International Journal of Microbiology

WILEY

RESEARCH ARTICLE OPEN ACCESS

Genome-Based Reclassification of *Curtobacterium plantarum* Dunleavy 1989 as a Later Heterotypic Synonym of *Pantoea agglomerans* (Beijerinck 1888) Gavini *et al.* 1989

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Received: 26 August 2025 | **Revised:** 5 October 2026 | **Accepted:** 21 October 2026

Academic Editor: Syed Hassan

Keywords: comparative genomics | *Curtobacterium* | heterotypic synonym | *Pantoea* | phylogeny | taxonomy

ABSTRACT

In this study, we examined the taxonomic relationship between *Curtobacterium plantarum* and *Pantoea agglomerans*. Comparison of the 16S rRNA gene sequences showed 99.86% sequence similarity between the type strains. Analyses of the whole-genome sequence revealed that *C. plantarum* LMG 16222^T shared 88.40% digital DNA-DNA hybridization (dDDH), 98.25% average nucleotide identity by blast (ANIb), and 98.67% average nucleotide identity using MUMmer (ANIm) with *P. agglomerans* NBRC 102470^T. These values exceeded the accepted thresholds for species delineation, which are 70% for dDDH and 95%-96% for both ANIb and ANIm. Moreover, the two strains showed an average amino acid identity (AAI) of 99.13% and a percentage of conserved proteins (POCP) of 92.72%. Both values clearly exceed the established genus-level criteria: 60%-85% for AAI and more than 50% for POCP. Phylogenetic analyses based on the 16S rRNA gene, a concatenated set of 81 conserved bacterial core genes, and whole-genome data consistently placed *C. plantarum* LMG 16222^T in a well-supported clade with *P. agglomerans* NBRC 102470^T within the genus *Pantoea*. Accordingly, the phylogenetic and genomic evidence indicates that the two strains are conspecific and represent the same species. We consequently propose that *C. plantarum* Dunleavy 1989 be reclassified as a later heterotypic synonym of *P. agglomerans* (Beijerinck 1888) Gavini *et al.* 1989.

1 | Introduction

The genus *Pantoea* is classified within the family Erwiniaceae, order Enterobacterales, class Gammaproteobacteria, and phylum Pseudomonadota [1]. The genus was first proposed by Gavini et al. in 1989, with *Pantoea agglomerans* (Beijerinck 1888) Gavini *et al.* 1989 designated as the type species. *P. agglomerans* has been isolated from a variety of environments including water, plant seeds, soil, and surfaces [2, 3] and has also been associated with human infections [4–7]. The genus *Curtobacterium* was first proposed by Yamada and Komagata in 1972 [8], with *Curtobacterium citreum* (Komagata and Iizuka 1964) Yamada and Komagata 1972 designated as the type species [9]. The genus *Curtobacterium* falls within the family Microbacteriaceae, order Micrococcales, class Actinomycetes, and phylum Actinomycetota [1]. Dunleavy was the first to isolate *Curtobacterium plantarum* from the leaves of various plants and described the species in 1989. Traditionally, phenotypic traits, such as pigment formation and carbohydrate utilization, have been used to differentiate *C. plantarum* [10]. This species is Gram-positive, rod-shaped, and motile with produces a yellow pigment. It is strictly

