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Comparative phylogenetic analysis of bacterial *acdS* genes reveals a combination of evolutionary patterns and ecological adaptation

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Abstract

ACC deaminase-producing bacteria play a crucial role in alleviating plant stress by modulating ethylene levels, thereby enhancing plant growth under adverse conditions. Although the *acdS* gene that encodes for ACC deaminase is found in many different bacterial taxa, limited information is known about its ecological relationships and evolutionary trends. The phylogenetic relationships, taxonomic similarity, and environmental distribution of *acdS* gene sequences were all exhaustively analyzed in this review. A total of 177 *acdS* sequences were retrieved from public databases, of which 107 representative sequences for each species were selected for multiple sequence alignment using the MUSCLE algorithm. Phylogenetic analysis was conducted using the maximum likelihood method with the Kimura 2-parameter model, and tree robustness was assessed through bootstrap analysis with 1000 replications. The phylogenetic analysis grouped the sequences into seven major clades. Congruence and incongruence patterns were assessed by comparing the resulting phylogeny with taxonomic classification. Additionally, metadata including ecological niches, stress conditions, and geographic origin of isolates, were integrated to identify potential correlations with phylogenetic clustering. The analysis revealed that most sequences clustered according to their taxonomy, suggesting vertical inheritance; however, a significant number of sequences deviated from this pattern, indicating possible horizontal gene transfer of the *acdS* gene, potentially driven by environmental stress conditions and associated selective pressures. These findings provide insights into the evolution and ecological significance of ACC deaminase-producing bacteria and highlight their potential applications in sustainable agriculture.

Keywords: ACDS gene, 1-aminocyclopropane-1-carboxylate deaminase, ACC deaminase, horizontal gene transfer, stress-responsive genes, phylogenetic analysis

Introduction

The primary challenge to the sustainability of global agricultural output is the abrupt and unpredictable shift in climate, in addition to population growth (Oyebamiji *et al.*, 2024) [37]. Since they are sessile, plants must adjust to the variety of environmental pressures they face. There are two types of environmental stresses: biotic and abiotic. Drought, flooding, salinity, heat, cold, injury, and exposure to xenobiotics, heavy metals, and ultraviolet radiation are examples of abiotic stressors. In addition, biotic stressors that affect plants include microbial infections including fungi, bacteria, and nematodes. These stressors have the potential to negatively impact plant development and productivity, either separately or in combination. In response to biotic and abiotic stressors, the plant releases reactive oxygen species, activates a variety of ion channels, and accumulates hormones including salicylic acid, ethylene, jasmonic acid, and abscisic acid (Sachdev *et al.*, 2021) [41].

All plants generate ethylene, an important hormone that modulates many kinds of responses and developmental processes. Since the introduction of many stress signals, including mechanical wounding, salt, drought, water logging, severe temperatures, pathogenic infection, and pollutants, speeds up the synthesis of this hormone, it is also known as a stress hormone (Morgan and Drew, 1997) [33]. On the other hand, excessive ethylene generated during seed germination or by various environmental stressors may retard plant growth, particularly in the case of root growth retardation (Li, J. *et al.*, 2015) [27].

There are two steps in the entire ethylene manufacturing process: - Sadenosylmethionine (S-AdoMet) is converted by ACC synthase (ACS, S-adenosyl-L-methionine methylthioadenosine-lyase) into 1-aminocyclopropane-1-carboxylic acid (ACC) and 5-

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Methylthioadenosine (MTA). During high rates of ethylene synthesis, the 5-Methylthioadenosine (MTA) is then recycled back to methionine to restore the cell's concentration of methionine. The second step involves oxidizing 1-Aminocyclopropane-1-Carboxylic Acid (ACC) to ethylene and cyanoformate ion [NCCO₂] by ACC oxidase in the presence of oxygen (Yang and Hoffman, 1984). A schematic representation of ethylene biosynthesis is shown in Figure 1. One strategy to mitigate the harmful accumulation of stress-induced ethylene involves exploiting

plant-microbe interactions, which play a central role in sustainable agriculture. This interaction can be symbiotic (bacteria living inside root nodules), endophytic (bacteria inside plant tissues), rhizospheric (bacteria binding to root surface), or phyllospheric (bacteria binding on leaf or stem) (Compant *et al.*, 2010) [10]. Compared to fertilizers, pesticides, and insecticides based on inorganic chemicals, such microbe-based approaches are theoretically and economically practical (Daniel *et al.*, 2022) [12].

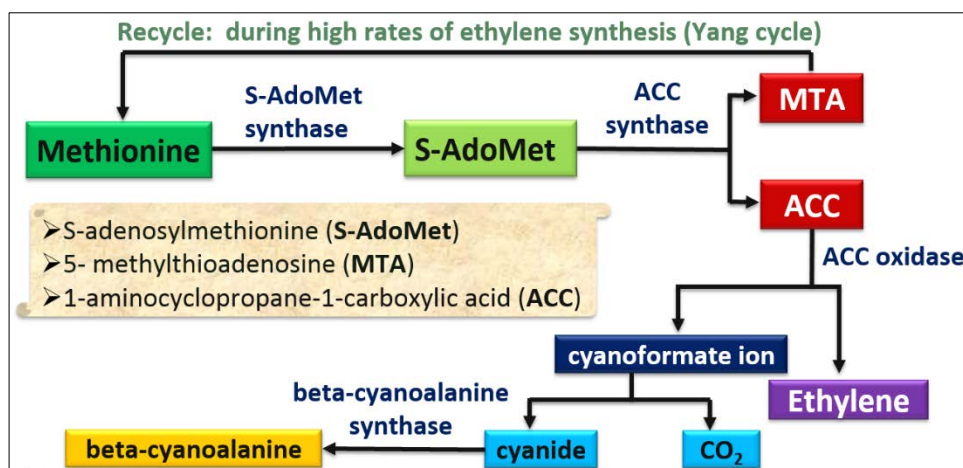


Fig 1: Flow chart representing the biosynthesis pathway of ethylene in plants

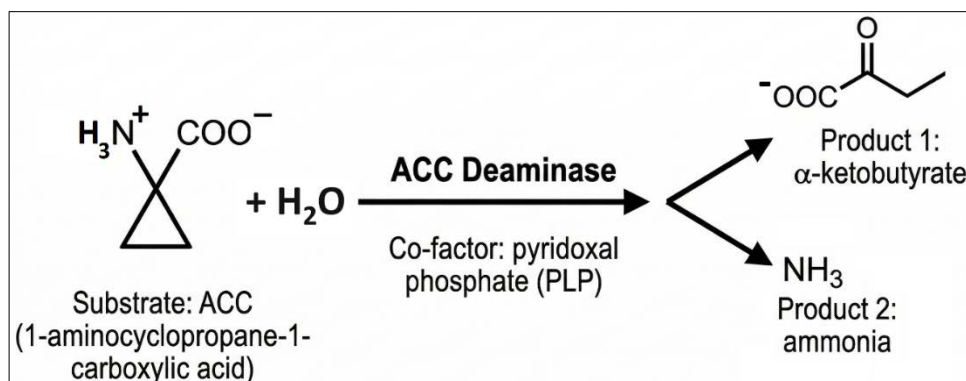


Fig 2: Schematic representation of enzymatic deamination of ACC by ACC deaminase

Plants produce ethylene in direct proportion to the amount of 1-aminocyclopropane-1-carboxylic acid (ACC), which is the precursor of ethylene. By cleaving ACC to α -ketobutyrate and ammonium ion, ACC deaminase, which is encoded by the *acdS* gene in various bacteria that promote plant growth, can lower the amount of ethylene produced by stressed plants. The mechanism of enzymatic deamination of ACC by ACC deaminase is schematically illustrated in Fig. 2. By reducing the amount of stress-induced ethylene in the plants, the plant growth-promoting bacteria (PGPR) with 1-Aminocyclopropane-1-Carboxylate (ACC) deaminase potential provide resistance to a variety of abiotic stress conditions, including high temperature, flood, drought, salinity, and acidity (Singh *et al.*, 2015) [44].

Despite this well-established functional significance, the evolutionary history of the *acdS* gene across bacterial lineages remains incompletely understood. Even though ACC deaminase's physiological role is well-known, the context presented by its evolutionary distribution is more complex. *Alphaproteobacteria*, *Betaproteobacteria*, *Gammaproteobacteria*, *Actinobacteria*, and *Firmicutes* are among the taxonomically diverse bacterial groups that have been identified with the *acdS* gene (Hontzeas *et al.*, 2005,

Blaha *et al.*, 2006) [4, 21]. The consistent clustering of *acdS* sequences with recognised taxonomic relationships in certain lineages suggests vertical inheritance. Others have questioned gene mobility and evolutionary reshaping due to incongruence between 16S rRNA trees and *acdS*-based phylogenies (Hontzeas *et al.*, 2005) [21].

In contrast to housekeeping genes like 16S rRNA, functional genes frequently evolve under different selective pressures. Therefore, it is possible to assess whether the evolutionary trajectory of *acdS* reflects lineage history, ecological adaptation, or genetic exchange mechanisms by comparing its phylogeny with established taxonomic frameworks (Hontzeas *et al.*, 2005, Blaha *et al.*, 2006) [4, 21]. Extensive *in silico* comparative analyses are now possible due to the growing availability of publicly accessible sequence databases. These methods make it possible to quantitatively evaluate genetic distance relationships across a wide range of taxa and to reconstruct gene-based phylogenies in a systematic manner. Therefore, patterns of conservation, divergence, and possible incongruence with respect to conventional phylogenetic markers can be clarified by integrating *acdS* sequence data from various bacterial representatives. In this context, the present study is

based on an *in silico* comparative analysis of publicly available *acdS* gene sequences. This review is aimed at analyzing the phylogenetic relationships among diverse representatives of bacterial taxa with the *acdS* gene as a molecular marker. The resulting *acdS*-based phylogenetic trees and their respective distance matrices are analyzed, and a comparison with established taxonomic (16S rRNA-based) phylogenies is made in an effort to establish the degree of concordance between them. Any incongruences that may be observed will be discussed in detail, focusing on the possible role of evolutionary and genetic factors such as horizontal gene transfer, gene duplication, and adaptive divergence. Hence, the present study aims to give a better understanding of how the *acdS* gene has changed over bacterial lineages and how its distribution reflects the relationship between function, taxonomy, and evolutionary dynamics by combining phylogenetic, genetic, and comparative insights.

Materials and methods

Retrieval of *acdS* gene sequences

An extensive set of *acdS* gene sequences were retrieved from the NCBI database as of December 2025. A wide range of bacterial taxa representing different genera and families were considered for analysis. From each species, a single representative strain was selected to avoid redundancy. Selection was based on the criterion that the selected sequence is found to be a representative of all the sequences of different strains of same species after aligning using the MUSCLE algorithm in MEGA software version 12 and care was taken to ensure all chosen *acdS* sequences were of comparable length to ensure reliable alignment and downstream phylogenetic analysis.

Taxonomic data collection

Taxonomic details of the selected bacterial species were obtained from the List of Prokaryotic names with Standing in Nomenclature (LPSN) database (<https://lpsn.dsmz.de>). These taxonomic assignments were used as the reference framework for comparison with the *acdS* gene-based phylogenetic tree.

Multiple sequence alignment

All analyses were performed using MEGA version 12. All the *acdS* gene sequences were aligned using the MUSCLE algorithm in MEGA software. The results were then examined and trimmed to remove any poorly aligned regions found at the ends of the sequences. These aligned and trimmed sequences were used for further phylogenetic and distance matrix analyses.

