes	Contigs				Phage ^c	Plasmid	
3,534	3,589	50	70.9	219	ND	45, 49, 50	ND	JAHEXD000000000
3,821	3,878	64	70.7	249	ND	7, 54, 59, 61, 63, 64	ND	JAHEXC000000000
3,396	3,450	54	71.0	219	ND	39, 53	ND	JAHEXB000000000
3,559	3,614	48	71.0	249	ND	ND	ND	JAHEXA000000000
3,682	3,739	52	70.5	204	ND	25, 41, 43, 46, 51, 52	40, 44, 45	JAHEWZ000000000
3,349	3,404	45	71.0	234	ND	2, 44	ND	JAHEWY000000000
3,549	3,604	48	70.8	264	ND	15, 22, 40, 46, 47, 48	36	JAHEWX000000000
3,540	3,595	52	70.9	310	ND	9, 17, 19, 40, 42, 43, 46, 47, 48, 49, 50	ND	JAHEWW000000000
3,464	3,518	43	70.9	332	ND	40, 42, 43	ND	JAHEWU000000000
3,497	3,553	73	70.9	189	ND	19, 56, 59, 63, 67	ND	JAHEWT000000000
3,504	3,556	63	70.8	219	ND	24, 44, 48, 53, 57, 60	ND	JAHEWS000000000
3,618	3,673	56	70.9	234	ND	24, 52, 55, 56	ND	JAHEWR000000000
3,417	3,470	47	71.0	189	ND	46, 47	ND	JAHEWQ000000000
3,495	3,549	47	71.0	219	ND	46, 47	ND	JAHEWP000000000
3,519	3,576	65	70.8	227	ND	12, 23, 53, 56, 59, 64	ND	JAHEWO000000000
3,369	3,422	35	71.0	287	ND	8, 33, 35	ND	JAHEWN000000000
3,487	3,542	47	71.0	189	ND	25, 45, 46	ND	JAHEWM000000000

(Tegli et al. 2020), quarantined members of the species require considerable cost and effort to prevent the risk of global spread and introduction into areas yet free of the disease (Harveson et al. 2015; Osdaghi et al. 2020a). Members of *C. flaccumfaciens* are well-known for variability in colony pigmentation and morphology possessing a wide range of colony variants including orange, pink, purple, red, and yellow phenotypes in either fluidal, mucoid, or dry form on culture media (Harveson and Vidaver 2008; Osdaghi and Lak 2015; Osdaghi et al. 2016). As a complex species, population structure and taxonomy of *C. flaccumfaciens* has rarely been examined using high throughput genomics techniques, leaving the phylogenetic relationships of different pathovars to each other uninvestigated. Further, due to the lack of whole-genome resources from different pathovars of *C. flaccumfaciens*, pathogenicity-associated genomic features and virulence strategies of its members are still almost entirely unknown. Unlike the other plant-pathogenic actinobacteria, for which the nucleotide sequence data from a wide range of strains are available (Ansari et al. 2019; Jacques et al. 2012; Osdaghi et al. 2020b), whole-genome sequence data of only a few *C. flaccumfaciens* strains are published in the literature (Chen et al. 2021). Among the pathotype strains of the species, *C. flaccumfaciens* pv. *flaccumfaciens* is the only one for which a whole-genome sequence is available (Gonçalves et al. 2019).

DNA fingerprinting-based investigations (Agarkova et al. 2012; Osdaghi et al. 2018a) and multilocus sequence analysis (MLSA) (Gonçalves et al. 2019; Osdaghi et al. 2018b) suggested high genetic diversity among plant pathogenic members of *C. flaccumfaciens* either in an intrapathovar or interpathovar level. For instance, it has been noted that yellow-pigmented

strains of the dry bean pathogen *C. flaccumfaciens* pv. *flaccumfaciens* are genetically and phylogenetically distinct from those of red- and orange-pigmented strains of the same pathovar (Osdaghi et al. 2018a, b). Interestingly, MLSA-based results showed that the red- and orange-pigmented strains of the latter pathogen are phylogenetically more related to the poinsettia pathogen *C. flaccumfaciens* pv. *poinsettiae* than to the pathotype strain of *C. flaccumfaciens* pv. *flaccumfaciens*. All these findings led us to conclude that an inclusive genome sequencing effort is warranted to shed light on the taxonomic structure, phylogenetic relationships, and genomic repertoires of *C. flaccumfaciens* members. Thus, the main objective of this study was to provide whole-genome resources for 17 *C. flaccumfaciens* strains, covering nearly the entire genetic diversity of the species, including the pathotype strains of *C. flaccumfaciens* pv. *betae*, *C. flaccumfaciens* pv. *oortii*, and *C. flaccumfaciens* pv. *poinsettiae*.

