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# *Bacillus cereus sensu lato* antimicrobial arsenal: An overview

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ABSTRACT

The *Bacillus cereus* group contains genetically closed bacteria displaying a variety of phenotypic features and lifestyles. The group is mainly known through the properties of three major species: the entomopathogen *Bacillus thuringiensis*, the animal and human pathogen *Bacillus anthracis* and the foodborne opportunistic strains of *B. cereus sensu stricto*. Yet, the actual diversity of the group is far broader and includes multiple lifestyles. Another less-appreciated aspect of *B. cereus* members lies within their antimicrobial potential which deserves consideration in the context of growing emergence of resistance to antibiotics and pesticides, and makes it crucial to find new sources of antimicrobial molecules. This review presents the state of knowledge on the known antimicrobial compounds of the *B. cereus* group members, which are grouped according to their chemical features and biosynthetic pathways. The objective is to provide a comprehensive review of the antimicrobial range exhibited by this group of bacteria, underscoring the interest in its potent biocontrol arsenal and encouraging further research in this regard.

## 1. Introduction

The *Bacillus cereus* group contains closely related bacteria exhibiting a broad range of properties associated with their diverse lifestyles (Jensen et al., 2003). Some members have known biotechnological applications, while others may pose a potential health risk (Ehling-Schulz et al., 2019). Eight historic species compose this group, for which the phylogeny has been intensively studied and the classification regularly discussed. On the bright side, *Bacillus thuringiensis* produces entomocidal toxins (Cry and Cyt proteins) and has been used as biopesticide for more than six decades. Another valued member is *Bacillus toyonensis* that possesses probiotic features used in animal husbandry. On the darker side, some strains of *B. cereus sensu stricto* (*s.s.*) are considered as foodborne pathogens due to their ability to cause the emetic and/or diarrhoeal syndromes, while *Bacillus anthracis* is the causal agent of anthrax disease. Another potential human pathogen is the thermotolerant *Bacillus cytotoxicus* for which some strains have also been associated to diarrhoeal syndromes and lethality. In the grey zone are the less studied species *Bacillus mycoides* and *Bacillus pseudomycoides*, forming rhizoid colonies, or the psychrotolerant *Bacillus weihenstephanensis*. New members, exhibiting distinct characteristics from previously documented species, have been reported, some of which being associated with human illnesses (e.g. *Bacillus paranthracis* , Bukharin et al., 2019) or antibiotic production (e.g. *Bacillus clarus*, Méndez Acevedo et al., 2020).

Besides this large lifestyle spectrum, antimicrobial compounds (AMCs) have also been frequently reported among members of the *B. cereus* group. The present review aims to provide a detailed overview of antimicrobial compounds produced by bacteria related to *B. cereus sensu lato* (*s.l.*) and to shed light on their properties. For the sake of clarity, this work focuses on AMCs produced by the eight historical *B. cereus* species and tested for antifungal and/or antibacterial activities. They are listed according to their chemical nature and biosynthetic pathways. Antimicrobial compounds reported from genome mining analysis, but not experimentally characterised and assessed for their activity, are discussed but not listed in the tables. The different mechanisms displayed by the various *B. cereus s.l.* antimicrobial molecules are illustrated in Fig. 1.

## 2. Amino acid-based antimicrobial compounds

The majority of *B. cereus s.l.* antimicrobial compounds contain amino acids (aa) which are used as building blocks of peptides, proteins or other complex molecules. Two synthetic pathways are recognised, namely the ribosome-dependent and ribosome-independent pathways.

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### 2.1. Ribosomally synthesized peptides

#### 2.1.1. Bacteriocins

Bacteriocins are defined as antibacterial ribosomally-synthesised peptides produced by bacteria (Chopra et al., 2015; Klaenhammer, 1988). The width of their target spectrum varies greatly, allowing their use as alternatives to classical chemical antibiotics or food preservatives (Cotter et al., 2013; O'Connor et al., 2020). Different bacteriocin classifications have been proposed over the years. In particular, the one established by Abriouel and his collaborators (2010) has been used as a reference for the *Bacillus* bacteriocins, but new classes have been described since. Therefore, the classification proposed by Acedo et al. (2018) is used in this review (Table 1). Note that a recent review on Bacilli bacteriocins can be found in Vaca et al. (2022).

As indicated in Table 1, class I contains post-translationally modified bacteriocins while class II comprises non-modified bacteriocins and class III gathers the larger bacteriocins (i.e. more than 10 kDa). Each class is divided into subclasses according to their structure, and some subclasses are themselves divided into different categories (Acedo et al., 2018). As shown in Table 2, the number and diversity of bacteriocins produced by *B. cereus* members are remarkable. Most of them belong to class I (Table 2, Fig. S1), among which lantibiotics and sactibiotics are the most abundant. However, many bacteriocins found in *B. cereus s.l.* have not been fully characterized yet (e.g. Risøen et al., 2004) and remain unclassified (Table 2). Similarly, although potent bacteriocins have been detected in genomes of *B. cereus*, their production and characterisation remain to be investigated. This encompasses heterocycloanthracins, a subgroup of thiazole/oxazole-modified microcins, and paeninodin, a lassopeptide (Fayad et al., 2021; Haft, 2009; Hollensteiner et al., 2017). Also, no class III bacteriocins have been reported in *B. cereus s.l.* so far.

Lantibiotics designate lanthipeptides displaying antimicrobial properties (Arnison et al., 2013). These molecules are polycyclic peptides characterised by the presence of 2,3-didehydroalanine (Dha) and (*Z*)-2,3-didehydrobutyrine (Dhb) formed by dehydration of serine and threonine residues, respectively, which can be cyclised with cysteine residues to form lanthionine (Lan) or methyl-lanthionine (MeLan) thioester bridges (Barbosa et al., 2015). Lanthipeptides are commonly produced by Firmicutes (Heilbronner et al., 2021), including by the *B. cereus* group (Table 2). This was confirmed by genome mining analyses that revealed *B. cereus s.l.* as an excellent reservoir of lantibiotics (Xin et al., 2015b).

The sactipeptide class has been recently defined. Antimicrobial sactipeptide or sactibiotic are bacteriocins containing thioester linkage between a cysteine sulfur and the α-carbon of another aa (Fig. S1) (Rea et al., 2011). Several well-characterised sactibiotics are produced by *B. cereus s.l.*: thuricin CD, thurincin H, thuricin S and thuricin Z (Table 2) (Chen et al., 2021). They were previously grouped in the class II subclass of "thuricin-like peptides" as they all share a particular conserved "DWTXWSXL" motif. This N-terminus pattern is also shared with other, not fully characterised, bacteriocins: bacthuricin F4, tolworthcin 524, thuricin 17, cerein MRX1 (Abriouel et al., 2010). Based on sequence similarity, these non-fully characterised bacteriocins could be part of sactibiotics, but structural elucidation is needed to confirm this grouping.

*B. cereus s.l.* bacteriocins are mostly active against Gram-positive bacteria, including other *Bacillus*, while only a limited number have shown to exhibit antibacterial activity against Gram-negative bacteria (e.g. thiocillins - Chan and Burrows, 2021a, or thuricin S - Chehimi et al., 2007; 2010). The main mode of action of bacteriocins from Gram-positive bacteria is the formation of pores in the membrane of the target cell, but other mechanisms have been reported such as the inhibition of peptidoglycan synthesis (Acedo et al., 2018; Cotter et al., 2013), or protein synthesis, as illustrated by the thiocillin thiopeptides (Fig. S1F,) that bind to 50 S ribosomal subunit (Chan and Burrows, 2021b; Vinogradov and Suga, 2020). For most *B. cereus s.l.* bacteriocins, their mechanisms of action have been inferred by analogy to other well-known bacteriocins. For lantibiotics, two mechanisms have been identified: inhibition of cell wall synthesis by attachment to the lipid II and/or pore formation (Barbosa et al., 2015). Cellular membrane damages caused by andalusicin a and bicereucin were reported to be