Genetic distance analysis

Pairwise genetic distances among the aligned *acdS* sequences were calculated using the Kimura 2-parameter (K2P) model. The generated distance matrix was used to assess genetic divergence of *acdS* gene among various taxa and to support phylogenetic interpretations.

Phylogenetic tree construction

Phylogenetic analysis was carried out using the Maximum Likelihood method based on the Kimura 2-parameter model in MEGA software. The statistical robustness of the inferred phylogenetic relationships was evaluated using bootstrap analysis with 1000 replications. The resulting *acdS* gene phylogeny was subsequently compared with the established taxonomic framework to evaluate congruence and incongruence patterns. The Kimura 2-parameter model was

selected as it accounts for differential rates of transition and transversion substitutions, while the Maximum Likelihood method was used for its robustness in phylogenetic inference. Similarity between the *acdS* gene phylogeny and the taxonomic framework was assessed by comparing clustering patterns of *acdS* phylogeny at the genus and family levels.

Results

Overview of retrieved *acdS* gene sequences

A total of 177 *acdS* gene sequences were retrieved from NCBI database as of December 2025. The details of these sequences are provided in Supplementary Table S1. For further phylogenetic analysis, a total of 107 sequences were selected so that there were maximum of one sequence as representative for that species. Organism names are presented in abbreviated form for clarity in the phylogenetic tree. The list of selected sequences for further analysis along with their corresponding species names and accession numbers is provided in Table 1.

Taxonomic profile of selected bacterial species

The taxonomic classification of the selected bacterial species was compiled based on data obtained from the LPSN database. These classifications were used as a reference for comparison with the *acdS* gene-based phylogenetic tree. The detailed taxonomic information of all selected species is provided in Table 2.

Phylogenetic clustering and diversity of *acdS* sequences

A circular maximum likelihood phylogenetic tree based on *acdS* gene sequences is presented in Figure 3, showing the evolutionary relationships among bacterial taxa. Phylogenetic analysis based on *acdS* gene sequences revealed various clustering patterns that were mostly similar with established bacterial taxonomy. Seven major clades were identified. The phylogenetic tree with highlighted clades is presented in Supplementary Figure 1, and the clade assignment of each organism is provided in Table 1. Many clades with strong bootstrap support were identified, which showed significant taxonomical congruence and incongruence. Most of the major clusters exhibited bootstrap support values above 70%, with several internal nodes showing support values of $\geq 90\%$, indicating reliable phylogenetic relationships among the *acdS* sequences. Members of *Methylobacterium*, *Methylobacterium*, *Bradyrhizobium*, *Mesorhizobium*, *Phyllobacterium*, *Rhizobium*, *Sinorhizobium*, *Roseibium*, and *Azospirillum*, that were primarily *Alphaproteobacteria*, were among the major cluster (referred to as Cluster F). Strong internal uniformity within this cluster indicated that the *acdS* gene had a conserved evolutionary history within *Alphaproteobacteria*. However, *Rhizobium* sp. TAL1145 was positioned separately in cluster C and did not group within cluster F, which deviates from the expected taxonomic placement.

Streptomyces, *Microbacterium*, *Mycobacterium*, *Rhodococcus*, and *Marmoricola* were among the *actinomycetes* that formed a unique cluster (Cluster D), confirming taxonomic similarity. *Zhihengliuella somnathii* JG05 was an exception; it clustered outside of the primary actinomycete group, indicating that the *acdS* gene may have undergone horizontal acquisition or divergence. Notably, *Herbaspirillum* sp. Os23 (*Betaproteobacteria*) clustered within this actinomycete-dominated group, representing a clear case of taxonomic incongruence. *Burkholderia*, *Paraburkholderia*, and *Cupriavidus* are among the members

of the *Burkholderiaceae* family, which primarily clustered into Cluster B, suggesting that *acdS* sequences are conserved within this family. *Burkholderia* sp. BL25 I3R1, on the other hand, was not included in this cluster and instead held a distinct phylogenetic position, cluster D. All *Achromobacter* species, at the genus level, exhibited strong concordance between taxonomic classification and *acdS*-based phylogeny, forming a well-supported clade (Cluster C). On the other hand, *Gammaproteobacteria*, were dispersed throughout several clades and failed to form a single coherent cluster. Members of *Enterobacter* and *Pseudomonas* were also scattered across various clusters, indicating a high degree of diversity in their *acdS* sequences. Two different clusters of *Bacillus* species were found, suggesting intragenomic divergence of the *acdS* gene. Members of the *Bacilli* (*Bacillus cereus*, *B. licheniformis*, and *B. amyloliquefaciens*), *Actinomycetes* (*Zhihengliuella somnathii*), *Betaproteobacteria* (*Ralstonia*, *Delftia*, *Variovorax* spp.), and *Gammaproteobacteria* (*Enterobacter*, *Klebsiella*, *Serratia*, *Halomonas*, and *Pseudomonas* spp.) were among the taxonomically diverse bacteria that clustered in Cluster A. These taxa formed a single large cluster despite being members of different bacterial classes, indicating that the *acdS* gene is subject to shared evolutionary pressures or functional convergence.

Members of *Alphaproteobacteria* (*Rhizobium* sp. TAL1145), *Betaproteobacteria* (*Achromobacter* spp.), *Gammaproteobacteria* (*Pseudomonas* and *Enterobacter* spp.), and *Bacilli* (*Priestia aryabhatai*) were found in another mixed cluster (Cluster E), emphasising the deviation between *acdS* phylogeny and taxonomic classification. A complex evolutionary trajectory of the gene could be explained by the observed inconsistency between *acdS*-based phylogeny and taxonomic classification. The *acdS* gene's complex evolutionary history among bacterial taxa have been emphasised by the *acdS*-based phylogenetic tree, which overall showed both conserved lineage-specific clustering and extensive taxonomic mixing.

Bootstrap support across major *acdS* clusters

Bootstrap analysis (1000 replicates) was used to assess the robustness of the *acdS*-based phylogenetic groupings, and support values differed among the main clusters (A-G). Cluster A, a taxonomically mixed cluster that includes *Bacilli*, *Actinomycetes*, *Betaproteobacteria*, and *Gammaproteobacteria* showed moderate to high bootstrap support and internal node values typically ranged from 59% to 99%, indicating a stable but evolutionarily diverse grouping. Cluster B (the *Burkholderiaceae*-dominated cluster) showed moderate bootstrap support with values generally ranging from 60% to 84%, indicating the family's general congruence with some internal divergence. With bootstrap values ranging from 73% to 100%, Cluster C (*Achromobacter* cluster) showed strong support, indicating that *Achromobacter* species are grouped together in the same clade based on the *acdS* gene. This suggests that the gene is likely inherited through vertical evolution and is an inherent part of their genome, rather than being acquired through horizontal transfer. *Herbaspirillum* sp. Os23 is part of Cluster D, which is dominated by *actinomycetes*. Despite taxonomic deviation, Cluster D showed moderate to high bootstrap support, with values ranging from 64% to 100%. The *acdS* sequences in the mixed cluster E (*Alphaproteobacteria*, *Betaproteobacteria*, *Gammaproteobacteria*, and *Bacilli*) showed evolutionary connection across diverse taxa, with moderate bootstrap

support values primarily between 43% and 99%. With the majority of nodes consistently supported by high bootstrap values between 75% and 100%, Cluster F (*Alphaproteobacteria*-dominated cluster) confirms strong *acdS* gene conservation within this group. With high bootstrap support ranging from 72% to 100%, Cluster G (*Bacilli* cluster, which includes *Bacillus*, *Priestia*, and *Lysinibacillus*) established a well-resolved grouping that was different from other *Bacilli* in the tree.

Overall, clusters dominated by taxonomically related groups exhibited higher bootstrap support, whereas mixed clusters showed moderate support, reflecting functional conservation of the *acdS* gene across phylogenetically diverse bacteria.

Evolutionary distance analysis

In addition to showing numerous instances of taxonomic similarity and mismatch, the distance matrix mostly confirmed the phylogenetic clustering identified in the Maximum Likelihood tree.

Overall, taxa belonging to the same major clusters showed low evolutionary distances, while clusters representing different bacterial classes confirmed high genetic divergence. Within their respective clusters, the *alphaproteobacteria* (Cluster F) and *Burkholderiaceae* (Cluster B) showed comparatively short pairwise distances, suggesting conserved *acdS* sequences. Comparisons of *Actinomycetes*, *Bacilli*, and *Alphaproteobacteria*, on the other hand, revealed significantly greater distances, which is consistent with deep evolutionary divergence. In several taxonomic groups, there was evident genetic congruence. *Alphaproteobacteria* showed concordance between taxonomy and *acdS*-based relationships by clustering together with low intra-group distances. Additionally, *Achromobacter* species (Cluster C) revealed strong internal coherence and low evolutionary distances. Similar to this, the majority of *Burkholderiaceae* members showed relatively low divergence within Cluster B, indicating concordance at the genus and family levels.

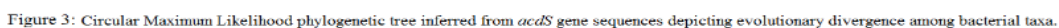
On the other hand, various taxa revealed notable intra-genomic diversity. Significant divergence of *acdS* within the genus has been confirmed by the broad evolutionary distances and multi-cluster distribution of *Pseudomonas* species. Similar patterns were seen for *Enterobacter* and *Bacillus*, where species from the same genus segregated into distinct clusters and exhibited significant genetic distances. *Bacillus* species' division into two separate clusters emphasises intra-genus diversity even more. Within mixed clusters, especially Cluster A, taxonomically unrelated bacteria were found to have unexpectedly low evolutionary distances. Members of *Bacilli*, *Actinomycetes*, *Betaproteobacteria*, and *Gammaproteobacteria* were found in this cluster, and their genetic similarity was closer than what taxonomy would have predicted. Likewise, *Herbaspirillum* sp. Os23 (*Betaproteobacteria*) showed lower evolutionary distance to *actinomycetes* than to other *Betaproteobacteria*.

Correlation between clades and environmental stress, ecological origin, and geographic distribution

The metadata of the sequences, including the stress conditions under which the bacteria were studied, their ecological sources, and geographical details, are presented in Table 1. Partial similarity as well as significant differences across clusters were found when *acdS*-based clades were compared with environmental stress, sample source, and country of isolation. Several clades (notably A, B, and C) included strains associated with abiotic stress mitigation, such as drought, salinity, heavy metal stress, and

associations, and non-plant environments, were often grouped together within those same clades. Genetic diversity within the same genus was evident from the frequent and significant divergence observed among members isolated from different ecological niches. While strains from the same country were distributed across multiple clades, indicating strong geographic divergence, isolates from different countries and continents clustered together with low genetic divergence, indicating the weakest correlation, according to geographic analysis. No clade was confined to a particular area.

