Updated taxonomy of *Pectobacterium* genus in the CIRM-CFBP bacterial collection: when newly described species reveal "old" endemic population

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Bacterial collections are invaluable tools for microbiologists. However, their practical use is compromised by imprecise taxonomical assignation of bacterial strains. This is particularly true for soft rotting plant pathogens of the *Pectobacterium* genus. To solve this difficulty, we analyzed the taxonomic status of 265 *Pectobacterium* strains deposited at CIRM-CFBP collection from 1944 to 2020. This collection gathered *Pectobacterium* strains isolated in 27 countries from 32 plant species representing 17 botanical families or from non-host environments. MLSA approach completed by genomic analysis of 15 strains was performed to update the taxonomic status of these 265 strains. Results showed that the CIRM-CFBP *Pectobacterium* collection harboured at least one strain of each species to the exception of *P. polonicum*. Yet, 6 strains could not be assigned to any of the described species and may represent at least two new species. Surprisingly, the *P. versatile* species, recently described in 2019, is the most prevalent species among CIRM-CFBP strains. Analysis of *P. versatile* strains revealed that this species is endemic all over the world on various host plants and environments. At the opposite, other species gathered strains isolated from only one botanical family or exclusively from fresh water environment. Our work also revealed new host plants for several *Pectobacterium* spp.

Key words: *Pectobacterium*, collection, taxonomy, host plants

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Introduction

Bacterial collections are invaluable tools for microbiologists as they host many strains isolated at different times on different hosts or environments and on different countries and continents. As such they summarize the collective sampling and research efforts performed by bacteriologists from all over the world on many different bacterial species. This collective treasure is nevertheless often underexploited for several reasons, the main one being the poor taxonomical assignation of many deposited strains to current taxonomical standard. This situation results from the fact that many strains are ancient strains that were deposited in collection before precise taxonomic delineation of species through genome analysis were performed. Even if most collections are doing great efforts to improve this situation, a lot of work is still necessary. Therefore, currently, collections harbour many strains with old names no longer informative of their actual taxonomical status. Such ancient strains are nevertheless important to understand the epidemiology of a given species, when and where a particular species was first isolated in the world and what is its historical prevalence all over the world.

Soft rot plant bacterial pathogens of the *Pectobacterium* genus represent an archetype of this situation. They are characterized by their ability to degrade plant cell wall through the secretion of a large cocktail of plant cell wall degrading enzymes (PCWDEs) [1,2]. *Pectobacterium* is a major cause of harvest loss for potato both on the field and during potato storage. However, strains of this genera have also been collected on large number of host plants and are thus known as large host range plant pathogens, although the extent of the host range varies between species [3,4]. *Pectobacterium* sp. were previously regrouped in the *Erwinia* genus founded in 1917 to unite all gram negative, fermentative, non-sporulating, peritrichous flagellated plant pathogenic bacteria [5]. Early taxonomy recognized 3 taxa within these soft rot bacteria, *Erwinia carotovora* subsp. *carotovora*, *Erwinia carotovora* subsp. *atroseptica* and *Erwinia chrysanthemi* [6,7] that were included in the Approved Lists of Bacterial Names in 1980 either under the species named *Erwinia* or *Pectobacterium* [8] and the *Pectobacterium* genus was formaly described in 1998 [9]. In 2005, on the basis of 16S RNA sequence, *P. chrysanthemi* was reclassified within the new *Dickeya* genus [10]. Furthermore, in addition to *Pectobacterium carotovorum* subsp. *carotovorum* and *Pectobacterium carotovorum* subsp. *atrosepticum* several new subspecies were progressively described for *P. carotovorum* : *Pectobacterium carotovorum* subsp. *brasiliense* [11,12], *Pectobacterium carotovorum* subsp. *wasabiae*, *Pectobacterium carotovorum* subsp. *betavasculorum*, *Pectobacterium carotovorum* subsp. *odoriferum* [9] and *P. carotovorum*

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subsp. *actinidiae* [13]. All these subspecies were latter elevated at species level [14,15] following genomic analysis [16]. In addition, new *Pectobacterium* species were progressively described, most of them recently on the basis of whole genome sequence analysis. Today, the *Pectobacterium* genus encompasses 17 recognized species *Pectobacterium actinidiae* [15], *Pectobacterium aquaticum* [17], *Pectobacterium aroidearum* [18], *Pectobacterium atrosepticum* [14], *Pectobacterium betavasculorum* [14], *Pectobacterium brasiliense* [15], *Pectobacterium cacticida* [9,19], *Pectobacterium carotovorum* [8,15,20], *Pectobacterium fontis* [21], *Pectobacterium odoriferum* [15], *Pectobacterium parmentieri* [22], *Pectobacterium parvum* [23], *Pectobacterium polaris* [24], *Pectobacterium polonicum* [25], *Pectobacterium punjabense* [26], *Pectobacterium versatile* [15] and *Pectobacterium wasabiae* [14] and 2 proposed species not yet validated by *had hoc* committees: '*Pectobacterium peruviense*' and '*Pectobacterium zantedeschiae'* [27,28]. Given the taxonomic evolution in the past ten years, the ecological importance, repartition and habitat of most species need to be evaluated. Bacterial collections are interesting tools to reach that goal. The CIRM-CFBP, French Collection for Plant-associated bacteria (DOI: 10.15454/1.5103266699001077E12) located in France at INRAE hosts many strains of the *Pectobacterium* genus isolated from 1944 to 2019. However, the taxonomical status of most of these strains is not stabilized. Indeed, many strains were deposited as *Pectobacterium* sp., which just indicates they belong to this genus. Furthermore, many strains were deposited as *P. carotovorum.* Since historically *P. carotovorum* has gathered until 7 subspecies that are now elevated at species level, it is currently difficult to known to which species these strains belong to. Finally, many ancient strains were likely characterized solely on the basis of phenotypic tests and this could have led to incorrect taxonomic assignation. As a result, it is currently impossible to have a synthetic view of the *Pectobacterium* collection hosted at the CIRM-CFBP.

The aim of this work was to clarify and update the taxonomic status of 265 *Pectobacterium* strains deposited at the CIRM-CFBP collection and to gain insight of the frequency and isolation habitat of the 19 described *Pectobacterium* species within the CIRM-CFBP collection. To do so, we performed phylogenetic analysis based on the partial sequences or *dnaX*, *leuS* and *recA* housekeeping genes that allocated strains to specific clades. To understand how clades were related to delineate species, this analysis was completed with genome sequencing of 15 strains. This allowed determining the frequency of each species within the CIRM-CFBP collection. Some species appeared to be endemic *Pectobacterium* species found all over the world on various host plants and environments while others, at the

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opposite, gathered strains isolated from only one botanical family or one specific environment.

