Original Article

# *Bacillus cereus*: Taxonomy, Pathogenicity, Toxin Diversity, Molecular Identification, and Heavy Metal Resistance: A Comprehensive Literature Review

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**Abstract** *Bacillus cereus* is a ubiquitous, endospore-forming, Gram-positive bacterium belonging to the family Bacillaceae and a leading cause of foodborne illness worldwide. As a member of the taxonomically complex *B. cereus* sensu lato group — comprising at least 28 validly described species, including *B. anthracis* and *B. thuringiensis* — it presents persistent challenges for both clinical and food safety microbiology. This review synthesises the current state of knowledge on the taxonomy, biological characteristics, ecology, pathogenicity, and toxin diversity of *B. cereus*, with a particular focus on its diarrhoeal enterotoxins (haemolysin BL [HBL], non-haemolytic enterotoxin [NHE], enterotoxin T, enterotoxin FM, and cytotoxin K) and the heat-stable emetic toxin cereulide. The review further covers phenotypic and genotypic approaches to bacterial identification — including restriction fragment length polymorphism (RFLP), plasmid profiling, 16S rRNA gene sequencing, and phylogenetic analysis — and examines the environmental fate of heavy metals and the molecular mechanisms by which *Bacillus* species develop resistance to chromium, zinc, nickel, and cadmium. Recent evidence from genomic and molecular studies confirms that *B. cereus* harbours a diverse arsenal of virulence and metal resistance genes, encoded on both chromosomal and plasmid loci. The integrative understanding of these traits is essential for the development of improved detection strategies, risk assessment frameworks, and bioremediation applications. The global prevalence of *B. cereus* in foods is estimated at 23.75%, with a mortality rate of 0.9% across all infection types, underscoring the continuing public health relevance of this versatile pathogen.

**Keywords:** *Bacillus cereus*; foodborne illness; cereulide; enterotoxin; heavy metal resistance; genotypic identification.

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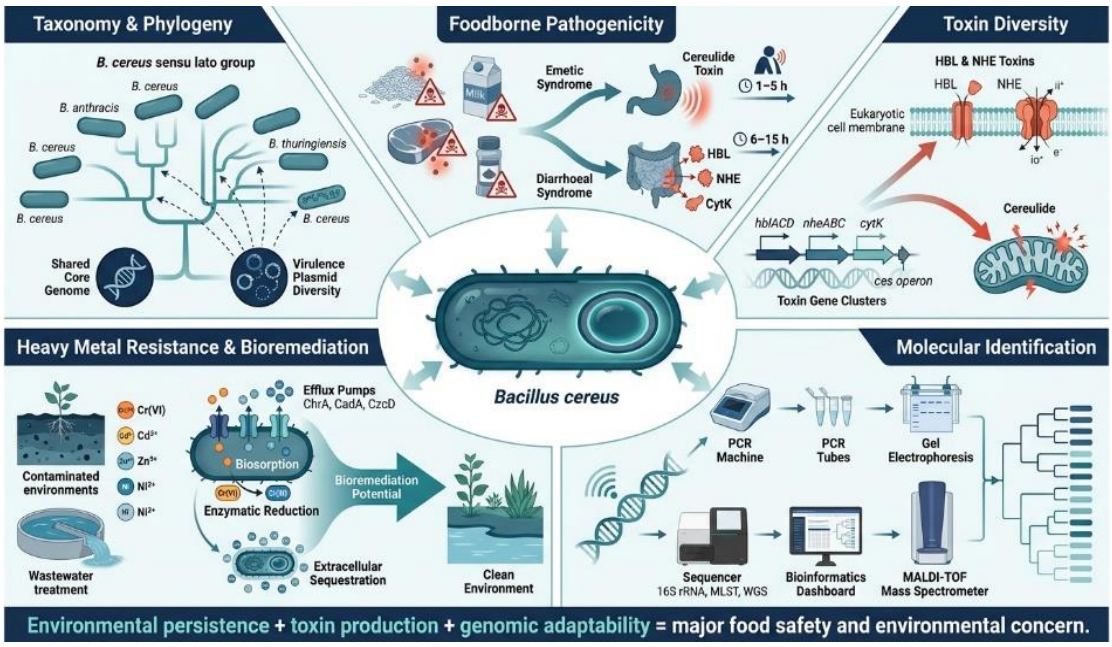
## Graphical abstract



## 1 Introduction

*Bacillus cereus* is a spore-forming, facultatively anaerobic, Gram-positive rod that has attracted sustained scientific interest due to its dual roles as a ubiquitous environmental saprophyte and a clinically significant foodborne pathogen. Since Ferdinand Cohn first formally described the genus *Bacillus* in 1872 by naming *B. subtilis*, the genus has expanded dramatically to encompass a highly diverse assemblage of organisms united by their capacity to form metabolically dormant endospores – among the most stress-resistant biological structures known. Within the genus, *B. cereus* occupies a position of particular importance for food microbiology, environmental science, and biotechnology. On one hand, it is a leading cause of food poisoning worldwide, responsible for an estimated 1.4–12% of all foodborne illness outbreaks globally and implicated in the contamination of a wide range of foods — from rice and cereals to dairy, meat, and spices. On the other hand, strains of *B. cereus* have attracted growing interest for their capacity to resist and biosorb toxic heavy metals, offering potential applications in the bioremediation of contaminated soils and effluents. A recent meta-analysis reported a worldwide prevalence of *B. cereus* in foods of 23.75% and a global infection mortality rate of 0.9%, confirming the enduring public health relevance of this organism [1, 2].

These figures are not merely descriptive: they indicate that *B. cereus* already ranks among the most consequential foodborne pathogens by both incidence and case burden, yet – unlike *Salmonella* or *Listeria* – it lacks harmonised regulatory thresholds and rapid confirmatory diagnostics in most jurisdictions, a gap this review aims to help close by consolidating the current toxin-detection and strain-typing evidence base [3].