Overall, the findings show that *acdS* sequences from bacteria that are geographically and taxonomically different from one another are similar, but they are also diverse within the same genera or classes. This suggests that functional conservation and diversification, rather than strict alignment with taxonomy, ecology, or geographic origin, have shaped the evolution of *acdS*.



bacterial taxa

Table 1: Cluster-wise details of retrieved acdS sequences and associated metadata, number of sequences analysed for each species

S No	Cluster	ACCESSION no.	Organism Name	No. of strains analyzed	Abbreviated name	Sample Source	country	stress	Ref No
1.	A	JN625726.1	<i>Bacillus cereus</i> AcdSPB4	2	B_cere_1	-	China	hyphal growth and primordium initiation	(Chen <i>et al.</i> , 2013) ^[8]
2.	A	FJ357241.1	<i>Klebsiella oxytoca</i> strain Rs-5	1	Kl_oxytoca	-	Not provided	-	
3.	A	JN625725.1	<i>Klebsiella pneumoniae</i> AcdSPB2	2	Kl_pneum_1	-	China	hyphal growth and primordium initiation	(Chen <i>et al.</i> , 2013; 174) ^[8]
4.	A	JN625724.1	<i>Serratia rubidaea</i> AcdSPB1	1	Se_rubid	-	China	hyphal growth and primordium initiation	(Chen <i>et al.</i> , 2013) ^[8]
5.	A	PP208627.1	<i>Pseudomonas mucidolens</i>	1	Ps_mucidol	-	Not provided	-	
6.	A	KM501059.2	<i>Bacillus licheniformis</i> strain HSW-16	1	B_lichen	-	Not provided	-	
7.	A	AF047840	<i>Enterobacter cloacae</i> CAL2	3	En_cloa_1	soil	Canada	-	(Shah <i>et al.</i> , 1998) ^[43]
8.	A	MN232215.1	<i>Pseudomonas</i> sp. strain Q1	6	Ps_sp_4	roots	Portugal	High Manganese Concentration	(Paço <i>et al.</i> , 2020) ^[38]
9.	A	KY451712	<i>Pseudomonas migulae</i> strain DR35	1	Ps_migul	root samples	China	Drought	(Niu <i>et al.</i> , 2018) ^[35]
10.	A	KY305919	<i>Pseudomonas</i> sp. strain SYC-RS-TSA-3	6	Ps_sp_5	River estuary, Rhizosphere roots	China	-	(Qin <i>et al.</i> , 2017) ^[40]
11.	A	KR080559.1	<i>Delftia</i> sp. 17(2015)	1	Del_sp	-	-	-	
12.	A	KX709841.1	<i>Bacillus amyloliquefaciens</i> strain BPSRB14	2	B_amylo_1	Rhizospheric soil and root samples	India	plant growth promotion and disease suppression	(Passari <i>et al.</i> , 2017) ^[39]
13.	A	KY305930	<i>Halomonas</i> sp. strain XB-RS-PIA-11	1	Halom_sp	River estuary, Rhizosphere roots	China	-	(Qin <i>et al.</i> , 2017) ^[40]
14.	A	HQ197346.1	<i>Zhihengliuella somnathii</i> strain JG 05	1	Zh_somnath	-	-	-	
15.	A	KU517662.1	<i>Ralstonia</i> sp. S1SM82	1	Ra_sp	-	-	-	
16.	A	AY604530	<i>Variovorax paradoxus</i> strain 2C1	3	Va_parad_1	Direct strain obtained	Canada	-	(Hontzeas <i>et al.</i> , 2005) ^[21]
17.	A	KP116958	<i>Variovorax</i> sp. DW01-1	1	Va_sp	Black locust nodule	China	drought	(Li, Z. <i>et al.</i> , 2015) ^[28]
18.	B	DQ125254.1	<i>Burkholderia tropica</i> strain BM273	1	Bu_tropic	Rhizosphere (PGPR)	Mexico	-	(Blaha <i>et al.</i> , 2006) ^[4]
19.	B	KX622567.1	<i>Paraburkholderia tropica</i> strain S39-2	1	Pa_tropica	-	-	-	
20.	B	EU886302.1	<i>Burkholderia graminis</i> strain C4D1M	1	Bu_gramin	Maize roots; environmental grasses	France	growth-promoting	(Onofre-Lemus <i>et al.</i> , 2009) ^[36]
21.	B	EU886303.1	<i>Burkholderia phenoliruptrix</i> strain LMG 22037	1	Bu_phenol	Soil; 2,4,5-trichlorophenoxyacetic acid degrader	-	-	(Onofre-Lemus <i>et al.</i> , 2009) ^[36]
22.	B	EU886312.1	<i>Burkholderia xenovorans</i> strain CAC-124	1	Bu_xenov	Rhizospheric; biphenyl degrader; N2 fixer	Mexico	-	(Onofre-Lemus <i>et al.</i> , 2009) ^[36]
23.	B	EU886299.1	<i>Burkholderia caledonica</i> strain LMG 19076	1	Bu_caledon	Rhizosphere soil	United Kingdom	-	(Onofre-Lemus <i>et al.</i> , 2009) ^[36]
24.	B	EU886316.1	<i>Burkholderia fungorum</i> strain	1	Bu_fungor	Fungus; aromatic compound degrader	France	-	(Onofre-Lemus <i>et al.</i> ,

			LMG 16225						2009) [36]
25.	B	EU886317.1	<i>Burkholderia kururiensis</i> strain M130	1	Bu_kurur	Trichloroethylene degrader; endophyte; N2 fixer	-	-	(Onofre-Lemus <i>et al.</i> , 2009) [36]
26.	B	EU886300.1	<i>Burkholderia caryophylli</i> strain LMG 2155	1	Bu_caryop	Plant pathogen (carnation)	USA	-	(Onofre-Lemus <i>et al.</i> , 2009) [36]
27.	B	DQ125252.1	<i>Burkholderia phenazinum</i> strain LMG2247	1	Bu_phenaz	Soil	-	-	(Blaha <i>et al.</i> , 2006) [4]
28.	B	EU886315.1	<i>Burkholderia caribensis</i> strain MWAP64	1	Bu_cariben	Soil; exopolysaccharide producer	-	-	(Onofre-Lemus <i>et al.</i> , 2009) [36]
29.	B	EU886307.1	<i>Burkholderia terricola</i> strain LMG 20594	1	Bu_terric	Agricultural soil	-	-	(Onofre-Lemus <i>et al.</i> , 2009) [36]
30.	B	EU886304.1	<i>Burkholderia silvatlantica</i> strain PPCR-2	1	Bu_silvat	Rhizospheric; endophyte; N2 fixer	-	-	(Onofre-Lemus <i>et al.</i> , 2009) [36]
31.	B	EU886314.1	<i>Burkholderia ambifaria</i> strain LMG 6991	1	Bu_ambif	Soil, maize roots	-	-	(Onofre-Lemus <i>et al.</i> , 2009) [36]
32.	B	EU886319.1	<i>Burkholderia stabilis</i> strain LMG 14294	1	Bu_stabil	Opportunistic human pathogen; rhizospheric	-	-	(Onofre-Lemus <i>et al.</i> , 2009) [36]
33.	B	EU886301.1	<i>Burkholderia cepacia</i> strain ATCC 25416	4	Bu_cepac_1	Rhizospheric; opportunistic human pathogen (cystic fibrosis)	-	-	(Onofre-Lemus <i>et al.</i> , 2009) [36]
34.	B	EU886309.1	<i>Burkholderia vietnamiensis</i> strain TVV75	1	Bu_vietnam	Rhizospheric; endophyte; opportunistic human pathogen; N2 fixer	-	-	(Onofre-Lemus <i>et al.</i> , 2009) [36]
35.	B	KY305933	<i>Cupriavidus</i> sp. strain XDPOP-RS-TSA-2	2	Cup_sp_2	River estuary, Rhizosphere roots	China	-	(Qin <i>et al.</i> , 2017) [40]
36.	C	KY305922	<i>Achromobacter</i> sp. strain DF-RS-ACC-6	10	Ach_sp_3	River estuary, Rhizosphere roots	China	-	(Qin <i>et al.</i> , 2017) [40]
37.	C	DQ133504.1	<i>Achromobacter xylosoxidans</i>	3	Ach_xylo_1	Rhizosphere soil	Russia	-	(Blaha <i>et al.</i> , 2006) [4]
38.	C	KP116957	<i>Achromobacter</i> sp. HZ167	10	Ach_sp_2	Black locust nodule	China	-	(Li, Z. <i>et al.</i> , 2015) [28]
39.	C	EU183544.1	<i>Rhizobium</i> sp. TAL1145	3	Rb_sp_3	root nodules	Thailand	promotes nodulation and growth	(Tittabutr <i>et al.</i> , 2008) [47]
40.	C	AY604540	<i>Achromobacter xylosoxidans</i> strain BM1	3	Ach_xylo_3	Direct strain obtained	Canada	-	(Hontzeas <i>et al.</i> , 2005) [21]
41.	C	MH939181.1	<i>Priestia aryabhatai</i> strain EWR29	1	Pr_aryab	-	-	-	
42.	C	JF741959.1	<i>Pseudomonas oryzihabitans</i> strain LP11	1	Ps_oryzi	-	-	-	
43.	C	MT779781.1	<i>Pseudomonas rhodesiae</i> strain GRC093	1	Ps_rhodes	-	-	-	
44.	C	PP208626.1	<i>Serratia marcescens</i>	1	Se_marces	-	-	-	
45.	C	AY604543	<i>Serratia proteamaculans</i> strain SUD	1	Se_proteam	Direct strain obtained	Canada	-	(Hontzeas <i>et al.</i> , 2005) [21]
46.	C	MH588718.1	<i>Enterobacter</i> sp. strain 7K	2	En_sp_1	rhizosphere soil	India	salinity stress	194
47.	C	AY604544	<i>Enterobacter aerogenes</i> strain Cal3	1	En_aerogen	Direct strain obtained	Canada	-	(Hontzeas <i>et al.</i> , 2005) [21]
48.	C	AY604545	<i>Pseudomonas syringae</i> strain GR12-2	1	Ps_syring	Direct strain obtained	Canada	-	(Hontzeas <i>et al.</i> , 2005) [21]
49.	D	AY604542	<i>Pseudomonas</i>	1	Ps_margin	Direct strain obtained	Canada	-	(Hontzeas <i>et</i>