Materials and Methods

Bacterial strains, culture conditions and DNA extraction

The 265 strains used in this study are provided Table S1. For house-keeping genes amplification, PCRs were conducted directly on colonies grown overnight on solid KingB medium (2g protease peptone, 15g agar, 10ml glycerol, 1,5g KH_2PO_4, 1,5g $MgSO_4$-$7H_2O$, per one liter of medium) and boiled at 100°C for 10 minutes. For preparation of genomic DNA, the strains were first grown overnight at 28°C on solid LB medium (10 g tryptone, 5 g yeast extract, 10 g NaCl, 15 g agar per one liter of medium). A single colony was then picked up and grown overnight in 2ml of liquid LB medium at 28°C agitated at 20 rpm. After centrifugation of the culture broth (5 min at 12,000 rpm), DNA was extracted with the wizard® genomic DNA extraction kit (Promega) following the supplier's instructions. DNA was suspended in 100µl of sterile distilled water and the quantity and quality of DNA was assessed by NanoDrop measurement, spectrophotometry analysis and agarose gel electrophoresis on 1% agarose gels.

dnaX-leuS-recA phylogeny

Housekeeping genes *dnaX leuS* and *recA* were amplified and sequenced for the 261 strains. PCR protocols and primers are described in Portier *et al*, 2019 [15]. Sequencing of PCR products was performed by Genoscreen (Lille, France). The consensus sequences for each gene for each strain were extracted from forward and reverse sequences assembly using Geneious Pro version 9.1.8 (www.geneious.com). The sequences were then aligned and trimmed using BioEdit version 5.0.6. All the obtained sequences were deposited in public databases and Table S1 summarizes the data. A phylogenetic tree was constructed with concatenated alignments of all genes with MEGA 7.0.26, using the neighbour-joining method with 1000 bootstrap replicates, and the evolutionary distances were computed by using the Kimura two-parameter method. All the *Pectobacterium* type strains were included in the phylogenetic tree. When type strains were not present at CIRM-CFBP (*P. polonicum* DPMP 315^T, *P. actinidiae* KKH3^T, *P. zantedeschiae* 9M^T and *P. peruviense* UGC32^T) *dnaX, leuS* and *recA* sequences were retrieved from genome sequences available at NCBI. In addition, to help species delineation on the phylogenetic tree, *dnaX, leuS* and *recA* sequences retrieved of

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other NCBI genomes recently reclassified in their correct assignation species by Portier et al., 2019 [15] were also included. To root the phylogenetic tree, *dnaX, leuS* and *recA* sequences were retrieved from the genome of *Dickeya solani* CFBP 7704 (RNS 08.23). Twelve strains were not included in the phylogenetic analysis provided Fig S1 because at least one of the three sequences *dnaX, leuS* or *recA* was not correctly amplified. However, for these 12 strains, the remaining amplified sequences (Data not shown) allowed their assignation to known species without ambiguities. Finally, 4 strains (CFBP 8719, CFBP 8720, CFBP 8723 and CFBP 8724) deposited at the CIRM-CFBP in 2019 were assigned to their species following amplification and sequencing of the *gap*A housekeeping gene as described by Cigna et al. [29]. All the sequences used for the phylogenetic tree in figure 2 and figure S1 were deposited at NCBI and the accession numbers are listed in table S1.

Genome analysis

Genome sequencing was performed at the next generation sequencing core facilities of the Institute for Integrative Biology of the Cell (Avenue de la Terrasse 91190 Gif-sur-Yvette France). Nextera DNA libraries were prepared from 50 ng of high-quality genomic DNA. Paired end 2x75pb sequencing was performed on an Illumina NextSeq500 apparatus, with a High Output 150 cycle kit. CLC Genomics Workbench (Version 9.5.2, Qiagen Bioinformatics) was used to assemble reads. Final sequencing coverage was between 118x and 216x (Table 1). Coding sequences were predicted using the RAST server [30] with the Glimmer 3 prediction tool [31]. Statistics of the 15 newly sequenced draft genomes are presented in Table 1.

Pairwise comparison of the genomes was computed using the average nucleotide identity (ANI) Pyani python module (https://github.com/widdowquinn/pyani [32] with the blast algorithm (ANIb). The species threshold was set at 96%. Digital DNA-DNA hybridization (dDDH) values were calculated between each sequenced genome and reference species genomes using a dedicated pipeline (http://ggdc.dsmz.de/) from the formula 2 (sum of all identities found in high-scoring segment pairs (HSPs) divided by overall HSP length), this measure is normalised to genome length and therefore is still robust when incomplete draft genomes are analysed. The species threshold was set to 70%.

Phylogenetic tree was constructed from concatenated sequences of 1053 homologous genes retrieved from the 15 newly sequenced genomes and 18 genomes of type strains or reference strains for each species. MLSA analysis was performed as described in Portier et al., 2019 [15]. The genome of *D. solani* strain RNS_08.23 was used to root the tree. The species *P.*

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cacticida was not included in this analysis as no reference genome has yet been published.

Results and discussion

The CIRM-CFBP studied strains

The 265 *Pectobacterium* CIRM-CFBP studied strains are presented in Fig 1. They were isolated from 1944 to 2019 covering therefore a 75 years period (Fig. 1A). For 56 strains, the year of isolation was not reported, however, for these strains the year of deposit at the CIRM-CFBP indicated that 22 strains were isolated at least 46 years ago (deposited at the CIRM-CFBP from 1970 to 1974), 1 strain was isolated at least 38 years ago (deposited in 1982), 6 strains were isolated at least 28 years ago (deposited from 1991 to 1992), and 28 strains were isolated at least 19 years ago (deposited in 2001). Concerning the host plants or environments from which these 265 strains were isolated, a large majority of 136 strains were isolated from potato tubers or potato plants accounting for the threat provoked by *Pectobacterium* sp. on this economically important crop plant (Fig. 1B) [4]. ~~Overall,~~ the studied collection gathers 100 strains isolated from 31 host plants covering 17 botanical families accounting for the broad host range of *Pectobacterium* species [3] as well as 29 strains isolated from freshwater, soil or rhizosphere. As the CIRM-CFBP collection is a French collection, it is not surprising that a large majority of 100 strains originated from this country (Fig. 1C). Fours strains originating from overseas French territories (Martinique, Guadeloupe and La Réunion) were considered apart, as these territories are located respectively on North American continent (Martinique, Guadeloupe) and African continent (La Réunion). Overall, the collection gathers strains originating from 27 countries in Europe, Africa, North America, South America, Asia and Indonesia. Finally, 94 strains were deposited at the CIRM-CFBP as *Pectobacterium* sp. without any indication of the species they belong to (Fig 1D). Furthermore, many strains were deposited under names that no longer exist or under the *P. carotovorum* name that could be misleading since it regrouped for a while many different subspecies. In summary, although this collection gathers many strains sampled at different times over different countries and environments, its practical use is hampered by the poor taxonomic designation of the deposited strains.

dnaX-leuS-recA phylogeny of the collection

The *dnaX-leuS-recA* phylogeny (Fig 2 and Fig S1) revealed that most strains spread out in clades that are separated from each other's, supported by usually high boostrap values, which

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gather strains and the type strain of a given species. This allowed assignation most of the strains of CIRM-CFBP to already described species. All these strains were assigned to 18 of the 19 described species within *Pectobacterium*, except to *P. polonicum*.

