ANALYSIS OF THE PANGENOME OF BACILLUS CEREUS AND ITS RELEVANCE IN FOOD SAFETY

José Carlos Parada Fabián[1]*, Ana Karen Álvarez Contreras[1], Iván Natividad Bonifacio[1], Marcos Francisco Hernández Robles[1], Carlos Ramón Vázquez Quiñones[1], Elsa Irma Quiñones Ramírez[1], Carlos Vázquez Salinas[2]

[1]Department of Microbiology, National School of Biological Sciences-IPN, Mexico City, Mexico

[2]Department of Biotechnology, Universidad Autónoma Metropolitana, Mexico City, Mexico

Abstract

The study of the pangenome of Bacillus cereus *through the analysis of 135 complete and validated genomes provides insight into its genetic diversity and implications for food safety. The pangenome, composed of a core genome (shared by all strains) and an accessory genome (variable between strains), can be classified as open, demonstrating a high adaptive capacity due to the acquisition of genes through horizontal gene transfer. This analysis identifies key genes associated with virulence, such as those responsible for producing toxins (Nhe, Hbl, cereulide), spore formation, and biofilm production. These factors are fundamental for understanding the differential pathogenicity of strains and their persistence in food-related environments. Additionally, exclusive genes and those within the accessory genome reveal specific adaptations, such as resistance to extreme conditions or metabolic advantages for colonizing diverse niches.*

Phylogenomic analysis based on core genome genes enables the identification of clades and lineages associated with outbreaks of foodborne diseases. Moreover, the detection of antibiotic resistance genes and mobile genetic elements, such as plasmids and transposons, highlights the risk of resistance dissemination in food and clinical environments. These findings are essential for developing targeted control strategies, improving detection methods in the food industry, and mitigating risks associated with the contamination and transmission of B. cereus*. The pangenomic approach integrates bioinformatics and microbiological analyses to advance the surveillance and control of this pathogen in the food chain, contributing to the protection of public health.*

Keywords: *Bacillus cereus, Pangenome, Virulence factors, Antibiotic resistance, Food safety*

1. INTRODUCTION

Bacillus cereus is a Gram-positive, spore-forming, facultative aerobic bacterium with widespread distribution in the environment, including soil, water, and food, owing to its ability to produce spores that are resistant to adverse conditions (Enosi *et al*., 2021). This microorganism is frequently associated with foodborne illnesses mediated by the production of specific toxins, such as cereulide (responsible for the emetic syndrome) and enterotoxins like Hbl, Nhe, and CytK (involved in the diarrheal syndrome) (Märtlbauer & Granum, 2021). Additionally, *B. cereus* acts as an opportunistic pathogen in severe systemic or localized infections, particularly in immunocompromised patients (Ehling-Schulz *et al*., 2019). Phylogenetically, it belongs to the *B. cereus sensu lato* group, a complex that includes closely related species such as *B. anthracis*, the primary pathogen of anthrax, and *B. thuringiensis*, known for its use as a bioinsecticide (Lin *et al*., 2022). This genetic and functional diversity highlights its genomic plasticity and its importance in clinical, environmental, and industrial contexts (Morandini *et al*., 2024).

The pangenome of a bacterial species, defined as the set of shared genes (core genome) and accessory or unique genes found in different strains, is a key tool for understanding its genetic and functional diversity (Azarian *et al*., 2020). In *B. cereus*, this concept reveals remarkable genomic plasticity, enabling adaptation to a wide variety of environments and selective pressures (Bazinet, 2017). This genomic variability is directly linked to the expression of specific virulence factors, such as toxins and extracellular enzymes, and to the acquisition of genes conferring antimicrobial resistance (Brito *et al*., 2018). Thus, pangenome analysis not only provides a comprehensive view of the evolution and

adaptability of *B. cereus* but also identifies critical genetic determinants of its pathogenicity and clinical relevance, offering insights for the development of control and treatment strategies (Zhou *et al*., 2022).

The virulence factors of *B. cereus* include a wide variety of toxins and enzymes that contribute to its pathogenic potential (Dietrich *et al*., 2021). Among the toxins, cereulide stands out as responsible for the emetic syndrome, along with the enterotoxins Hbl (hemolysin BL), Nhe (non-hemolytic enterotoxin), and CytK (cytotoxin K), which are implicated in the diarrheal syndrome (Jovanovic *et al*., 2021). These molecules not only play a role in food poisoning but also in severe systemic infections such as sepsis and endophthalmitis (Ramarao *et al*., 2020). Additionally, *B. cereus* secretes extracellular enzymes, such as phospholipases and proteases, that facilitate tissue invasion and damage, promoting bacterial dissemination (Aoyagi *et al*., 2020). The combined action of these virulence factors plays a crucial role in pathogenesis, increasing the severity of infections and broadening the spectrum of diseases caused by this species, particularly in immunocompromised individuals or in the presence of predisposing conditions (Zhang *et al*., 2022).

In *B. cereus*, genes associated with resistance to multiple classes of antimicrobials have been identified, including beta-lactams, aminoglycosides, and tetracyclines, reflecting its ability to persist in environments where selective pressures are applied (Ibrahim *et al*., 2022). Key resistance mechanisms include the production of beta-lactamases, which inactivate beta-lactam antibiotics (Fraccalvieri *et al*., 2022); efflux pumps, which expel antimicrobials from the cell interior, reducing their effectiveness (Mohammadi *et al*., 2023); and mutations in antibiotic targets, which lower drug affinity for their binding sites (Yu *et al*., 2019). Moreover, horizontal gene transfer, mediated by plasmids, transposons, and other mobile genetic elements, plays a fundamental role in the spread of resistance determinants among strains and related species (Mills *et al*., 2022). This phenomenon not only complicates infection treatment but also underscores the need to monitor and understand the genetic dynamics of *B. cereus* in clinical and environmental settings (Duan *et al*., 2023).

The study of *B. cereus* holds significant relevance for both public health and the food industry, given its role as an etiological agent of foodborne illnesses and its ability to cause severe opportunistic infections (Huang *et al*., 2020). The presence of antimicrobial-resistant strains and the production of potent virulence factors exacerbate its health impact (Pitt *et al*., 2015). In this context, genomic analysis is essential to unravel the mechanisms of pathogenesis, identify key genetic determinants, and understand the evolution of antimicrobial resistance (Carroll *et al*., 2020). This approach also enhances diagnostic tools and supports the development of effective control and treatment strategies, ranging from food safety measures to the design of targeted therapies (Glasset *et al*., 2021). Therefore, research on *B. cereus* not only addresses a global health concern but also strengthens our capacity to respond to emerging challenges in the management of bacterial infections.

2. MATERIALS AND METHODS

A total of 135 complete and curated genomes of *B. cereus* were downloaded from the NCBI Genome database. Genome annotation was performed using PROKKA 1.14.5. Virulence factors were identified with Abricate 1.0.1 using the VFDB database, while genes involved in antimicrobial resistance were identified using the CARD database. Subsequently, pangenome analysis was carried out using Roary 3.13.0.

3. RESULTS

An analysis of metadata from 135 complete *B. cereus* genomes downloaded from NCBI revealed notable diversity in isolation sources, geographic origins, and collection dates. However, a significant number of incomplete entries limited the depth of contextual interpretation. Isolation sources were unspecified in 42 strains (31.1%). Among those reported, soil was the most common (19 strains), followed by marine organisms such as *Apostichopus japonicus* (3 strains). Other sources, air, green onions, seawater, honey, and fermented foods, each accounted for two strains, reflecting the ecological adaptability of *B. cereus*. Geographically, most strains originated from Asia, particularly China (47 strains) and South Korea (16),

with fewer from the U.S. (9), Namibia, and Vietnam. Geographic data were missing or marked as "Not applicable" in 29 strains (21.5%), limiting full spatial interpretation. Collection dates ranged from 2006 to 2021, with peaks in 2013 (8 strains) and 2006 (7 strains). Several entries came from early 2016 and spring 2019. Only two records were marked "Not applicable," and 12 were labeled "Unknown". These metadata highlight the environmental and geographical breadth of *B. cereus*, especially in Asia, though the prevalence of incomplete records restricts broader conclusions. The dominance of environmental and food-related sources reinforces its relevance to public health and food safety (see Appendix).