Beyond these epidemiological figures, *B. cereus* itself is a large (3–5 × 1–1.2 μm), peritrichously flagellated, Gram-positive rod that grows across a wide temperature range (8–55 °C) and pH range (4.3–9.3) and whose defining survival trait — the metabolically dormant endospore — allows it to persist through cooking, pasteurisation, and many standard disinfection regimes. This combination of metabolic versatility, environmental ubiquity, and spore-mediated resilience underlies both its success as an opportunistic pathogen and its promise as a biotechnological agent and is the unifying thread connecting the otherwise disparate themes covered in this review [3].

This review integrates classical and contemporary literature on five interconnected themes: (i) the taxonomy and phylogenetics of the genus *Bacillus* and the *B. cereus* sensu lato group; (ii) the biological characteristics, ecology, and epidemiology of *B. cereus*; (iii) the molecular biology, diversity, and detection of its toxins; (iv) genotypic methods for bacterial identification, including RFLP, plasmid profiling, sequencing, and phylogenetic analysis; and (v) the environmental fate of heavy metals and the resistance mechanisms developed by *Bacillus* species, with particular reference to chromium, zinc, nickel, and cadmium. Where earlier foundational citations have been substantially superseded by more recent molecular and genomic evidence, updated references are incorporated throughout.

## 2 The Genus Bacillus: Taxonomy and Phylogenetics

In 1872, Ferdinand Cohn recognised and named the bacterium *Bacillus subtilis*, establishing the type species for what would become one of the largest and most taxonomically complex genera in bacteriology. The genus *Bacillus* belongs to Family Bacillaceae, Order Bacillales, Class Bacilli, Phylum Firmicutes, based on Bergey's Manual of Systematic Bacteriology [4]. The family's defining characteristic is the production of endospores — highly refractile, metabolically dormant structures of extraordinary resistance to heat, radiation, desiccation, and chemical disinfectants.

*Bacillus* is distinguished from phenotypically similar endospore-forming genera by its combination of aerobic or facultatively anaerobic growth, rod-shaped morphology, and (usually) catalase-positive reaction [5]. Other endospore-forming genera include *Sporolactobacillus* (microaerophilic, catalase-negative), *Clostridium* (strictly anaerobic, non-sulphate-reducing), *Desulfotomaculum* (anaerobic, sulphate-reducing), *Sporosarcina* (coccal morphology), and *Thermoactinomycetes* (actinomycete-like characteristics). Despite phenotypic similarities, genotypic analysis has revealed that these genera are more distantly related phylogenetically than their shared endospore phenotype would suggest.

Early classification of *Bacillus* species relied exclusively on aerobic growth and endospore morphology, often grouping organisms of diverse physiological and genetic backgrounds into the same species. The advent of molecular sequencing technologies fundamentally transformed this landscape. Ash et al. [6] were among the first to apply molecular phylogenetic analysis based on 16S rRNA sequences to the classification of *Bacillus* members, revealing substantial diversity within the genus. Today, molecular data – including whole-genome sequencing, multi-locus sequence typing (MLST), and pan-genome analyses – have replaced purely morphological approaches, enabling much more precise and reliable species delineation [7].

### 2.1 The B. cereus sensu lato Group

The *B. cereus* sensu lato (*Bcsl*) group, formerly comprising six species, has been expanded through whole-genome-based taxonomic revision to encompass at least 28 validly and effectively published species [8]. This group includes *B. cereus* sensu stricto, *B. anthracis*, *B. thuringiensis*, *B. mycoides*, *B. pseudomycoides*, *B. weihenstephanensis*, *B. cytotoxicus*, *B. toyonensis*, and several recently described species. The phylogenetic boundaries between these species are remarkably fluid: *B. cereus*, *B. thuringiensis*, and *B. anthracis* share > 99% 16S rRNA sequence identity and are differentiated primarily by the virulence plasmids they carry rather than core genome differences [9, 10].

The only established genomic distinction between *B. cereus* and *B. thuringiensis* is the presence of plasmids encoding insecticidal crystal (Cry) protein toxins in the latter; upon plasmid curing, *B. thuringiensis* strains become indistinguishable from *B. cereus* by standard phenotypic and genotypic methods. Similarly, *B. anthracis*—the causative agent

of anthrax—is distinguished by two pathogenicity plasmids (pXO1 and pXO2), which encode the anthrax toxin complex and the polyglutamate capsule synthesis genes. These observations led early researchers to suggest that the entire *Bcsl* group may represent a single species with different plasmid profiles – a view supported by pan-genome studies demonstrating highly conserved core genomes across group members [8] (Figure 1).

This proposal, however, remains actively contested rather than settled. Carroll et al. [11] instead proposed a hybrid nomenclatural framework that preserves clinically and industrially meaningful species names (*B. anthracis*, *B. thuringiensis*, and *B. cereus* sensu stricto) as genomic ‘‘groups’’ nested within the wider Bcsl complex, arguing that collapsing the group into a single species would strip away information critical for biosafety and food-safety decision-making even though it is genomically defensible. Comparative phylogenomic analyses have similarly shown that *B. thuringiensis* itself is polyphyletic with respect to *B. cereus* sensu stricto, further undermining any simple one-species-per-plasmid-profile model [12]. Carroll et al. [13] reviewed the resulting proliferation of conflicting taxonomic frameworks and cautioned that repeated, poorly harmonised renaming has already caused laboratory misidentifications with real diagnostic and regulatory consequences. The debate therefore centres on a genuine trade-off: genomic lumping best reflects evolutionary relatedness, whereas phenotype-anchored splitting better serves clinical and biosecurity communication — and no consensus framework has yet reconciled the two.