The relative position of the *P. caticida* species inside the *Pectobacterium* genus has remained questionable since no genome of this species have been sequenced and, at the time of the description in 1991 by Alcorn et al. [19], most of the *Pectobacterium* species were not yet described. Interestingly, the *leuS*, *recA* and *dnaX* phylogeny performed here grouped all the *P. cacticida* strains in the same clade as a deep branching species within the *Pectobacterium* genus (Fig 2).

For seven strains (CFBP 797, CFBP 5380, CFBP 6067, CFBP 6168, CFBP 6588, CFBP 8736 and CFBP 8739), the assignation to an already described species was either not possible or their position on the phylogenetic tree was ambiguous (Figure 2). These seven strains may belong to not yet described species, however the *dnaX-leuS-recA* phylogeny performed here is not adequate to delineate new species. Three of these strains grouped together in the same *dnaX-leuS-recA* clade and may represent a single species (only two of which being displayed in the phylogenetic tree in Fig 2), while the 4 remaining strains each represent a different clade. We sequenced the genomes of 2 strains out of these 7 strains. Furthermore, in order to check that large clades revealed by the *dnaX-leuS-recA* phylogeny indeed represented a single species, we sequenced 13 genomes to complete this analysis.

Whole genome strains analysis

The 15 sequenced genomes are presented in Table 1. Pairewise ANIb and dDDH were performed between these the genomes of these 15 strains and the genomes of type strains or species representative. A phylogenetic tree, constructed from concatenated sequences of 1053 homologous genes retrieved from the 15 analysed genomes and the genomes of type strain or species representative is presented in figure 3. Results of ANIb and dDDH (Table S2) allowed to classify all the newly sequenced strains but two to already described species: 4 of the sequenced strains were classified as *P. carotovorum*, 4 as *P. versatile*, 3 as *P. brasiliense*, 1 as *P. odoriferum*, and 1 as *P. aroidearum*.

Strain CFBP 8736 displays pairwise ANI and DDH values below the species threshold with the *P. brasiliense* type strain (ANI: 94.7%; DDH 61.1%) (Table 2). However, the pairwise ANI/DDH values are higher (95.5% to 95.7% and 64.7% to 65.3% respectively) between CFBP 8736 and the other *P. brasiliense* genomes (Table 2). The *P. brasiliense* species shows a relatively high level of divergence between its strains and is probably ongoing a

 doi:10.20944/preprints202008.0608.v1

diversification process (Portier et al., 2019). Our results show that strain CFBP 8736 belongs to a separate species but is very close to *P. brasiliense*.

The remaining genome, corresponding to strain CFBP 8739, could not be assigned to known or proposed species. Analysis of the pairwise ANI/dDDH values obtained for this latter genome with type strains or reference strains of other species indicated that its closest species was *P. aroidearum* with pairwise ANI value of 91.1% and dDDH value of 43.2%, well below the cut-off values of species limit (Table 2). Strain CFBP 8739 therefore belongs to a still uncharacterized species. Its position in the *dnaX-leu*S-*recA* phylogenetic tree was distinct but close to two other strains, CFBP 6588 and CFBP 797, which could not be assigned to any known species (Fig 2, Fig S1). However, it remains ambiguous to decipher if CFBP 6588 and CFBP 797 could be grouped either with *P. aroidearum* or with this new species represented by strain CFBP 8739 or if each strain represents a new species.

Comparison of the updated taxonomy with the former one

Following *dnaX-leuS-recA* phylogeny and genome analysis, out of the 265 strains analysed, 261 strains could be assigned to 18 known or proposed species. The only species not represented in the CIRM-CFBP collection is *P. polonicum.* We performed comparison of the updated taxonomy with the former one (Fig 4). Among the 94 formely unassigned *Pectobacterium* sp. strains, 90 were taxonomically assigned to 10 different species. The more frequently assigned species were *P. versatile* (41/94 strains), *P. carotovorum* (21/94 strains) and *P. brasiliense* (11/94). Interestingly, 3 strains formely unassigned *Pectobacterium* sp. were finally assigned to *P. zantedeschiae*, a species without known representative in the CIRM-CFBP collection before our work. Most of the 27 former *P. carotovorum* subsp. *carotovorum* strains were splitted between *P. carotovorum* (12/27) and *P. versatile* (8/27). As well, the 13 strains previously classified as *P. carotovorum*, were mostly splitted between *P. versatile* (8/13) and *P. carotovorum* (4/13). This highlights the close proximity between *P. versatile* and *P. carotovorum*, as already noted by [15]. Conversely, strains assigned to the former *P. carotovorum* subsp. *brasiliense* and *P. carotovorum* subsp. *odoriferum* were mostly assigned to their cognate species *P. brasiliense* (16/17) and *P. odoriferum* (14/16) (Fig 4). As well, strains assigned to the species *P. atrosepticum* (27/33), *P. betavasculorum* (18/19), *P. aquaticum* (8/8), *P. cacticida* (6/7) and *P. wasabiae* (5/6) remained mostly associated to the same species indicating former good taxonomic resolution of these groups. Finally, while the former classification assigned only 2 strains to the *P. aroidearum* species this species was enriched of 5 strains following our taxonomical update. Out of these 5 strains, 4 were

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previously designated as *Pectobacterium* sp. and 1 as *P. carotovorum*.

Finally, 7 strains could not be assigned to any known or proposed species. Three strains (CFBP 5380, CFBP 6067 and CFBP 6068, the latter not displayed in the phylogenetic tree Fig 2) could probably be gathered in the same new species since they are closely clustered in the same clade following *dnaX-leuS-recA* analysis (Fig 2). It remains unclear how many different species could be described with the 4 remaining strains. Among these, CFBP 8736 and CFBP 8739 whose genome were sequenced, represent potentially two new species close to *P. brasilense* and *P. aroidearum* respectively.