3.1 Analysis of Virulence Factors in Bacillus cereus

The genomic analysis of *B. cereus* revealed the presence of 17 genes associated with the biosynthesis of virulence factors. These can be grouped into three main categories: capsule, toxins, and adhesion/biofilm, each playing a crucial role in the pathogenesis of the bacterium.

3.2 Genes involved in capsule biosynthesis (capABCDE)

The presence of the *capABCDE* genes suggests that the analyzed *B. cereus* strains have the ability to produce a capsule, which can perform various functions in virulence, such as immune evasion, as the capsule can prevent phagocytosis by macrophages and neutrophils; resistance to adverse conditions, contributing to protection against desiccation and antimicrobial agents and increased persistence in the host or in the environment.

3.3 Toxin-related genes (cya, cytK, hblACD, inhA, lef, nheABC, pagA)

The identification of eleven genes involved in toxin biosynthesis suggests that these strains have pathogenic potential. These genes are associated with different toxicity mechanisms (see Table 1). The combination of these toxins indicates a high potential to cause severe gastrointestinal infections and possibly systemic illness under certain conditions.

3.4 Gene associated with adhesion and biofilm formation (bslA)

The detection of *bslA* is significant because this gene encodes a surface layer (S-layer) protein that facilitates adhesion to both biotic and abiotic surfaces, allowing colonization of host tissues, biofilm formation, which provides resistance to antibiotics and disinfectants, supporting persistence in hospital environments or the food industry and greater survival capacity in different ecological niches.

3.5 Analysis of the Frequencies of Virulence Factor Genes in B. cereus

A total of 17 virulence genes were analyzed across *B. cereus* genomes. The results show significant variability in the presence of these genes, suggesting differences in the pathogenic potential of the various strains (Figure 1).

1. Genes involved in capsule biosynthesis (capA, capB, capC, capE, dep/capD)

• capA, capB, capC, capE (5.19%) and dep/capD (5.19%)

These genes are involved in capsule production, a factor that can protect the bacterium from the host immune system. The low frequency (5.19%) suggests that most of the analyzed strains do not have a functional capsule, which may indicate that *B. cereus* relies on other virulence mechanisms for infection in these cases.

2. Toxin-related genes

• pagA (1.48%): Gene associated with the protective antigen of *B. anthracis*. Its low frequency suggests that this trait is rare in *B. cereus* strains and does not play a significant role in their pathogenicity.

• cya (3.70%): This gene encodes adenylate cyclase, an enzyme that interferes with host cell signaling. Its low frequency suggests it is not an essential virulence factor in most of the strains analyzed.

• lef (3.70%): A lethal factor like that of *B. anthracis*. Its low frequency indicates it is not common in these *B. cereus* strains, suggesting a different pathogenic mechanism from *B. anthracis*.

• hblA (69.63%), hblC (59.26%), hblD (57.78%): These genes encode Hemolysin BL, a tripartite toxin that damages cell membranes and contributes to virulence. The high frequency (over 50%) suggests that many strains have hemolytic and cytotoxic potential, reinforcing their pathogenic capabilities.

• cytK (73.33%): Cytolysin K is a pore-forming toxin strongly associated with severe foodborne illness. Its high frequency indicates that more than 70% of the strains may be pathogenic and capable of causing gastrointestinal symptoms.

• inhA (100.00%): Encodes a serine protease inhibitor that enables the bacterium to evade immune responses. Its presence in 100% of strains indicates that this mechanism is essential for *B. cereus* survival and virulence.

• nheA, nheB, nheC (100.00%): These genes encode the non-hemolytic enterotoxin (NHE), a key cytotoxic complex involved in gastrointestinal infections. Their presence in all strains indicates that this toxin is a central virulence factor in *B. cereus*.

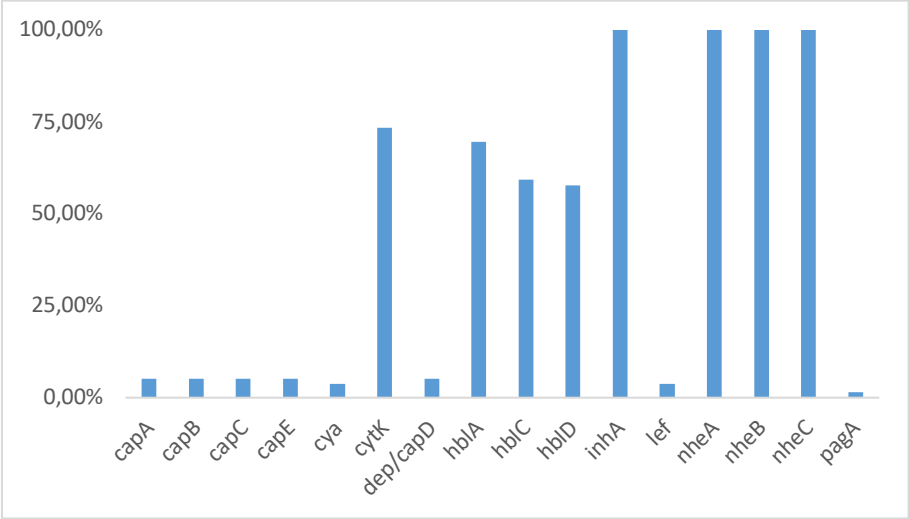

Figure 1. Frequency of virulence factors present in *B. cereus* genomes. It can differentiate between two groups, high frequency and low frequency genes.

Gene	Product	Process	Reference
capA	Required for Poly-gamma-glutamate transport	Capsule biosynthesis codified in pXO2 plasmid (*Bacillus* spp.)	Jang *et al*., 2011
capB	Involved in Poly-gamma-glutamate synthesis		
capC	Involved in Poly-gamma-glutamate synthesis		
capD	Gamma-glutamyltranspeptidase, required for polyglutamate anchoring to peptidoglycan		
capE	Involved in Poly-gamma-glutamate synthesis		
Cya	Calmodulin sensitive adenylate cyclase, edema factor	Anthrax toxin (*B. anthracis*)	Feld *et al*., 2010
Lef	Anthrax toxin lethal factor precursor		

pagA	Anthrax toxin moiety, protective antigen		
cytK	Cytotoxin K	Toxins (*B. cereus*)	Ramarao & Sanchis, 2013
hblA	Hemolysin BL binding component precursor		Madegowda *et al*., 2008
hblC	Hemolysin BL lytic component L2		
hblD	Hemolysin BL lytic component L1		
nheA	Non-hemolytic enterotoxin A		Jeßberger *et al*., 2014
nheB	Non-hemolytic enterotoxin B		
nheC	Non-hemolytic enterotoxin C		
InhA	Immune inhibitor A metalloprotease	Protease (*B. anthracis*)	Tonry *et al*., 2012
bslA	S-layer protein	Adhesion process and biofilm formation (*B. anthracis*)	Morris *et al*., 2017

Table 1. Virulence factors detected in *B. cereus* genomes

3.6 Analysis of the Co-occurrence of Virulence Factor Genes in B. cereus

The analysis of gene co-occurrence in *B. cereus* strains allows for the identification of key associations among virulence factors and potential patterns of genetic regulation or functional synergy in pathogenesis (Figure 2).

3.7 Co-occurrence Pattern Analysis

*3.7.1 Association among capsule genes (*capA, capB, capC, capE, dep/capD*)*

The capsule genes (capA, capB, capC, capE, dep/capD) show strong co-occurrence among themselves (weight = 7). They are also associated with nheABC, inhA, and cya (weight = 5–7), suggesting a potential link between capsule production and mechanisms related to adhesion or cytotoxicity. However, co-occurrence with hemolytic toxin genes such as hblA and hblC is low (weight = 2), indicating that encapsulated strains may rely less on these toxins.