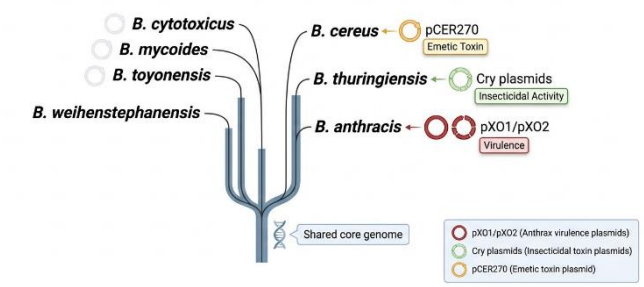



**Figure 1.** Simplified phylogenetic and taxonomic relationships within the *Bacillus cereus* sensu lato group. The closely related species share highly conserved core genomes but differ primarily in plasmid-associated virulence determinants, including anthrax toxin plasmids (pXO1/pXO2), Cry toxin plasmids, and the cereulide megaplasmid (pCER270).

## 3 *Bacillus cereus*: Biology, Ecology, and Epidemiology

### 3.1 Biological Characteristics

*B. cereus* is a facultatively anaerobic organism with large, vegetative rod-shaped cells (3–5 × 1–1.2 μm). It grows over a temperature range of 8–55 °C, with optimal growth at 28–35 °C. The organism is classified as a mesophile, though psychrotrophic strains capable of growth at 4–5 °C have been documented. Growth and enterotoxin production have been observed in rice meal after storage at 4 °C, indicating that refrigeration alone is insufficient for safety. The bacterium grows within a pH range of 4.3–9.3. Endospore production is a key survival trait; *B. cereus* spores resist boiling, pasteurisation, and many chemical disinfectants, enabling survival and subsequent germination during food storage and processing.

Recent genomic studies have revealed the molecular basis for many of these phenotypic characteristics. Whole-genome sequencing of diverse *B. cereus* strains has identified regulatory networks controlling sporulation, germination, and stress response, providing insights into the organism's exceptional environmental persistence. The presence of biofilm-forming genes in many strains further enhances their survival on food processing surfaces — a critical factor in repeat contamination events in food production facilities [1].

### 3.2 Ecology and Environmental Distribution

*B. cereus* is ubiquitous in the environment and is routinely recovered from soil, water, air, vegetation, and the gastrointestinal tracts of invertebrates and mammals. It is commonly found in dried foodstuffs, spices, cereals, meat, eggs, milk and dairy products, and cooked foods held at improper temperatures [14]. Its ecological success is underpinned by an extensive enzymatic repertoire, including lipases, proteases, xylanases, and amylases that enable it to exploit a wide range of organic substrates.

The organism's adaptability is also evident in its colonisation of unusual ecological niches. The "*Arthromitus*" filamentous stage of *B. cereus* has been documented in the guts of soil-dwelling arthropods — including insects and larvae — where the bacterium maintains a symbiotic intestinal relationship, representing an important reservoir in the environment. From these invertebrate hosts, *B. cereus* can be disseminated to soil, water, and ultimately food products. A meta-analysis of *B. cereus* prevalence across 266 studies confirmed a worldwide food contamination prevalence of 23.75% — with the highest prevalence in starchy foods, cereals, and spices — underscoring the near-ubiquitous environmental distribution of this organism [2] (Figure 2).

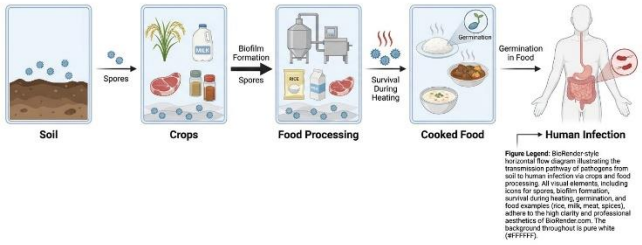



**Figure 2.** Ecological distribution, endospore-mediated persistence, and routes of food contamination by *Bacillus cereus*. Environmental reservoirs and stress-resistant spores facilitate contamination of food products and survival through processing and storage conditions.

### 3.3 Pathogenicity and Epidemiology

Outbreaks of food poisoning due to *B. cereus* have been documented since the early twentieth century, with the first confirmed outbreak occurring in Norway in 1950. The organism is now recognised as one of the most common causes of foodborne illness globally, responsible for an estimated 1.4–12% of all food poisoning outbreaks worldwide [18]. In Europe, *B. cereus* sensu lato is the second most frequently confirmed causative agent of foodborne outbreaks [15].

A systematic review encompassing 6,135 cases across 266 studies reported a global food poisoning mortality rate of 0.05%, but a higher mortality of 0.9% when non-gastrointestinal systemic infections are included – reflecting the spectrum of severity that *B. cereus* infections can manifest [1].

Two distinct clinical syndromes characterise *B. cereus* food poisoning: the emetic syndrome, caused by the preformed heat-stable cyclic peptide cereulide in contaminated food, and the diarrhoeal syndrome, caused by the in vivo production of proteinaceous enterotoxins in the small intestine. The emetic syndrome presents 1–5 hours after ingestion, while diarrhoeal symptoms typically develop 6–15 hours post-exposure. A notable foodborne outbreak at two middle schools in Chongqing, China, in 2021 illustrated the severity of *B. cereus* poisoning: it involved 198 cases with a 24.63% attack rate, and *B. cereus* was isolated from contaminated rice noodles at counts exceeding $10^3$ CFU/g [16]. Beyond gastrointestinal disease, *B. cereus* is an opportunistic pathogen capable of causing severe non-gastrointestinal infections — including endophthalmitis, bacteraemia, meningitis, endocarditis, cutaneous infections, and pneumonia — particularly in immunocompromised patients, neonates, and intravenous drug users. Cases of severe or fatal pneumonia in apparently healthy welders have raised concern about occupational exposure as a risk factor for invasive *B. cereus* disease [17].

## 4 Toxins of *Bacillus cereus*: Diversity, Molecular Biology, and Detection

The pathogenicity of *B. cereus* is mediated by a diverse arsenal of secreted toxins encoded on both chromosomal and plasmid loci. These toxins fall into two broad functional categories: enterotoxins causing diarrhoeal syndrome and the heat-stable emetic toxin cereulide (Figure 3). A comprehensive updated summary of these toxins, their associated genes, sizes, and detection methods is presented in Table 1, which extends the classical characterisation to include cytotoxin K (CytK) and recent molecular detection advances.