Analysis of strains isolated on potato plant

As already stated, a large majority of 136 strains were isolated from potato tubers or potato plants. These 136 strains were isolated in 16 countries covering 4 continents (Fig 5). We were therefore interested in understanding which species were isolated from this economically important crop. We found that strains isolated from potato belong to 11 different already described *Pectobacterium* species (Table 3). The most frequently deposited species was the recently described species *P. versatile* (42/136) followed by *P. atrosepticum* (27/136), *P. carotovorum* (26/136) and *P. brasiliense* (24/136). Less frequently, other recently described species known to infect potato such as *P. parmentieri*, *P. polaris*, *P. parvum*, *P. peruviense* and *P. punjabense* were also deposited to the collection (Table 3). Surprisingly, our taxonomical update also identified one strain of *P. actinidiae* and one strain of *P. betavasculorum* that were isolated from potato in Syria in 2004 and Romania in 1992 respectively. Among the non-classified strains, the three strains that grouped into a putative new species (CFBP 5380, CFBP 6067 and CFBP 6068) were isolated from potato plants and may represent a new pathogen species on this host plant.

On potato, soft rot is the name usually used for tuber rotting while the blackleg disease refers to the spread of the pathogen to the base of the potato stem, where it causes darkening and decay of the aerial part [4]. Not all *Pectobacterium* species cause blackleg but we could infer that a strain isolated from stem or aerial part of the potato plant was isolated from blackleg disease symptoms. Out of the 136 strains isolated from potato, 31 were isolated from stem or leaf, 33 from tuber and, unfortunately, it was not clearly documented for the remaining 71 strains (Table 3). The 31 strains isolated from stem or leaf belonged to 6 species, 5 of which *P. brasiliense, P. atrosepticum, P. parvum, P. parmentieri* and *P. punjabense* are well known species triggering blackleg disease [4,23,26]. Interestingly, the newly described *P. versatile* species was also isolated from potato stem or leaf in UK, Morocco and France from 1972 to

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2016. Whether *P. versatile* could be responsible of blackleg outbreak or whether it is associated with blackleg symptoms as a secondary invader remains to be determined.

Analysis of species host range and geographic distribution

The update of taxonomical assignation prompted us to check the host range and geographic distribution of species deposited at the CIRM-CFBP collection (Table 4).

The *P. versatile* species is by far the most represented species of CIRM-CFBP collection. The 72 *P. versatile* strains were isolated from 12 host plants representing 9 botanical families and from water. *P. versatile* strains were isolated from 11 countries on 3 continents. This highlights the broad ecological and geographical distribution of this species. The most ancient *P. versatile* strain deposited in CIRM-CFBP was isolated in 1946. This contrasts with the recent description of this species in 2019. The reason why this species was so long neglected probably comes from its close genomic proximity with *P. carotovorum* [15] and the taxonomical update performed here confirms that these two species were often mixed up by bacteriologists (Fig. 5). *P. carotovorum* is the second most represented species deposited in CIRM-CFBP and, as *P. versatile*, it also has a broad ecological and geographical distribution (Table 4) also explaining why these two species were often mixed up. Another species with broad ecological and geographical distribution is *P. brasiliense* (Table 4). This is in contrast with *P. atrosepticum* strains which were isolated from only one botanical family *Solanaceae*, with 27 strains isolated from potato, 2 from tomato and 1 from soil environment, certainly indicating a narrower ecological niche. The host range of *Pectobacterium* sp. was reviewed by Ma et al. in 2007 and updated by Charkowski in 2018 [3,4]. Our taxonomical update of the CIRM-CFBP extends the number of plant hosts from which *Pectobacterium* strains. were isolated (Table 4 new plant hosts in bold). For example, we found that *P. brasiliense* and *P. versatile* could be isolated from *Chrysanthemum sp.*, an ornamental plant previously described as infected by *Dickeya sp.* and not by *Pectobacterium sp.* [3]. As well, *P. brasiliense* was isolated from *Musa* sp., a plant also previously reported to be infected only by *Dickeya* sp. [3].

The recently described "*P. zantedeschiae"* [27] and *P. parvum* species [23] had only a few representatives in CIRM-CFBP (Table 4). Nevertheless, some of the strains were isolated more than 50 years ago. Indeed, the first *P. parvum* strain was isolated in 1969 and the three "*P. zandeteschiae"* strains were respectively isolated in 1960, 1964 and 1966. This indicates that both species were already present on their respective host plants well before their description. Interestingly, although most of the *P. parvum* strains were isolated from potato

 doi:10.20944/preprints202008.0608.v1

plant, the *P. parvum* strain of 1969 was isolated from sunflower enlarging the host range of this species. For "*P. zantedeschiae"*, the 3 strains hosted at CIRM-CFBP were all isolated from *Araceae* plants as the other strains described for this species [27]. Concerning the recently described fresh water environmental species *P. aquaticum* [17], *P. fontis* [21], *P. polonicum* [25] and the strain CFBP 8739, we were surprised that these species had either no representative in the CIRM-CFBP or only strains deposited following the recent description of the species. The fact that no strain representative of these three species were isolated from crop plants and ornementals along the 75 years period that cover our analysis strongly suggests that these species are not an important threat for crop plants and ornementals. Whether these species evolved toward saprophytism and are no longer able to damage living plants or whether they infect living plants with no economic value remains to be determined.

Conclusion

Bacterial culture collections hold resources that are diverse and can help scientists to better understand, in the case of pathogens, the history of the epidemics, the emergence of diseases, and the host range of pathogenic bacteria. However, even if the situation improved a lot during the last decade, the quality of associated data to deposited resources, often scarce for old resources, can hamper the benefit that could be gained from bacterial collection

By this publication we wanted to show that the effort made by the collections to cure their resources is really beneficial to the whole scientist community, and brings a better understanding of the dynamic of the taxa considered. We strongly encourage culture collections to initiate or continue their efforts to update the identity of their resources.

We also encourage scientists to deposit their resources in public culture collections, where they will be made available long term for the benefit of the whole scientific community. The quality of the resources being dependent to the quality of the associated data, the depositors are also strongly encouraged to transmit the most accurate and complete data even if they can appear to not to be important at the time of deposit. Indeed, while the plant specie or environment from which strains have been isolated is generally indicated the type of symptoms is often missing and for environmental strains isolated from water, the water temperature is often not indicated. As well, the year of isolation is an important data that is sometimes neglected.

In the case of *Pectobacterium*, our work permitted to have a much better overview of the extend of the diversity in the collection, uncover potential new species and give insights in the epidemiology and ecology of this genera.

Supplementary materials

Two supplementary Tables (Table S1 and Table S2) and 1 supplementary Figure (Figure S1) are available with the on-line version of this article.

Data availability statement

The 15 newly whole genome sequenced *Pectobacterium* strains are deposited in the GenBank database. Accession numbers for genomes and *recA, dnaX, leuS* partial sequences are listed in Table 1 and Table S1.