*3.7.2 Association among hemolytic toxin genes (*hblACD, cytK, nheABC, inhA*)*

A strong co-occurrence is observed among hemolytic toxin genes:

o hblA ↔ hblC (80), hblA ↔ hblD (78), hblC ↔ hblD (78)

o cytK ↔ hblA (82), cytK ↔ hblC (69), cytK ↔ hblD (69)

o cytK ↔ nheABC (99), inhA ↔ nheABC (135)

These values indicate that hemolytic and cytotoxic toxins are highly correlated, suggesting that the most pathogenic strains tend to carry multiple toxin genes simultaneously.

3.7.3 The central role of inhA

inhA shows the highest co-occurrence with nheABC (135), cytK (99), and hblA (94). This gene encodes a serine protease inhibitor, suggesting that its presence is essential for modulating the activity of toxins in the host and protecting the bacterium from immune responses.

3.7.4 Association of virulence genes with pagA *and* lef

pagA and *lef* show very low co-occurrence (weight = 2–5) with other genes. This suggests that genes associated with *B. anthracis* are present in some strains but are not part of the dominant virulence profile in *B. cereus*.

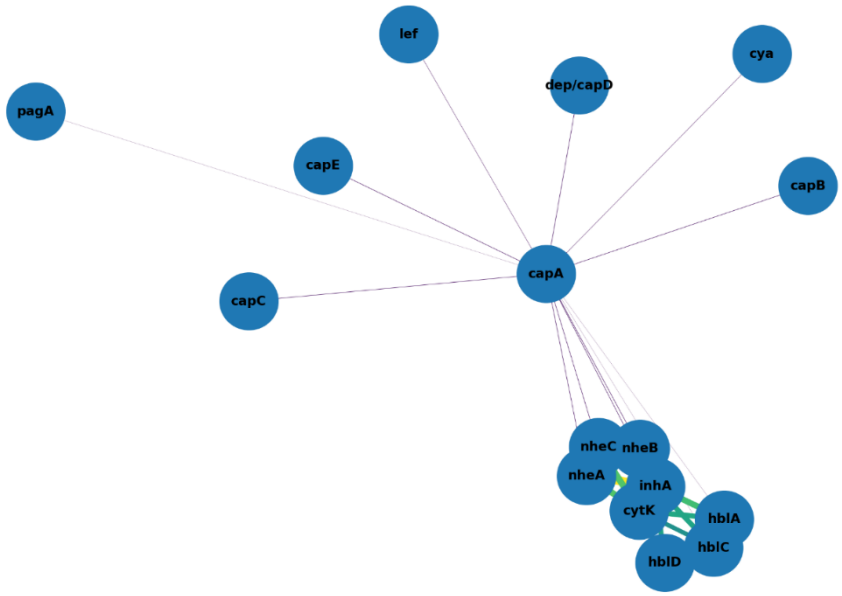

Figure 2. Network graph visualizing the co-occurrence of virulence factor genes in *Bacillus cereus*. Nodes represent individual genes, while edges indicate co-occurrence between them. The thickness of the edges is proportional to the strength (weight) of the co-occurrence. Large, highly connected nodes such as *inhA*, *cytK*, *nheABC*, and *hblACD* suggest that these genes are commonly found together in the most pathogenic strains. Thicker lines represent stronger co-occurrence (e.g., *inhA* ↔ *nheABC* and *cytK* ↔ *nheABC*). Capsule-related genes (*capABCDE*, *dep/capD*) display weaker connections with toxin genes, reinforcing the idea that encapsulated strains may follow a different virulence strategy.

3.8 Analysis of Antimicrobial Resistance Genes Frequency

The frequency analysis of antimicrobial resistance genes identified in *B. cereus* strains reveals marked variability in the distribution of these genetic determinants within the analyzed population (Figure 3). The most common gene was *FosB*, associated with resistance to fosfomycin, found in 135 strains, indicating a widespread dissemination of this resistance mechanism. It was followed by *vanZF*, a gene linked to glycopeptide resistance, detected in 107 strains, suggesting a significant presence of resistance determinants against clinically important antibiotics such as vancomycin. Similarly, the *BcI* and *BcII* genes, which encode beta-lactamases, were found in 85 and 67 strains, respectively. Other beta-lactam resistance genes, such as *Bla2* and *BLA1*, were present in 54 and 50 strains, respectively, reflecting an extensive distribution of beta-lactam resistance across the strains analyzed.

Among macrolide resistance genes, *mphL* stood out, being present in 52 strains. In contrast, other genes from the same group, such as *mel*, *mphM*, and *ErmC*, showed very low frequencies, detected in only one or two strains. The co-occurrence of *vanRA* and *vanSA* in 26 strains each was also observed, which is consistent with the typical organization of glycopeptide resistance operons. In contrast, some genes such as *tet(45)* (tetracycline resistance), *vanYA*, *fexA*, *mel*, and less common variants such as *AAC(6')-Ie-APH(2'')-Ia* and a *B. clausii* acetyltransferase, showed very limited distribution, being found in eight or fewer strains. These genes may represent sporadic events of horizontal acquisition or emerging resistance (Table 2).

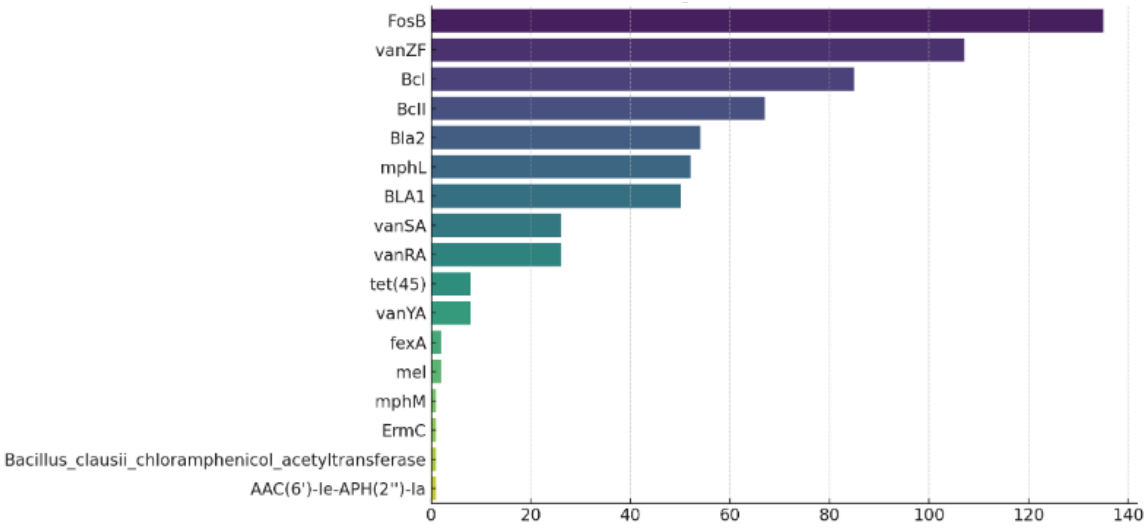

Figure 3. Frequency of antimicrobial resistance genes detected in *B. cereus* strains. The figure shows the number of strains in which each gene was identified. Genes such as *FosB*, *vanZF*, and *BcI* show high prevalence, suggesting widespread dissemination within the analyzed population. In contrast, genes like *mel*, *fexA*, and *ErmC* exhibit limited distribution, possibly related to sporadic acquisition events or emerging resistance.