			<i>marginalis</i>						<i>al.</i> , 2005) ^[21]
50.	D	AY604529	<i>Acidovorax facilis</i> strain 4P6	1	Aci_facil	Direct strain obtained	Canada	-	(Hontzeas <i>et al.</i> , 2005) ^[21]
51.	D	KR154507	<i>Burkholderia</i> sp. BL25 I3R1	3	Bu_sp_1	Roots nodules	South Africa	-	(Lemaire <i>et al.</i> , 2015) ^[25]
52.	D	KY352308	<i>Pseudomonas fluorescens</i> strain DR7	5	Ps_fluor_3	root samples	China	Drought	(Niu <i>et al.</i> , 2018) ^[35]
53.	D	OR227281.1	<i>Pseudomonas</i> sp. strain BApK9	6	Ps_sp_3	root	Egypt	inhibiting tumor formation	(Amer <i>et al.</i> , 2024) ^[2]
54.	D	MF040749	<i>Pseudomonas palleroniana</i> strain DPB16	2	Ps_pall_2	Rhizosphere soil	India	Drought	(Chandra <i>et al.</i> , 2018) ^[6]
55.	D	KY352309	<i>Enterobacter hormaechei</i> strain DR16	1	En_hormaec	root samples	China	Drought	(Niu <i>et al.</i> , 2018) ^[35]
56.	D	AY604528	<i>Pseudomonas brassicacearum</i> strain Am3	2	Ps_brass_1	Direct strain obtained	Canada	-	(Hontzeas <i>et al.</i> , 2005) ^[21]
57.	E	>KF612321.1	<i>Pseudomonas psychrotolerans</i> strain TP5-04	1	Ps_psychro	Roots, stems, seeds and leaves	China	low night temperature	(Chen <i>et al.</i> , 2014) ^[7]
58.	E	MN065177.1	<i>Pseudomonas putida</i> strain PSE-3	3	Ps_putid_2	rhizospheric soils	India	improves growth, nodulation and yield	(Ahmad <i>et al.</i> , 2013) ^[1]
59.	E	HQ728588.1	<i>Herbaspirillum</i> sp. Os23	1	Herbas_sp	-	-	-	
60.	E	KP116956	<i>Marmoricola</i> sp. LR61	1	Mar_sp	Mung bean nodule	China	-	(Li, Z. <i>et al.</i> , 2015) ^[28]
61.	E	KP116955.1	<i>Microbacterium</i> sp. GLR25	1	Mib_sp	-	-	-	
62.	E	OU548656.1	<i>Streptomyces</i> sp. CMB-FB	1	St_sp	-	-	-	
63.	E	KP116952.1	<i>Mycobacterium</i> sp. GDR13	1	Myb_sp	-	-	-	
64.	E	AY604538	<i>Rhodococcus</i> sp. 4N4	2	Rc_sp_1	Direct strain obtained	Canada	-	(Hontzeas <i>et al.</i> , 2005) ^[21]
65.	F	EU430449.1	<i>Methylobacterium fujisawaense</i> strain KACC 10744	1	Mb_fujisaw	-	-	-	
66.	F	MF124310.1	<i>Methylobacterium gregans</i> strain 002-074	1	Mb_gregans	-	Russia	-	(Ekimova <i>et al.</i> , 2018) ^[15]
67.	F	EU430439.1	<i>Methylobacterium oryzae</i> strain CBMB110	1	Mb_oryzae	-	-	-	
68.	F	EU430438.1	<i>Methylobacterium phyllosphaerae</i> strain CBMB27	1	Mb_phyllos	phyllosphere	Korea	-	(Madhaiyan <i>et al.</i> , 2009) ^[30]
69.	F	MF124311.1	<i>Methylobacterium longum</i> strain 440	1	Mb_longum	-	Russia	-	(Ekimova <i>et al.</i> , 2018) ^[15]
70.	F	OR958551.1	<i>Methylorubrum</i> sp. strain C44s	1	Mer_sp	-	-	-	
71.	F	MF124313.1	<i>Methylobacterium mesophilicum</i> strain A47	1	Mb_mesoph	-	Russia	-	(Ekimova <i>et al.</i> , 2018) ^[15]
72.	F	MG495925.1	<i>Methylobacterium tardum</i> strain RB677	1	Mb_tardum	-	Russia	-	(Ekimova <i>et al.</i> , 2018) ^[15]
73.	F	MF124309.1	<i>Methylobacterium goesingense</i> strain iEII3	1	Mb_goesin	-	Russia	-	(Ekimova <i>et al.</i> , 2018) ^[15]
74.	F	MF124312.1	<i>Methylobacterium marchantiae</i> strain JT1	1	Mb_marchan	-	Russia	-	(Ekimova <i>et al.</i> , 2018) ^[15]
75.	F	KY289001.1	<i>Bradyrhizobium elkanii</i> strain PV1.1	12	Br_elka_1	-	-	-	

76.	F	KC969411.1	<i>Bradyrhizobium ganzhouense</i> strain RITF807	2	Br_ganz_2	nodules	China	-	(Lu <i>et al.</i> , 2014)
77.	F	JF937710.1	<i>Bradyrhizobium japonicum</i> strain KA-B j	1	Br_japonic	-	-	-	
78.	F	AF421376	<i>Rhizobium leguminosarum</i>	7	Rb_legum_1	Direct strain obtained	Canada	-	(Hontzeas <i>et al.</i> , 2005) ^[21]
79.	F	EF525234	<i>Rhizobium gallicum</i> strain PB2	1	Rb_gallic	rhizosphere soil	Canada	-	(Duan <i>et al.</i> , 2009) ^[14]
80.	F	MN255491.1	<i>Sinorhizobium meliloti</i> strain ATCC 9930	2	Si_melit_2	specific microsymbionts	Portugal	High Manganese Concentration	(Paço <i>et al.</i> , 2020) ^[38]
81.	F	KC143168.1	<i>Sinorhizobium</i> sp. Mc1	3	Si_sp_2	-	-	-	
82.	F	FJ624149	<i>Methylobacterium radiotolerans</i> strain CoLR1	1	Mb_radiot	phyllosphere	India	-	(Chinnadurai <i>et al.</i> , 2009) ^[9]
83.	F	KU517661.1	<i>Rhizobium</i> sp. S1SS148	3	Rb_sp_2	rhizosphere soil and plant endosphere (root, stem, leaf)	China	soil fertility intensification	(Solanki <i>et al.</i> , 2018) ^[45]
84.	F	DQ125257.1	<i>Azospirillum lipoferum</i> strain TVV3	4	Az_lipo_4	roots	Vietnam	-	(Blaha <i>et al.</i> , 2006) ^[4]
85.	F	OR296837.1	<i>Roseibium aggregatum</i> strain MSSRFCCM_2	1	Ro_aggreg	-	-	-	
86.	F	EF452620.1	<i>Phyllobacterium brassicacearum</i>	1	Ph_brassic	rhizoplane (root surface)	France.	local root responses to plant growth-promoting	(Contesto <i>et al.</i> , 2008) ^[11]
87.	F	AY604534	<i>Rhizobium sullae</i> strain ATCC 43676	1	Rb_sullae	Direct strain obtained	Canada	-	(Hontzeas <i>et al.</i> , 2005) ^[21]
88.	F	JQ013381.1	<i>Mesorhizobium chacoense</i>	1	Mr_chacoen	root nodules	Portugal	nodulation	(Nascimento <i>et al.</i> , 2012) ^[34]
89.	F	KR154567	<i>Mesorhizobium</i> sp. MM5343	10	Mr_sp_6	Roots nodules	South Africa	-	(Lemaire <i>et al.</i> , 2015) ^[25]
90.	F	JQ013380.1	<i>Mesorhizobium albiziae</i>	1	Mr_albiz	root nodules	Portugal	nodulation	(Nascimento <i>et al.</i> , 2012) ^[34]
91.	F	JQ013382.1	<i>Mesorhizobium ciceri</i>	2	Mr_ciceri_1	root nodules	Portugal	nodulation	(Nascimento <i>et al.</i> , 2012) ^[34]
92.	F	JQ013384.1	<i>Mesorhizobium mediterraneum</i>	1	Mr_mediterr	root nodules	Portugal	nodulation	(Nascimento <i>et al.</i> , 2012) ^[34]
93.	F	JQ013399.1	<i>Mesorhizobium</i> sp. 101-Evora	10	Mr_sp_1	root nodules	Portugal	nodulation	(Nascimento <i>et al.</i> , 2012) ^[34]
94.	F	KU745724.1	<i>Mesorhizobium</i> sp. AG1	10	Mr_sp_4	root nodules	Poland, Ukraine, and Canada	growth promotion	(Wdowiak-Wróbel and Małek, 2016) ^[50]
95.	F	JQ013385.1	<i>Mesorhizobium plurifarum</i>	1	Mr_plurif	root nodules	Portugal	nodulation	(Nascimento <i>et al.</i> , 2012) ^[34]
96.	F	KP117016.1	<i>Mesorhizobium septentrionale</i> strain CCBau 83284	1	Mr_septent	-	-	-	
97.	F	JQ013388.1	<i>Mesorhizobium tianshanense</i>	1	Mr_tiansh	root nodules	Portugal	nodulation	(Nascimento <i>et al.</i> , 2012) ^[34]
98.	F	JQ013389.1	<i>Mesorhizobium thiogangeticum</i>	1	Mr_thiogang	root nodules	Portugal	nodulation	(Nascimento <i>et al.</i> , 2012) ^[34]
99.	F	JQ013383.1	<i>Mesorhizobium loti</i>	2	Mr_loti_1	root nodules	Portugal	nodulation	(Nascimento

									<i>et al.</i> , 2012) [34]
100	F	JQ013387.1	<i>Mesorhizobium tarimense</i>	1	Mr_tarimen	root nodules	Portugal	nodulation	(Nascimento <i>et al.</i> , 2012) [34]
101	F	KU248370.1	<i>Rhizobium</i> sp. OA132	3	Rb_sp_1	root nodules	Poland.	heavy metal, salinity	(Wdowiak-Wróbel <i>et al.</i> , 2017) ^[51]
102	G	LT795007.1	<i>Pseudomonas</i> sp. VKh13	6	Ps_sp_6	rhizosphere and roots	Iran	-	(Keshavarz-Tohid <i>et al.</i> , 2017) ^[22]
103	G	MK652706	<i>Bacillus subtilis</i> strain ACCD-SF48	1	B_subtil	rhizosphere soil	India	drought	(Gowtham <i>et al.</i> , 2020) ^[19]
104	G	PV166437.1	<i>Bacillus pumilus</i> strain UA15-3	3	B_pumil_1	-	-	-	
105	G	PV166431.1	<i>Bacillus thuringiensis</i> strain UA20-1	3	B_thurin_1	-	-	-	
106	G	PV166433.1	<i>Lysinibacillus fusiformis</i> strain UA14-1	1	Ly_fusifor	-	-	-	
107	G	PV166436.1	<i>Priestia megaterium</i> strain UA18-1	1	Pr_megater	-	-	-	

Table 2: Taxonomic positions of the bacterial strains of the sequences used in this analysis