Authors contributions

MAB : Conceptualization, Funding acquisition, Writing original draft PP, MAB : Supervision, Project administration PP, JP : Writing - review & editing, Formal analysis, PP, PJ, MAB: Validation PP, PJ, MAB, GT : Visualization PP, JP, GT: Data curation, Methodology PP, MAB, GT, CD : Investigation CD : Resources . all authors have approved the manuscript.

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Conflicts of interests

The authors declare that there are no conflicts of interest

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Figure Legends

Figure 1: Overview of the 265 CIRM-CFBP *Pectobacterium* strains at the beginning of our study

A: Decade of isolation, B Host or Environment from which the strains were isolated, C: country from which the strains were isolated, D: name under which the strains were deposited. Diagrams B, C and D: legends are restricted to groups ~~of~~ 5 strains or more. . Complete details for strains are available in Table S1.

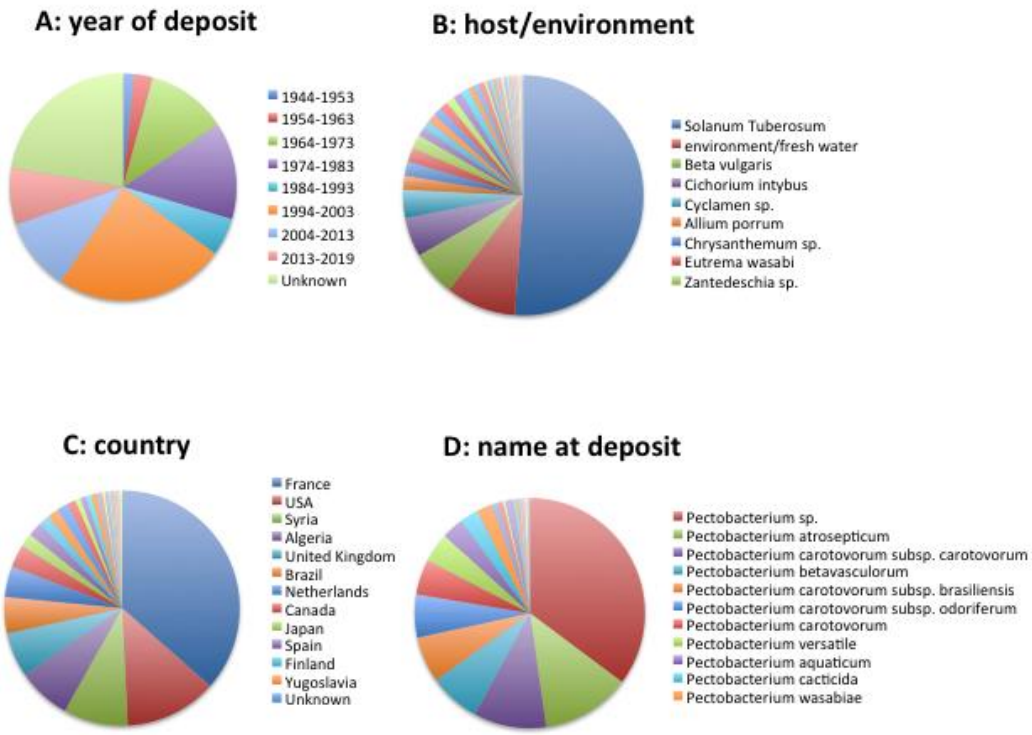

Figure 2: Phylogenetic tree reconstructed from concatenated partial sequences from *dnaX*, *leuS* and *recA* housekeeping genes. The phylogenetic tree was reconstructed with concatenated alignments of all genes with MEGA 7.0.26, using the neighbour-joining method with 1000 bootstrap replicates, and the evolutionary distances were computed by using the Kimura two-parameter method. Bootstrap values are shown when over 70. Full view of this tree and the accession numbers of the sequences are available in Fig. S1 and Table S1 respectively.

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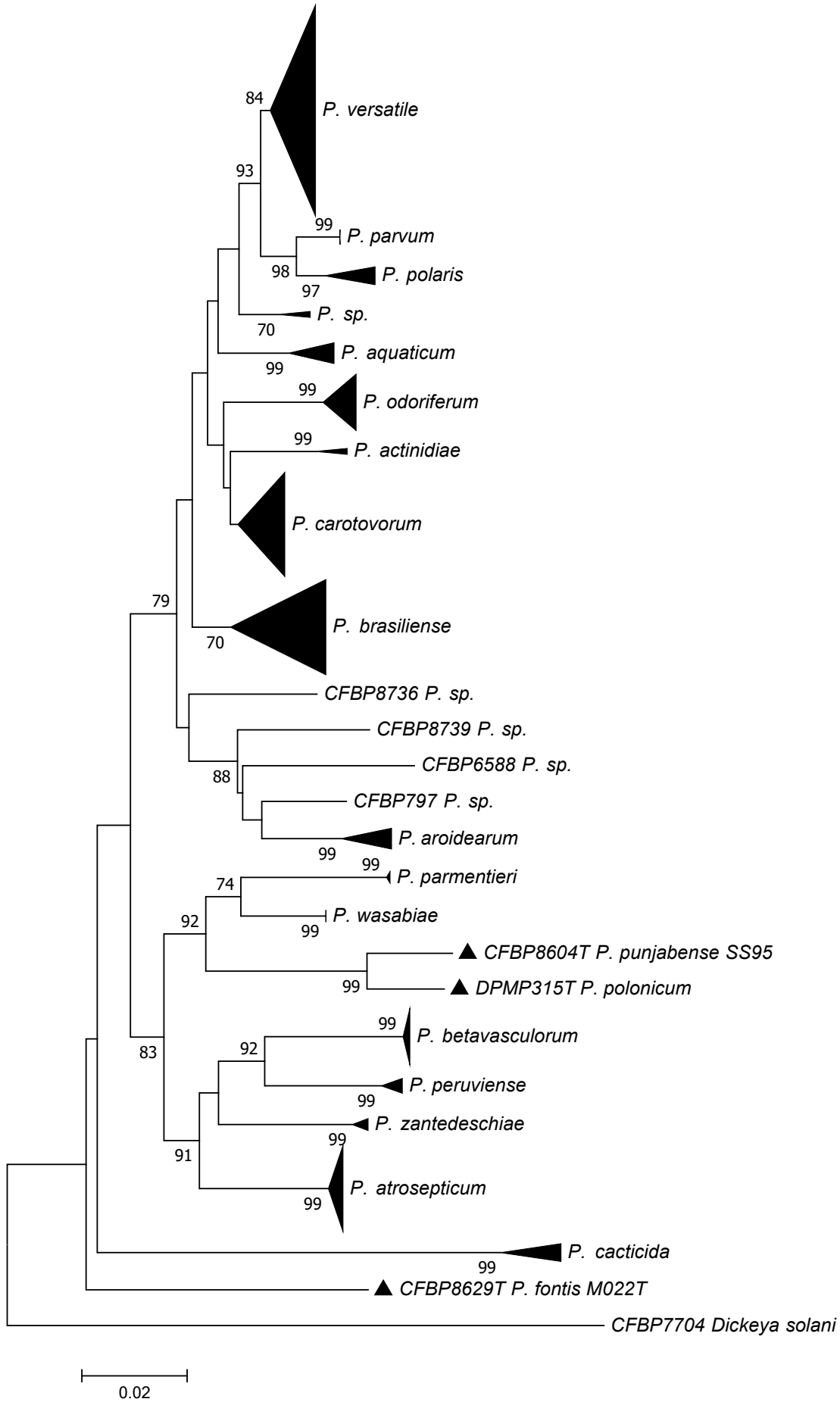