Gene	Product	Resistant	Reference
AAC(6')-Ie-APH(2'')-Ia	Aminoglycoside acetyltransferase encoded by plasmids and transposons in *S. aureus, E. faecalis, E. faecium* and *Staphylococcus warneri*	Aminoglycoside	Behnood *et al*., 2013
BLA1	Chromosomal-encoded beta-lactamase found in *B. anthracis* which hydrolyzes penicillins	Beta lactams	Song *et al*., 2019
BcI	Zinc metallo-beta-lactamase that hydrolyzes many penicillins and cephalosporins	Beta lactams	
BcII	Zinc metallo-beta-lactamase that hydrolyzes many penicillins and cephalosporins	Beta lactams	
Bla2	Chromosomal-encoded beta-lactamase found in *B. anthracis*	Beta lactams	
***B. clausii* chloramphenicol acetyltransferase**	Chloramphenicol_acetyltransferase	Amphenicol	Glenwright *et al*., 2017
fexA	Plasmid-encoded chloramphenicol exporter that is found in *S. lentus*	Amphenicol	
ErmC	Methyltransferase that catalyzes the methylation of A2058 of the 23S ribosomal RNA in two steps	Macrolides	Kowalska *et al*., 2024
Mel	Protein associated with macrolide resistance	Macrolides	

mphL	Chromosomally-encoded macrolide phosphotransferases that inactivate 14- and 15-membered macrolides	Macrolides	
mphM	Chromosomally-encoded macrolide phosphotransferases that inactivate 14- 15- and 16-membered macrolides	Macrolides	
FosB	A thiol transferase that leads to the resistance of Fosfomycin	Fosfomycin	Travis *et al*., 2023
tet(45)	Tetracycline efflux pump	Tetracycline	Glenwright *et al*., 2017
vanRA	vanR variant found in the vanA gene cluster glycopeptide	Glycopeptide	Schmid *et al*., 2024
vanSA	vanS variant found in the vanA gene cluster glycopeptide	Glycopeptide	
vanYA	vanY variant found in the vanA gene cluster glycopeptide	Glycopeptide	
vanZF	vanZ variant found in the vanF gene cluster glycopeptide	Glycopeptide	

Table 2. Antimicrobial Resistance Genes detected in *B. cereus* genomes

3.9 Analysis of the Co-occurrence of Antimicrobial Resistance Genes in B. cereus

Based on the co-occurrence analysis of antimicrobial resistance genes present in various *B. cereus* strains, a binary presence/absence matrix was generated to identify co-occurrence patterns among different genetic determinants. This matrix was then transformed into a co-occurrence matrix, which quantifies the number of times each pair of genes appears together in the same strain. The results show that certain genes tend to frequently coexist, suggesting potential functional or genomic associations, or mechanisms of joint transfer. For example, the gene *BcI* co-occurs with *FosB* in 85 strains, indicating a strong association between them. Similarly, *BLA1* and *mphL* co-occur in 47 strains, while the glycopeptide resistance genes *vanRA* and *vanSA* consistently co-occur in 26 strains, suggesting these genes may be part of the same operon or genetic resistance module. Other relevant pairs include the co-occurrence of *BcII* and *BcI* in 57 strains, as well as *vanRA* and *FosB* in 26 strains. These patterns may reflect shared selective pressures or horizontal transfer events of mobile genetic elements (Figure 4).

Figure 4. Heatmap of co-occurrence between antimicrobial resistance genes in *B. cereus* strains. The heatmap displays the number of times each pair of resistance genes was found together in the same strain. Darker red tones indicate higher co-occurrence frequencies, highlighting potential genetic linkages, shared selective pressures, or joint horizontal gene transfer events. This visualization aids in identifying gene clusters that may be functionally or genomically associated.

3.10 Pangenome analysis of B. cereus *genomes*

Based on the pangenome analysis of *B. cereus* from 135 strains, a remarkable genetic diversity within this species is evident. The gene presence/absence matrix, together with the associated phylogenetic tree, reveals the distribution of 44,539 orthologous gene groups across the analyzed strains. Visually, a dense band of genes present in almost all strains, corresponding to the core genome, is distinguishable, followed by a gradient of genes that appear intermittently or sporadically, representing the accessory genome (soft-core and shell) and the cloud genome (Figure 5).

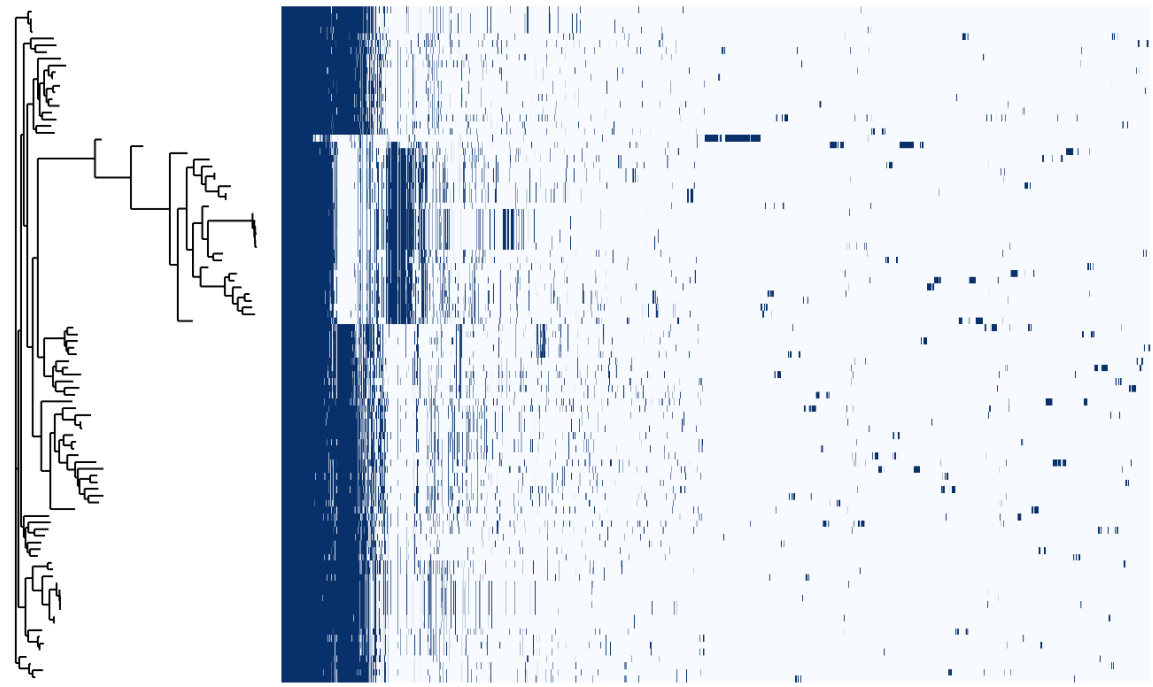

Figure 5. Presence/absence gene matrix of the *Bacillus cereus* pangenome based on 135 strains. The visualization displays 44,539 orthologous gene groups distributed across strains, where a dense band represents the core genome (genes present in almost all strains), followed by a gradient of intermittent genes comprising the accessory genome (soft-core and shell) and the cloud genome, highlighting the genetic diversity within the species. The associated phylogenetic tree indicates the evolutionary relationships among the analyzed strains.

It is observed that most genes (36,398; 81.7%) belong to the cloud genome, meaning they are present in fewer than 15 strains, which indicates a high rate of gene acquisition and suggests that *B. cereus* possesses an open pangenome. This characteristic is common in bacteria with a high degree of genomic plasticity, allowing them to adapt to diverse ecological niches, acquire antimicrobial resistance mechanisms, or increase their pathogenic potential. In contrast, the core genome consists of only 2,185 genes (4.9%), those present in 99% or more of the strains. These genes likely encode essential and conserved functions throughout the species' evolution. In addition, there are 245 genes (0.6%) in the soft-core genome and 5,711 genes (12.8%) in the shell genome, which represent fewer essential functions but are shared among a considerable number of strains (Figure 6).

Together, these results highlight that *B. cereus* is a species with great genomic diversity, characterized by a small set of conserved genes and a large proportion of variable genes. This landscape has important implications for understanding its evolution as well as for epidemiological surveillance, as it reflects its ability to adapt, evolve, and acquire new functions, including antimicrobial resistance.