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aerobic, does not form endospores, and is not acid-fast. The organism has been isolated from soybean and corn leaves, suggesting a close ecological association with these plant hosts. To date, there is no evidence that it is pathogenic to these plants. It grows optimally at 28°C-30°C and can tolerate up to 10% (w/v) NaCl. Furthermore, it is susceptible to bacteriophage PYB-3 [10]. Comparison of the 16S rRNA gene sequences revealed 99.86% sequence similarity between *C. plantarum* CIP 108988^T and *P. agglomerans* NCTC 9381^T, suggesting that the two type strains may belong to the same species. The high degree of phylogenetic relatedness between *C. plantarum* and *P. agglomerans* prompted a re-evaluation of the taxonomic placement of *C. plantarum*. Although the 16S rRNA gene sequence similarity exceeds the widely accepted species-level threshold of 98.65% [11], phylogenetic inference based on a single gene does not provide sufficient resolution for reliable species delineation. In order to make clear the taxonomic relationship between these organisms, we carried out extensive genome-based comparative analyses to determine whether *C. plantarum* and *P. agglomerans* represent separate species or the same species. According to the List of Prokaryotic Names With Standing in Nomenclature [1] (https://lpsn.dsmz.de, accessed 20 June 2026), *C. plantarum* and *P. agglomerans* are currently recognized as separate species. This apparent contradiction therefore calls for a thorough reassessment of their taxonomic relationship based on whole-genome sequence analyses. Therefore, the present study is aimed at clarifying the taxonomic position of *C. plantarum* by means of comparative genomic analyses using overall genome relatedness indices (OGRIs), including digital DNA-DNA hybridization (dDDH), average nucleotide identity calculated using BLAST (ANIb), average nucleotide identity calculated using MUMmer (ANIm), average amino acid identity (AAI), and percentage of conserved proteins (POCP). Furthermore, phylogenetic and phylogenomic analyses were carried out to investigate the evolutionary relationships of *C. plantarum* and to determine whether its assignment to the genus *Curtobacterium* is consistent with genome-based taxonomic evidence.

2 | Materials and Methods

According to LPSN, 15 species had validly published and correct names in the genus *Curtobacterium*, whereas 25 species had validly published and correct names in the genus *Pantoea*, as of September 8, 2026. To investigate the taxonomic relationship between *C. plantarum* and *P. agglomerans*, the 16S rRNA gene sequences of all the validly published names of the genera *Curtobacterium* and *Pantoea* were obtained from the National Center for Biotechnology Information (NCBI) database. The EzBioCloud server [12] was used to determine the 16S rRNA gene sequence similarity between the two type strains. The alignment of the 16S rRNA gene sequences was carried out using the MAFFT program version 7.525 [13] and the phylogenetic tree was constructed using MEGA version 12 [14]. The evolutionary relationships were determined by means of the neighbor-joining (NJ) [15], as well as the maximum likelihood (ML) and maximum parsimony (MP) methods [14, 16]. The percentages of replicate trees that clustered the associated taxa together during the bootstrap test (with 1000 replicates) [17] are shown next to the branches. Evolutionary distances were calculated using the Kimura 2-parameter model [18]. The genome sequences of all validly published species from the two genera were retrieved from the NCBI Assembly database in FASTA format. Genome quality, including completeness and contamination, was initially assessed using CheckM version 2 [19]. The genomic characteristics are presented in Table S1 on the basis of the data obtained from the NCBI database. For further genomic analysis, a phylogenetic tree was generated using the UBCG (up-to-date bacterial core gene) program version 2.0, based on the nucleotide sequences of 81 bacterial core genes [20]. The phylogenomic relationships were inferred by means of the TYGS platform using the Genome BLAST Distance Phylogeny (GBDP) method [21] and was subsequently visualized and edited using iTOL version 7.6 [https://itol.embl.de/]. Pairwise genomic relatedness was assessed based on dDDH values calculated using version 3.0 of the Genome-to-Genome Distance Calculator (GGDC) [22]. The ANIb and ANIm values were calculated using the Jspecies web server [23], whereas the average AAI values were estimated using EzAAI software [24] version 1.2.4. The POCP [25–28] was calculated using the POCP pipeline to further assess genomic relatedness between *C. plantarum* LMG 16222^T and *P. agglomerans* NBRC 102470^T. The genomes were also examined for secondary metabolite biosynthetic gene clusters using antiSMASH [29] version 8.0. Additionally, acquired antimicrobial resistance genes, chromosomal point mutations, and disinfectant resistance genes were identified using the ResFinder program [30] version 4.7.2, with a threshold of 90% and a minimum length of 60%.