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Figure 3: Phylogenetic tree reconstructed from concatenated sequences of 1053 homologous gene sequences retrieved from complete genome sequences for the 15 sequenced strains and type strains or reference strains of other species.

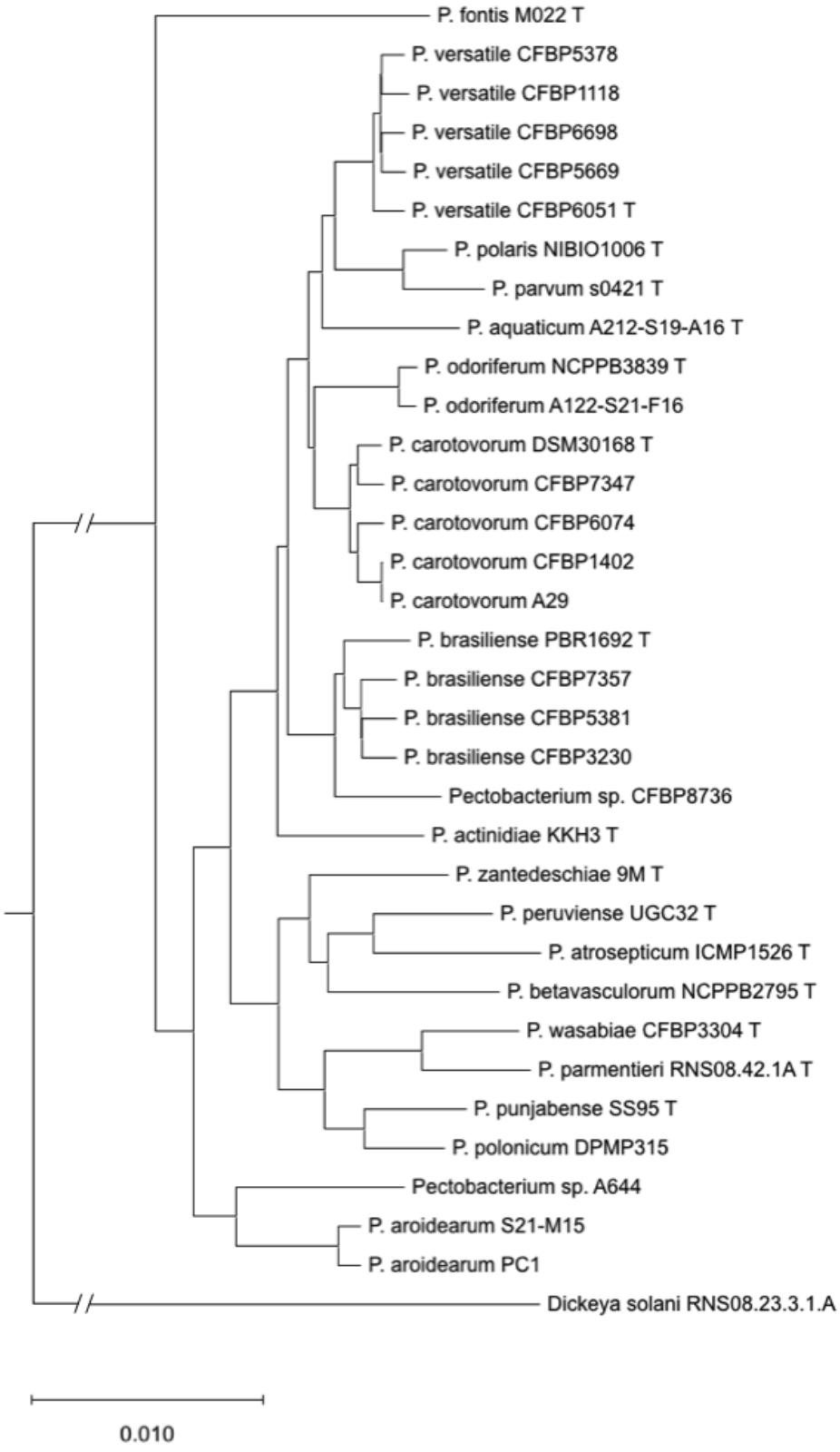

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Figure 4: Comparison of the updated taxonomy with the former one

On the left are displayed the taxonomic names under which the strains were deposited, on the right the updated taxonomy for the 265 strains is displayed.