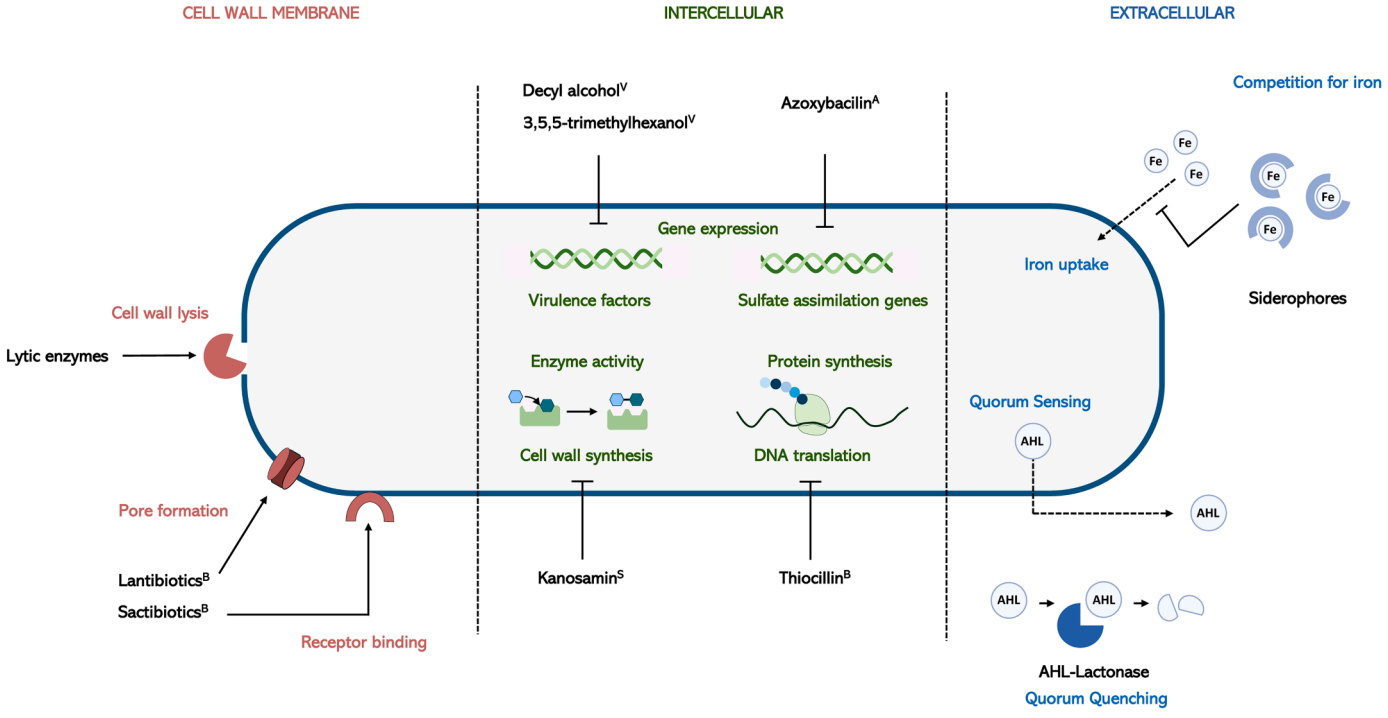


**Fig. 1.** Summary of the mechanisms of antimicrobial molecules originating from *Bacillus cereus s.l.* Three distinct types of mechanism can be distinguished based on the location of the inhibition event: cell envelop (cell wall or membrane), intracellular or extracellular. Abbreviations are as follows: A, amino acid derivatives, AHL: N-Acyl Homoserine Lactone, B: bacteriocins, Fe: iron, S: sugar derivatives and V: volatile compounds.

similar to the one observed with nisin, a pore-forming lantibiotic, but the exact mechanism remains to be determined (Fan et al., 2022; Huo and van der Donk, 2016). In the case of sactibiotics, their high potency, and in some cases narrow specificity, suggested that they target specific (yet unknown) receptors, but several modes of action could be present in this subclass (Acedo et al., 2018; Arnison et al., 2013). Among them, thuricins CD, S and Z effects on bacteria are similar to those caused by nisin (Chehimi et al., 2010; Mathur et al., 2017; Mo et al., 2019), while thurincin H, as it has been shown to interfere with cell integrity and rigidity which differs from the effects observed with nisin, is suggested to use another mechanism (Wang et al., 2014a).

Interestingly, bacteriocins also have other biological effects, notably antifungal (e.g. cerein 8 A, entomocin 9 and morrocin 269, active against ascomycetes) (Table 2) and, in the case of thuricin 17, plant growth stimulation (Lee et al., 2009b), which extends their potential beyond bactericidal applications.Table 1,Table 2

### 2.1.2. Antimicrobial proteins

As indicated in Table 3, three classes of antimicrobial proteins can be distinguished based on their primary mode of action: quorum quenching (QQ), cell wall degradation, and entomotoxicity. As indicated below, it should be noted that members of the last group are better known for their entomocidal activities than their antimicrobial ones.

The ability of bacteria to regulate the expression of specific genes based on their population density is referred to as quorum sensing (QS). By contrast, the inhibition of QS is called quorum quenching. Activation of QS can trigger the virulence of some pathogenic bacteria and, as a consequence, its inactivation by QQ results in silencing the virulence behaviour. N-acyl homoserine lactone (AHL) is a well-characterised mediator of QS signal used by Gram-negative bacteria. Since AHL regulates different biological functions, including the production of virulence factors or the formation of biofilm, it is an attractive target for QQ. Such approach has been demonstrated against the plant pathogen *Pectobacterium carotovorum* using strains of *B. cereus s.l.* that produce AHL-lactonase (Table 3) (Dong et al., 2002; 2004; Lee et al., 2002; Park et al., 2008). AHL lactonase activity has also been associated with the biological control of other plant pathogens such as *Agrobacterium tumefaciens*, *Pseudomonas syringae*, and the human pathogen *Pseudomonas aeruginosa* (Ananda et al., 2019; Raafat et al., 2019; Zamani et al., 2013).

Lytic enzymes like chitinases or glucanases can breach cell wall constituents leading to the cell lysis and death. Chitinases are widespread among *B. cereus s.l.* and they have mainly been studied in *B. thuringiensis* in the frame of their insecticidal role (Martínez-Zavala et al., 2020). Nevertheless, as shown in Table 3, their activities have been demonstrated towards several plant pathogens as well, including *Ascomycota, Basidiomycota, Mucoromycota* and *Oomycota*. These proteins are indeed particularly interesting to control fungal diseases since their cell walls are also primarily made of chitin and glucans and their use against fungal pathogens has been suggested using *B. cereus s.l.* (Caulier et al., 2018; Jadhav et al., 2017; Shrestha et al., 2015). Similarly, Hollensteiner and coll. reported the antagonistic activity of several *B. thuringiensis* and *B. weihenstephanensis* against *Verticillium* species and suggested that chitinases could be responsible for this effect (Hollensteiner et al., 2017).

As already indicated, *B. thuringiensis* has been used for several decades in the control of specific insects, mainly crop pests or vectors of human and animal diseases. The two major types of insecticidal proteins, both produced during sporulation, are the Cry- and Cyt-toxins (Crickmore et al., 2021). Besides their known activity towards insect larvae, experiments have suggested their potential antimicrobial potential (Cahan et al., 2008; Kamenek et al., 2012; Yudina et al., 2003), but these presumptive activities remain to be adequately confirmed.

Finally, a rather unusual way of niche colonization was reported in milk where a *B. cereus* strain was shown to secrete endoproteases that generate antimicrobial peptides from casein (Ouertani et al., 2018). Similar competitive mechanisms might occur in other specific environments.Table 3

**Table 1**
Classification of bacteriocins from Gram-positive bacteria (Acedo et al., 2018).

| Classes | Subclasses | Main characteristics |
|---|---|---|
| Class I – Post-translationally modified | **Lantibiotic** | (Methyl)lanthionine residues |
| | **Sactibiotic** | Cysteine sulfur to α-carbon bridges |
| | **Circular bacteriocin** (Head-to-tail cyclised bacteriocin) | N- to C-terminal cyclization |
| | **Glycocin** | Glycosylated residue(s) |
| | **Thiopeptide** | 6-membered nitrogen heterocycle, azol(in)e rings, dehydro residues |
| | Lassopeptide | N-terminal amine to γ -acid residue cyclization, C-terminal tail threaded through ring |
| | Bottromycin | Macrocyclic amidine, decarboxylated C-terminal thiazole, β-methylated residues |
| | Linear azol(ine)-containing bacteriocin | Thiazole and (methyl)oxazole rings, linear backbone |
| | Lipolanthine | N-terminal fatty acid, avionin moiety (aminovinylcysteine-labionin hybrid) |
| Class II – Non-modified | YGNG-motif containing bacteriocins (pediocin-like) | YGNG consensus motif, minimum one disulfide bridge |
| | Two-peptides bacteriocin | Act as one unit for synergistic activity* |
| | **Leaderless** | Produced with no leader sequence |
| | **Other linear non-modified bacteriocins** | Single linear non-leaderless-peptide bacteriocins |
| Class III – Large peptides | Bacteriolysin | Large bacteriolytic bacteriocins |
| | Non-lytic | Large non-bacteriolytic bacteriocins |
| | Tailocin | Multi-protein complex, bacteriophage tail-like structure |

*Activity is optimal when both peptides are present in equimolar concentration (Acedo et al., 2018).
The sub-classes of bacteriocins in bold are those produced by *B. cereus* group members.

## 2.2. Ribosomally-independent synthesized peptides

Classification of ribosome-independent peptide biosynthesis pathways has recently been based on the enzymes involved, resulting in five classes (Dell et al., 2022). The first three types comprise non-ribosomal peptide synthases (NRPSs) that use a thiotemplate mechanism to bind their substrate during the peptide synthesis, and are differentiated on the basis of their domain organisation. The last two classes are non-thiotemplate enzymes discriminated by their dependence on aminoacyl-tRNA as substrate Table 4.