3 | Results and Discussion

The analysis of the 16S rRNA gene sequence of *C. plantarum* CIP 108988^T (GenBank Accession Number: JN175348) revealed that the species most closely related to this bacterium is *P. agglomerans* DSM 3493^T (GenBank Accession Number: AJ233423), with 99.86% sequence identity. This high degree of sequence similarity indicates a close taxonomic relationship between the two organisms and warranted further genome-based analyses. Yarza et al. reported that the 16S rRNA gene sequences of *C. plantarum* CIP 108988^T and *P. agglomerans* share 99.86% sequence similarity [31]. Likewise, Ludwig et al. assigned *C. plantarum* CIP 108988^T to the family Enterobacteriaceae on the basis of 16S rRNA gene sequence analysis rather than to the Actinobacteria [32]. The phylogenetic tree based on the 16S rRNA gene showed that *C. plantarum* clustered within the genus *Pantoea* and was clearly distinct from the other *Curtobacterium* species (Figure 1). The phylogenetic relationships were also examined using the ML and MP methods based on the 16S rRNA gene sequences. Both analyses consistently showed that *C. plantarum* belonged to the *Pantoea* lineage (Figures S1 and S2). The genomic DNA of *C. plantarum* LMG 16222^T had a G+C content of 55.0 mol%, which was much lower than the 68.0-72.0 mol% range observed for other members of the genus *Curtobacterium* (Table S1). On the other hand, *C. plantarum* LMG 16222^T and *P. agglomerans* NBRC 102470^T had the same genomic DNA G+C content (55.0 mol%). Notably, this value lies within the range