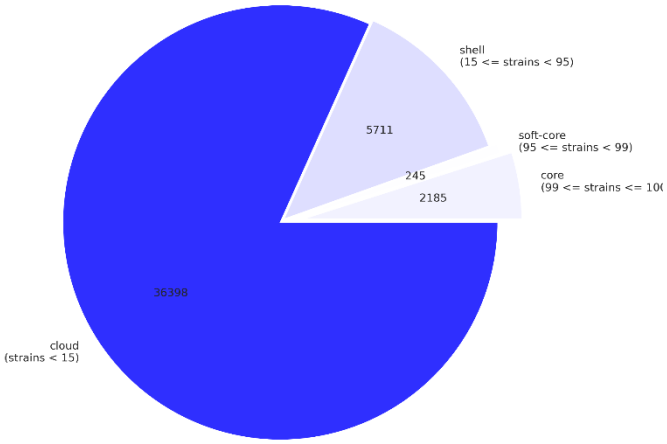

Figure 6. Distribution of gene categories in the *B. cereus* pangenome based on 135 strains. Most genes (36,398; 81.7%) belong to the cloud genome, present in fewer than 15 strains, indicating a high gene acquisition rate and supporting the existence of an open pangenome. Smaller fractions correspond to the core genome (2,185 genes; 4.9%), the soft-core genome (245 genes; 0.6%), and the shell genome (5,711 genes; 12.8%), highlighting the species' genomic variability and plasticity.

4. DISCUSSION

The genomic and functional analyses of *B. cereus* reveal a bacterium of remarkable complexity, combining diverse virulence mechanisms, extensive antimicrobial resistance, and high genomic plasticity. These traits together contribute to its ecological versatility and capacity to act as an opportunistic pathogen.

The metadata analysis of 135 *B. cereus* genomes reveals significant ecological and geographical diversity, although interpretation is limited by incomplete information in a substantial portion of records. Most strains originated from environmental or food-related sources, reflecting the bacterium's ability to persist across diverse niches. The strong representation of Asian strains, particularly from China and South Korea, suggests a geographic bias likely related to regional surveillance or research efforts. The collection dates, ranging from 2006 to 2021, indicate ongoing isolation efforts that are valuable for evolutionary and antimicrobial resistance studies. However, missing key metadata in many records hinders comparative and epidemiological context. Overall, these findings reinforce the role of *B. cereus* as a ubiquitous pathogen relevant to both natural environments and the food chain, emphasizing the need to improve the quality and completeness of metadata associated with publicly available genomes.

4.1 Virulence factors profile in B. cereus *Strains*

The genomic characterization of *B. cereus* virulence determinants reveals a complex and heterogeneous profile among analyzed strains. The identification of 17 virulence-associated genes, categorized into capsule formation, toxin production, and adhesion/biofilm-related functions, highlights the multifactorial nature of *B. cereus* pathogenicity, which is consistent with its role as both an environmental microorganism and an opportunistic pathogen (Ehling-Schulz *et al.*, 2019; Bottone, 2010).

Capsule biosynthesis genes (*capABCDE*) were found in only 5.19% of the strains, indicating that encapsulation is not a predominant trait across the population analyzed. However, their strong co-occurrence (weight = 7) suggests that when present, these genes operate as a coordinated module. The capsule provides resistance to phagocytosis and contributes to immune evasion, as well as environmental persistence (Scorpio *et al.*, 2010). The association of capsule genes with *nheABC* and *inhA* (co-occurrence weights = 5–7) might suggest a synergy between immune evasion and cytotoxicity in specific pathogenic profiles. The lack of frequent co-occurrence with hemolytic toxin genes (e.g., *hblA*, *hblC*) may indicate a division of virulence strategies among strains—those relying on encapsulation may compensate with lower expression or absence of pore-forming toxins.

Toxin-related genes were more prevalent and exhibited higher levels of co-occurrence, reflecting their central role in *B. cereus* pathogenicity. Notably, *nheA*, *nheB*, *nheC*, and *inhA* were present in 100% of the genomes analyzed, suggesting that these genes constitute the core virulome of the species. The *nhe* operon encodes the non-hemolytic enterotoxin, a tripartite cytotoxin strongly implicated in diarrheal illness caused by *B. cereus*. Its universal presence, together with *inhA*, which inhibits host proteases, may reflect a conserved mechanism to damage host tissues while simultaneously modulating host immune responses to prolong survival and dissemination (Granum & Lund, 1997).

High frequencies of *cytK* (73.33%) and *hblACD* (over 57%) further emphasize the cytotoxic potential of these strains. *CytK* encodes a β-barrel pore-forming toxin that has been associated with food poisoning outbreaks and necrotic enteritis (Lund et al., 2000). The strong co-occurrence of *cytK* with both *nheABC* and *hblACD* suggests that highly virulent strains may possess a "toxin synergy," allowing for additive or even synergistic cytolytic effects on host cells. The co-expression of multiple toxins may not only enhance pathogenicity but also complicate clinical outcomes (Stenfors Arnesen et al., 2008).

Importantly, *inhA* exhibited the highest co-occurrence scores across the dataset, 135 with *nheABC*, 99 with *cytK*, and 94 with *hblA*, underlining its central regulatory or protective role in the virulence network. Its ubiquitous presence and strong correlations suggest that *inhA* may be critical not only for countering host immune factors but also for maintaining bacterial viability during toxin-mediated host damage.

Genes *pagA*, *lef*, and *cya*, typically associated with the anthrax toxin complex in *B. anthracis*, were found at low frequencies (1.48–3.70%) and exhibited minimal co-occurrence with other virulence genes. This aligns with the known genetic proximity between *B. cereus* and *B. anthracis*, which can share plasmid-encoded virulence factors (Rasko *et al*., 2005). Nevertheless, the limited presence of these genes suggests they are not central to *B. cereus* pathogenicity and likely represent horizontal gene transfer events or vestigial elements retained in certain lineages.

The presence of the *bslA* gene in several strains adds an additional layer to the virulence landscape. *bslA* encodes a hydrophobic surface-layer protein involved in biofilm formation, which enhances bacterial survival in hostile environments such as food-processing surfaces or medical devices (Branda *et al*., 2001). Although this gene was not universally present, its detection highlights the ecological versatility of *B. cereus*, which may support persistence outside the host and facilitate repeated opportunities for infection.

The observed variability in virulence gene distribution, particularly the combination of high-prevalence core genes (*nheABC*, *inhA*, *cytK*) with low-frequency accessory genes (*capABCDE*, *pagA*, *lef*), points to significant heterogeneity in virulence potential among *B. cereus* strains. This supports a growing body of evidence indicating that *B. cereus* comprises a complex species cluster with a flexible genome and dynamic virulence repertoire (Carroll *et al*., 2020; Miller *et al*., 2018). Consequently, strain-level genotyping and virulome profiling should be considered essential for risk assessment in clinical and food safety contexts.

4.2 Antimicrobial Resistance Gene Profiles in B. cereus *Strains*

The presence and distribution of antimicrobial resistance genes in *B. cereus* reveal a complex and diverse resistome that may contribute to treatment challenges in both clinical and foodborne contexts. The detection of numerous resistance determinants across different antibiotic classes supports the notion that *B. cereus* has evolved or acquired a broad repertoire of resistance mechanisms, likely shaped by selective pressures in both natural and anthropogenic environments (Nielsen *et al*., 2022).

Fosfomycin resistance, mediated by the *fosB* gene, was the most frequently detected determinant, found in 135 strains. This gene encodes a thiol transferase that inactivates fosfomycin via glutathione conjugation. Its widespread presence suggests a conserved resistance mechanism that may have been acquired early in the evolution of the species or spread via mobile genetic elements in response to environmental exposure. *B. cereus* is known to persist in soil and hospital surfaces, ecosystems where exposure to fosfomycin and other antibiotics may select for such traits (Bottone, 2010).