**Table 1.** Toxins of Bacillus cereus and their properties, associated genes, and current detection methods. Updated from Märtlbauer and Granum [18] and Jovanovic et al. [19].

| Toxin | Syndrome | Gene(s) | Size | Detection Methods |
|---|---|---|---|---|
| Haemolysin BL (HBL) | Diarrhoeal | hblA, hblC, hblD | 35–45 kDa (3-component) | Vero cell cytotoxicity, PCR, ELISA, commercial kits |
| Non-haemolytic enterotoxin (NHE) | Diarrhoeal | nheA, nheB, nheC | 36–105 kDa (3-component) | ELISA, PCR, BDE-VIA kit |
| Enterotoxin T (BceT) | Diarrhoeal | bceT | 41 kDa | PCR, Vero cell assay |
| Enterotoxin FM | Diarrhoeal | entFM | 39, 45, 105 kDa | PCR, Tecra ELISA kit |
| Cytotoxin K (CytK) | Diarrhoeal /Necrotic | cytK | 34 kDa | PCR, cytotoxicity assay |
| Cereulide (emetic toxin) | Emetic | ces operon (pCER270) | 1.2 kDa cyclic peptide | LC-MS/MS, MALDI-TOF, HEp-2 vacuolation |

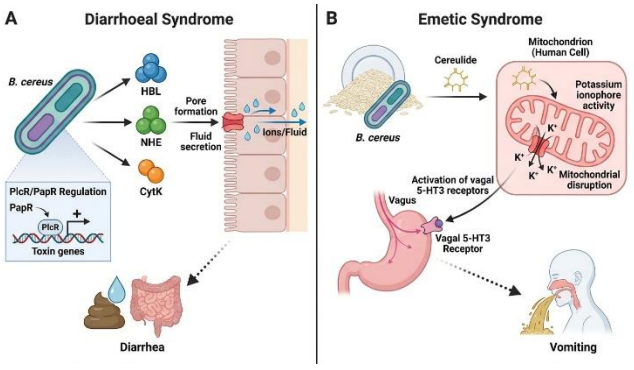



**Figure 3.** Molecular mechanisms underlying the diarrhoeal and emetic syndromes caused by *Bacillus cereus*. Diarrhoeal disease results from enterotoxin-mediated pore formation in intestinal epithelial cells, whereas emetic disease is caused by cereulide-induced mitochondrial dysfunction and stimulation of vagal emetic pathways.

### 4.1 Haemolysin BL (HBL)

Haemolysin BL (HBL) is a three-component protein complex (B, L1, and L2) encoded by the *hblA*, *hblC*, and *hblD* genes within the *hbl* operon and is considered the major diarrhoeal toxin of *B. cereus*. All three components must be present for full haemolytic and enterotoxic activity. Beecher and MacMillan [20] demonstrated that individual components are non-haemolytic but that combined reconstitution restores activity. Approximately 40–74% of *B. cereus* strains carry the *hbl* operon, with prevalence estimates varying by geographic region, isolation source, and PCR primer design.

HBL exerts its cytotoxic effects by forming pores in target cell membranes, leading to osmotic lysis. The toxin acts on intestinal epithelial cells and vascular endothelium, explaining both the diarrhoeal and vascular permeability-increasing properties documented in animal models. Recent transcriptomic analyses have demonstrated that *hbl* gene expression is regulated by the PlcR/PapR quorum-sensing system — a master virulence regulator in the *B. cereus* group — linking toxin production to population density-dependent signalling [1].

### 4.2 Non-Haemolytic Enterotoxin (NHE)

The non-haemolytic enterotoxin (NHE) is a three-component complex encoded by the *nheA*, *nheB*, and *nheC* genes, and it is the most prevalent diarrhoeal toxin complex found in *B. cereus* strains. Unlike HBL, NHE does not induce haemolysis but shares similar pore-forming cytotoxic activity on Vero cells and intestinal epithelial cells. The *nhe* operon is present in >95% of *B. cereus* strains—a substantially higher prevalence than the *hbl* operon—making it the dominant diarrhoeal toxin in many clinical settings [18]. Commercial immunoassay kits (BDE-VIA; Tecra International) and PCR-based methods are routinely used for NHE detection in food samples.

### 4.3 Enterotoxin T (BceT) and Enterotoxin FM

Enterotoxin T, encoded by the *bceT* gene and initially identified by Agata et al. [21], is a single 41 kDa protein exhibiting Vero cell cytotoxicity and fluid accumulation in the ligated mouse ileal loop model. The prevalence of *bceT* among *B. cereus* strains is inconsistent across studies (40–100%), reflecting genuine geographic diversity and methodological differences in primer design. Enterotoxin FM, a three-component complex encoded by the chromosomal *entFM* gene, was first described by Asano et al. [22]. The *entFM* gene is the most prevalent enterotoxin gene in the *B. cereus* group, detected in 93–96% of food and outbreak strains surveyed by Tran et al. [23]. Both BceT and EntFM require commercial ELISA or PCR confirmation for routine food safety monitoring.

### 4.4 Cytotoxin K (CytK)

Cytotoxin K (CytK) is a 34 kDa pore-forming toxin encoded by the *cytK* gene that was first identified as the causative agent of a severe necrotic food poisoning outbreak in France in 1998, in which three of 17 affected individuals died. CytK-1, the more potent variant, is found only in a subset of highly virulent strains, while the less toxic CytK-2 is more widely distributed. CytK is particularly associated with the newly recognised species *B. cytotoxicus*, which has been taxonomically separated from *B. cereus* sensu stricto. Recent genomic surveillance studies have highlighted CytK as an underappreciated virulence determinant whose contribution to the global burden of *B. cereus* illness may be substantially underestimated due to limited routine screening [18].