### 2.2.1. Peptides from non-ribosomal peptides synthases (NRPSs)

The detailed synthesis mechanisms used by NRPSs have been described in different reviews (e.g. Dell et al., 2022; Süssmuth and Mainz, 2017). Briefly, the main domains of NRPSs are the adenylation (A), condensation (C) and thiolation (peptidyl carrier protein - PCP or T) domains, responsible for the recruitment, transport and incorporation of the aa in the forming peptide chain, respectively. A last thioesterase domain (TE) catalyses the reaction to release the peptide from the NRPS. Other additional domains can be present in NRPSs, adding modifications to the peptide chain, and creating various compound structures (Miller and Gulick, 2016). Type I NRPSs are mega-enzymes organised in multimodal and acting as assembly lines. Each module is responsible for the incorporation of one aa into the peptide chain. Type II NRPSs are similar to type I but are composed of catalytic units non-covalently bound to each other (Jaremko et al., 2020). Type III NRPSs do not use

**Table 2**
Bacteriocins from *B. cereus s.l.*

| Class | Subclass | Name | Molecular weight [kDa] | Producer | Antibacterial activity | Reference |
|---|---|---|---|---|---|---|
| I | Lantibiotic | Andalusicin | 2.26 | *B. thuringiensis* sv. *andalousiensis* NRRL B23139 | **Gram** +: *Arthrobacter* sp., *B. cereus, B. mycoides, Paenibacillus polymyxa, Staphylococcus aureus* | Grigoreva et al., (2021) |
| | | Bicereucin | Bsjα: 3.48; Bsjβ: 4.10 | *B. cereus* SJ1 | **Gram** +: *Bacillus subtilis, Enterococcus faecium, Lactococcus lactis, Micrococcus luteus, S. aureus, Staphylococcus epidermidis, Streptococcus mutans* | Huo and van der Donk, (2016) |
| | | Cerecidin A1 | 1.99 | *B. cereus* As 1.1846 | **Gram** +: *B. cereus, Bacillus pumilus, B. subtilis, B. thuringiensis, Enterococcus durans, Enterococcus faecalis, Enterococcus pernyi, Lactobacillus acidophilus, Lactobacillus buchneri, Lactobacillus coprophilus, Lactobacillus curvatus, Lactobacillus plantarum, Lactobacillus rhamnosus, L. lactis, Leuconostoc dextranicum, Levilactobacillus brevis, Micrococcus flavus, S. aureus, Streptococcus bovis, Streptococcus gordonii, Streptococcus salivarius, Streptococcus thermophilus* | Wang et al., (2014b) |
| | | Cerecidin A7 | 1.96 | *B. cereus* As 1.1846 | **Gram** +: *B. cereus, B. pumilus, B. subtilis, B. thuringiensis, E. durans, E. faecalis, E. pernyi, L. acidophilus, L. buchneri, L. coprophilus, L. curvatus, L. plantarum, L. rhamnosus, L. lactis, L. dextranicum, L. brevis, M. flavus, S. bovis, S. gordonii, S. salivarius, S. thermophilus* | *Ibid.* |
| | | Pseudomycoicidin | 2.79 | *B. pseudomycoides* DSM 12442 | **Gram** +: *Bacillus* spp., *Enterococcus* spp., *Lactococcus* spp., *M. luteus, S. aureus, Staphylococcus simulans, Streptococcus* spp. | Basi-Chipalu et al., (2015); Janssen et al., (2022) |
| | | Thuricin 4A-4 | 2.784 | *B. thuringiensis* T01001 | **Gram** +: *B. cereus, Bacillus firmus, B. thuringiensis, B. pumilus, B. subtilis, E. faecalis, Microbacterium* sp., *Paenibacillus* sp., *S. aureus, Staphylococcus sciuri* | Xin et al., (2015a) |
| | | Thuricin 4A-4d | 2.89 | *Ibid.* | *Ibid.* | *Ibid.* |
| | | Thusin | Thsα: 3.93; Thsβ: 2.91 | *B. thuringiensis* BGSC 4BT1 | **Gram** +: *Bacillus amyloliquefaciens, B. cereus, B. pumilus, B. subtilis, B. thuringiensis, E. faecalis, Listeria monocytogenes, S. aureus, S. sciuri, Streptococcus pneumoniae* | Xin et al., (2016) |
| | | Ticin A1 | 4.06 | *B. thuringiensis* BMB3201 | **Gram** +: *B. amyloliquefaciens, B. cereus, B. firmus, B. thuringiensis, B. subtilis, B. pumilus, E. faecalis, L. monocytogenes, Paenibacillus* sp., *S. aureus, S. sciuri* | Xin et al., (2015b) |
| | | Ticin A3 | 4.05 | *Ibid.* | *Ibid.* | *Ibid.* |
| | | Ticin A4 | 4.06 | *Ibid.* | *Ibid.* | *Ibid.* |
| | Sactibiotic | Huazacin (Thuricin Z) | 12.41 | *B. thuringiensis* sv. *huazhongensis* | **Gram** +: *B. cereus, L. monocytogenes* | Hudson et al., (2019); Mo et al., (2019) |
| | | Thuricin CD | Trn-α: 2.76; Trn-β: 2.86 | *B. thuringiensis* DPC 6431 | **Gram** +: *B. firmus, Clostridioides difficile* | Mathur et al., (2017); Rea et al., (2010) |
| | | Thuricin S | 3.14 | *B. thuringiensis* sv. *entomocidus* HD198 | **Gram** +: *B. cereus, B. subtilis, B. thuringiensis sv. darmstadiensis, L. monocytogenes, Pediococcus acidilactici, S. thermophilus*<br>**Gram** -: *Pseudomonas aeruginosa, Pseudomonas fluorescens, Pseudomonas putida, Pseudomonas stutzeri, Salmonella choleraesuis, Salmonella enterica* sv. Enteritidis, *Salmonella* Newport, *Shigella flexneri* | Chehimi et al., (2007) |
| | | Thurincin H | 3.14 | *B. thuringiensis* SF361 | **Gram** +: *B. cereus, Bacillus megaterium, B. subtilis, B. thuringiensis, Enterococcus mundtii, Geobacillus stearothermophilus, Listeria innocua, Listeria ivanovii, L. monocytogenes, S. aureus* | Lee et al., (2009a); Ortiz-Rodríguez et al., (2023); Sit et al., (2011); Wang et al., (2014a) |
| | Circular | Bacicyclicin XIN-1 | 5.85 | *B. cereus s.l.* Xin1 | **Gram** +: *B. cereus, E. faecalis, E. faecium, L. monocytogenes, S. aureus, S. epidermidis, S. pneumoniae, Streptococcus pyogenes* | Xin et al., (2021) |
| | | Cerecyclin | 7.07 | *B. cereus* DDD103 | **Gram** +: *B. amyloliquefaciens, B. cereus, B. firmus, B. pumilus, B. subtilis, B. thuringiensis, E. faecalis, L. monocytogenes* | Xin et al., (2020) |
| | Glycocin | Bacillicin BAG2O | 3.65 | *B. cereus* BAG20 | **Gram** +: *B. cereus* | Ren et al., (2018) |
| | | Bacillicin CER074 | 4.58 | *B. cereus* CER074 | **Gram** +: *B. cereus* | *Ibid.* |
| | Thiopeptide | Thiocillin I | 1.16 | *B. cereus* G-15 and ATCC 14579 | **Gram** +: *B. anthracis, B. subtilis, S. aureus, S. pneumoniae, S. pyogenes*<br>**Gram** -: *Pseudomonas aeruginosa* | Chan and Burrows, (2021a); Shoji et al., (1976a); (1981); Wieland Brown et al., (2009) |
| | | Thiocillin II | 1.17 | *B. cereus* G-15 and ATCC 14579 | *Ibid.* | *Ibid.* |
| | | Thiocillin III* | 1.16 | *B. cereus* ATCC 14579 | *Ibid.* | *Ibid.* |
| | | Thiocillin IV | 1.16 | *B. cereus* ATCC 14579 | **Gram** +: *S. aureus, E. faecalis* | Wieland Brown et al., (2009); Son et al., (2023) |
| II | Leaderless | Cereucin H | CehA: 2.85; CehB: 3.14; CehC: 2.84; CehD: 2.99 | *B. cereus* HuA2–4 | **Gram** +: B. *subtilis, B. cereus, E. durans, E. faecalis, E. faecium, Lactococcus garvieae, L. lactis, L. plantarum, Latilactobacillus sakei, L. innocua, L. monocytogenes, Pediococcus pentosaceus, S. aureus, S. epidermidis* | Ovchinnikov et al., (2016) |

(*continued on next page*)