The second most prevalent resistance determinant was *vanZF*, associated with resistance to glycopeptides like vancomycin. Detected in 107 strains, its high frequency is concerning, as

glycopeptides are considered last-resort antibiotics for Gram-positive infections (Courvalin, 2006). The co-occurrence of *vanZF* with *vanRA* and *vanSA* in 26 strains each mirrors the canonical structure of *van* operons, suggesting that complete resistance modules may be present in a significant subset of strains. The modular organization of vancomycin resistance operons supports their mobility and integration into various genomic contexts, facilitating dissemination across bacterial populations (Arthur *et al*., 1993).

Beta-lactam resistance was also prominent, with *BcI* and *BcII* (encoding class A and class B beta-lactamases, respectively) found in 85 and 67 strains. Additionally, *BLA1* and *Bla2* were detected in 50 and 54 strains, respectively, indicating extensive beta-lactamase-mediated resistance. These enzymes hydrolyze a wide range of β-lactam antibiotics, including penicillins and cephalosporins, and are frequently reported in *B. cereus* clinical isolates (Torki-Baghbadorani *et al*., 2023). The co-occurrence of *BcI* and *BcII* in 57 strains further suggests that multiple resistance genes can be harbored simultaneously, potentially resulting in additive or redundant protection against β-lactam antibiotics.

Macrolide resistance genes were less prevalent, with *mphL* found in 52 strains, while *mel*, *mphM*, and *ermC* appeared only in one or two strains each. *mphL* encodes a macrolide phosphotransferase, which inactivates macrolides via phosphorylation. The low prevalence of other macrolide resistance genes may reflect limited selective pressure from macrolide use or suggest recent, sporadic acquisition via horizontal gene transfer. These findings are consistent with other studies reporting variable and often low frequencies of macrolide resistance in environmental *B. cereus* isolates (Leclercq & Courvalin, 1991).

Interestingly, rare resistance genes such as *tet(45)*, *fexA*, and the bifunctional aminoglycoside-modifying enzyme *AAC(6')-Ie-APH(2'')-Ia* were detected in a very small number of strains (≤8). These genes may represent emerging resistance traits or artifacts of horizontal gene transfer from other genera, including enterococci and staphylococci, especially in environments such as food-processing facilities where multispecies biofilms are common (Harada *et al*., 2021).

The co-occurrence analysis of AMR genes revealed clear association patterns that likely reflect physical linkage within mobile genetic elements or coordinated selection pressures. The strong co-occurrence between *BcI* and *FosB* (85 strains), and *BLA1* with *mphL* (47 strains), suggests that these genes may be located on the same plasmid or genomic island, facilitating their joint transmission. Similarly, the consistent co-occurrence of *vanRA* and *vanSA* supports their location within the same operon, reinforcing their role in glycopeptide resistance.

Moreover, the co-occurrence of *vanRA* with *FosB* in 26 strains underscores the possibility of multi-resistance profiles, where strains harbor determinants against both glycopeptides and phosphonic acid antibiotics. This could indicate exposure to multiple antibiotics in certain ecological niches—especially in hospital, agricultural, or industrial environments where antibiotic residues or biocides may co-select for broad resistance (Gillings, 2013).

Overall, the detected resistance patterns support the hypothesis that *B. cereus* possesses an open resistome, highly influenced by horizontal gene transfer and environmental adaptability (Rasko *et al*., 2005). The presence of multi-drug resistance traits in environmental isolates of *B. cereus* raises significant concerns for food safety and public health, particularly given the bacterium's ability to form biofilms, survive disinfection, and cause outbreaks through contaminated foods.

4.3 Pangenome Structure and Genomic Plasticity of B. cereus

The pangenome analysis of 135 *B. cereus* genomes revealed a species with striking genomic plasticity and extensive gene content variability. The identification of 44,539 orthologous gene groups, of which over 81% (36,398 genes) belong to the cloud genome, reflects the highly dynamic nature of *B. cereus*, driven by frequent gene gain and loss events. This characteristic strongly supports the classification of *B. cereus* as a bacterium with an open pangenome, a feature typically associated with environmental bacteria capable of adapting to a broad range of ecological niches and selective pressures (Tettelin *et al*., 2005; Rouli *et al*., 2015).

The core genome, consisting of only 2,185 genes (4.9%), represents the minimal set of conserved genes shared by ≥99% of the strains. These likely encode essential housekeeping functions related to

metabolism, replication, and basic cellular structures (Medini *et al*., 2005). The relatively small size of the core genome, when compared to the total gene pool, is consistent with previous studies on *B. cereus sensu lato* and reflects the species' taxonomic complexity and ecological versatility (Carroll *et al*., 2020; Bazinet, 2017). It also indicates a low degree of genome conservation, which has important implications for the development of diagnostics, vaccines, and control strategies.

The shell genome (5,711 genes; 12.8%) and soft-core genome (245 genes; 0.6%) represent intermediate genomic elements, present in multiple but not all strains. These regions may contribute to niche-specific adaptations, such as sporulation efficiency, temperature tolerance, or interactions with hosts or surfaces. The variable distribution of these genes across the phylogeny suggests they may be under diversifying selection or linked to mobile genetic elements such as plasmids, phages, or transposons (Didelot *et al*., 2012).

The predominance of cloud genes (i.e., genes found in <15 strains) indicates a high level of horizontal gene transfer and genomic innovation. These genes may include recently acquired functions such as antibiotic resistance determinants, virulence factors, metabolic capabilities, or stress response systems (McInnes, 2020). Given the previously described high frequency and co-occurrence of certain antimicrobial resistance and virulence genes, it is likely that many of these accessory genes are functionally relevant for pathogenesis or survival in clinical and industrial environments.

Furthermore, the observed gene content variability aligns with the phylogenetic divergence of the strains, supporting the idea that the *B. cereus* species complex encompasses genetically and functionally diverse lineages. This diversity complicates taxonomic delineation within the group but enhances the ecological success and pathogenic potential of the species (Guinebretière *et al*., 2008).

From a practical standpoint, the open nature of the *B. cereus* pangenome implies that the discovery of new genes, including virulence and resistance factors, will likely continue as more genomes are sequenced. This has significant epidemiological implications, as it underscores the need for whole-genome-based surveillance approaches rather than relying solely on core genome markers or classical phenotyping methods (Rasko *et al*., 2005; Didelot *et al*., 2018).

The genomic landscape of *B. cereus*, shaped by a compact core genome and an expansive and diverse accessory genome, underpins its ecological adaptability, capacity for opportunistic pathogenicity, and potential for acquiring resistance. These findings reinforce the importance of pangenomic frameworks for understanding the evolutionary and functional trajectories of bacterial pathogens.

5. CONCLUSIONS

The metadata analysis of *B. cereus* genomes shows that this species has a wide ecological and geographical distribution, with a marked prevalence in environmental and food-related sources. Despite limitations due to incomplete data, the findings highlight its relevance as an opportunistic pathogen and emphasize the need to improve the quality of genomic records to enhance surveillance and research.

The comprehensive genomic analysis of *B. cereus* strains revealed a complex and diverse landscape of virulence and antimicrobial resistance determinants, underscoring the species' high pathogenic and adaptive potential. The presence of key virulence genes, particularly those encoding enterotoxins such as *nheABC*, *cytK*, and *hblACD*, suggests that gastrointestinal pathogenicity is a widespread trait among the analyzed strains. Furthermore, the ubiquitous presence of *inhA* reinforces its essential role in immune evasion and bacterial survival within the host.

In terms of antimicrobial resistance, the high frequency of genes such as *FosB*, *vanZF*, and various beta-lactamase-encoding genes (e.g., *BcI*, *BcII*) indicates a broad capacity of *B. cereus* to resist multiple classes of antibiotics, including those of clinical relevance. The co-occurrence patterns observed among resistance genes suggest that horizontal gene transfer and genomic plasticity play crucial roles in the dissemination of resistance traits.