C. flaccumfaciens strains representing members of different pathovars with various colony morphology (pigmentation) and diverse geographic origins were obtained from the French Collection for Plant-Associated Bacteria CIRM-CFBP (Table 1). The strains were streaked onto yeast-extract peptone glucose agar medium, were resuspended in sterile distilled water and stored at 4°C for further use, and were stored in 15% glycerol at –70°C for long-term purposes. Bacterial DNAs were extracted using the Wizard genomic DNA purification kit (Promega, Madison WI, U.S.A.). The 17 strains were sequenced using NovaSeq 6000 Illumina with Nextera XT Preparation kit and paired-end 150 bp (Institut du Cerveau, CHU Pitié-Salpêtrière, Paris). Genome assembly was performed using SPAdes 1 (Bankevich et al. 2012) after a quality filtration with CheckM (Parks et al. 2015). For each strain, sequencing coverage, genome size, number of contigs, and G+C percentage are summarized in Table 1. Genome annotation was performed using the GeneMarkS+ suite implemented in the National Center for Biotechnology Information (NCBI) Prokaryotic Genome Annotation Pipeline with default settings (Borodovsky and Lomsadze 2014). Total number of genes and coding sequences were determined for all the genomes (Table 1).

Whole-genome sequences of the 17 *C. flaccumfaciens* strains obtained in this study were assembled in contigs varying in number from 35 to 73, while sequencing coverage was between 189x and 332x (Table 1). Genome size of the strains ranged from 3,587,123 bp in *C. flaccumfaciens* pv. *flaccumfaciens* CFBP 3422 to 4,024,422 bp in the pathotype strain of *C. flaccumfaciens* pv. *oortii* CFBP 1384^{PT}, while G+C% content was between 70.5 and 71.0% (Table 1). It has previously been shown that a number of *C. flaccumfaciens* strains possess plasmids harboring various biological functions (Chen et al. 2021; Hendrick et al. 1984; Vaghefi et al. 2021). Hence, the genome sequences obtained in this study were investigated for the presence of plasmid and phage sequences via online services PlasmidFinder 2.0 and SourceFinder 1.0 (Carattoli et al. 2014). While PlasmidFinder did not find any plasmid in the genome sequences, SourceFinder suggested the presence of plasmid in the *C. flaccumfaciens* pv. *flaccumfaciens* strains CFBP 3423 and CFBP 3417. Phage fragments were also frequently detected in all the genomes except *C. flaccumfaciens* pv. *oortii* CFBP 3400, as detailed in Table 1. Agarose gel-based plasmid profiling is recommended to decipher the precise plasmid profile of the strains sequenced in this study. Furthermore, a preliminary average nucleotide identity (ANI) and digital DNA-DNA hybridization calculation among the strains sequenced in this study suggest a need for an in-depth taxonomic investigation on the phylogenetic relationships of the *C. flaccumfaciens* members. For instance, ANI between the type strain of *C. flaccumfaciens* CFBP 3418^T and the pathotype strain of *C. flaccumfaciens* pv. *poinsettiae* CFBP 2403P^T was 93.5%, which was below the accepted threshold (95 to 96%) for definition of prokaryotic species (Kim et al. 2014). A comprehensive multiphasic taxonomic study is ongoing to re-evaluate the taxonomy of *C. flaccumfaciens* complex species.

Data Availability

The whole-genome shotgun sequences obtained in this study are deposited at the NCBI GenBank database under the accession numbers shown in Table 1. Furthermore, a pure culture of the 17 strains is available in CIRM-CFBP culture collection.

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