Scientific name	Genus	Family	Order	Class	Phylum
<i>Streptomyces</i> sp. CMB-FB	<i>Streptomyces</i>	<i>Streptomycetaceae</i>	Kitasatosporales	<i>Actinomycetes</i>	<i>Actinomycetota</i>
<i>Microbacterium</i> sp. GLR25	<i>Microbacterium</i>	<i>Microbacteriaceae</i>	Micrococcales	<i>Actinomycetes</i>	<i>Actinomycetota</i>
<i>Zhihengliuella somnathii</i> strain JG 05	<i>Zhihengliuella</i>	<i>Micrococcaceae</i>	Micrococcales	<i>Actinomycetes</i>	<i>Actinomycetota</i>
<i>Mycobacterium</i> sp. GDR13	<i>Mycobacterium</i>	<i>Mycobacteriaceae</i>	Mycobacteriales	<i>Actinomycetes</i>	<i>Actinomycetota</i>
<i>Rhodococcus</i> sp. 4N4	<i>Rhodococcus</i>	Nocardiaceae	Mycobacteriales	<i>Actinomycetes</i>	<i>Actinomycetota</i>
<i>Marmoricola</i> sp. LR61	<i>Marmoricola</i>	Nocardioidaceae	Propionibacteriales	<i>Actinomycetes</i>	<i>Actinomycetota</i>
<i>Bacillus amyloliquefaciens</i> strain BPSRB14	<i>Bacillus</i>	<i>Bacillaceae</i>	Caryophanales	<i>Bacilli</i>	<i>Bacillota</i>
<i>Bacillus cereus</i> AcdSPB4	<i>Bacillus</i>	<i>Bacillaceae</i>	Caryophanales	<i>Bacilli</i>	<i>Bacillota</i>
<i>Bacillus licheniformis</i> strain HSW-16	<i>Bacillus</i>	<i>Bacillaceae</i>	Caryophanales	<i>Bacilli</i>	<i>Bacillota</i>
<i>Bacillus pumilus</i> strain UA15-3	<i>Bacillus</i>	<i>Bacillaceae</i>	Caryophanales	<i>Bacilli</i>	<i>Bacillota</i>
<i>Bacillus subtilis</i> strain ACCD-SF48	<i>Bacillus</i>	<i>Bacillaceae</i>	Caryophanales	<i>Bacilli</i>	<i>Bacillota</i>
<i>Bacillus thuringiensis</i> strain UA20-1	<i>Bacillus</i>	<i>Bacillaceae</i>	Caryophanales	<i>Bacilli</i>	<i>Bacillota</i>
<i>Priestia aryabhattai</i> strain EWR29	<i>Priestia</i>	<i>Bacillaceae</i>	Caryophanales	<i>Bacilli</i>	<i>Bacillota</i>
<i>Priestia megaterium</i> strain UA18-1	<i>Priestia</i>	<i>Bacillaceae</i>	Caryophanales	<i>Bacilli</i>	<i>Bacillota</i>
<i>Lysinibacillus fusiformis</i> strain UA14-1	<i>Lysinibacillus</i>	Caryophanaceae	Caryophanales	<i>Bacilli</i>	<i>Bacillota</i>
<i>Methylobacterium fujisawaense</i> strain KACC 10744	<i>Methylobacterium</i>	<i>Methylobacteriaceae</i>	Hyphomicrobiales	Alphaproteobacteria	Pseudomonadota
<i>Methylobacterium goesingense</i> strain iEII3	<i>Methylobacterium</i>	<i>Methylobacteriaceae</i>	Hyphomicrobiales	Alphaproteobacteria	Pseudomonadota
<i>Methylobacterium gregans</i> strain 002-074	<i>Methylobacterium</i>	<i>Methylobacteriaceae</i>	Hyphomicrobiales	Alphaproteobacteria	Pseudomonadota
<i>Methylobacterium longum</i> strain 440	<i>Methylobacterium</i>	<i>Methylobacteriaceae</i>	Hyphomicrobiales	Alphaproteobacteria	Pseudomonadota
<i>Methylobacterium marchantiae</i> strain JT1	<i>Methylobacterium</i>	<i>Methylobacteriaceae</i>	Hyphomicrobiales	Alphaproteobacteria	Pseudomonadota
<i>Methylobacterium mesophilicum</i> strain A47	<i>Methylobacterium</i>	<i>Methylobacteriaceae</i>	Hyphomicrobiales	Alphaproteobacteria	Pseudomonadota
<i>Methylobacterium oryzae</i> strain CBMB110	<i>Methylobacterium</i>	<i>Methylobacteriaceae</i>	Hyphomicrobiales	Alphaproteobacteria	Pseudomonadota
<i>Methylobacterium phyllosphaerae</i> strain CBMB27	<i>Methylobacterium</i>	<i>Methylobacteriaceae</i>	Hyphomicrobiales	Alphaproteobacteria	Pseudomonadota
<i>Methylobacterium radiotolerans</i> strain CoLR1	<i>Methylobacterium</i>	<i>Methylobacteriaceae</i>	Hyphomicrobiales	Alphaproteobacteria	Pseudomonadota
<i>Methylobacterium tardum</i> strain RB677	<i>Methylobacterium</i>	<i>Methylobacteriaceae</i>	Hyphomicrobiales	Alphaproteobacteria	Pseudomonadota

<i>Methylobacterium</i> sp. strain C44s	<i>Methylobacterium</i>	<i>Methylobacteriaceae</i>	<i>Hyphomicrobiales</i>	<i>Alphaproteobacteria</i>	<i>Pseudomonadota</i>
<i>Bradyrhizobium elkanii</i> strain PV1.1	<i>Bradyrhizobium</i>	<i>Nitrobacteraceae</i>	<i>Hyphomicrobiales</i>	<i>Alphaproteobacteria</i>	<i>Pseudomonadota</i>
<i>Bradyrhizobium ganzhouense</i> strain RITF807	<i>Bradyrhizobium</i>	<i>Nitrobacteraceae</i>	<i>Hyphomicrobiales</i>	<i>Alphaproteobacteria</i>	<i>Pseudomonadota</i>
<i>Bradyrhizobium japonicum</i> strain KA-B j	<i>Bradyrhizobium</i>	<i>Nitrobacteraceae</i>	<i>Hyphomicrobiales</i>	<i>Alphaproteobacteria</i>	<i>Pseudomonadota</i>
<i>Mesorhizobium albiziae</i>	<i>Mesorhizobium</i>	<i>Phyllobacteriaceae</i>	<i>Hyphomicrobiales</i>	<i>Alphaproteobacteria</i>	<i>Pseudomonadota</i>
<i>Mesorhizobium chacoense</i>	<i>Mesorhizobium</i>	<i>Phyllobacteriaceae</i>	<i>Hyphomicrobiales</i>	<i>Alphaproteobacteria</i>	<i>Pseudomonadota</i>
<i>Mesorhizobium ciceri</i>	<i>Mesorhizobium</i>	<i>Phyllobacteriaceae</i>	<i>Hyphomicrobiales</i>	<i>Alphaproteobacteria</i>	<i>Pseudomonadota</i>
<i>Mesorhizobium loti</i>	<i>Mesorhizobium</i>	<i>Phyllobacteriaceae</i>	<i>Hyphomicrobiales</i>	<i>Alphaproteobacteria</i>	<i>Pseudomonadota</i>
<i>Mesorhizobium mediterraneum</i>	<i>Mesorhizobium</i>	<i>Phyllobacteriaceae</i>	<i>Hyphomicrobiales</i>	<i>Alphaproteobacteria</i>	<i>Pseudomonadota</i>
<i>Mesorhizobium plurifarium</i>	<i>Mesorhizobium</i>	<i>Phyllobacteriaceae</i>	<i>Hyphomicrobiales</i>	<i>Alphaproteobacteria</i>	<i>Pseudomonadota</i>
<i>Mesorhizobium septentrionale</i> strain CCBAU 83284	<i>Mesorhizobium</i>	<i>Phyllobacteriaceae</i>	<i>Hyphomicrobiales</i>	<i>Alphaproteobacteria</i>	<i>Pseudomonadota</i>
<i>Mesorhizobium</i> sp. 101-Evora	<i>Mesorhizobium</i>	<i>Phyllobacteriaceae</i>	<i>Hyphomicrobiales</i>	<i>Alphaproteobacteria</i>	<i>Pseudomonadota</i>
<i>Mesorhizobium</i> sp. AG1	<i>Mesorhizobium</i>	<i>Phyllobacteriaceae</i>	<i>Hyphomicrobiales</i>	<i>Alphaproteobacteria</i>	<i>Pseudomonadota</i>
<i>Mesorhizobium</i> sp. MM5343	<i>Mesorhizobium</i>	<i>Phyllobacteriaceae</i>	<i>Hyphomicrobiales</i>	<i>Alphaproteobacteria</i>	<i>Pseudomonadota</i>
<i>Mesorhizobium tarimense</i>	<i>Mesorhizobium</i>	<i>Phyllobacteriaceae</i>	<i>Hyphomicrobiales</i>	<i>Alphaproteobacteria</i>	<i>Pseudomonadota</i>
<i>Mesorhizobium thioganicum</i>	<i>Mesorhizobium</i>	<i>Phyllobacteriaceae</i>	<i>Hyphomicrobiales</i>	<i>Alphaproteobacteria</i>	<i>Pseudomonadota</i>
<i>Mesorhizobium tianshanense</i>	<i>Mesorhizobium</i>	<i>Phyllobacteriaceae</i>	<i>Hyphomicrobiales</i>	<i>Alphaproteobacteria</i>	<i>Pseudomonadota</i>
<i>Phyllobacterium brassicacearum</i>	<i>Phyllobacterium</i>	<i>Phyllobacteriaceae</i>	<i>Hyphomicrobiales</i>	<i>Alphaproteobacteria</i>	<i>Pseudomonadota</i>
<i>Rhizobium gallicum</i> strain PB2	<i>Rhizobium</i>	<i>Rhizobiaceae</i>	<i>Hyphomicrobiales</i>	<i>Alphaproteobacteria</i>	<i>Pseudomonadota</i>
<i>Rhizobium leguminosarum</i>	<i>Rhizobium</i>	<i>Rhizobiaceae</i>	<i>Hyphomicrobiales</i>	<i>Alphaproteobacteria</i>	<i>Pseudomonadota</i>
<i>Rhizobium</i> sp. OA132	<i>Rhizobium</i>	<i>Rhizobiaceae</i>	<i>Hyphomicrobiales</i>	<i>Alphaproteobacteria</i>	<i>Pseudomonadota</i>
<i>Rhizobium</i> sp. S1SS148	<i>Rhizobium</i>	<i>Rhizobiaceae</i>	<i>Hyphomicrobiales</i>	<i>Alphaproteobacteria</i>	<i>Pseudomonadota</i>
<i>Rhizobium</i> sp. TAL1145	<i>Rhizobium</i>	<i>Rhizobiaceae</i>	<i>Hyphomicrobiales</i>	<i>Alphaproteobacteria</i>	<i>Pseudomonadota</i>
<i>Rhizobium sullae</i> strain ATCC 43676	<i>Rhizobium</i>	<i>Rhizobiaceae</i>	<i>Hyphomicrobiales</i>	<i>Alphaproteobacteria</i>	<i>Pseudomonadota</i>
<i>Sinorhizobium meliloti</i> strain ATCC 9930	<i>Sinorhizobium</i>	<i>Rhizobiaceae</i>	<i>Hyphomicrobiales</i>	<i>Alphaproteobacteria</i>	<i>Pseudomonadota</i>
<i>Sinorhizobium</i> sp. Mc1	<i>Sinorhizobium</i>	<i>Rhizobiaceae</i>	<i>Hyphomicrobiales</i>	<i>Alphaproteobacteria</i>	<i>Pseudomonadota</i>
<i>Roseibium aggregatum</i> strain MSSRFCCM_2	<i>Roseibium</i>	<i>Stappiaceae</i>	<i>Hyphomicrobiales</i>	<i>Alphaproteobacteria</i>	<i>Pseudomonadota</i>
<i>Azospirillum lipoferum</i> strain TVV3	<i>Azospirillum</i>	<i>Azospirillaceae</i>	<i>Rhodospirillales</i>	<i>Alphaproteobacteria</i>	<i>Pseudomonadota</i>
<i>Achromobacter</i> sp. HZ167	<i>Achromobacter</i>	<i>Alcaligenaceae</i>	<i>Burkholderiales</i>	<i>Betaproteobacteria</i>	<i>Pseudomonadota</i>
<i>Achromobacter</i> sp. strain DF-RS-ACC-6	<i>Achromobacter</i>	<i>Alcaligenaceae</i>	<i>Burkholderiales</i>	<i>Betaproteobacteria</i>	<i>Pseudomonadota</i>
<i>Achromobacter xylosoxidans</i>	<i>Achromobacter</i>	<i>Alcaligenaceae</i>	<i>Burkholderiales</i>	<i>Betaproteobacteria</i>	<i>Pseudomonadota</i>
<i>Achromobacter xylosoxidans</i> strain BM1	<i>Achromobacter</i>	<i>Alcaligenaceae</i>	<i>Burkholderiales</i>	<i>Betaproteobacteria</i>	<i>Pseudomonadota</i>
<i>Burkholderia ambifaria</i> strain LMG 6991	<i>Burkholderia</i>	<i>Burkholderiaceae</i>	<i>Burkholderiales</i>	<i>Betaproteobacteria</i>	<i>Pseudomonadota</i>
<i>Burkholderia caledonica</i> strain LMG 19076	<i>Burkholderia</i>	<i>Burkholderiaceae</i>	<i>Burkholderiales</i>	<i>Betaproteobacteria</i>	<i>Pseudomonadota</i>
<i>Burkholderia caribensis</i> strain MWAP64	<i>Burkholderia</i>	<i>Burkholderiaceae</i>	<i>Burkholderiales</i>	<i>Betaproteobacteria</i>	<i>Pseudomonadota</i>
<i>Burkholderia caryophylli</i> strain LMG 2155	<i>Burkholderia</i>	<i>Burkholderiaceae</i>	<i>Burkholderiales</i>	<i>Betaproteobacteria</i>	<i>Pseudomonadota</i>
<i>Burkholderia cepacia</i> strain ATCC 25416	<i>Burkholderia</i>	<i>Burkholderiaceae</i>	<i>Burkholderiales</i>	<i>Betaproteobacteria</i>	<i>Pseudomonadota</i>
<i>Burkholderia fungorum</i> strain LMG 16225	<i>Burkholderia</i>	<i>Burkholderiaceae</i>	<i>Burkholderiales</i>	<i>Betaproteobacteria</i>	<i>Pseudomonadota</i>
<i>Burkholderia graminis</i> strain C4D1M	<i>Burkholderia</i>	<i>Burkholderiaceae</i>	<i>Burkholderiales</i>	<i>Betaproteobacteria</i>	<i>Pseudomonadota</i>
<i>Burkholderia kururiensis</i> strain M130	<i>Burkholderia</i>	<i>Burkholderiaceae</i>	<i>Burkholderiales</i>	<i>Betaproteobacteria</i>	<i>Pseudomonadota</i>
<i>Burkholderia phenazinium</i> strain LMG2247	<i>Burkholderia</i>	<i>Burkholderiaceae</i>	<i>Burkholderiales</i>	<i>Betaproteobacteria</i>	<i>Pseudomonadota</i>
<i>Burkholderia phenoliruptrix</i> strain LMG 22037	<i>Burkholderia</i>	<i>Burkholderiaceae</i>	<i>Burkholderiales</i>	<i>Betaproteobacteria</i>	<i>Pseudomonadota</i>
<i>Burkholderia silvaticola</i> strain PPCR-2	<i>Burkholderia</i>	<i>Burkholderiaceae</i>	<i>Burkholderiales</i>	<i>Betaproteobacteria</i>	<i>Pseudomonadota</i>
<i>Burkholderia</i> sp. BL25 I3R1	<i>Burkholderia</i>	<i>Burkholderiaceae</i>	<i>Burkholderiales</i>	<i>Betaproteobacteria</i>	<i>Pseudomonadota</i>
<i>Burkholderia stabilis</i> strain LMG 14294	<i>Burkholderia</i>	<i>Burkholderiaceae</i>	<i>Burkholderiales</i>	<i>Betaproteobacteria</i>	<i>Pseudomonadota</i>
<i>Burkholderia terricola</i> strain LMG 20594	<i>Burkholderia</i>	<i>Burkholderiaceae</i>	<i>Burkholderiales</i>	<i>Betaproteobacteria</i>	<i>Pseudomonadota</i>