The pangenome analysis confirmed that *B. cereus* possesses an open pangenome, with a relatively small core genome and a vast cloud genome comprising genes with sporadic distribution. This genetic

architecture reflects the species' evolutionary dynamics and its ability to adapt to diverse ecological niches, acquire novel traits, and pose variable risks to public health.

Altogether, these findings highlight the importance of continuous genomic surveillance of *B. cereus*, particularly in food, clinical, and environmental contexts. Such efforts are vital for understanding its epidemiological behavior, mitigating its pathogenic potential, and informing public health strategies and antimicrobial stewardship.

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Appendix: Metadata of the *B. cereus* genomes used

RefSeq	Description	Isolation source	Collection date	Geographic location
GCF_002220285.1	Pathogen: environmental/food/other sample from *Bacillus cereus*	Not applicable	Aug,2015	South Korea
GCF_045287585.1	Microbe sample from *Bacillus cereus* ATCC14579	Soil	Not applicable	Not applicable
GCF_006094295.1	Microbe sample from *Bacillus cereus*	Not applicable	Dec, 2018	Not applicable
GCF_000007825.1	Microbe sample from *Bacillus cereus* ATCC14579	Not applicable	Jun,2014	Not applicable
GCF_041879445.1	Microbe sample from *Bacillus cereus*	Milk powder factory	Oct, 2013	China
GCF_021655335.1	30075	Not applicable	2016	Not applicable
GCF_029201265.1	Microbe sample from *Bacillus cereus*	Not applicable	Mar, 2022	China
GCF_030064245.1	*Bacillus cereus* IBA1	Food Waste	Sep, 2021	Hong Kong
GCF_021391515.1	Microbe sample from *Bacillus cereus*	Contaminated soil	Oct,2020	USA
GCF_047557475.1	Microbe sample from *Bacillus cereus*	Not applicable	2020	China
GCF_023094015.1	Microbe sample from *Bacillus cereus*	Dry soil	Jul, 2019	China
GCF_002813875.1	MIGS Cultured Bacterial/Archaeal sample from *Bacillus cereus*	Activated sludge	Oct, 2017	China
GCF_016774555.1	Microbe sample from *Bacillus cereus*	Not applicable	2017	China
GCF_030518615.1	Microbe sample from *Bacillus cereus*	Not applicable	Sep, 2021	China
GCF_008041975.1	MISAG Single Amplified Genome sample from *Bacillus cereus*	Not applicable	Oct, 2018	Not applicable
GCF_009739965.1	*BacillusCereus*-DLOU-Tangshan	Apostichopus japonicus	Nov, 2018	China
GCF_001635915.1	Microbe sample from *Bacillus cereus*	Soil	1979	China
GCF_016774535.1	Microbe sample from *Bacillus cereus*	Not applicable	Nov, 2017	China
GCF_034078685.1	Microbe sample from *Bacillus cereus*	Soil	May, 2023	China
GCF_001635955.1	Microbe sample from *Bacillus cereus*	Soil	1984	China
GCF_002216125.1	Microbe sample from *Bacillus cereus* M13	Fermented food	Jan, 2016	South Korea
GCF_013394245.1	Microbe sample from *Bacillus cereus*	Shinkaia crosnieri	Jul, 2016	China
GCF_030406205.1	Pathogen: environmental/food/other sample from *Bacillus cereus*	Spleen of cattle	Apr, 2019	China
GCF_003568565.1	Microbe sample from *Bacillus cereus*	Air in Laboratory	Jul, 2016	China
GCF_004006495.1	Microbe sample from *Bacillus cereus*	Soil	Jun, 2017	China
GCF_009497015.2	Microbe sample from *Bacillus cereus*	Soil	Oct, 2018	Australia
GCF_021655215.1	J62	Not applicable	Not applicable	Not applicable
GCF_030517775.1	Microbe sample from *Bacillus cereus*	Marine sediments	2023	Pacific ocean
GCF_001721145.1	Pathogen: environmental/food/other sample from *Bacillus cereus*	Not applicable	Sep, 2019	South Korea
GCF_022700995.1	Microbe sample from *Bacillus cereus*	Soil	Mar,2019	China
GCF_001518875.1	Pathogen *Bacillus cereus* FORC 013	Fried eel	2013	South Korea
GCF_003013315.1	Muestra de *Bacillus* sp. TG1 6	Sporobolus anglicus	Apr, 2016	China
GCF_013267775.1	Pathogen	Clinical sample	Not applicable	Not applicable
GCF_001635995.1	Microbe sample from *Bacillus cereus*	Vomit of food poisoning patient	2000	China
GCF_024498915.1	Microbe sample from *Bacillus cereus*	Soil	Jan, 2020	China
GCF_009739925.1	*BacillusCereus*-DLOU-Changhai	Apostichopus japonicus	Dec, 2017	China
GCF_016917795.1	Microbe sample from *Bacillus cereus*	Bombyx mori	1887	Armenia
GCF_013267255.1	Pathogen: clinical or host-associated sample from *Bacillus cereus*	Not applicable	Mar, 2019	USA
GCF_013267275.1	Pathogen: clinical or host-associated sample from *Bacillus cereus*	Not applicable	Mar, 2019	USA
GCF_040210495.1	Microbe sample from *Bacillus cereus*	Soil	Mar, 2021	China
GCF_045277855.1	Repositorio abierto de recursos para secuenciación de nanoporos y NGS	Seawater	Jun, 2023	China
GCF_021655015.1	MRY14 0105	Not applicable	2013	Not applicable
GCF_021654895.1	MRY14-0057	Not applicable	2013	Not applicable
GCF_021654875.1	MRY14-0045	Not applicable	2013	Not applicable
GCF_001277915.1	Complete genome of *Bacillus cereus* strain NJ_W	Soil	Mar, 2014	China