**Table 2** (*continued*)

| Class | Subclass | Name | Molecular weight [kDa] | Producer | Antibacterial activity | Reference |
|---|---|---|---|---|---|---|
| | | Cereucin V | CevA: 2.97; CevB: 2.83; CevC: 3.11 | *B. toyonensis* VD148 | *Ibid.* | *Ibid.* |
| | | Cereucin X | CexA: 2.94; CexB: 3.14; CexC: 2.79 | *B. cereus* BAG2O-1 | *Ibid.* | *Ibid.* |
| | | Thucin A1 | 5.55 | *B. thuringiensis* P86 | **Gram** +: *B. cereus, B. firmus, B. pumilus, Bacillus siamensis, Bacillus simplex, B. subtilis, B. thuringiensis, Glutamicibacter arilaitensis, L. monocytogenes, Lysinibacillus fusiformis, Rhodococcus sp., S. aureus, Staphylococcus succinus* | Zhang et al., (2022) |
| | | Toyoncin | 7.82 | *B. toyonensis* XIN-YC13 | **Gram** +: *B. cereus, L. monocytogenes* | Wang et al., (2021) |
| | Other | Cerein 7 A | 3.94 | *B. cereus* Bc7 | **Gram** +: *B. cereus, B. subtilis, Clostridium acetobutylicum, Clostridium botulinum, Clostridium butyricum, Clostridium perfringens, Enterococcus avium, G. stearothermophilus, L. lactis, L. lactis subsp. cremoris, L. innocua, L. ivanovii, L. monocytogenes, Listeria seeligeri, M. luteus, S. aureus, S. bovis, Streptococcus equinus* | Oscáriz et al., (1999) |
| | | Cerein 7B | 4.89 | *Ibid.* | **Gram** +: *L. lactis* | Oscáriz et al., (2006) |
| ND | ND | Bacthuricin F103 | ca. 11.00 | *B. thuringiensis* BUPM103 | **Gram** +: *B. cereus, Bacillus licheniformis, B. subtilis, B. thuringiensis, L. monocytogenes*<br>**Gram** -: *Agrobacterium tumefaciens* | Kamoun et al., (2011) |
| | | Bacthuricin F4*** | 3.16 | *B. thuringiensis* BUPM4 | **Gram** +: *B. cereus, B. licheniformis, B. subtilis, B. thuringiensis* sv. *kurstaki*, *Brevibacterium flavum, S. aureus*<br>**Gram** -: *Klebsiella pneumoniae* | Kamoun et al., (2005) |
| | | BLISm387 | ND | *B. cereus* m387 | **Gram** +: *B. cereus, B. megaterium, B. mycoides, B. subtilis, B. thuringiensis, Paenibacillus larvae, Paenibacillus macerans* | Minnaard and Alippi, (2016) |
| | | BLISm6c | ND | *B. cereus* m6c | **Gram** +: *B. mycoides, B. subtilis, B. thuringiensis, P. larvae, P. macerans* | *Ibid.* |
| | | BtCspB | ND | *B. thuringiensis* BRC-ZYR2 | **Gram** +: *B. cereus* | Huang et al., (2016); Jin et al., (2019) |
| | | Cerein 8 A** | ca. 26 | *B. cereus* 8 A | **Gram** +: *B. cereus, Bacillus coagulans, B. subtilis, Brevibacterium linens, Cellulomonas fimi, C. perfringens, Clostridium septicum, E. faecalis, G. stearothermophilus, L. acidophilus, L. innocua, L. monocytogenes, M. luteus, P. macerans, S. bovis, Streptococcus uberis*<br>**Gram** -: *Pasteurella haemolytica, Salmonella* Enteritidis | Bizani and Brandelli, (2002); Bizani et al., (2005a); (2005b); (2008); Lappe et al., (2009) |
| | | Cerein BS229 | ca. 8.20 | *B. cereus* BS229 | **Gram** +: *B. cereus, B. pumilus, B. subtilis, B. thuringiensis, M. flavus, Propionibacterium thoenii*<br>**Gram** -: *Escherichia coli* | Paik et al., (2000) |
| | | Cerein GN105 | ca. 9.00 | *B. cereus* GN105 | **Gram** +: *B. cereus* | Naclerio et al., (1993) |
| | | Cerein MRX1*** | 3.14 | *B. cereus* MRX1 | **Gram** +: *Bacillus badius, B. cereus, Bacillus circulans, B. coagulans, B. licheniformis, Bacillus maroccanus, B. megaterium, B. mycoides, B. subtilis, B. pumilus, B. weihenstephanensis, Bacillus laterosporus, C. acetobutylicum, Clostridium saccharoperbutylacetonicum, E. faecium, E. faecalis, L. lactis subsp. Lactis, L. plantarum, L. sakei* subsp. *sakei, L. innocua, Leuconostoc mesenteroides, L. brevis, M. luteus, Paenibacillus alvei, P. macerans, P. polymyxa, P. pentosaceus, S. aureus, S. epidermidis, S. bovis, Virgibacillus pantothenticus*<br>**Gram** -: *E. coli, Pseudomonas oleovorans* | Sebei et al., (2007) |
| | | Entomocin 110 | ca. 4.80 | *B. thuringiensis* sv. *entomocidus* HD110 | **Gram** +: *B. cereus, B. coagulans, B. megaterium, B. mycoides, B. pseudomycoides, B. thuringiensis, B. weihenstephanensis, L. lactis, L. monocytogenes, P. alvei, P. larvae, P. polymyxa* | Cherif et al., (2008) |
| | | Entomocin 420 | ca. 10.00 | *B. thuringiensis* sv. *entomocidus* LBIT 420 | **Gram** +: *B. cereus, B. subtilis, B. thuringiensis, E. faecium, L. innocua*<br>**Gram** -: *Vibrio cholerae* | Barboza-Corona et al., (2007); de la Fuente-Salcido et al., (2008) |
| | | Entomocin 9** | ca. 12.40 | *B. thuringiensis* sv. *entomocidus* HD9 | **Gram** +: *B. cereus, B. mycoides, B. pseudomycoides, B. thuringiensis, B. weihenstephanensis, Lactobacillus spp., L. lactis, L. monocytogenes*<br>**Gram** -: *P. aeruginosa* | Cherif et al., (2003) |
| | | Kenyacin 404 | ca. 10.00 | *B. thuringiensis* sv. *kenyae* LBIT 404 | *Ibid.* | Barboza-Corona et al., (2007); de la Fuente-Salcido et al., (2008) |
| | | Kurstacin 287 | ca. 10.00 | *B. thuringiensis* sv. *kurstaki* LBIT 287 | **Gram** +: *B. cereus, B. thuringiensis*<br>**Gram** -: V. cholerae | *Ibid.* |
| | | Morricin 269** | ca. 10.00 | *B. thuringiensis* sv. *morrisoni* LBIT 269 | *Ibid.* | *Ibid.* |
| | | Thuricin 17*** | 3.16 | *B. thuringiensis* NEB17 | **Gram** +: *B. cereus, B. licheniformis, B. megaterium, B. pumilus, B. thuringiensis, G. stearothermophilus, L. brevis,* | Gray et al., (2006) |

(*continued on next page*)

**Table 2** (*continued*)

| Class | Subclass | Name | Molecular weight [kDa] | Producer | Antibacterial activity | Reference |
|---|---|---|---|---|---|---|
| | | | | | *P. polymyxa, Paenibacillus dendritiformis*<br>**Gram -**: *E. coli* | |
| | | Thuricin 4AJ1 | ca. 6.5 | *B. thuringiensis* 4AJ1 | **Gram +**: *B. cereus* | Su et al., (2020) |
| | | Thuricin 439 | A: 2.92;<br>B: 2.80 | *B. thuringiensis* B439 | **Gram +**: *B. cereus, B. thuringiensis, L. innocua* | Ahern et al., (2003) |
| | | Thuricin 7 | ca. 11.60 | *B. thuringiensis* BMG 1.7 | **Gram +**: *B. cereus, B. mycoides, B. pseudomycoides, B. subtilis, B. thuringiensis, B. weihenstephanensis, L. monocytogenes, S. pyogenes* | Cherif et al., (2001) |
| | | Thuricin Bn1 | 3.14 | *B. thuringiensis* sv. *kurstaki* Bn1 | **Gram +**: *B. cereus, B. thuringiensis, B. weihenstephanensis, L. monocytogenes*<br>**Gram -**: *Paucimonas lemoignei, Pseudomonas savastanoi, Pseudomonas syringae* | Ugras et al., (2013) |
| | | Thuricin HD-2 | ND | *B. thuringiensis* HD2 | **Gram +**: *B. thuringiensis* | Favret and Yousten, (1989) |
| | | Tochicin | ca. 10.50 | *B. thuringiensis* sv. *tochigiensis* HD868 | **Gram +**: *B. cereus, B. thuringiensis, L. mesenteroides subsp mesenteroides* | Paik et al., (1997) |
| | | Tolworthcin 524*** | ca. 6.00 | *B. thuringiensis* sv. *tolworthi* LBIT 524 | **Gram +**: *B. cereus, B. subtilis, B. thuringiensis, E. faecalis, E. faecium, L. innocua, L. monocytogenes, Micrococcus* sp., *S. aureus, Staphylococcus xylosus* | Barboza-Corona et al., (2007); Pacheco-Cano et al., (2014) |

* Antibacterial activity was determined by thiocillin III produced by *B. badius* AR-91 (Shoji et al., 1976a). Thiocillin III was later discovered in *B. cereus* ATCC 14579 (Wieland Brown et al., 2009).

** Antifungal activity:

Cerein 8 A: Ascomycetes: *Penicillium* sp. (Bizani and Brandelli, 2002).

Morricin 269: Ascomycetes: *Fusarium oxysporum*, *Mucor rouxii, Rhizopus* sp., *Trichoderma* sp. (de la Fuente-Salcido et al., 2008).

Entomocin 9: Ascomycetes: *Aspergillus nidulans, Fusarium graminis* (Cherif et al., 2003).

*** Thuricin-like bacteriocin or potential sactibiotic (shares N-terminal motif with thuricin S but lacks information to class the compound as sactibiotic).