<i>Burkholderia tropica</i> strain BM273	<i>Burkholderia</i>	<i>Burkholderiaceae</i>	<i>Burkholderiales</i>	<i>Betaproteobacteria</i>	<i>Pseudomonadota</i>
<i>Burkholderia vietnamiensis</i> strain TVV75	<i>Burkholderia</i>	<i>Burkholderiaceae</i>	<i>Burkholderiales</i>	<i>Betaproteobacteria</i>	<i>Pseudomonadota</i>
<i>Burkholderia xenovorans</i> strain CAC-124	<i>Burkholderia</i>	<i>Burkholderiaceae</i>	<i>Burkholderiales</i>	<i>Betaproteobacteria</i>	<i>Pseudomonadota</i>
<i>Cupriavidus</i> sp. strain XDPOP-RS-TSA-2	<i>Cupriavidus</i>	<i>Burkholderiaceae</i>	<i>Burkholderiales</i>	<i>Betaproteobacteria</i>	<i>Pseudomonadota</i>
<i>Paraburkholderia tropica</i> strain S39-2	<i>Paraburkholderia</i>	<i>Burkholderiaceae</i>	<i>Burkholderiales</i>	<i>Betaproteobacteria</i>	<i>Pseudomonadota</i>
<i>Ralstonia</i> sp. S1SM82	<i>Ralstonia</i>	<i>Burkholderiaceae</i>	<i>Burkholderiales</i>	<i>Betaproteobacteria</i>	<i>Pseudomonadota</i>
<i>Acidovorax facilis</i> strain 4P6	<i>Acidovorax</i>	<i>Comamonadaceae</i>	<i>Burkholderiales</i>	<i>Betaproteobacteria</i>	<i>Pseudomonadota</i>
<i>Delftia</i> sp. 17(2015)	<i>Delftia</i>	<i>Comamonadaceae</i>	<i>Burkholderiales</i>	<i>Betaproteobacteria</i>	<i>Pseudomonadota</i>
<i>Variovorax paradoxus</i> strain 2C1	<i>Variovorax</i>	<i>Comamonadaceae</i>	<i>Burkholderiales</i>	<i>Betaproteobacteria</i>	<i>Pseudomonadota</i>
<i>Variovorax</i> sp. DW01-1	<i>Variovorax</i>	<i>Comamonadaceae</i>	<i>Burkholderiales</i>	<i>Betaproteobacteria</i>	<i>Pseudomonadota</i>
<i>Herbaspirillum</i> sp. Os23	<i>Herbaspirillum</i>	<i>Oxalobacteraceae</i>	<i>Burkholderiales</i>	<i>Betaproteobacteria</i>	<i>Pseudomonadota</i>
<i>Enterobacter aerogenes</i> strain Cal3	<i>Enterobacter</i>	<i>Enterobacteriaceae</i>	<i>Enterobacterales</i>	<i>Gammaproteobacteria</i>	<i>Pseudomonadota</i>
<i>Enterobacter cloacae</i> CAL2	<i>Enterobacter</i>	<i>Enterobacteriaceae</i>	<i>Enterobacterales</i>	<i>Gammaproteobacteria</i>	<i>Pseudomonadota</i>
<i>Enterobacter hormaechei</i> strain DR16	<i>Enterobacter</i>	<i>Enterobacteriaceae</i>	<i>Enterobacterales</i>	<i>Gammaproteobacteria</i>	<i>Pseudomonadota</i>
<i>Enterobacter</i> sp. strain 7K	<i>Enterobacter</i>	<i>Enterobacteriaceae</i>	<i>Enterobacterales</i>	<i>Gammaproteobacteria</i>	<i>Pseudomonadota</i>
<i>Klebsiella oxytoca</i> strain Rs-5	<i>Klebsiella</i>	<i>Enterobacteriaceae</i>	<i>Enterobacterales</i>	<i>Gammaproteobacteria</i>	<i>Pseudomonadota</i>
<i>Klebsiella pneumoniae</i> AcdSPB2	<i>Klebsiella</i>	<i>Enterobacteriaceae</i>	<i>Enterobacterales</i>	<i>Gammaproteobacteria</i>	<i>Pseudomonadota</i>
<i>Serratia marcescens</i>	<i>Serratia</i>	<i>Yersiniaceae</i>	<i>Enterobacterales</i>	<i>Gammaproteobacteria</i>	<i>Pseudomonadota</i>
<i>Serratia proteamaculans</i> strain SUD	<i>Serratia</i>	<i>Yersiniaceae</i>	<i>Enterobacterales</i>	<i>Gammaproteobacteria</i>	<i>Pseudomonadota</i>
<i>Serratia rubidaea</i> AcdSPB1	<i>Serratia</i>	<i>Yersiniaceae</i>	<i>Enterobacterales</i>	<i>Gammaproteobacteria</i>	<i>Pseudomonadota</i>
<i>Halomonas</i> sp. strain XB-RS-PIA-11	<i>Halomonas</i>	<i>Halomonadaceae</i>	<i>Oceanospirillales</i>	<i>Gammaproteobacteria</i>	<i>Pseudomonadota</i>
<i>Pseudomonas brassicacearum</i> strain Am3	<i>Pseudomonas</i>	<i>Pseudomonadaceae</i>	<i>Pseudomonadales</i>	<i>Gammaproteobacteria</i>	<i>Pseudomonadota</i>
<i>Pseudomonas fluorescens</i> strain DR7	<i>Pseudomonas</i>	<i>Pseudomonadaceae</i>	<i>Pseudomonadales</i>	<i>Gammaproteobacteria</i>	<i>Pseudomonadota</i>
<i>Pseudomonas marginalis</i>	<i>Pseudomonas</i>	<i>Pseudomonadaceae</i>	<i>Pseudomonadales</i>	<i>Gammaproteobacteria</i>	<i>Pseudomonadota</i>
<i>Pseudomonas migulae</i> strain DR35	<i>Pseudomonas</i>	<i>Pseudomonadaceae</i>	<i>Pseudomonadales</i>	<i>Gammaproteobacteria</i>	<i>Pseudomonadota</i>
<i>Pseudomonas mucidolens</i>	<i>Pseudomonas</i>	<i>Pseudomonadaceae</i>	<i>Pseudomonadales</i>	<i>Gammaproteobacteria</i>	<i>Pseudomonadota</i>
<i>Pseudomonas oryzae</i> strain LP11	<i>Pseudomonas</i>	<i>Pseudomonadaceae</i>	<i>Pseudomonadales</i>	<i>Gammaproteobacteria</i>	<i>Pseudomonadota</i>
<i>Pseudomonas palleroniana</i> strain DPB16	<i>Pseudomonas</i>	<i>Pseudomonadaceae</i>	<i>Pseudomonadales</i>	<i>Gammaproteobacteria</i>	<i>Pseudomonadota</i>
<i>Pseudomonas psychrotolerans</i> strain TP-04	<i>Pseudomonas</i>	<i>Pseudomonadaceae</i>	<i>Pseudomonadales</i>	<i>Gammaproteobacteria</i>	<i>Pseudomonadota</i>
<i>Pseudomonas putida</i> strain PSE-3	<i>Pseudomonas</i>	<i>Pseudomonadaceae</i>	<i>Pseudomonadales</i>	<i>Gammaproteobacteria</i>	<i>Pseudomonadota</i>
<i>Pseudomonas rhodesiae</i> strain GRC093	<i>Pseudomonas</i>	<i>Pseudomonadaceae</i>	<i>Pseudomonadales</i>	<i>Gammaproteobacteria</i>	<i>Pseudomonadota</i>
<i>Pseudomonas</i> sp. strain BAPK9	<i>Pseudomonas</i>	<i>Pseudomonadaceae</i>	<i>Pseudomonadales</i>	<i>Gammaproteobacteria</i>	<i>Pseudomonadota</i>
<i>Pseudomonas</i> sp. strain Q1	<i>Pseudomonas</i>	<i>Pseudomonadaceae</i>	<i>Pseudomonadales</i>	<i>Gammaproteobacteria</i>	<i>Pseudomonadota</i>
<i>Pseudomonas</i> sp. strain SYC-RS-TSA-3	<i>Pseudomonas</i>	<i>Pseudomonadaceae</i>	<i>Pseudomonadales</i>	<i>Gammaproteobacteria</i>	<i>Pseudomonadota</i>
<i>Pseudomonas</i> sp. VKh13	<i>Pseudomonas</i>	<i>Pseudomonadaceae</i>	<i>Pseudomonadales</i>	<i>Gammaproteobacteria</i>	<i>Pseudomonadota</i>
<i>Pseudomonas syringae</i> strain GR12-2	<i>Pseudomonas</i>	<i>Pseudomonadaceae</i>	<i>Pseudomonadales</i>	<i>Gammaproteobacteria</i>	<i>Pseudomonadota</i>

Discussion

In order to understand the evolutionary forces that impact the distribution of the *acdS* gene, the current study discusses phylogenetic patterns of the gene across taxonomically and ecologically diverse bacteria. Several plant systems have been examined by experimental inoculation studies, which have consistently shown that bacteria carrying functional *acdS* enhance plant resilience when exposed to abiotic and biotic stresses such as salinity, drought, heavy metal exposure, hydrocarbon contamination, temperature stress, and pathogen-associated stress. All of these studies show that by modifying host ethylene levels during stress

responses, *acdS* improves the efficiency of bacteria in plant-associated environments, indirectly enhancing plant performance and promoting microbial colonization (Belimov *et al.*, 2001; Grichko and Glick, 2001; Mayak *et al.*, 2004; Chen *et al.*, 2014; Govindasamy *et al.*, 2014; Kukla *et al.*, 2014; Saikia *et al.*, 2018; Paço *et al.*, 2020; Amer *et al.*, 2024) [2, 3, 7, 18, 24, 20, 31, 38, 42].