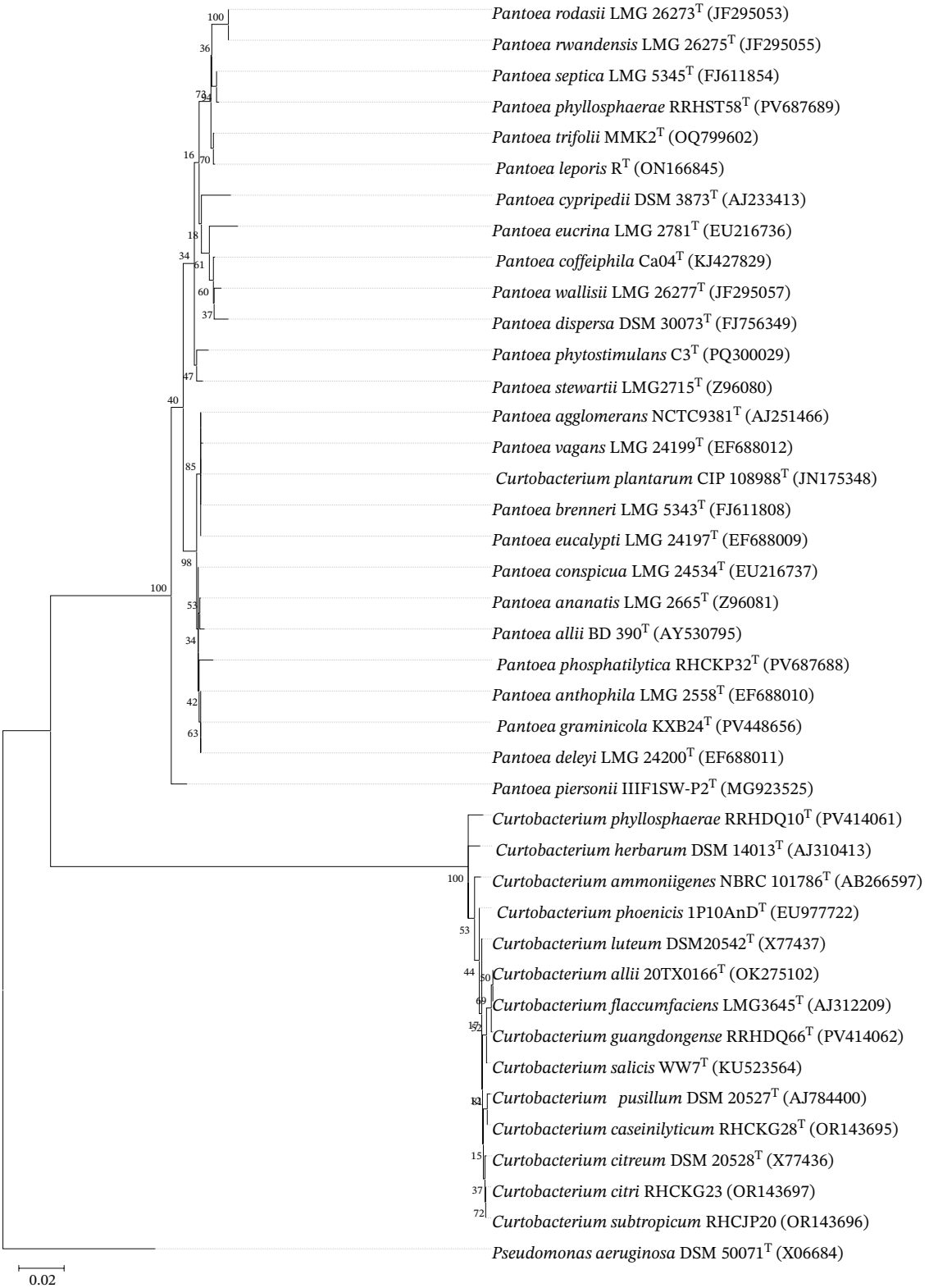

FIGURE 1 | This phylogenetic tree indicates the taxonomic placement of *C. plantarum* based on the analysis of the 16S rRNA gene sequences from members of the *Curtobacterium* and *Pantoea*. All positions containing gaps and missing data were eliminated. The optimal tree with the sum of branch length = 0.466 is shown. The final dataset comprised 857 positions, with the scale bar representing 0.02 substitutions per nucleotide position. *Pseudomonas aeruginosa* DSM 50071^T was used as an outgroup. GenBank accession numbers of the 16S rRNA gene nucleotide sequences are in parentheses. Superscript T indicates the type strain.

of genomic DNA G+C content reported for members of the genus *Pantoea* (51.0-58.5 mol%) (Table S1). The genome annotation carried out by NCBI showed that *C. plantarum* LMG 16222^T had 4692 genes, of which 4529 were protein coding. Among validly published species of *Pantoea*, the total number of genes ranged from 3758 to 6210, whereas the number of protein-coding genes ranged from 3462 to 5978 (Table S1). Genome quality assessment with the CheckM2 program indicated that both genome assemblies were of high quality. The assembly of *C. plantarum* LMG 16222^T (NCBI GenBank assembly Accession Number: GCF_003710245.1) had an estimated completeness of 100.0% and contained 0.25% contamination, whereas the assembly of *P. agglomerans* NBRC 102470^T (NCBI GenBank assembly Accession Number: GCF_001598475.1) showed 100.0% completeness with no detectable contamination. Comparative genomic analyses