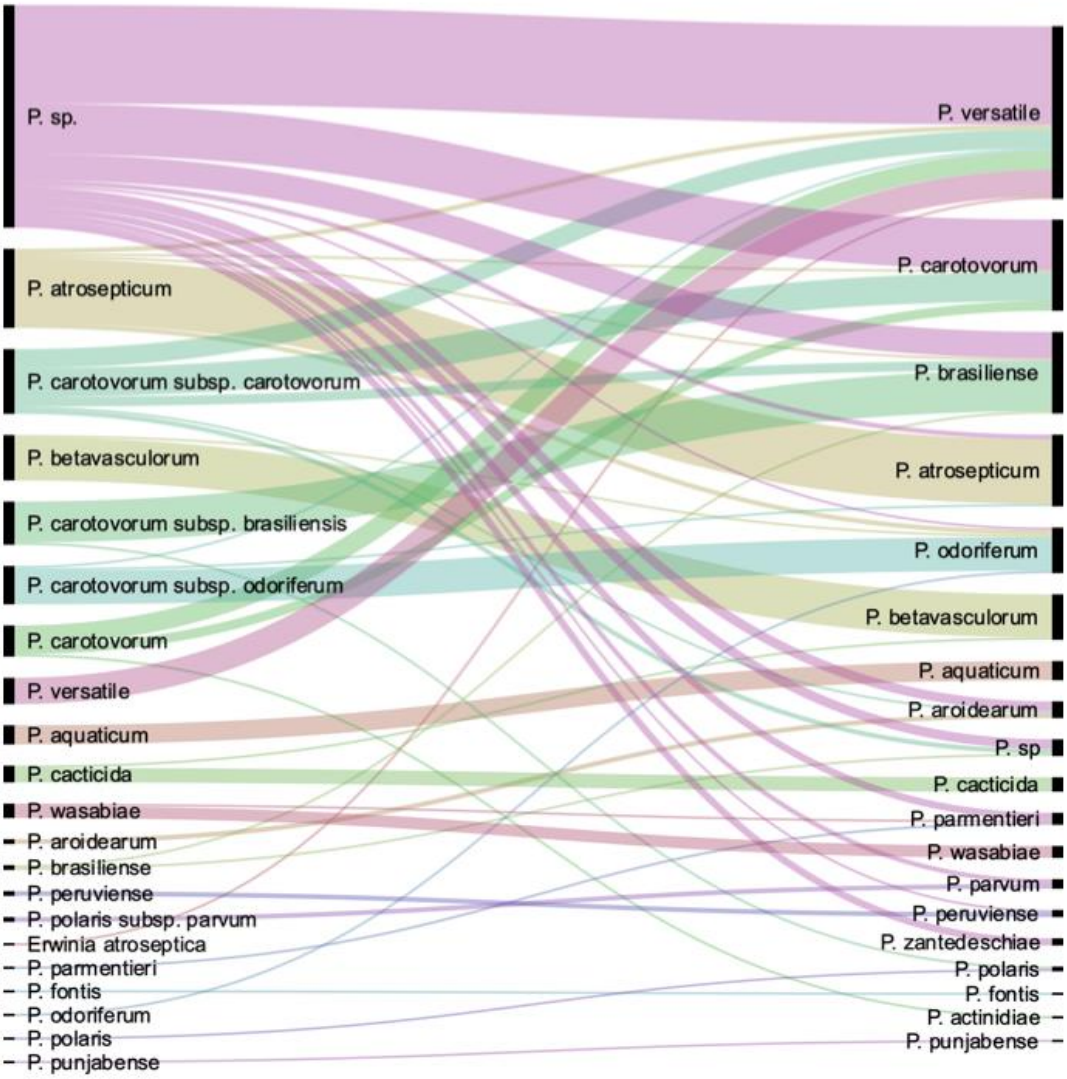

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Figure 5: Updated taxonomy of the 136 strains isolated from potato

A: country of isolation B: proportion of strain isolated in each *Pectobacterium* species.

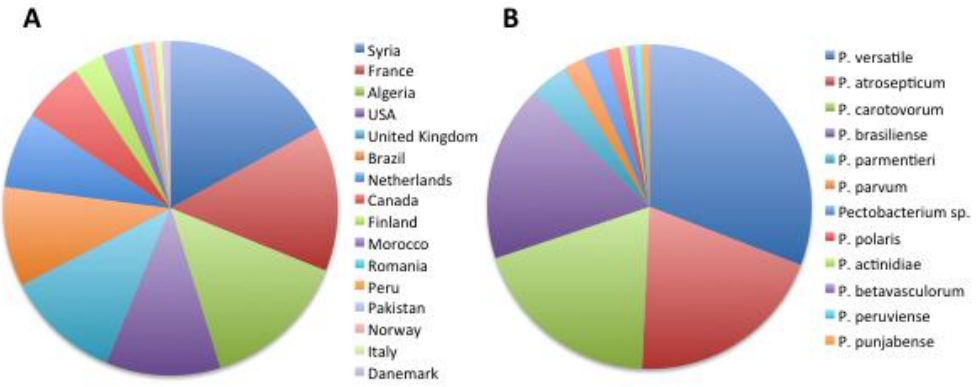

Table 1: General informations for the 15 sequenced *Pectobacterium* genomes

Strain	Accession	Size	Scaffolds	%GC	N50	Coverage	CDS	RNA
Psp CFBP8736	JACDSF000000000	4,665,864	169	51,2	107,870	118	4,322	52
Pb CFBP7357	JACDSB000000000	4,805,970	50	51,8	231,494	143	4,236	62
Pb CFBP3230	JACDSD000000000	4,850,518	50	52,1	394,958	179	4,243	62
Pb CFBP5381	JACDSC000000000	4,600,084	60	52,0	230,522	126	4,059	62
Pc CFBP6074	JACDRY000000000	4,691,819	92	52,0	207,976	156	4,171	62
Pc CFBP8734	JACDSA000000000	4,702,111	58	51,9	325,663	216	4,190	55
Pc CFBP1402	JACDRZ000000000	4,667,513	62	52,0	312,332	177	4,146	58
Pc CFBP7347	JACDRX000000000	4,694,461	42	52,0	317,373	189	4,148	63
Po CFBP8735	JACDRW000000000	4,974,102	129	51,4	131,982	203	4,466	71
Psp CFBP8739	JACDRR000000000	4,359,644	64	51,7	341,883	149	3,874	57
Pv CFBP1118	JACDRV000000000	4,968,197	210	51,9	51,811	180	4,419	41
Pv CFBP6698	JACDRS000000000	4,963,578	87	50,8	120,001	124	4,401	61
Pv CFBP5378	JACDRU000000000	4,942,943	57	51,8	277,607	154	4,338	61
Pv CFBP5669	JACDRT000000000	4,960,228	45	51,7	245,703	150	4,367	61
Pa CFBP8737	JACDSE000000000	4,898,716	50	51,8	326,273	178	4,357	60

P. sp: P. unassigned species, Pb: *P. brasiliense*, Pc: *P. carotovorum*, Po: *P. odoriferum*, Pv: *P. versatile*, Pa: *P. aroidearum*

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Table 2: Closest ANI (below diagonal) and dDDH (above diagonals) for 6 of the analyzed genomes

		CFBP7357	CFBP5381	CFBP3230	PBR1692 T	CFBP8736	PC1	CFBP8737	CFBP8739
Pb	CFBP7357	1.000	0.772	0.766	0.678	0.647	0.416	0.417	0.415
	CFBP5381	0.973	1.000	0.765	0.683	0.653	0.416	0.415	0.417
	CFBP3230	0.973	0.973	1.000	0.684	0.649	0.415	0.415	0.414
	PBR1692^{T}	0.962	0.962	0.962	1.000	0.611	0.413	0.412	0.410
Psp	CFBP8736	0.955	0.957	0.956	0.947	1.000	0.412	0.409	0.407
Pa	PC1	0.905	0.906	0.905	0.904	0.903	1.000	0.832	0.432
	CFBP8737	0.906	0.906	0.905	0.904	0.904	0.980	1.000	0.429
Psp	CFBP8739	0.905	0.905	0.905	0.903	0.903	0.911	0.910	1.000

Pb: *P. brasiliense*. Pa: *P. aroidearum*. Psp: *Pectobacterium* unassigned species.
The genomes analysed in this study are indicated in black.
The reference genomes are indicated in red.