**Table 3**
Antimicrobial proteins from the *B. cereus* group.

| Class/Activity | Name | Producer | Antimicrobial activity | | References |
|---|---|---|---|---|---|
| | | | Antibacterial | Antifungal | |
| Quorum quenching | AHL-lactonase | *B. thuringiensis* sv. *israelensis* 4Q7 | **Gram -**: *Pectobacterium carotovorum* | ND | Park et al., (2008) |
| | | *B. thuringiensis* sv. *israelensis* B23 | **Gram -**: *P. carotovorum* | ND | Dong et al., (2004) |
| Cell wall degradation | Chitinase Chi255 | *B. thuringiensis* BUPM255 | ND | **Ascomycetes**: *Aspergillus niger* | Driss et al., (2005) |
| | Chitinase ChiA Btt | *B. thuringiensis* sv. *tenebrionis* DSM 2803 | ND | **Ascomycetes**: *Colletotrichum gloeosporioides* | de la Fuente-Salcido et al., 2016 |
| | Chitinase A | *B. thuringiensis* sv. *colmeri* | ND | **Ascomycetes**: *Botrytis cinerea, Penicillium chrysogenum, Penicillium glaucum, Phylasospora piricola*<br>**Basidiomycetes**: *Rhizoctonia solani* | Liu et al., (2010a) |
| | Chitinase A | *B. cereus s.l.* B25 | ND | **Ascomycetes**: *Fusarium verticillioides* | Morales-Ruiz et al., (2021) |
| | Chitinase chiCW | *B. cereus* 28–9 | ND | **Ascomycetes**: *Botrytis elliptica* | Huang et al., (2005) |
| | Chitinase B | *B. cereus s.l.* B25 | ND | **Ascomycetes**: *F. verticillioides* | Morales-Ruiz et al., (2021) |
| | Chitinase ChiIO8 | *B. cereus* IO8 | ND | **Ascomycetes**: *Alternaria citri, Alternaria solani, A. nidulans, Fusarium sambucinum, Fusarium solani, Penicillium occitanis, Verticillium dahliae*<br>**Oomycetes**: *Phytophthora capsici* | Hammami et al., (2013) |
| | Chitinase | *B. cereus* YQ 308 | ND | **Ascomycetes**: *F. oxysporum, F. solani*<br>**Oomycetes**: *Pythium ultimum* | Chang et al., (2003) |
| | Chitinase | *B. thuringiensis* H3 | ND | **Ascomycetes**: *Fusarium graminearum, F. oxysporum* f. sp. *vasinfectum, Pyricularia grisea*<br>**Basidiomycetes**: *Thanatephorus cucumeris* | Tang et al., (2012) |
| | Chitinase | *B. thuringiensis* sv. *aizawai* | ND | **Ascomycetes**: *Athelia* (*Sclerotium*) *rolfsii, Fusarium* sp., *Helminthosporium* sp., *Macrophomina phaseolina, Pestalotia* sp. | de la Vega et al., (2006) |
| | Chitinase | *B. thuringiensis* NM101–19 | ND | **Ascomycetes**: *Aspergillus flavus, A. niger, Aspergillus terreus, F. oxysporum, Fusarium* sp.<br>**Mucoromycetes**: *Rhizopus* sp. | Gomaa, (2012) |

**Table 4**
Ribosome-independent peptide biosynthesis classification (Dell et al., 2022).

| Enzyme type | Description |
|---|---|
| I | Thio-templated and modular peptide synthetases. Type I NRPS |
| II | Thio-templated and freestanding peptide synthetases. Type II NRPS |
| III | Thio-templated, freestanding and non-canonical peptide synthetases Type III NRPS |
| IV | Non thio-templated and tRNA-independent peptide synthetases |
| V | Non thio-templated and tRNA-dependent peptide synthases |

typical C domain to bind the aa together, but do instead require proteases or ATP-dependent enzymes (Dell et al., 2022). NRPSs possess a broad range of substrates beyond the 20 canonical aa and can use non-proteinogenic aa as well (Koglin and Walsh, 2009). In fact, NRPSs can potentially use more than 500 different building blocks (Flissi et al., 2020). Besides, tailoring enzymes can provide further modifications (Walsh et al., 2001). Atypical NRPSs with non-canonical organisation or rare domains have also been described (Duban et al., 2022).

*2.2.1.1. Cereulide.* The emetic cereulide toxin is a cyclic dodecadepsipepide (Fig. S2) produced by some strains of *B. cereus s.s.* and *B. weihenstephanensis*, often referred to as emetic strains (Ehling-Schulz et al., 2005a; Guérin et al., 2017; Thorsen et al., 2006). The cereulide biosynthetic gene cluster is located on the mega plasmid pCER270 (Ehling-Schulz et al., 2006; Hoton et al., 2005). Cereulide production is ensured by the enzyme CesNRPS, a heterodimer of CesA and CesB, which uses an iterative process (Ehling-Schulz et al., 2005b; 2006). Cereulide is resistant to proteases, heat and extreme pH and it maintains its pathogenic activity even after food processing (Agata et al., 1995; Rajkovic et al., 2008; Shinagawa et al., 1995). Cereulide is considered as highly toxic. It is assumed that its virulence mechanism is based on the disruption of the ionic balance of cells and the transmembrane potential of mitochondria, which can lead to harmful damage to the liver or other organs, and even death in case of severe infection (Dierick et al., 2005; Rouzeau-Szynalski et al., 2020). Strikingly, cereulide structure is similar to the antibiotic valinomycin. The antimicrobial activity of cereulide has also been observed against Gram-positive bacteria (Tempelaars et al., 2011) and fungal phytopathogens (Ladeuze et al., 2011) (Table 5), suggesting its potential involvement into the ecology of the producing strains (Ladeuze et al., 2011; Jenull et al., 2023; Tempelaars et al., 2011).

*2.2.1.2. Lipopeptides.* Lipopeptides (LPs) are composed of a hydrophilic peptide joined to a hydrophobic carbon chain. The attachment of the fatty acid chain to the peptide moiety is set up by a condensation domain present in the NRPS initiation module (Bloudoff and Schmeing, 2017; Ongena and Jacques, 2008). This structure confers to LPs amphiphilic and biosurfactant properties. LPs are involved in different functions such as antagonism, biofilm formation, motility and surface attachment (Raaijmakers et al., 2010). It is assumed that their antimicrobial properties are driven by their ability to interact with the cell membrane of microorganisms and to form deleterious pores (Deleu et al., 2013; Etchegaray et al., 2008; Wu et al., 2020b). A similar hypothesis applies to the stimulation of plant defences, which are activated by the interaction between LPs and plant cell membranes. However, in both cases, the detailed mechanisms remain mostly elusive (Crouzet et al., 2020). Surfactin, fengycin (or plipastatin) and iturin are three main LP families traditionally described for *Bacillus* sp. Although lipopeptides were mainly reported from the *Bacillus subtilis* group, members of *B. cereus s.l.* produce antimicrobial LPs too (Roy et al., 2013; Théatre et al., 2022) (Table 5 and Fig. S3).

Surfactin is an important LP family of cyclic heptapeptides often encountered among *B. subtilis* group members (Théatre et al., 2022). However, surfactin-like compounds are also present in *B. cereus s.l.* For instance, kannurin was identified in B. cereus AK1 and has a strong antifungal activity through a wide range of pH and temperatures (Ajesh et al., 2013). More recently, Kannurin variants and their antibacterial effects have also been characterized (Shabeer Ali et al., 2020). Another, yet not fully characterised surfacting-like LP has been reported from *B. thuringiensis* pak2310 together with its antifungal activity against *Fusarium graminearum* (Deepak and Jayapradha, 2015).

Plipastatins are cyclic lipodecapeptides discovered in *B. cereus* and reported as inhibitors of phospholipase A2 with antagonistic activity against *Corynebacterium bovis* (Nishikiori et al., 1986). Similarly, fengycin was described as an antifungal agent produced by *B. subtilis* (Vanittanakom et al., 1986). Fengycins and plipastatins are now considered as synonyms (Théatre et al., 2022). Fengycins are mainly reported among *B. subtilis* members, especially for their antifungal effects. Fengycin genetic determinants are often reported in *B. cereus s.l.* (Xia et al., 2022) but true production or characterisation of such compounds remain scarce. A fengycin-like compound was found in *B. thuringiensis* CMB26 (Kim et al., 2004) and the genetic determinants were also detected in other *B. cereus s.l.* strains (Athukorala et al., 2009; Hussein, 2019).

Other *B. cereus s.l.* LPs, unrelated to those of *B. subtilis* group, have also been described. Kurstakin is a LP family containing partially cyclic lipoheptapeptides and initially identified from *B. thuringiensis* sv. *kurstaki* HD1. Kurstakins seem to be specific to the *B. cereus* group and are involved in different functions such as biofilm formation (Gélis-Jeanvoine et al., 2017), antifungal activity against *Stachybotrys charatum* (black mould) (Béchet et al., 2012; Hathout et al., 2000) or the control of rice diseases (Yu et al., 2023).

Cerexins are linear cationic lipodecapeptides with antagonistic activity against Gram-positive bacteria (Cochrane et al., 2015; Shoji et al., 1975; 1976b). They were identified in two *B. cereus* strains, in different isoforms (Shoji et al., 1975; 1976b). New cerexin analogues have also been reported from *B. clarus* (Cochrane et al., 2015; Méndez Acevedo et al., 2020). Despite their promising antibacterial effects and their discovery dating nearly fifty years ago, only limited research has been conducted on cerexins and little is known about their biosynthesis.

Lately, a new biosynthetic gene cluster of a LP named thumolycin was found on a 312-kb plasmid from *B. thuringiensis* BMB171 through genome mining. Although its production was confirmed by chemical analysis, its structure has not been elucidated yet (Zheng et al., 2018). Other studies have reported antimicrobial effects of other *B. cereus s.l.* putative lipopeptides or biosurfactants identified through genetic determinants without identifying the actual molecules (Hsueh et al., 2007; Ming et al., 2022; Sriram et al., 2011; Tapi et al., 2010).