### 4.5 Cereulide: The Emetic Toxin

Cereulide is a small (1.2 kDa), heat- and acid-stable cyclic dodecadepsipeptide synthesised non-ribosomally by a peptide synthetase complex encoded by the *ces* operon, located on the large pCER270 megaplasmid. It is the causative agent of the emetic syndrome in *B. cereus* food poisoning and is preferentially produced in starchy foods — most notably cooked rice — at temperatures of 15–37 °C [24, 25]. Cereulide is structurally analogous to the potassium ionophore valinomycin and acts by disrupting mitochondrial function through potassium transport across mitochondrial membranes, ultimately triggering emesis via stimulation of 5-HT3 receptors on vagal afferent neurones.

A key food safety concern is the extreme stability of cereulide: it withstands autoclaving at 121 °C for 90 minutes, is resistant to pH 2–11, and is not inactivated by pepsin or trypsin. Standard cooking and heat treatment of contaminated rice therefore cannot eliminate pre-formed cereulide, making prevention of *B. cereus* growth in cooked rice the only effective control strategy. Wang et al. [26] published an updated review of cereulide characterisation, confirming that emetic strains are predominantly found in specific *B. paranthracis* clades within the *B. cereus* sensu lato group and that the ces operon prevalence is approximately 4–9% of *B. cereus* strains in food environments.

Advanced detection methods for cereulide have evolved rapidly. Liquid chromatography-tandem mass spectrometry (LC-MS/MS) using stable isotope dilution assays (SIDA) has been standardised by the ISO (ISO/TS 18999:2024) as the reference method for quantifying cereulide in food. Matrix-assisted laser desorption/ionisation-time of flight (MALDI-TOF) mass spectrometry has been validated as a rapid, colony-based screening tool for cereulide-producing strains, with a limit of detection of 30 pg/mL from optimised extracts [27]. These technologies dramatically reduce the time to detection compared with the classical HEp-2 cell vacuolation assay. Figure 4 illustrates these technologies.

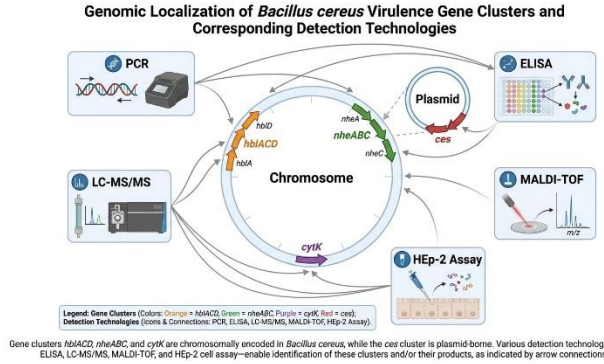



**Figure 4.** Genetic organisation of major *Bacillus cereus* toxin genes and current laboratory detection methods. Enterotoxin genes are predominantly chromosomal, whereas the cereulide synthetase operon (*ces*) is plasmid-encoded on the pCER270 megaplasmid.

### 4.6 Identification of *Bacillus cereus*: Phenotypic Methods

Phenotypic identification of *B. cereus* relies on its distinctive characteristics: haemolysis on blood agar, lecithinase activity, inability to ferment mannitol, and motility. The most widely used selective medium is polymyxin pyruvate egg yolk mannitol bromothymol blue agar (PEMBA), on which *B. cereus* produces characteristic turquoise-blue colonies with surrounding lecithinase halos due to its inability to ferment mannitol [28]. However, phenotypic methods alone are insufficient for differentiation of *B. cereus* from closely related *Bcsl* species, necessitating molecular confirmation.

### 4.7 Critical Appraisal of Toxin Gene Prevalence and Detection Data

The prevalence figures summarised above should be interpreted with caution rather than treated as fixed biological constants. Reported carriage rates for individual toxin genes vary substantially between studies — for example, bceT prevalence ranging from 40% to 100% and hbl prevalence from 40% to 74% — and much of this variability is attributable to methodological rather than genuinely biological differences: primer design and target region, PCR annealing stringency, strain source (clinical versus food versus environmental isolates), and geographic sampling bias all confound direct comparison across the literature. Toxin gene presence, moreover, does not equate to toxin expression or clinical relevance; phenotypic virulence assays (Vero cell cytotoxicity and HEp-2 vacuolation) and genotypic screening frequently disagree, and few studies systematically reconcile the two. This gap is compounded in the clinical setting: standard phenotypic identification does not distinguish B. cereus sensu stricto from other Bcsl members, so that invasive-infection case series attributed to ‘‘B. cereus’’ may in fact include misclassified relatives, complicating any critical synthesis of pathogenicity data across studies [29, 30]. Future comparative work would benefit from standardised, whole-genome-anchored reporting of both gene carriage and confirmed expression, rather than PCR-only prevalence surveys.

## 5 Genotypic Methods for Bacterial Identification

Genotypic methods, which directly analyse DNA rather than phenotypic expression, offer superior reproducibility, discrimination power, and taxonomic precision compared to traditional phenotypic approaches [31]. For *B. cereus* specifically — where high phenotypic plasticity and horizontal gene transfer complicate phenotypic classification — molecular methods are indispensable for definitive identification, strain typing, and outbreak investigation (Figure 5).

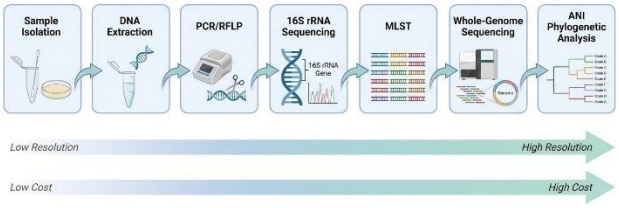



**Figure 5.** Progressive hierarchy of molecular identification and phylogenetic methods used for *Bacillus cereus* characterisation, ranging from PCR-RFLP to whole-genome sequencing and ANI-based phylogenomics.

### 5.1 Restriction Fragment Length Polymorphism (RFLP)

RFLP exploits sequence polymorphisms at restriction endonuclease recognition sites within conserved DNA regions to produce strain-specific banding patterns. For *Bacillus* species, RFLP of the 16S or 23S rDNA loci—amplified by PCR with conserved primers and then digested with appropriate restriction enzymes—generates fragment patterns that can distinguish between species and closely related strains. RFLP is particularly suited to intra-specific level comparisons among closely related taxa and is cost-effective for screening large strain collections [32, 33]. Its primary limitation is reduced discriminatory power among strains sharing identical restriction patterns despite minor genomic differences.