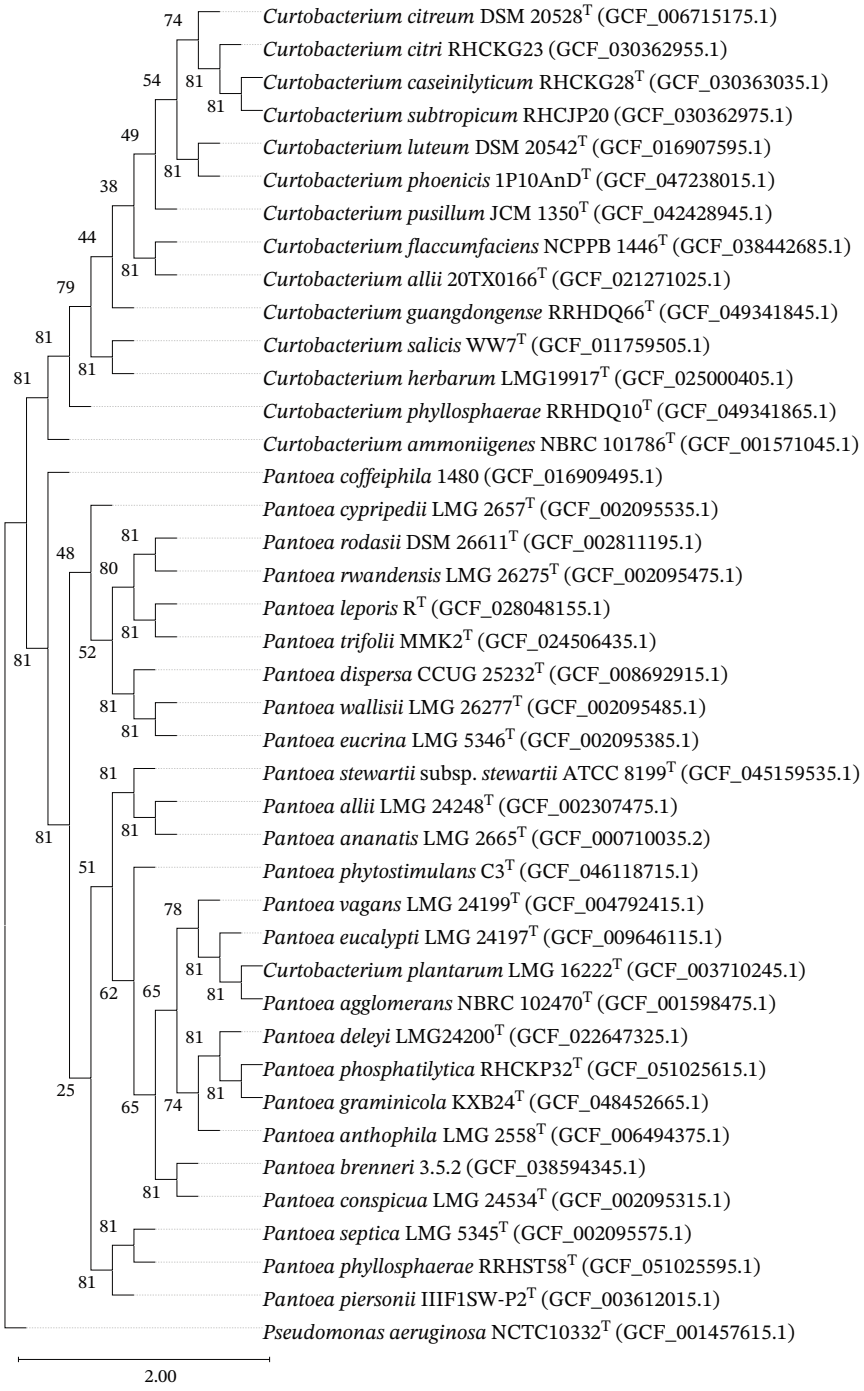

FIGURE 2 | Phylogenomic tree inferred from 81 bacterial core genes showing the relationship between *C. plantarum* LMG 16222^T and *P. agglomerans* NBRC 102470^T. *Pseudomonas aeruginosa* NCTC10332^T was used as an outgroup. The scale bar represents 2.00 substitutions per nucleotide position. Branch lengths are shown as equal for visualization purposes only. GenBank accession numbers for the genome nucleotide sequences are provided in parentheses. Superscript T indicates the type strain.