Table 3: Species isolated from potato plants and reported symptoms.

	nb of strains isolated on potato /species			
	Stems or Leaves	Tubers	Not reported	Total
P. versatile	6	7	29	42
P. atrosepticum	6	11	10	27
P. carotovorum	0	4	22	26
P. brasiliense	14	7	3	24
P. parmentieri	2	3	0	5
P. sp	0	1	2	3
P. parvum	2	0	1	3
P. polaris	0	0	2	2
P. punjabense	1	0	0	1
P. peruviense	0	0	1	1
P. betavasculorum	0	0	1	1
P. actinidiae	0	0	1	1
Total	31	33	72	136

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Table 4: host plant, environment and country of isolation for each of the *Pectobacterium* species deposited at the CIRM-CFBP

Species	nb of strains	Isolated from (number of strains)	Country of isolation (nb of strains)
P. versatile *	72	Solanum tuberosum (42) **Cyclamen sp. (4)** **Chrysanthemum sp. (3)** Cichorium intybus (3) **Iris (3)** **Primula sp. (3)** **Allium porrum, (2)** Brassica oleracea (2) Cynara scolymus L. **(1)** **Daucus carota (1)** **Hyacinthus orientalis, (1)** Rhizosphere of **Solanum dulcamara** (1) fresh water (6)	Algeria (3) Canada(3) Finland (1) France (35) La Réunion island (France) (1) Morocco (3) Netherland (8) Spain (1) Syria (6) UK (7) USA (4)
*P. carotovorum**	38	**Aloe arborescens (1)** **Apium graveolens (1)** Brassica oleracea (1) **Capsicum annuum (1)** **Cyclamen sp (5)** Solanum tuberosum (26) fresh water (3)	Algeria (3) Canada (4) Denmark (1) France (5) Greece (2) Spain (2) Syria (11) USA (7) Yugoslavia (3)
P. brasiliense	34	**Carica papaya (1)** **Chrysanthemum morifolium (2)** Cucurbita pepo (1) **Cyclamen sp. (1)** **Gossypium sp. (1)** **Musa sp. (1)** Solanum tuberosum, (23) Rhizosphere of **Solanum dulcamara,** (1) Fresch water (2) Unknown (1)	Algeria (7) Brazil (13) France (3) Italy (1) La Réunion island (France) (1) Martinique island (France) (1) Spain (2) Syria(3) USA (2) unknown (1)
P. atrosepticum	30	**Lycopersicon esculentum (2)** Solanum tuberosum, (27) soil (1)	Algeria (6) Canada (1) France (11) Italy (1) Syria (1) UK (7) USA (3)
P.betavasculorum	19	Beta vulgaris (15) **Helianthus annuus (2)** **Opuntia phaeacantha (1)** **Solanum tuberosum (1)**	France (9) Mexico (1) Romania (1) USA (7) Unknown (1)
P. odoriferum	19	**Allium porrum (3)**	France (17)

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		Apium graveolens (1) **Beta vulgaris (1)** Cichorium intybus, (11) **Hyacinthus sp. (2)** Fresh water (1)	Unknown (2)
P. aroidearum	10	**Dieffenbachia sp, (1)** **Lycopersicon esculentum (1)** **Musa sp. (1)** **Nicotiana tabacum (1)** **Philodendron floridi (1)** Zantedeschiae (3) fresch water (2)	France (5) Guadeloupe island (France) (2) South Africa (1) USA (2)
P. aquaticum	8	fresh water (8)	France (8)
P. cacticida	6	**Acanthocereus pentagonus (1)** Carnegiea gigantea (3) **Lemaireocereus thurberi (1)** **Opuntia fulgida (1)**	USA (6)
P. parmentieri	5	Solanum tuberosum (5)	UK (2) Netherlands (1) France (1) Finland (1)
P. wasabiae	5	Eutrema wasabi (syn *Eutrema japonicum*) (5)	Japan (5)
P. parvum **	4	Solanum tuberosum, (3) Helianthus annuus (1)	Yugoslavia (1) Netherlands (1) Finland (2)
*P. sp.14***	3	Solanum tuberosum (3)	Netherland (1) USA (2)
*P. peruviense***	3	Solanum tuberosum, (1) fresch water (2)	France (2) Peru (1)
*P. zantedeschiae***	3	Zantedeschia sp (2), Arum sp. (1)	France (3)
*P. polaris***	2	Solanum tuberosum (2)	Syria (1) Norway (1)
*P. sp***	1	fresh water (1)	France (1)
P. actinidiae	1	**Solanum tuberosum** (1)	Syria (1)
*P. fontis***	1	fresh water (1)	Malaysia (1)
*P. punjabense***	1	Solanum tuberosum (1)	Pakistan (1)

Plant indicated in bold correspond to plant not described as host plant for the indicated species by Charkowski 2018

* as *P. carotovorum* and *P. versatile* were often mixed up, new host plants indicated in bold correspond to host plants not described as P. *carotovorum* host plants by Charkowski 2018

** *Pectobacterium* sp. whose host range is not described by Charkowski 2018.

The number of isolated strains on each host or country is indicated between brakets.

Table S1: detailed list of the studied strains, including genome accession numbers when available and accession numbers of *dnaX, leuS* and *recA* sequences used for the phylogenetic trees displayed in Figure 1 and Figure S1.

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The star after the NCBI accession number indicates sequences produced for this study.

Table S2: Pairwise ANI (lower diagonal) and dDDH (top diagonal) between the 15 analyzed genomes (indicated in black) and reference genomes (indicated in red).
Pc : *P. carotovorum*. Pv : *P. versatile*. Po : *P. odoriferum*. Pb : *P. brasiliense*. Pa : *P. aroidearum*. Psp : *Pectobaterium* unassigned species.

Figure S1: Extended view of the phylogenetic tree displayed Fig 1. Phylogenetic tree reconstructed from concatenated partial sequences from *dnaX*, *leuS* and *recA* housekeeping genes. The strains indicated in red correspond to strains whose genomes are deposited in NCBI database, ~~the~~ genomes references are provided Table S1. The phylogenetic tree was reconstructed with concatenated alignments of all genes with MEGA 7.0.26, using the neighbour-joining method with 1000 bootstrap replicates, and the evolutionary distances were computed by using the Kimura two-parameter method. Bootstrap values are shown when over 70%