### 5.2 Plasmid Profiling

Plasmid profiling exploits the presence and size distribution of extrachromosomal genetic elements as a strain fingerprinting tool. Within the *B. cereus* group, plasmid complement is of particular importance given the central role of plasmid-encoded genes in virulence (pCER270 for cereulide; pXO1/pXO2 in *B. anthracis*; Cry toxin plasmids in *B. thuringiensis*). Many studies have used plasmid patterns to differentiate among *Bacillus* subspecies in food safety and environmental monitoring contexts [34, 35]. However, the reliability of plasmid profiles is contingent on plasmid stability: plasmids may be lost spontaneously during culture or may be acquired through horizontal transfer, limiting epidemiological interpretability.

### 5.3 DNA Sequencing and Multi-Locus Sequence Typing (MLST)

Nucleotide sequencing of important genetic areas gives the best detail for identifying bacteria and understanding their evolutionary relationships. Partial or full 16S rRNA gene sequencing remains the gold standard for genus- and species-level identification of *Bacillus* isolates, with the 5' hypervariable region (HV region) providing the highest discriminatory power for grouping *Bacillus* species [36]. However, the very high 16S rRNA sequence identity within the *B. cereus* sensu lato group (>99% between *B. cereus*, *B. anthracis*, and *B. thuringiensis*) necessitates the use of multi-locus approaches for definitive

differentiation.

Multi-locus sequence typing (MLST), which analyses sequence polymorphisms at multiple housekeeping loci, offers substantially greater discriminatory power than single-locus 16S analysis. A DNA nanomachine (DNM) biplex assay targeting unamplified 16S rRNA has recently been validated for rapid, instrument-accessible differentiation of *B. cereus* group species, offering single-nucleotide variant (SNV) discrimination without PCR amplification — a promising development for rapid food safety screening [37]. Whole-genome sequencing (WGS), now increasingly accessible through short-read (Illumina) and long-read (Oxford Nanopore, PacBio) platforms, is progressively replacing MLST as the reference method for outbreak investigation and strain source attribution in high-income settings [8].

### 5.4 Phylogenetic Analysis

Phylogenetic reconstruction based on 16S rRNA sequences or whole-genome data provides the evolutionary framework for understanding relationships among *Bacillus* species. Classical 16S rRNA phylogenetics, pioneered for *Bacillus* by Ash et al. [6], revealed that the genus as traditionally circumscribed is not monophyletic, with members of the *Bacillaceae* distributed across multiple deep phylogenetic lineages in Firmicutes. Contemporary whole-genome phylogenomics has refined these relationships substantially. Average nucleotide identity (ANI) analysis now provides the definitive species delineation threshold (95–96% ANI for conspecificity) in the *B. cereus* group, enabling objective, reproducible species assignment in the absence of universal phenotypic markers [7, 8].

## 6 Environmental Fate of Heavy Metals and Bacterial Resistance

### 6.1 Heavy Metals in the Environment

Heavy metals constitute a persistent class of environmental contaminants whose non-biodegradable and non-thermodegradable nature enables indefinite accumulation in soil, sediment, and water. Essential metals such as calcium, cobalt, chromium, copper, iron, potassium, magnesium, manganese, nickel, and zinc serve as enzymatic cofactors and osmoregulatory agents at trace concentrations; non-essential metals including cadmium, lead, mercury, and arsenic serve no known biological function and are toxic even at low concentrations [38].

The primary pathways of heavy metal entry into the environment include industrial effluents from tanneries, electroplating plants, and mining operations; atmospheric deposition; agricultural inputs (sewage sludge, fertilisers, and pesticides); and wastewater irrigation of agricultural soils. Contamination of aquatic ecosystems by heavy metals is particularly concerning due to bioaccumulation in aquatic organisms and biomagnification through food chains. Serious systemic health consequences — including renal toxicity, neurological damage, and carcinogenesis — result from chronic dietary exposure to cadmium, chromium (VI), and lead accumulated through the food chain [39]. The co-contamination of many industrial sites with both heavy metals and organic pollutants has driven intensified interest in metal-resistant microorganisms as tools for bioremediation.

### 6.2 Bacterial Metal Resistance Mechanisms

Selective pressure from metal-contaminated environments has driven the evolution of resistance systems in bacteria targeting virtually all toxic metals. Research since the 1970s has identified multiple classes of metal resistance mechanisms operating at different levels of cellular organisation (Figure 6). Table 2 presents an updated summary of the six principal resistance mechanisms identified in *Bacillus* species, incorporating recent genomic evidence.

**Table 2.** Mechanisms of heavy metal resistance in Bacillus species. Updated from Nies [40] and Ayangbenro and Babalola [41], incorporating genomic evidence from B. cereus NWUAB01.

| No. | Mechanism | Description | Example in *Bacillus* sp. |
|---|---|---|---|
| 1 | Permeability barrier | Reduction in membrane permeability limiting metal entry into the cell | Outer membrane modification in Cr(VI)-exposed strains |
| 2 | Active efflux | Energy-dependent pumping of metal ions out of the cytoplasm via P-type ATPases or RND transporters | CadA ($Cd^{2+}$), ChrA ($Cr^{6+}$), ZntA ($Zn^{2+}$) |
| 3 | Intracellular sequestration | Binding of metal ions by intracellular proteins (e.g., metallothioneins) | Metal-binding proteins in *B. cereus* NWUAB01 |
| 4 | Extracellular sequestration | Exopolysaccharide or biosurfactant-mediated metal chelation outside the cell | Lipopeptide biosurfactant in *B. cereus* NWUAB01 |
| 5 | Enzymatic detoxification | Biotransformation of toxic metal species to less toxic forms (e.g., Cr(VI) → Cr(III); $Hg^{2+} \rightarrow Hg^0$) | Cr(VI) reductase in *B. cereus* b-525k |
| 6 | Target modification | Alteration of cellular components to reduce their affinity for metal ions | Ribosomal or enzyme modifications in resistant strains |