*2.2.1.3. Siderophores.* Siderophores are secondary metabolites chelating iron, which makes them essential in terms of competition. Siderophores classification is based on their chelating moieties (Kramer et al., 2020). Bacillibactin and petrobactin are two catecholic siderophores found in the *B. cereus* group (Fig. S4) (Wilson et al., 2006). Both are produced by two distinct ribosomal-independent pathways. Bacillibactin is synthesised by a hybrid type I/II NRPS pathway using an iterative process (Hotta et al., 2010; Jaremko et al., 2020; May et al., 2001) while petrobactin synthesis uses a type I/III NRPS combination (Dell et al., 2022; Hagan et al., 2016). Different biological effects of siderophores have been reported, including plant growth promoters, bio-remediators and antibiotics (Ahmed and Holmström, 2014). *B. cereus s.l.* siderophores are mainly studied for their role in the virulence of pathogenic strains (Hagan et al., 2016; Hotta et al., 2010; Segond et al., 2014) but their roles could be more versatile since antifungal effects of bacillibactin, produced by members of the *B. subtilis* group members have been observed (Chakraborty et al., 2022; Dimopoulou et al., 2021). In addition, siderophore production of *B. cereus* NRRL 100132 was suggested to facilitate the competitive exclusion effect against the fish pathogen *Aeromonas hydrophila* (Lalloo et al., 2010).

**Table 5**
Antimicrobial NRPS and NRPS/PKS hybrid from the *B. cereus* group.

| Class | Subclass | Name | Producer | Antimicrobial activity | | Reference |
|---|---|---|---|---|---|---|
| | | | | Antibacterial | Antifungal | |
| NRP | Cyclic dodecadepsipeptide | Cereulide | *B. cereus* Kinrooi 5975c | **Gram** +: *Arthrobacter globiformis, Arthrobacter oxydans, Arthrobacter viscosus, B. cereus, B. subtilis, B. linens, Corynebacterium casei, L. innocua, L. monocytogenes, Micrococcus aurantiacus, Microbacterium lacticum, Propionibacterium freudenreichii, Rhodococcus fascians, S. aureus* | **Ascomycetes**: *Alternaria alternata, B. cinerea, Candida albicans, Cladosporium cucumerinum, Magnaporthe grisea, Monographella nivalis, Sclerotinia minor, V. dahliae* **Basidiomycetes**: *Rhodotorula glutinis, Rhodotorula mucilaginosa* **Mucoromycetes**: *Mortierella isabellina* | Ladeuze et al., (2011); Jenull et al., (2023); Tempelaars et al., (2011) |
| | Lipopeptide - cyclic | Kannurin | *B. cereus* AK1 | **Gram** +: *Staphylococcus spp.* | **Ascomycetes**: *Alternaria* sp., *A. flavus, Aspergillus fumigatus, A. niger, C. albicans, Candida krusei, Candida parapsilosis, Candida tropicalis, Cryptococcus albidus, Cryptococcus laurentii, Curvularia* sp., *Cladosporium* sp., *F. oxysporum, Trichoderma* spp. **Basidiomycetes**: *Cryptococcus neoformans* **Mucoromycetes**: *Mucor* sp., *Rhizopus* sp. | Ajesh et al., (2013); Shabeer Ali et al., (2020) |
| | Lipopeptide - cyclic (fengycin family) | Plipastatin A1, A2,B1,B2 | *B. cereus* BMG3O2-fF67 | **Gram** +: *Corynebacterium bovis* | ND | Nishikiori et al., (1986) |
| | Lipopeptide - partially cyclic | Kurstakin | *B. thuringiensis* sv. *kurstaki* HD1 | ND | **Ascomycetes**: *Stachybotrys chartarum* | Hathout et al., (2000); Yu et al., (2023) |
| | Lipopeptide - linear | Cerexin A | *B. cereus* 60–6 | **Gram** +: *B. anthracis, B. subtilis, S. pneumoniae, S. aureus, S. pyogenes* | ND | Shoji et al., (1975) |
| | | Cerexin A1 | *B. clarus* ATCC 21929* | **Gram** +: *B. subtilis, S. aureus* | ND | Cochrane et al., (2015) |
| | | Cerexin B | *B. cereus* Gp-3 | **Gram** +: *B. anthracis, B. subtilis, S. aureus, S. pneumoniae, S. pyogenes* | ND | Shoji et al., (1975) |
| | | Cerexins C and D | *B. cereus* 60–6 | **Gram** +: *B. subtilis, S. aureus, S. pneumoniae, S. pyogenes* | ND | Shoji et al., (1976b) |
| | Lipopeptide** | Thumolycin | *B. thuringiensis* BMB171 | **Gram** +: *B. amyloliquefaciens, B. pumilus, B. subtilis, B. thuringiensis, E. avium, S. aureus* **Gram -**: *Erwinia amylovora, Pantoea agglomerans* | ND | Zheng et al., (2018) |
| | Siderophores*** | Bacillibactin | *B. anthracis* Sterne, *B. cereus* ATCC 14579, *B. thuringiensis* ATCC 33679 | ND | ND | Wilson et al., (2006) |
| | | Petrobactin | *B. anthracis* Sterne, *B. cereus* ATCC 14579 | ND | ND | Wilson et al., (2006) |
| Hybrid PK/ NRP | Aminopolyol | Zwittermicin A | *B. cereus* UW85, *B. thuringiensis* MORWBS1.1, *B. thuringiensis* GAO03.1, *B. thuringiensis* HD1 | **Gram** +: *B. megaterium, L. acidophilus, S. aureus* **Gram -**: *A. tumefaciens, Bradyrhizobium japonicum, E. coli, K. pneumoniae, P. agglomerans, P. carotovorum, Rhizobium tropici, Rhodobacter sphaeroides, Rhodospirillum rubrum, Salmonella* Typhimurium, *Sinorhizobium meliloti, Yersinia pseudotuberculosis* | **Ascomycetes**: *A. alternata, Alternaria panax, Alternaria tagetica, B. cinerea, Colletotrichum phomoides, Colletotrichum trifolii, Drechslera poae, Epicoccum nigrum, F. graminearum, F. solani, Fusarium sporotrichioides, Helminthosporium carbonum, Helminthosporium sativum, Monilinia oxycocci, Ophiostoma ulmi, Phomopsis obscurans, Sclerotinia sclerotiorum, Septoria musiva, Venturia inaequalis, Verticillium albo-atrum, V. dahliae* **Basidiomycetes**: *R. solani, Ustilago maydis* **Oomycetes**: *Aphanomyces euteiches, Phytophthora medicaginis, Pythium aphanidermatum, Pythium torulosum* | Hao et al., (2015); Luo et al., (2011); Silo-Suh et al., (1994); (1998) |

* Formerly named *B. mycoides* ATCC 21929 (Méndez Acevedo et al., 2020).
** Structure non elucidated.
*** The actual antimicrobial activities of *B. cereus s.l.* siderophores have not been demonstrated yet, but are mentioned by analogy to the activities displayed by identical molecules produced by other Bacilli (Dimopoulou et al., 2021).
ND: Not determined.

### 2.2.2. Hybrid polyketides and non-ribosomal peptides

Polyketides (PKs) are formed by the successive condensation of acetyl or malonyl units and are considered as a wide source of biological active compounds (Nivina et al., 2019). The condensation forming the C-C bond between PK monomers is carried by enzymes called polyketides synthases (PKSs) (Chan et al., 2009; Hertweck, 2009). The PK biosynthesis machinery has been described in detail (Chen and Du, 2016; Nivina et al., 2019; Shimizu et al., 2017; Wang et al., 2020; Weissman, 2020; Wong and Morita, 2020). Briefly, the main PK synthase domains are the acyltransferase (AT), acyl carrier protein (ACP) and ketosynthase (KS) domains, responsible for the recruitment, transport and incorporation in the building block in the forming PK, respectively. A thioesterase domain (TE) catalyses the macrolactonization and release of the PK. Additional domains and tailoring enzymes can also bring further modifications (Katsuyama and Ohnishi, 2012; Nivina et al., 2019; Wang et al., 2020). Three types of PKS are defined based on their domain organisation and modes of operation (Cox, 2007; Hertweck, 2009; Nivina et al., 2019; Shimizu et al., 2017).