Our phylogenetic analysis showed that several major *acdS* clades show close correspondence with accepted bacterial taxonomy. Specifically, members of the *Burkholderiaceae* and subsets of *Alphaproteobacteria* formed well-supported clusters, indicating that vertical inheritance played a

dominant role in *acdS* evolution within these lineages. Comparative sequencing studies show that the *acdS* gene can be stably inherited when it becomes part of the main genome. This is supported by the fact that different strains from the same genus often have very similar *acdS* sequences, even when they come from different environments (Blaha *et al.*, 2006)^[4].

On the other hand, significant phylogenetic deviation throughout the tree at times contradicted with this vertical inheritance. Despite being clearly separated in 16S rRNA phylogenies, taxonomically distant genera clustered together based on *acdS* sequence similarity. *Rhizobium* sp. TAL1145, *Zhihengliuella somnathii* JG05, *Herbaspirillum* sp. Os23, *Burkholderia* sp. BL25, *Gammaproteobacteria*, *Enterobacter*, *Pseudomonas* and *Bacillus* are the major instances which were not placed in the phylogenetic tree similar to their taxonomy. This pattern is extensively inferred as strong confirmation for Horizontal Gene Transfer (HGT). Multiple independent studies have experimentally and phylogenetically reported this incongruence, demonstrating that the *acdS* phylogeny is inconsistent with evolutionary relationships, suggesting frequent sharing of genes across distant groups (Hontzeas *et al.*, 2005; Blaha *et al.*, 2006)^[4, 21]. This pattern appears frequently across several clades in our analysis, proving that *acdS* mobility is an aspect of its evolutionary history rather than an uncommon or isolated occurrence. Another possible explanation for the clustering of *acdS* sequences disagreement from the taxonomic classification maybe gene loss followed by re-acquisition. Gene loss can occur due to reduced selective pressure or genome streamlining, leading to the absence of functional genes in certain lineages (Mira *et al.*, 2001)^[32]. These genes may later be re-acquired through horizontal gene transfer, restoring functional capabilities under changing environmental conditions (Soucy *et al.*, 2015)^[46]. Such gene gain-loss dynamics contribute to genome plasticity and evolutionary adaptation in bacteria (Koonin *et al.*, 2001)^[23]. Consequently, these processes can result in phylogenetic inconsistencies, where some organisms cluster with different genera rather than their expected taxonomic groups in the *acdS* phylogenetic tree (Boto, 2009)^[5].

This intra-generic diversity correlates with results from culture-based surveys that showed significant differences in gene sequences and *acdS* activity levels between strains of the same species or genus. Blaha *et al.* (2006)^[4] reported significant sequence heterogeneity and functional variation among *acdS*-positive bacteria isolated from similar environments, suggesting that microevolutionary processes like recombination, differential regulation, and controlled selection pressures play a role in post-acquisition diversification. The persistence of functional *acdS* appears to be influenced by the environment despite its mobility. In the data we've collected, closely related *acdS* sequences were found in bacteria isolated from bulk soils, endophytic tissues, rhizosphere soils, and habitats under environmental stress. Essentially, these niches link with conditions in which ethylene-mediated stress responses play a significant role, either directly in plants or indirectly through microbial adaptation to stress. Functional ACC deaminase-producing bacteria have been recovered from rhizospheres, internal plant tissues, contaminated soils, saline soils, and metal-polluted sites in isolation-based studies, which provide evidence to this wider ecological

distribution (Glick, 2014)^[16]. All these results suggest that ecological conditions influence *acdS* genes in a way that allows horizontally transferred genes to remain functional rather than undergoing neutral degeneration. (Hontzeas *et al.*, 2005)^[21]. Strong research evidence for the adaptive significance of the *acdS* gene in plant-bacterial interactions is supported by gene mutation studies. Chemically induced ACC deaminase-deficient mutants in *Pseudomonas putida* GR12-2 were unable to use ACC and, contrary to the wild type, were unable to induce canola root elongation under gnotobiotic conditions (Glick *et al.*, 1994)^[17]. This made it significantly evident that the promotion of plant growth was directly inhibited by the loss of ACC deaminase activity. Similar to this, *Enterobacter cloacae* UW4's targeted *acdS* gene replacement produced a mutant strain with significantly reduced ACC deaminase activity and being unable to stimulate root elongation. More recently, precise genome editing in *Bradyrhizobium* verified that while overexpression increased enzyme activity, deletion of *acdS* significantly decreased ACC degradation capacity (Wang *et al.*, 2025)^[49]. Furthermore, in our analysis, *acdS* clustering was not significantly impacted by geographic origin. Low biogeographic structuring was suggested by the frequent grouping of isolates from different continents with high bootstrap support. This observation corresponds to worldwide sampling studies that indicates ecological function has a stronger influence on the distribution of *acdS* than geographic isolation. Blaha *et al.* (2006)^[4] suggested that *acdS*-positive bacteria from geographically distant regions frequently shared closely related gene sequences, confirming that dispersal and horizontal transfer can overcome geographic barriers when selective conditions are favourable. In addition, methodological caution is crucial when comprehending *acdS* diversity. Li, Z. *et al.* (2015)^[28] explicitly confirmed that overestimation of gene distribution and incorrect identification of ACC deaminase-producing bacteria were resulting from non-specific amplification of *acdS* homologs. Their study showed that key active-site residues such as Glu295 and Leu322 distinguish true ACC deaminase from closely related homologs, including D-cysteine desulphydrase. Similarly, established experimentally that ACC deaminase can be modified into D-cysteine desulphydrase and vice versa by making minor amino acid substitutions. Together, these results demonstrate that phylogenetic placement alone is not enough for accurate identification; in order to correct any misannotation, residue-level analysis and biochemical validation of enzyme activity are supplemental prerequisites.

Conclusion

This review is an attempt to comprehend how a single functional gene can reflect both ancestry and adaptation. With strong bootstrap support, our phylogenetic reconstruction identified seven major clades (A-G), displaying patterns of significant incongruence in some groups and evident lineage conservation in others. Sequences from different environmental stress often clustered together, while closely related taxa occasionally split into separate clades. These explain the vertical inheritance and horizontal gene transfer. Overall, the *acdS* gene shows up as a dynamic evolutionary marker influenced by both taxonomy and ecological pressure, rather than just as a trait linked to stress.

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Supplementary Figure 1

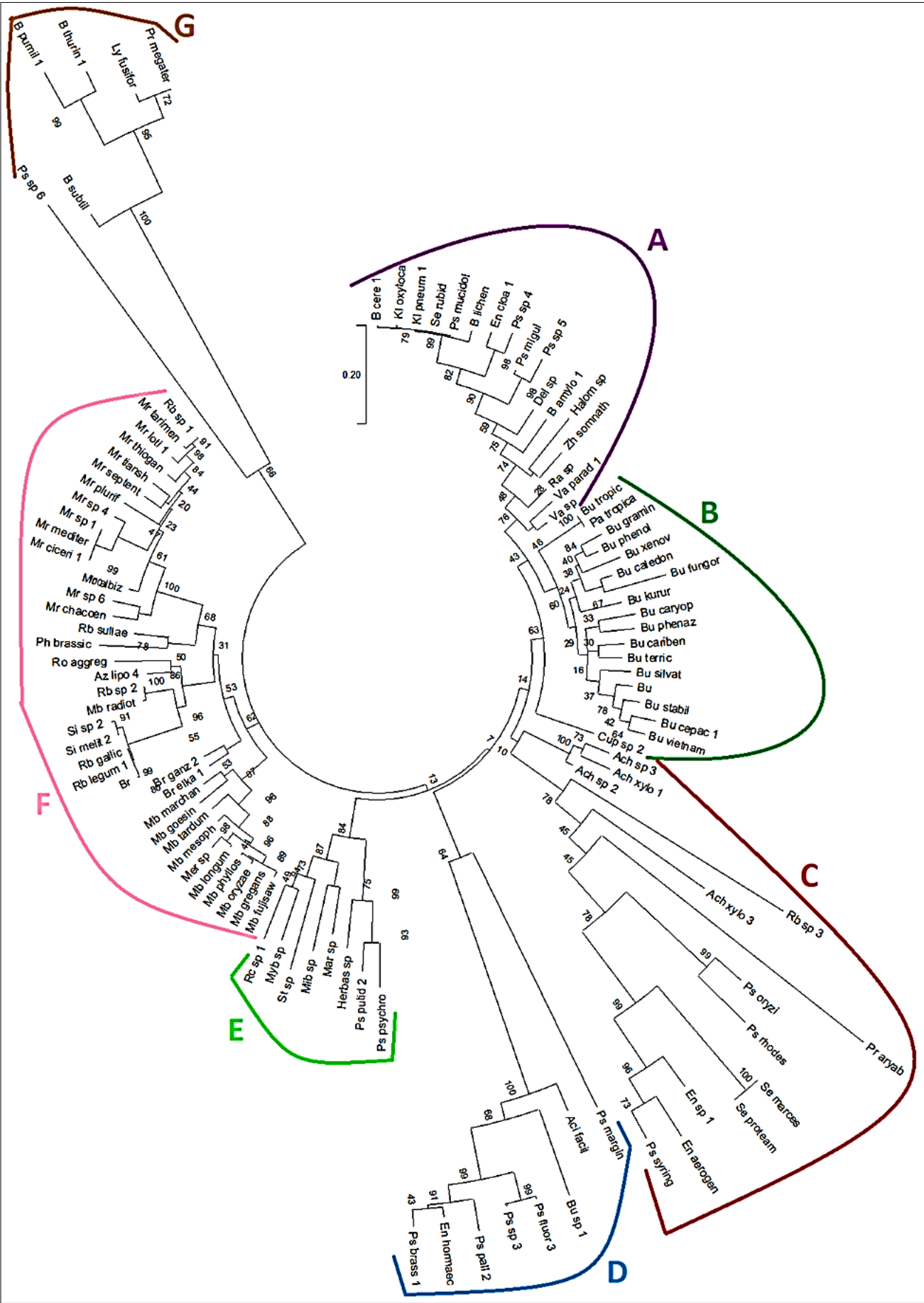


Fig 1: Circular maximum likelihood phylogenetic tree of *acdS* gene sequences showing their evolutionary relationships. Distinct clades are highlighted in different colors to indicate major phylogenetic groupings