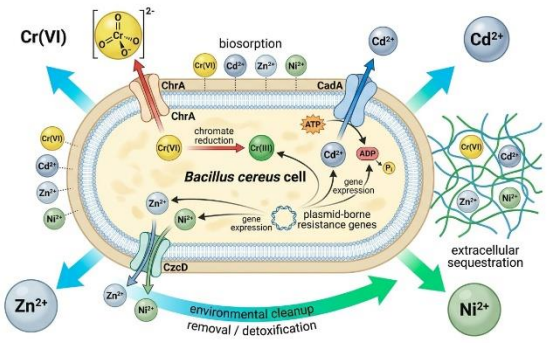



**Figure 6.** Heavy metal resistance mechanisms in *Bacillus cereus* and their relevance to bioremediation. Resistance involves coordinated efflux, sequestration, enzymatic detoxification, and biosorption systems encoded on chromosomal and plasmid-associated loci.

Metal resistance is frequently encoded on plasmids and is commonly co-located with antibiotic resistance genes on the same mobile genetic element, creating a linkage between antibiotic and heavy metal resistance that has significant implications for antimicrobial resistance surveillance [42]. Genomic analysis of *B. cereus* NWUAB01 — a multi-metal-resistant strain isolated from a gold mining site — identified putative resistance genes for cadmium (*cadA*), chromium (*chrA*), cobalt-zinc-cadmium (*czcD*), copper, arsenic, lead, and zinc on both chromosomal and extrachromosomal elements, confirming the genomic basis for the broad-spectrum metal tolerance of this strain [41].

### 6.3 Chromium Resistance in *Bacillus*

Chromium exists primarily in two stable oxidation states in the environment: Cr(III), which is relatively insoluble and of low biological availability, and Cr(VI), which is highly water-soluble, rapidly membrane-permeable, and strongly oxidising — making it markedly more toxic to microorganisms than the trivalent form. Industrial effluents from tanneries, chrome plating facilities, and textile dyeing operations are major sources of Cr(VI) contamination in soil and groundwater.

*Bacillus* species exhibit multiple Cr(VI) resistance mechanisms, most significantly the enzymatic reduction of Cr(VI) to the less toxic Cr(III) — a reaction catalysed by chromate reductases under both aerobic and anaerobic conditions. *B. cereus* b-525k, isolated from tannery effluent, demonstrated a minimum inhibitory concentration (MIC) for Cr(VI) of 32 mM — among the highest reported for any *Bacillus* strain — along with resistance to $Pb^{2+}$ (23 mM), $As^{3+}$ (21 mM), and $Zn^{2+}$ (17 mM) and maximum biosorption efficiency of 51 mM $Cr^{6+}$/g biomass after 6 days [43]. Chromosomal and plasmid-borne chromate resistance determinants — particularly the *chrA* gene encoding a chromate transport efflux protein — mediate Cr(VI) exclusion from the cytoplasm, reducing intracellular genotoxic damage from reactive Cr(VI) intermediates.

### 6.4 Zinc, Nickel, and Cadmium Resistance

Zinc, while an essential trace element and structural component of zinc-finger proteins and numerous metalloenzymes, becomes toxic to microorganisms at elevated concentrations. Bacterial resistance to zinc relies primarily on two efflux mechanisms: the P-type ATPase ZntA system, which hydrolyses ATP to drive $Zn^{2+}$ export across the cytoplasmic membrane, and the RND (resistance-nodulation-division) transporter system powered by the proton gradient, which exports zinc across the entire cell envelope of Gram-negative bacteria. The cobalt-zinc-cadmium resistance protein CzcD, identified in *B. cereus* NWUAB01, mediates efflux of all three metals through a cation diffusion facilitator (CDF) mechanism [41, 44].

Nickel (Ni(II)) resistance in *Bacillus* species is less extensively characterised than zinc or chromium resistance. Ni(II) toxicity is mediated by binding to cell surfaces and inhibiting sulphur-oxidising enzymes. Although other genera have described multiple nickel efflux systems, researchers have yet to fully characterise the dedicated Ni(II) resistance determinants in *B. cereus*. Cadmium toxicity, mediated by displacement of zinc and other essential metals from cellular binding sites, is countered in Gram-positive bacteria primarily through the CadA P-type ATPase efflux system, which was first characterised in *Staphylococcus aureus* [45]. The *cadA* gene and its homologues in *B. cereus* NWUAB01 and related strains confer specific $Cd^{2+}$ efflux capacity and have been verified by genomic analysis [41].

### 6.5 *Bacillus cereus* in Bioremediation: Current Status and Future Directions

The combination of metal resistance, biosurfactant production, endospore resilience, and extensive enzymatic repertoire makes *B. cereus* and related *Bacillus* species attractive candidates for bioremediation of heavy metal-contaminated soils and effluents. *B. cereus* NWUAB01 demonstrated metal removal efficiencies of 69% (Pb), 54% (Cd), and 43% (Cr) from experimentally contaminated soils using its lipopeptide biosurfactant as a metal chelation and mobilisation agent. Genetically engineered strains with enhanced efflux pump expression or metal-sequestering protein production represent the next frontier in bioremediation biotechnology. Regulatory and ecological risks associated with deliberate environmental release of genetically modified *Bacillus* strains must, however, be carefully evaluated given the persistence of *B. cereus* endospores in the environment [41, 46].