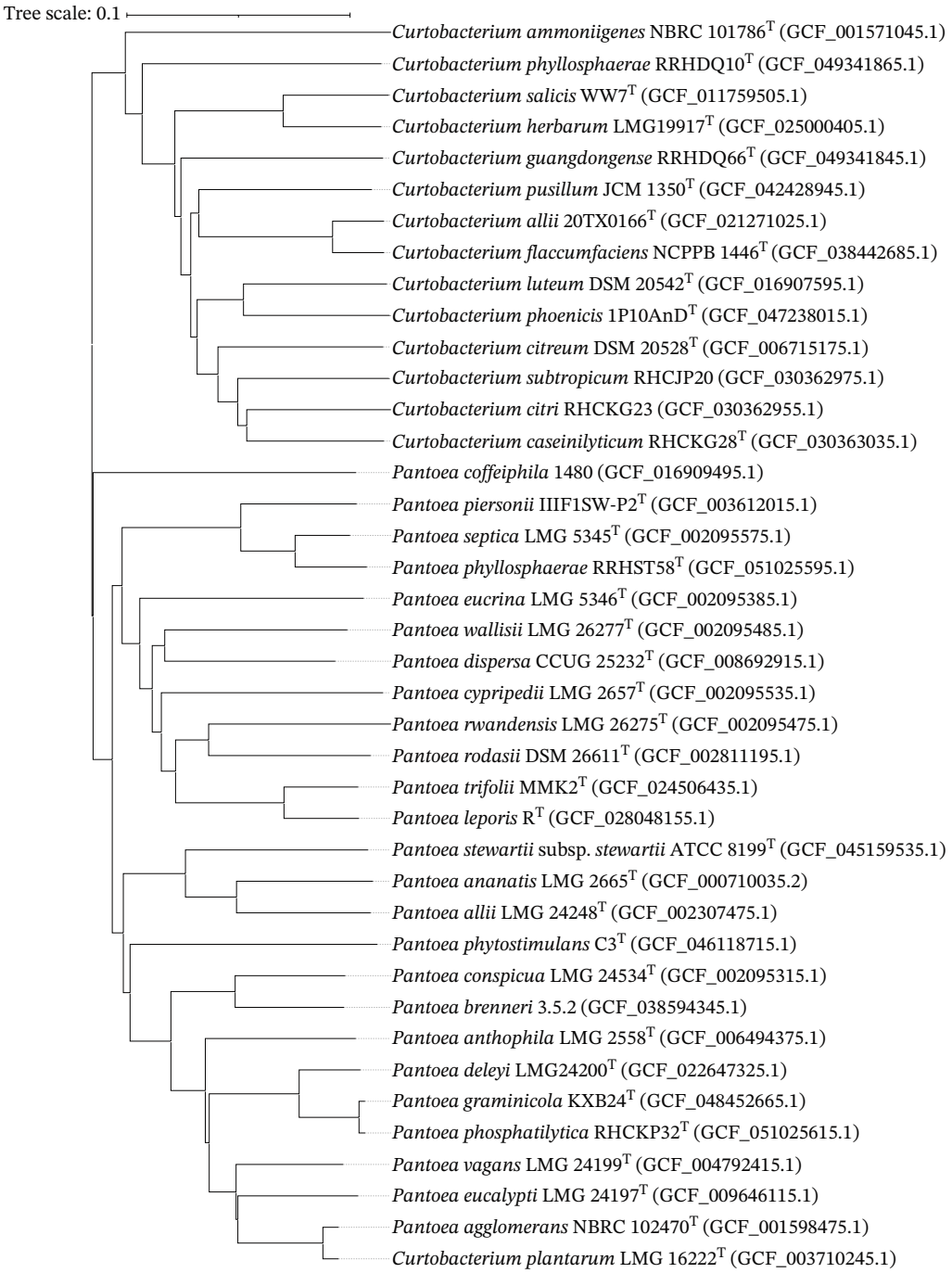

FIGURE 3 | The phylogenomic tree based on Genome BLAST Distance Phylogeny (GBDP) revealed that *C. plantarum* LMG 16222^T (GCF_003710245.1) formed a tight cluster with *P. agglomerans* NBRC 102470^T (GCF_001598475.1). The resulting phylogenomic tree was mid-point-rooted, and the branch-length scale corresponded to a genomic distance of 0.01.

revealed that *C. plantarum* LMG 16222^T (GCF_003710245.1) is highly genetically related to *P. agglomerans* NBRC 102470^T (GCF_001598475.1), with dDDH, ANIb, ANIm, and AAI values of 88.40%, 98.25%, 98.67%, and 99.13%, respectively. All genomic indices went beyond the accepted thresholds for species delimitation, including 70% for dDDH [33, 34] and 95%-96% for both ANIb [33] and ANIm [35]. The AAI value was also well above the range generally accepted for genus delineation (60%-85%) [33]. These results support the conclusion that the two type strains are conspecific. In contrast, the ANIb, ANIm, and dDDH values between *C. plantarum* LMG 16222^T and other members of the genus *Curtobacterium* ranged from 62.44% to 63.08%, 80.14% to 80.56%, and 15.20% to 19.20%, respectively (Tables S2 and S3). The corresponding values between this bacterium and other species of *Pantoea*, except *P. agglomerans* NBRC 102470^T, ranged from 76.68% to 90.49%, 83.75% to 91.36%, and 20.40% to 43.00%, respectively (Tables S2 and S3). Furthermore, the AAI values between *C. plantarum* LMG 16222^T and the other members of the genus *Curtobacterium* ranged from 47.97% to 48.77% (Table S4),