GCF_002214705.1	Microbe sample from *Bacillus cereus*	Fermented food	Jan, 2016	South Korea
GCF_021654975.1	MRY14-0079	Not applicable	2013	No aplicable
GCF_045780845.1	Microbe sample from *Bacillus cereus*	Epinephelus fuscoguttatus	Dec, 2020	China
GCF_016774575.1	Microbe sample from *Bacillus cereus*	Not applicable	Nov, 2017	China
GCF_003020845.1	Pathogen: environmental/food/other sample from *Bacillus cereus*	Cucumber	Jan, 2016	South Korea
GCF_021655355.1	30077	Not applicable	2016	Not applicable
GCF_002214765.1	Pathogen: environmental/food/other sample from *Bacillus cereus*	Sesame leaf	Jun, 2014	South Korea
GCF_021655255.1	30040	Not applicable	2016	Not applicable
GCF_021655275.1	30043	Not applicable	2016	Not applicable
GCF_021655135.1	J7	Not applicable	2006	Not applicable
GCF_030067875.1	Microbe sample from *Bacillus cereus*	Soil	2012	Namibia
GCF_000635895.2	Microbe sample for *Bacillus cereus*	Sludge of an anaerobic digestion reactor	Apr, 2011	China
GCF_021655195.1	J51	Not applicable	2006	Not applicable
GCF_000978375.1	*Bacillus cereus* FORC_005 food isolate from chicken cutlett	Chicken cutlett	Mar, 2014	South Korea
GCF_021655295.1	30048	Not applicable	2016	Not applicable
GCF_021655035.1	J1	Not applicable	2006	Not applicable
GCF_021442085.1	Microbe sample from *Bacillus cereus*	Mangrove sediment	Mar, 2019	China
GCF_018884185.1	MIGS Cultured Bacterial/Archaeal sample from *Bacillus cereus*	Not applicable	Sep, 2012	China
GCF_021655175.1	J39	Not applicable	2006	Not applicable
GCF_013267235.1	Pathogen: clinical or host-associated sample from *Bacillus cereus*	Not applicable	Unknown	USA
GCF_021655155.1	J10	Not applicable	2006	Not applicable
GCF_005707595.1	Pathogen: environmental/food/other sample from *Bacillus cereus*	Chives	Jan, 2016	South Korea
GCF_019704155.2	*Bacillus cereus* HT18:isolated 2018_Hashimoto_trunk	Hashimoto Trunk	Nov, 2018	Japan
GCF_002000005.1	Pathogen: environmental/food/other sample from *Bacillus cereus*	Knife	Nov, 2015	South Korea
GCF_040937925.1	Microbe sample from *Bacillus cereus*	Tobacco rhizosphere soil	Jul, 2023	China
GCF_004771155.1	Pathogen: environmental/food/other sample from *Bacillus cereus*	Young radish kimchi	2014	South Korea
GCF_021655235.1	J75	Not applicable	2006	Not applicable
GCF_002215175.1	Microbe sample from *Bacillus cereus* K8 isolated from Korean fermented food	Korean fermented food	Jan, 2016	South Korea
GCF_022699365.1	Microbe sample from *Bacillus cereus*	Buffalo Rumen	Oct, 2020	China
GCF_013112375.1	*Bacillus cereus* WPySW2 isolated from healthy pyropia conchocelis	Seawater	Dec, 2005	China
GCF_024299105.1	Microbe sample from *Bacillus cereus*	Deep-sea water	Dec, 2019	Pacific Ocean
GCF_025035865.1	*Bacillus cereus* FORC_010 food isolate from chinese cabbage geotjeori	Chinese cabbage geotjeori	Feb, 2014	South Korea
GCF_018309165.1	Microbe sample from *Bacillus cereus*	Bee Honey	Jul, 2020	China
GCF_016727405.1	Pathogen: clinical or host-associated sample from *Bacillus cereus*	Not applicable	Unknown	Germany
GCF_025502485.1	Microbe sample from *Bacillus cereus*	Soil	Oct, 2020	South Korea
GCF_023516415.1	Microbe sample from *Bacillus cereus*	Oil contaminated soil	Jan, 2020	China
GCF_027625975.1	Microbe sample from B*acillus cereus*	Penaeus vannamei pond water	Jan, 2015	China
GCF_006349715.2	Microbe sample from *Bacillus cereus*	Coffee Root	May, 2018	Vietman
GCF_032595315.1	Microbe sample from *Bacillus cereus*	Unknown	Oct, 2023	EUA
GCF_029590375.1	Pathogen: clinical or host-associated sample from *Bacillus cereus*	Liver	Oct, 2022	China
GCF_009739985.1	*BacillusCereus*-DLOU-Weihai	Apostichopus japonicus	Nov, 2016	China
GCF_027920485.1	MIGS Cultured Bacterial/Archaeal sample from *Bacillus cereus*	Not applicable	Sep, 2022	China
GCF_006384875.1	Pathogen: environmental/food/other sample from *Bacillus*	Chives	Jan, 2016	South Korea
GCF_000835185.1	Microbe sample *Bacillus cereus* S2-8	Soil	1993	USA
GCF_013267475.1	Pathogen: clinical or host-associated sample from *Bacillus cereus*	Not applicable	Unknown	USA
GCF_013267455.1	Pathogen: clinical or host-associated sample from *Bacillus cereus*	Not applicable	Unknown	USA
GCF_000832765.1	Microbe sample *Bacillus cereus* 3a	Unknown	Unknown	Not applicable

GCF_016027015.1	Pathogen: clinical or host-associated sample from *Bacillus cereus*	Not applicable	Unknown	Not applicable
GCF_021655315.1	30052	Not applicable	2016	Not applicable
GCF_024584625.1	Microbe sample from *Bacillus cereus*	Soil	Jun, 2020	China
GCF_006349735.2	Microbe sample from *Bacillus cereus*	Black pepper root	May, 2018	Vietman
GCF_033452345.1	Microbe sample from *Bacillus cereus*	Leaves	Nov, 2022	China
GCF_032145515.1	Microbe sample from *Bacillus cereus*	Plant	2022	South Korea
GCF_040959295.1	Microbe sample from *Bacillus cereus*	Soil	Sep, 2021	China
GCF_023008425.1	Microbe sample from *Bacillus cereus*	Pond silt	Apr, 2021	China
GCF_031216075.1	*Bacillus cereus* MO2 isolated from root surface of Moringa oleifera	Root surface	Jun, 2014	Israel
GCF_021654935.1	MRY14-0074	Not applicable	2013	Not applicable
GCF_004801195.1	Producing collagenase sample from *Bacillus cereus* MH19	Not applicable	Aug, 2017	China
GCF_001941885.1	Microbe sample from *Bacillus cereus*	Air	May, 2011	Not applicable
GCF_001941905.1	Microbe sample from *Bacillus cereus*	Air	May, 2011	Not applicable
GCF_021655055.1	J2	Not applicable	2006	Not applicable
GCF_031325985.1	MIGS Cultured Bacterial/Archaeal sample from *Bacillus cereus*	Not applicable	Nov, 2020	China
GCF_001941925.1	Microbe sample from *Bacillus cereus*	Surface	Apr, 2009	Not applicable
GCF_025917685.1	Microbe sample from *Bacillus cereus*	Soil	Sep, 2019	China
GCF_018309125.1	Microbe sample from *Bacillus cereus*	Honey	Jul, 2020	China
GCF_021654915.1	MRY14-0060	Not applicable	2013	Not applicable
GCF_030067855.1	Microbe sample from *Bacillus cereus*	Soil	2012	Namibia
GCF_018309145.1	Microbe sample from *Bacillus cereus*	Bee Honey	Jul, 2020	China
GCF_021654995.1	MRY14-0100	Not applicable	2013	Not applicable
GCF_026684175.1	Microbe sample from *Bacillus cereus*	Petroleum sludge	Dec, 2021	China
GCF_028607045.1	MIGS Cultured Bacterial/Archaeal sample from *Bacillus cereus*	Ocean	Sep, 2018	Pacific ocean
GCF_025946485.2	Pathogen: environmental/food/other sample from *Bacillus cereus*	Peper	2014	Slovenia
GCF_013284505.2	Microbe sample from *Bacillus cereus*	Soil from tomato plant	Apr, 2019	Vietman
GCF_013284455.2	Microbe sample from *Bacillus cereus*	Soil from tomato plant roots	Apr, 2019	Vietman
GCF_013177495.2	Microbe sample from *Bacillus cereus*	Soil	2011	Namibia
GCF_030291955.1	Microbe sample from *Bacillus cereus*	Grassland soil	Oct, 2017	Denmark
GCF_040268315.1	Microbe sample from *Bacillus cereus*	Soil	Jun, 2021	China
GCF_964341285.1	BcbvaCA	BcbvaCA	Nov, 2024	Cameroon
GCF_000832865.1	Microbe sample *Bacillus cereus* 03BB108	Dust	2003	USA
GCF_002224345.1	*Bacillus cereus* C1L	Rhizosphere	Jul, 2003	Taiwan
GCF_000833045.1	Microbe sample *Bacillus cereus* E33L	Animal, carcass of dead zebra	1966	Namibia
GCF_000011625.1	Sample from *Bacillus cereus* E33L	Unknown	Unknown	Unknown
GCF_000022505.1	Sample from *Bacillus cereus* 03BB102	Unknown	Unknown	Unknown
GCF_000832405.1	Microbe sample from *Bacillus cereus* 03BB102	Human blood	2003	USA
GCF_000021205.1	Sample from *Bacillus cereus* B4264	Not applicable	1969	Not applicable
GCF_000021305.1	Sample from *Bacillus cereus* G9842	Not applicable	Unknown	Not applicable
GCF_000832385.1	Microbe sample from *Bacillus cereus* D17	Not available	Not available	Not available
GCF_000021785.1	Sample from *Bacillus cereus* AH820	Unknown	Unknown	Unknown
GCF_000239195.1	Sample from *Bacillus cereus* F837/76	Unknown	Unknown	Unknown
GCF_000143605.1	Sample from *Bacillus cereus* biovar *anthracis* str. CI	Unknown	Unknown	Unknown