Supplementary Table S1

Table 1: List of total sequences retrieved for analysis

S.No	ACCESSION no.	Organism Name
1	AAT35837	Achromobacter sp. CM1
2	KP116957	Achromobacter sp. HZ167
3	KY305922	Achromobacter sp. strain DF-RS-ACC-6
4	KY305925	Achromobacter sp. strain DF-RS-PIA-1
5	KY305928	Achromobacter sp. strain DW-RS-PIA-1
6	KY305921	Achromobacter sp. strain JP-R-ACC-12
7	KY305917	Achromobacter sp. strain LW-RS-ACC-3
8	KY305926	Achromobacter sp. strain SYC-RS-PIA-8
9	KY305927	Achromobacter sp. strain SYC-RS-PIA-9
10	KY305920	Achromobacter sp. strain SYC-RS-TSA-4
11	DQ133504.1	Achromobacter xylosoxidans
12	AY604539	Achromobacter xylosoxidans strain A551
13	AY604540	Achromobacter xylosoxidans strain BM1
14	AY604529	Acidovorax facilis strain 4P6
15	GU727865.1	Azospirillum lipoferum strain AZm5
16	DQ125253	Azospirillum lipoferum strain CN1
17	DQ125255.1	Azospirillum lipoferum strain N4
18	DQ125257.1	Azospirillum lipoferum strain TVV3
19	KX709841.1	Bacillus amyloliquefaciens strain BPSRB14
20	KX709840.1	Bacillus amyloliquefaciens strain BPSRB4
21	JN625726.1	Bacillus cereus AcdSPB4
22	PV166435.1	Bacillus cereus strain UA15-1
23	KM501059.2	Bacillus licheniformis strain HSW-16
24	PV166437.1	Bacillus pumilus strain UA15-3
25	PV166434.1	Bacillus pumilus strain UA19-2
26	PV166430.1	Bacillus pumilus strain UA21-3
27	MK652706	Bacillus subtilis strain ACCD-SF48
28	PV166431.1	Bacillus thuringiensis strain UA20-1
29	PV166429.1	Bacillus thuringiensis strain UA8-2
30	PV166432.1	Bacillus thuringiensis strain UA9-1
31	KY289001.1	Bradyrhizobium elkanii strain PV1.1
32	KY289008.1	Bradyrhizobium elkanii strain PV1.14
33	KY289010.1	Bradyrhizobium elkanii strain PV3.1
34	KY288998.1	Bradyrhizobium elkanii strain PV3.16
35	KY289003.1	Bradyrhizobium elkanii strain PV3.17
36	KY289009.1	Bradyrhizobium elkanii strain PV3.2
37	KY289006.1	Bradyrhizobium elkanii strain PV3.24
38	KY288997.1	Bradyrhizobium elkanii strain PV3.5
39	ON597815.1	Bradyrhizobium elkanii strain VK10
40	ON597816.1	Bradyrhizobium elkanii strain WB74
41	ON597818.1	Bradyrhizobium elkanii strain XFH12
42	ON597819.1	Bradyrhizobium elkanii strain XFH13
43	KC969430.1	Bradyrhizobium ganzhouense strain RITF211
44	KC969411.1	Bradyrhizobium ganzhouense strain RITF807
45	JF937710.1	Bradyrhizobium japonicum strain KA-B j
46	EU886314.1	Burkholderia ambifaria strain LMG 6991
47	EU886299.1	Burkholderia caledonica strain LMG 19076
48	EU886315.1	Burkholderia caribensis strain MWAP64
49	EU886300.1	Burkholderia caryophylli strain LMG 2155
50	EU886301.1	Burkholderia cepacia strain ATCC 25416
51	DQ125243.1	Burkholderia cepacia strain LMG16656
52	EU886316.1	Burkholderia fungorum strain LMG 16225
53	EU886302.1	Burkholderia graminis strain C4D1M

54	EU886317.1	Burkholderia kururiensis strain M130
55	DQ125252.1	Burkholderia phenazinium strain LMG2247
56	EU886303.1	Burkholderia phenoliruptrix strain LMG 22037
57	EU886304.1	Burkholderia silvatlantica strain PPCR-2
58	KR154507	Burkholderia sp. BL25 I3R1
59	HQ728595.1	Burkholderia sp. CZ152S
60	KU517660.1	Burkholderia sp. D1SS235
61	EU886319.1	Burkholderia stabilis strain LMG 14294
62	EU886307.1	Burkholderia terricola strain LMG 20594
63	DQ125254.1	Burkholderia tropica strain BM273
64	EU886308.1	Burkholderia unamae strain CAC-98
65	EU886309.1	Burkholderia vietnamiensis strain TVV75
66	EU886312.1	Burkholderia xenovorans strain CAC-124
67	JX233794.1	Cupriavidus sp. SaCR1
68	KY305933	Cupriavidus sp. strain XDPOP-RS-TSA-2
69	KR080559.1	Delftia sp. 17(2015)
70	AY604544	Enterobacter aerogenes strain Cal3
71	AF047840	Enterobacter cloacae CAL2
72	KM501058.2	Enterobacter cloacae strain SBP8
73	AF047710	Enterobacter cloacae UW4
74	KY352309	Enterobacter hormaechei strain DR16
75	MH588718.1	Enterobacter sp. strain 7K
76	MH492008.1	Enterobacter sp. strain KA36
77	KY305930	Halomonas sp. strain XB-RS-PIA-11
78	HQ728588.1	Herbaspirillum sp. Os23
79	FJ357241.1	Klebsiella oxytoca strain Rs-5
80	JN625725.1	Klebsiella pneumoniae AcdSPB2
81	JN625725.1	Klebsiella pneumoniae AcdSPB2
82	PV166433.1	Lysinibacillus fusiformis strain UA14-1
83	KP116956	Marmoricola sp. LR61
84	JQ013380.1	Mesorhizobium albiziae
85	JQ013381.1	Mesorhizobium chacoense
86	JQ013382.1	Mesorhizobium ciceri
87	EF495226.2	Mesorhizobium ciceri
88	JQ013383.1	Mesorhizobium loti
89	KC143169.1	Mesorhizobium loti strain Le2
90	JQ013384.1	Mesorhizobium mediterraneum
91	JQ013385.1	Mesorhizobium plurifarum
92	KP117016.1	Mesorhizobium septentrionale strain CCBAU 83284
93	JQ013399.1	Mesorhizobium sp. 101-Evora
94	JQ013398.1	Mesorhizobium sp. 6b-Beja
95	KU745729.1	Mesorhizobium sp. ACMP18
96	KU745724.1	Mesorhizobium sp. AG1
97	JQ013390.1	Mesorhizobium sp. BR-8-Braganca
98	KR154567	Mesorhizobium sp. MM5343
99	KR154562	Mesorhizobium sp. MM5357
100	KR154565	Mesorhizobium sp. MM5462
101	KR154563	Mesorhizobium sp. MM5675
102	KR154566	Mesorhizobium sp. OD119
103	JQ013387.1	Mesorhizobium tarimense
104	JQ013389.1	Mesorhizobium thioglycolicum
105	JQ013388.1	Mesorhizobium tianshanense
106	EU430449.1	Methylobacterium fujisawaense strain KACC 10744
107	MF124309.1	Methylobacterium goesingense strain iEII3
108	MF124310.1	Methylobacterium gregans strain 002-074
109	MF124311.1	Methylobacterium longum strain 440
110	MF124312.1	Methylobacterium marchantiae strain JT1

111	MF124313.1	Methylobacterium mesophilicum strain A47
112	EU430439.1	Methylobacterium oryzae strain CBMB110
113	EU430438.1	Methylobacterium phyllosphaerae strain CBMB27
114	FJ624149	Methylobacterium radiotolerans strain CoLR1
115	MG495925.1	Methylobacterium tardum strain RB677
116	OR958551.1	Methylorubrum sp. strain C44s
117	KP116955.1	Microbacterium sp. GLR25
118	KP116952.1	Mycobacterium sp. GDR13
119	KX622567.1	Paraburkholderia tropica strain S39-2
120	EF452620.1	Phyllobacterium brassicacearum
121	MH939181.1	Priestia aryabhattai strain EWR29
122	PV166436.1	Priestia megaterium strain UA18-1
123	AY604528	Pseudomonas brassicacearum strain Am3
124	KC430107.1	Pseudomonas brassicacearum strain KY5404
125	MF040748	Pseudomonas fluorescens strain DPB15
126	KY451713	Pseudomonas fluorescens strain DR11
127	KY352308	Pseudomonas fluorescens strain DR7
128	FJ465155	Pseudomonas fluorescens strain FY32
129	MW328565.1	Pseudomonas fluorescens strain GL-RE-29
130	AY604542	Pseudomonas marginalis
131	KY451712	Pseudomonas migulae strain DR35
132	PP208627.1	Pseudomonas mucidolens
133	JF741959.1	Pseudomonas oryzihabitans strain LP11
134	MF040747	Pseudomonas palleroniana strain DPB13
135	MF040749	Pseudomonas palleroniana strain DPB16
136	>KF612321.1	Pseudomonas psychrotolerans strain TPs-04
137	AY604533	Pseudomonas putida strain Bm3
138	MN065177.1	Pseudomonas putida strain PSE-3
139	AY823987	Pseudomonas putida strain UW4
140	MT779781.1	Pseudomonas rhodesiae strain GRC093
141	M73488	Pseudomonas sp.
142	KR080557.1	Pseudomonas sp. 12(2015)
143	OR227281.1	Pseudomonas sp. strain BApK9
144	MN232215.1	Pseudomonas sp. strain Q1
145	KY305919	Pseudomonas sp. strain SYC-RS-TSA-3
146	LT795007.1	Pseudomonas sp. VKh13
147	AY604545	Pseudomonas syringae strain GR12-2
148	KU517662.1	Ralstonia sp. S1SM82
149	EF525234	Rhizobium gallicum strain PB2
150	AF421376	Rhizobium leguminosarum
151	JN110340.1	Rhizobium leguminosarum bv. phaseoli strain KA-PH7-10
152	JN110344.1	Rhizobium leguminosarum bv. trifolii strain KA-F-12
153	JF937709.1	Rhizobium leguminosarum bv. viciae strain KA-CP11
154	AY604535	Rhizobium leguminosarum strain 99A1
155	JN110342.1	Rhizobium leguminosarum strain KA-P-28
156	EF525255	Rhizobium leguminosarum strain PB165
157	KU248370.1	Rhizobium sp. OA132
158	KU517661.1	Rhizobium sp. S1SS148
159	EU183544.1	Rhizobium sp. TAL1145
160	AY604534	Rhizobium sullae strain ATCC 43676
161	AY604538	Rhodococcus sp. 4N4
162	AY604537	Rhodococcus sp. Fp2
163	OR296837.1	Roseibium aggregatum strain MSSRFCCM_2
164	PP208626.1	Serratia marcescens
165	AY604543	Serratia proteamaculans strain SUD
166	JN625724.1	Serratia rubidaea AcdSPB1
167	AEG57205	Sinorhizobium meliloti AK83

168	MN255491.1	<i>Sinorhizobium meliloti</i> strain ATCC 9930
169	KP117017.1	<i>Sinorhizobium</i> sp. CCBAU 05008
170	KC143168.1	<i>Sinorhizobium</i> sp. Mc1
171	ON597820.1	<i>Sinorhizobium</i> sp. strain RF36
172	OU548656.1	<i>Streptomyces</i> sp. CMB-FB
173	AY604530	<i>Variovorax paradoxus</i> strain 2C1
174	AY604532	<i>Variovorax paradoxus</i> strain 3C3
175	AY604531	<i>Variovorax paradoxus</i> strain 5C2
176	KP116958	<i>Variovorax</i> sp. DW01-1
177	HQ197346.1	<i>Zhihengliuella somnathii</i> strain JG 05