*B. cereus* zwittermicin A (Zma) is produced through a hybrid pathway between PKS and NRPS (Kevany et al., 2009). Two aa, namely L-serine and β-ureidoalanine are used as precursors by NRPS-modules and the precursors used by the PKS-modules are malonyl-CoA (2 S)-amino-malonyl-ACP and (2 R)-hydroxy-malonyl-ACP. This particular biosynthesis confers the unusual linear amino-polyol structure (Fig. S5). Zma was originally identified in *B. cereus* strain UW85 (He et al., 1994). However, Zma-producing strains of *B. cereus s.l.* are common and seem to be widespread in soil (Adeniji et al., 2021; Moshe et al., 2023; Stabb et al., 1994; Zhao et al., 2007). Zma was first studied for its role in controlling alfalfa disease (Silo-Suh et al., 1994; 1998) but it displays a particularly wide antimicrobial spectrum (Table 5), including several plant pathogens (Table 5). Zma also improves the insect killing potential of *B. thuringiensis* preparations (Broderick et al., 2000; 2003). Despite the interest in Zma, its mode of action remains not fully understood. Several hypotheses have been proposed for Zma activity, such as potential inhibition of protein synthesis or disruption of bacterial membrane potential (Silo-Suh et al., 1998). The same authors also pointed out Zma similarities with chitosan suggesting that both polycations could display similar antimicrobial mechanisms.Table 5

### 2.2.3. Cyclic dipeptides

Cyclic dipeptides (CDPs), also called cyclo-dipeptides or 2,5-diketopiperazines, are the smallest form of cyclic peptides and represent a highly diversified class of molecules. CDPs are heterocyclic compounds formed by two aa attached together and organised around a central ring of six elements containing two amine linkages (Fig. S6) (Milne and Kilian, 2010). A wide variety of organisms, especially microorganisms, produce CDPs that exhibit a broad range of biological effects (Mishra et al., 2017; Prasad, 1995; Song et al., 2021; Widodo and Billerbeck, 2023; Zhao et al., 2021). Two enzyme families have been described as catalysing the assembly of CDPs: non-ribosomal peptide synthetases and cyclodipeptide synthases (CDPSs) (Mishra et al., 2017). The latter are small (~30k Da) non-thio-templated tRNA-dependent peptide synthases (Mishra et al., 2017; Song et al., 2021). They are divided in two main families named NYH or XYP based on the conserved sequence residues in their active site domains (Jacques et al., 2015; Moutiez et al., 2014).

Kumar and his collaborators have studied the antimicrobial potential of ten CDPs produced by *B. cereus* MTCC 5234 and displaying antimicrobial properties against bacteria and fungi (Table 6). Remarkably, anticancer effects of cyclo(L-Pro-D-Arg) were also highlighted (Kumar et al., 2014a). Other works have reported the production of CDPs by *B. cereus s.l.* without studying their antimicrobial effects, as was the case for the production of Cyclo(L-Pro-L-OMet) by *B. thuringiensis* (Mukherjee, 2021). Still, the biosynthetic pathway of CDPs in *B. cereus s.l.* has not been detailed yet. Of note, CDPs are also found in other Gram-positive bacteria such as cyclo(L-Pro-L-Val) and cyclo(L-Pro-L-Tyr) produced by *Bacillus endophyticus* (Sansinenea et al., 2016), or cyclo(L-Pro-L-Tyr)

**Table 6**
Antimicrobial cyclic dipeptides from *B. cereus s.l.*

| TH | Producer | Antimicrobial activity | | Reference |
|---|---|---|---|---|
| | | Antibacterial | Antifungal | |
| Cyclo(L-Pro-D-Leu) | *B. cereus* MTCC 5234* | ND | **Ascomycetes**: *A. flavus, A. niger* | Kumar et al., (2013) |
| Cyclo(4-hydroxy-L-Pro-L-Trp) Cyclo(L-Phe-Gly) Cyclo(L-Tyr-L-Tyr) | *Ibid.* | ND | **Ascomycetes**: A. *flavus, A. fumigatus, A. niger, Aspergillus parasiticus, Aspergillus tubingensis, C. albicans, C. tropicalis, F. oxysporum, Penicillium expansum, Trichophyton rubrum*<br>**Basidiomycetes**: *Cryptococcus gastricus, R. solani* | Kumar et al., (2014b) |
| Cyclo(D-Tyr-D-Phe) Cyclo(L -Pro-D -Arg) | *Ibid.* | **Gram +**: *B. subtilis, S. aureus, S. epidermidis*<br>**Gram -**: *E. coli, K. pneumoniae, P. aeruginosa, Proteus mirabilis, V. cholerae* | ND | Kumar et al., (2014a); 2014c |
| Cyclo(L-Pro-Gly) | *Ibid.* | ND | **Ascomycetes**: *T. rubrum* | Kumar et al., (2014b) |
| Cyclo(D-Pro-L-Leu) | *Ibid.* | **Gram +**: B. *subtilis, S. aureus*<br>**Gram -**: *E. coli, P. aeruginosa* | **Ascomycetes**: *A. flavus, C. albicans, F. oxysporum, P. expansum*<br>**Basidiomycetes**: *R. solani*<br>**Oomycetes**: *P. capsici, Phytophthora colocasiae* | Kumar et al., (2012a); Kumar and Nambisan, (2014) |
| Cyclo(D-Pro-L-Tyr) | *Ibid.* | **Gram +**: *B. subtilis, S. aureus*<br>**Gram -**: *E. coli* | *Ibid.* | *Ibid.* |
| Cyclo(L-Pro-L-Leu) | *Ibid.* | **Gram +**: *B. subtilis, S. aureus* | *Ibid.* | *Ibid.* |
| Cyclo(L-Pro-L-Phe) | *B. thuringiensis* | ND | **Ascomycetes**: *F. oxysporum, Penicillium* sp. | Sansinenea et al., (2016) |
| Cyclo(L-Pro-L-Tyr) | *Ibid.* | ND | *Ibid.* | *Ibid.* |
| Cyclo(L-Pro-L-Val) | *Ibid.* | ND | *Ibid.* | *Ibid.* |

* This strain is also called *Bacillus* sp. N which was identified as a *B. cereus* according to the sequence of its 16 S rDNA. The strain was deposited under the accession number MTCC 5234 in IMTECH (Institute of Microbial Technology, Chandigarh, India) (Kumar et al., 2012b).
ND: Not determined.

and cyclo(D-Pro-L-leu) synthesised by *Streptomyces* sp. and *Bacillus amyloliquefaciens*, respectively (Jamal et al., 2017; Wattana-Amorn et al., 2016).

#### 2.2.4. Unclassified antimicrobial aa-based compounds

Other aa-based compounds (small peptides, aa derivatives, Fig. S7) displaying antimicrobial activities have been reported, but their biosynthetic pathway is still unknown (Table 7). Cispentacin is a beta-cyclic amino acid present in *B. cereus* and *Streptomyces setonii* (Iwamoto et al., 1990; Konishi et al., 1989). A biosynthetic gene cluster responsible for its synthesis has been recently described in *Streptomyces* sp. as a type II PKS-like hybrid synthesis system (Hibi et al., 2023). It is also thought to act by interfering with the autoregulatory processes of amino acid metabolism in *C. albicans* (Capobianco et al., 1993). Azoxybacilin inhibits sulfate assimilation in *S. cerevisiae* by the inhibition of genes expression related to sulfite reductase activity (Aoki et al., 1996).

Cereusitin a is a cyclic tetrapeptide, identified in *B. cereus* RKHC-09, that exhibits mild antifungal activity against *Colletotrichum gleosporoides* (Pinzón-Espinosa et al., 2017), and mycocerein is a peptide partially characterised, with the sequence N/D-S-E/Q-L-Y-P-X, related to that of iturin. Also, the cyclic hexapeptide bacicyclin, (cyclo-[-Gly-Leu-Val-IIe-Ala-Phe]) has antibacterial activity against Gram-positive, but not Gram-negative bacteria, suggesting a specific target spectrum (Wiese et al., 2018). Finally, mycrocin produced by *B. cereus* SW displays diverse antifungal activities (Table 7) but no bactericidal effect has been observed (Kerr, 1999; Wakayama et al., 1984).

## 3. Sugar derivatives

Carbohydrates and other sugar derivatives represent an important class of antibiotics (Horton, 2013). Within the *B. cereus* group, two sugar derivatives have been reported for their antimicrobial potential: kanosamine and thuringiensin. Kanosamine is an amino-sugar (Fig. S8A) discovered in *B. cereus* UW-85 (Milner et al., 1996; Silo-Suh et al., 1994). Its antifungal activity was reported against various human and plant pathogens (e.g. ascomycetes, basidiomycetes and oomycetes) (Table 8) and targets the glucosamine-6-phosphate synthase, as demonstrated by using *C. albicans* as a fungal pathogenic model. It was indeed shown to enter the cell via glucose permeases and to be phosphorylated into kanosamine-6-phosphate, which further inhibits glucosamine -6-phosphate synthase, a pivotal player in cell wall assembly (Janiak and Milewski, 2001; Wojciechowski et al., 2005). Kanosamine biosynthetic gene cluster was found within the gene cluster involved in zwittermicin A synthesis (Kevany et al., 2009; Prasertanan and Palmer, 2019). Interestingly, the use of kanosamine combined with Zma demonstrated synergistic antimicrobial effects (Silo-Suh et al., 1998).