which were below the AAI threshold for bacterial genus delineation [33]. In contrast, the AAI value between *C. plantarum* LMG 16222^T and the other *Pantoea* species, with the exception of *P. agglomerans*, ranged from 81.98% to 95.47% (Table S4). Further evidence supporting the suggested reclassification is provided by the NCBI Taxonomy quality control framework. The genome assembly GCF_003710245.1, which corresponds to the type strain LMG 16222^T, was identified as containing a taxonomic inconsistency because its nearest type-strain match was *P. agglomerans*, with an ANI value of 98.68% (available at https://www.ncbi.nlm.nih.gov/datasets/genome/GCF_003710245.1/ accessed 20 June 2026). This value exceeds the widely accepted species-level ANI threshold and independently supports the close genomic relationship between *C. plantarum* and *P. agglomerans*. The POCP value between *C. plantarum* LMG 16222^T and *P. agglomerans* NBRC 102470^T was 92.72%, which is considerably above the 50% threshold suggested to define a genus [25], providing further evidence that the two strains belong to the same genus. Genome-based phylogenomic analysis using 81 bacterial core genes showed that *C. plantarum* clustered in a well-supported clade with *P. agglomerans* within the genus *Pantoea*. Furthermore, *C. plantarum* was clearly separated from all other members of the genus *Curtobacterium* (Figure 2). The phylogenomic relationships among the strains examined were inferred using the GBDP method (Figure 3). The analysis showed that *C. plantarum* LMG 16222^T (GCF_003710245.1) is closely related to *P. agglomerans* NBRC 102470^T (GCF_001598475.1), indicating that the two strains have a relatively low genomic distance. The placement of the type strains LMG 16222^T, ATCC 49174^T, DSM 7069^T, and CIP 108988^T within the genus *Curtobacterium* has been questioned by the respective culture collections. In the ATCC database, the type strain ATCC 49174^T is classified as *P. agglomerans* (available at https://www.atcc.org/products/49174, accessed June 20, 2026). Similarly, BCCM/LMG indicates, based on fatty acid profiling and MALDI-TOF MS analysis, that the type strain LMG 16222^T does not belong to the genus *Curtobacterium* but is identified as *P. agglomerans* (https://bccm.belspo.be/LMG-catalogue-search). Likewise, DSMZ assigns the type strain DSM 7069^T to the genus *Pantoea* based on fatty acid composition and 16S rRNA gene sequence analysis (available at https://www.dsmz.de/collection/catalogue/details/culture/DSM-7069, accessed June 20, 2026). Consistent with these assessments, CIP also assigns the type strain CIP 108988^T to the genus *Pantoea* based on 16S rRNA gene sequence analysis (available at https://catalogue-crbip.pasteur.fr/fiche_catalogue.xhtml?crbip=CIP%2520108988, accessed June 20, 2026). However, these taxonomic reassessments were not based on genome-based analyses. The genome-based analyses performed in the present study provide independent genomic evidence supporting these taxonomic assessments. The original description of *C. plantarum* [10] was based mainly on phenotypic, biochemical, and ecological characteristics, as molecular phylogenetic and genome-based methods were not available at that time. As a result, the placement of this organism in the genus *Curtobacterium* was determined without the use of sequence-based taxonomic evidence. On the other hand, current molecular evidence provides a different perspective on the taxonomic position of *C. plantarum*. Some phenotypic characteristics are shown for *C. plantarum* and *P. agglomerans* in

TABLE 1 | Phenotypic and biochemical comparison between *C. plantarum* and *P. agglomerans*.

Characteristic	Motility	Pigment	Rhamnose	Mannose	Raffinose	Cellobiose	Lactose	Glucose	Fructose	Glycerol	Galactose	Maltose	Sorbose	Sucrose	Trehalose	Xylose	Sorbitol	Erythritol	Urea hydrolysis	Gelatin hydrolysis
Name of organism																				
C. plantarum [10]	+	Y	+	+	–	+	–	+	+	–	+	+	–	+	–	+	–	–	–	+
P. agglomerans [2]	+	Y	+	+	–	+	–	+	+	+	+	+	–	+	+	+	–	–	–	+

Note: Data for *C. plantarum* and *P. agglomerans* were obtained from references [2, 10], respectively.
Abbreviations: +, positive; –, negative; Y, yellow.