These risks are not merely theoretical. Field-scale deployment of metal-resistant *Bacillus* strains faces the same barriers documented for microbial bioremediation more broadly: bioremediation kinetics that are orders of magnitude slower than physicochemical treatment; sensitivity of resistance and biosorption phenotypes to fluctuating field conditions (pH, co-contaminants, and competing microbiota); the absence of standardised performance metrics or certification protocols in many jurisdictions; and precautionary regulatory frameworks that restrict environmental release of living or genetically modified organisms even where laboratory evidence suggests low risk [46]. A further, *B. cereus*-specific concern is that metal-resistance determinants are frequently co-located on the same mobile plasmids as antibiotic-resistance genes and, in some strains, virulence factors; releasing large populations of metal-tolerant *B. cereus* into contaminated soils could therefore inadvertently seed reservoirs of multidrug-resistant or toxigenic spores that persist indefinitely once introduced, given the very endospore resilience that makes the organism attractive for bioremediation in the first place. Ecological risk assessment specific to endospore-forming bioremediation agents – rather than generic microbial-release frameworks – is still largely lacking and represents a priority for translating

these laboratory findings into field practice.

## 7 Conclusions

*Bacillus cereus* is a taxonomically complex, metabolically versatile, and clinically significant organism whose importance spans food microbiology, environmental science, and biotechnology. This review has synthesised evidence across five interconnected domains — taxonomy, biology, toxin diversity, molecular identification, and heavy metal resistance — revealing a coherent picture of an organism whose ecological success is rooted in its genetic flexibility, endospore resilience, and capacity to exploit diverse environments and resistance strategies.

In practical terms, these findings carry significance for three distinct stakeholder groups. Food safety regulators require updated, genomically grounded criteria for risk assessment and outbreak attribution rather than the historically inconsistent phenotypic thresholds still in use in many jurisdictions. Clinical microbiologists need to recognise *B. cereus* as a genuine, probably underdiagnosed opportunistic pathogen in immunocompromised and neonatal populations, not merely as a presumed food-poisoning contaminant. Environmental biotechnologists, in turn, can draw on the same organism's metal-resistance traits as an underexploited, if not yet field-ready, bioremediation resource. Bridging these three domains, rather than treating them in isolation, is the central practical contribution of this review.

Four key conclusions emerge from this review. First, the *B. cereus* sensu lato group has expanded substantially beyond the classical six-species circumscription to encompass at least 28 species, whose boundaries are best defined by whole-genome-based metrics (ANI) rather than phenotypic or single-locus molecular markers. The genetic fluidity among *B. cereus*, *B. thuringiensis*, and *B. anthracis* — unified by highly conserved core genomes but differentiated by virulence plasmid content — underscores the inadequacy of 16S rRNA sequencing alone for reliable intra-group species discrimination.

Second, the toxin portfolio of *B. cereus* is more complex than historically recognised. Beyond the classical HBL and emetic toxin cereulide, NHE is now recognised as the most prevalent diarrhoeal toxin in clinical strains (>95% prevalence) and CytK as an underappreciated determinant of necrotic disease. Production of this entire toxin repertoire is coordinated by the quorum-sensing PlcR/PapR system. Advanced detection technologies — LC-MS/MS and MALDI-TOF for cereulide, multiplex PCR and commercial immunoassay kits for enterotoxins — have dramatically improved the sensitivity and speed of *B. cereus* toxin surveillance in food safety monitoring.

Third, genetic methods are now preferred over traditional methods for accurately identifying *B. cereus* and investigating outbreaks. Whole-genome sequencing now offers the highest resolution for strain typing and source attribution, while emerging platforms such as DNA nanomachine (DNM) assays targeting unamplified 16S rRNA represent promising rapid diagnostic tools for resource-limited settings.

Fourth, *B. cereus* harbours a genomically diverse heavy metal resistance repertoire — including chromate efflux (ChrA), cadmium-exporting ATPases (CadA), cobalt-zinc-cadmium transporters (CzcD), and Cr(VI) reductases — that enables survival in metal-contaminated environments and confers bioremediation potential. The close genetic linkage between metal resistance and antibiotic resistance genes on mobile plasmid elements raises concern for the co-selection of antimicrobial resistance in metal-contaminated environments.

Future research priorities include: (i) standardisation of WGS-based typing protocols for routine food safety surveillance of *B. cereus*; (ii) elucidation of the environmental triggers and regulatory networks controlling cereulide biosynthesis at different temperatures and food matrices; (iii) characterisation of CytK prevalence and contribution to the global burden of *B. cereus* illness; and (iv) development of safe, effective bioremediation strategies harnessing the metal resistance capabilities of *B. cereus* and related species while managing the ecological risks associated with endospore-forming soil bacteria. Interdisciplinary integration of genomics, food safety engineering, and environmental microbiology will be essential for advancing these priorities.

Beyond these four priorities, we further recommend: (v) reconciliation of the currently competing Bcsl taxonomic frameworks (lumping versus hybrid/splitting) into guidance that clinical and regulatory laboratories can apply consistently, given the demonstrated risk of misidentification under the status quo [47]; (vi) ecological risk assessment protocols specific to endospore-forming bioremediation agents, addressing the co-location of metal- and antibiotic-resistance genes prior to any field-scale release; and (vii) prospective, genomically confirmed cohort studies – rather than retrospective PCR-only surveys – to establish which toxin genotypes are reliably associated with clinical severity.

## Abbreviations

Bcsl — *Bacillus cereus* sensu lato

HBL — Haemolysin BL

NHE — Non-haemolytic enterotoxin

BceT — Enterotoxin T

EntFM — Enterotoxin FM

CytK — Cytotoxin K

RFLP — Restriction fragment length polymorphism

MLST — Multi-locus sequence typing

WGS — Whole-genome sequencing

ANI — Average nucleotide identity

PEMBA — Polymyxin pyruvate egg yolk mannitol bromothymol blue agar

MIC — Minimum inhibitory concentration

CDF — Cation diffusion facilitator

RND — Resistance-nodulation-division (transporter system)

SIDA — Stable isotope dilution assay

LC-MS/MS — Liquid chromatography-tandem mass spectrometry

MALDI-TOF — Matrix-assisted laser desorption/ionisation-time of flight

ISO — International Organization for Standardisation

EFSA — European Food Safety Authority

DNM — DNA nanomachine

SNV — Single-nucleotide variant

CFU — Colony-forming unit

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