Table 1. Both species are able to produce acid from rhamnose, mannose, glucose, fructose, cellobiose, galactose, maltose, and xylose but not from raffinose, lactose, sorbose, or sorbitol. Moreover, both bacteria are motile, produce a yellow pigment, do not have urease activity, and show gelatinase activity. The two taxa also differ phenotypically in their utilization of glycerol, sucrose, and trehalose. *P. agglomerans* utilizes all three substrates, whereas *C. plantarum* has been reported to be unable to utilize them [2, 10]. A notable finding of the current study is the discrepancy between the Gram-staining characteristic originally reported for *C. plantarum* and its genomic affiliation with *P. agglomerans*. In the original description, *C. plantarum* was reported to be Gram-positive [10], whereas *P. agglomerans* was described as Gram-negative. Although this discrepancy is inconsistent with the strong genomic relatedness observed in the present study, current bacterial taxonomy places greater emphasis on taxonomic relationships inferred from robust genomic evidence rather than from individual phenotypic characteristics. The Gram-staining characteristic of *C. plantarum* LMG 16222^T was predicted from its genome sequence using Traitar software [36] version 1.1.2, which showed that the organism has a Gram-negative cell envelope. The discrepancy between the originally described phenotype and the genome-based prediction may reflect limitations in the original phenotypic characterization. However, no phenotypic characterization was performed in the present study; therefore, the Traitar result should be considered an in silico prediction that requires experimental verification. Analysis of the biosynthetic gene clusters associated with secondary metabolites revealed that both type strains possess gene clusters for aryl polyenes, frederiksenibactin, carotenoid, and desferrioxamine E. Nevertheless, the herbicolin O biosynthetic gene cluster was detected only in *C. plantarum* LMG 16222^T. Neither of the type strains carried any acquired antimicrobial resistance genes.

4 | Conclusion

According to the priority rules, the priority of the names must be assessed independently for the generic name and the specific epithet. Specifically, the generic names *Curtobacterium* and *Pantoea*, as well as the specific epithets *plantarum* and *agglomerans*, must be considered separately with respect to their publication dates. The crucial year for the epithet *P. agglomerans* (Beijerinck 1888) Gavini *et al.* 1989 is actually 1888 (because that was the year Beijerinck coined the epithet). The crucial year for the epithet in *C. plantarum* Dunleavy 1989 is 1989. As a result, *P. agglomerans* takes precedence over *C. plantarum*. Based on this evidence, we propose that *C. plantarum* Dunleavy 1989 be considered as a later heterotypic synonym of *P. agglomerans* (Beijerinck 1888) Gavini *et al.* 1989.

Acknowledgments

The authors sincerely thank Dr. Markus Göker and Dr. Marko Kostovski for their valuable guidance on nomenclatural issues during the preparation of this manuscript. The authors also gratefully acknowledge the financial support provided by the Research Center for Health Technology Assessment and Medical Informatics, Shahid Sadoughi University of Medical Sciences, Yazd, Iran.

Funding

This study was funded by the Shahid Sadoughi University of Medical Sciences (10.13039/50110001503).

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that support the findings of this study are available in the supplementary material of this article.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Supporting Information 1.** Figure S1: The phylogeny was inferred using the maximum likelihood method and Tamura–Nei (1993) model of nucleotide substitutions, and the tree with the highest log likelihood (-3027.68) is shown. The percentage of replicate trees in which the associated taxa clustered together (1000 replicates) is shown next to the branches. The NJ tree was generated using a matrix of pairwise distances computed using the Tamura-Nei (1993) model. The evolutionary rate differences among sites were modeled using a discrete gamma distribution across five categories (+G, parameter = 0.2001). The complete deletion option was applied to eliminate positions containing gaps and missing data resulting in a final dataset comprising 871 positions. **Supporting Information 2.** Figure S2: The evolutionary history was inferred using the maximum parsimony method. The consistency index is 0.805195 (0.773414), the retention index is 0.971815 (0.971815), and the composite index is 0.782500 (0.751615) for all sites and parsimony-informative sites. The MP tree was obtained using the subtree-pruning-degrafting (SPR) algorithm. The complete deletion option was applied to eliminate positions containing gaps and missing data resulting in a final data set comprising 857 positions. **Supporting Information 3.** Table S1: The genomic features of bacteria used in this study. **Supporting Information 4.** Table S2: dDDH values among *Curtobacterium plantarum* and other members of the genus *Curtobacterium*. **Supporting Information 5.** Table S3: ANIb values between *Curtobacterium plantarum* and members of the genera *Curtobacterium* and *Pantoea*. **Supporting Information 6.** Table S4: AAI values among *Curtobacterium plantarum* and species of the genera *Curtobacterium* and *Pantoea*.