Thuringiensin (Thu), or β-exotoxin (Fig. S8B), is a thermostable adenine nucleoside oligosaccharide with a broad insecticidal spectrum produced by some strains of *B. thuringiensis*. Its biosynthetic gene cluster was found in a 110-kb plasmid carrying insecticidal protein (Liu et al., 2010b; 2014). Rosenberg and coll. have reported a thuringiensin antimicrobial effect on Gram-positive bacteria, such as *Staphylococcus aureus*, *Sarcina flava* and *Sporosarcina globispora* (Rosenberg et al., 1971). However, the potential role of this molecule in the ecology of its bacterial hosts has never been studied and therefore remains so far dubious. Moreover, because of its anti-mammalian effects, the use of *B. thuringiensis* strains producing thuringiensin as biopesticide has been banned by the World Health Organisation in 1999 (Liu et al., 2014; Palma et al., 2014).Table 8

## 4. Volatile compounds

Volatile compounds (VCs) are molecules that easily evaporate under normal atmospheric conditions. VCs comprise a large range of different chemical families and share different features as a low boiling point,

**Table 7**
Antimicrobial aa-based compounds from *B. cereus s.l.*

| Class | Subclass | Name | Producer | Antimicrobial activity | | Reference |
|---|---|---|---|---|---|---|
| | | | | Antibacterial | Antifungal | |
| Aa derivative | Aliphatic aa | Azoxybacilin | *B. cereus* NR2991 | ND | **Ascomycetes**: *Candida* spp., *Aspergillus* spp., *Trichophyton* spp. | Fujiu et al., (1994) |
| Aa derivative | Cyclic β-aa | Cispentacin | *B. cereus* L450-B2 | ND | **Ascomycetes**: *Candida* spp. | Capobianco et al., (1993); Konishi et al., (1989) |
| Peptide | Cyclic hexapeptide | Bacicyclin | *B. cereus s.l.* BC028** | **Gram** +: *E. faecalis*, *S. aureus* | ND | Wiese et al., (2018) |
| Peptide | Cyclic tetrapeptide | Cereusitin A | *B. cereus* RKHC-09 | ND | **Ascomycetes**: *C. gloeosporioides* | Pinzón-Espinosa et al., (2017) |
| Peptide | ND | Mycocerein* | *B. cereus* SW | ND | **Ascomycetes**: *A. nidulans*, *Eurotium chevalieri*, *F. oxysporum*, *Hansenula wingei*, *P. chrysogenum*, *Saccharomyces cerevisiae* **Basidiomycetes**: *Crepidotus luteolus* **Entomophthoromycetes**: *Conidiobolus lamprauges* *Mucoromycetes*: *M. rouxianus* | Wakayama et al., (1984) |

* Partially characterised.
** This strain was named *Bacillus* sp. BC028 but was also reported as a *B. cereus* based on its 16 S rRNA sequence (Wiese et al., 2018).
ND: Not determined.

**Table 8**
Antimicrobial sugar derivatives compounds from *B. cereus s.l.*

| Class | Subclass | Name | Producer | Antimicrobial activity | | Reference |
|---|---|---|---|---|---|---|
| | | | | Antibacterial | Antifungal | |
| Sugar derivative | Amino-sugar | Kanosamine | *B. cereus* UW85 | ND | **Ascomycetes**: *A. alternata, A. tagetica, C. albicans, D. poae, F. sporotrichioides, H. carbonum, H. sativum, P. obscurans, S. cerevisiae, V. inaequalis*<br>**Basidiomycetes**: *U. maydis*<br>**Oomycetes**: *A. euteiches, P. aphanidermatum, P. medicaginis, P. torulosum* | Janiak and Milewski, (2001); Milner et al., (1996); Silo-Suh et al., (1994) |

ND: not determined

small molecular weight and low water solubility (Bitas et al., 2013; Netzker et al., 2020; Schulz and Dickschat, 2007). Bacterial VCs were first considered as by-products remaining at the end of the metabolic pathway (Schmidt et al., 2015). In recent years, increasing biological functions have been accredited to VCs, leading to a growing interest (Netzker et al., 2020; Piechulla et al., 2020; Weisskopf et al., 2021). These molecules are classified according to their respective pathways (Schulz et al., 2020; Weisskopf et al., 2021).

As shown in Table 9, various effects of *B. cereus s.l.* VCs on target microorganisms have been described. Different VOCs produced by *B. cereus* SV40 have an impact on the morphology and conidiation of *Moniliophthora perniciosa* and *F. graminearum* (Chaves-López et al., 2015). Decyl alcohol and 3,5,5-trimethylhexanol showed biocontrol properties against *Xanthomonas oryzae* pv. *oryzae*, presumably through

**Table 9**
Antimicrobial volatile compounds from *B. cereus s.l.*

| Class | Subclass | Name | Producer | Antimicrobial activity | | Reference |
|---|---|---|---|---|---|---|
| | | | | Antibacterial | Antifungal | |
| Aromatic compound | Benzenoid - Amine | β-benzeneethanamine | *B. thuringiensis* TB72 | ND | **Ascomycetes**: *C. gloeosporioides* | Zheng et al., (2013) |
| | Benzenoid - Carboxylic acid | Phenylacetic acid | *B. mycoides* BM02 | ND | **Ascomycetes**: *F. oxysporum* f. sp. *lycopersici* | Wu et al., (2020a) |
| | Benzenoid - Ester | Methylphenyl acetate | Ibid. | ND | *Ibid.* | *Ibid.* |
| Fatty acid and derivative | Alcohol | 3,5,5-trimethylhexanol | *B. cereus* D13 | **Gram -**: *P. syringae* pv. *tomato*, *Ralstonia solanacearum*, *Xanthomonas oryzae* pv. *oryzae*, *X. oryzae* pv. *oryzicola* | ND | Xie et al., (2018) |
| | Alcohol | 3-methyl-1-butanol | *B. cereus* SV40 | ND | **Ascomycetes**: *F. oxysporum*<br>**Basidiomycetes**: *Moniliophthora perniciosa* | Chaves-López et al., (2015) |
| | Alcohol | Decyl alcohol | *B. cereus* D13 | **Gram -**: *X. oryzae* pv. *oryzae*, *X. oryzae* pv. *oryzicola* | ND | Xie et al., (2018) |
| | Alkane | Heptadecane,2,6,10,14-tetramethyl | *B. thuringiensis* IMC8 | ND | **Ascomycetes**: *Erysiphe pulchra* | Rotich et al., (2020) |
| | Ketone | Propanone | *B. cereus* SV40 | ND | **Ascomycetes**: *F. oxysporum*<br>**Basidiomycetes**: *M. perniciosa* | Chaves-López et al., (2015) |
| Primary metabolism derivatives | Alcohol | 1-butanol | *Ibid.* | ND | *Ibid.* | *Ibid.* |
| | Carboxylic acid | 2-methylpropanoic acid | *Ibid.* | ND | *Ibid.* | *Ibid.* |
| | Carboxylic acid | Acetic acid | *Ibid.* | ND | *Ibid.* | *Ibid.* |
| | Ester | Ethyl acetate | *Ibid.* | ND | *Ibid.* | *Ibid.* |
| | VIC - Nitrogen containing compound | Ammonia | *B. mycoides* CHT2401 and CHT2402 | ND | **Basidiomycetes**: *R. solani*<br>**Oomycetes**: *P. aphanidermatum* | Huang et al., (2018) |
| Pyrazine | Alkyl pyrazine | 2-methylpyrazine | *B. thuringiensis* TB72 | ND | **Ascomycetes**: *C. gloeosporioides* | Zheng et al., (2013) |
| Sulphur-containing compounds | - | Dimethyl disulphide | *B. mycoides* CHT2401 and CHT2402 | ND | **Basidiomycetes**: *R. solani*<br>**Oomycetes**: *P. aphanidermatum* | Huang et al., (2018) |
| Terpenoid | Terpene - Alcohol | Thymol | *Ibid* | ND | *Ibid.* | *Ibid.* |

ND: Not determined

their impact on the transcriptional expression of virulence-associated genes (Xie et al., 2018). *B. mycoides* BM02 produced phenylacetic acid and methylphenyl acetate that suppressed spore germination of *Fusarium oxysporum* f. sp. *lycopersici*, but had no effect on hyphal growth (Wu et al., 2020a). Dimethyl disulfide (DMDS) and trisulfide are also frequently reported as microbial VCs and have been involved in different biological effects. *B. cereus s.l.* DMDS production showed antifungal effects, along with the stimulation of plant natural defences. Similarly *B. mycoides* CHT2401 and 2402 produce DMDS and ammonia. Both compounds inhibit the growth of *Rhizoctonia solani* and *Pythium aphanidermatum*, and have morphological impacts such as rigidity weakening, shrinkage, curling or swelling of hyphae (Huang et al., 2012; 2018). Rotich et al. (2020) showed the effect of VCs from *B. thuringiensis* IMC8 on the powdery mildew *Erysiphe pulchra* and identified potential antifungal VOCs without determining the purified compounds involved.

Additional *B. cereus s.l.* VCs have been reported in the mVOC database (Lemfack et al., 2018) (Table S1). Certain *B. cereus s.l.* strains may still produce other antimicrobial VCs. For instance, nonan-2-one production by *B. weihenstephanensis* was reported to be active against nematodes (Gu et al., 2007). Interestingly, nonan-2-one produced by *Pseudomonas chlororaphis* 450 displayed antifungal activity against *Sclerotinia sclerotiorum* (Popova et al., 2014). Despite the challenges in setting up the application of VCs due to their high diffusion, various methods have been developed, including encapsulation systems (Sharifi and Ryu, 2020), or using them in closed environments (e.g. fruit or legume storage).Table 9

## 5. Miscellaneous compounds: indole, stilbene and benzenoid

Studies on antimicrobial effects of *B. cereus s.l.* indole, stilbene derivatives and benzenoids are seldom (Table 10). Two benzenoid antimicrobial compounds have been reported from *B. cereus* RKHC-09 supernatant (Pinzón-Espinosa et al., 2017). Interestingly, benzenoid compounds can also be related to volatile aromatic compounds. Indole is a six-membered benzene ring attached to a five-membered pyrrole ring. *Bacillus* production of the indole derivative indole-3-acetic acid, a phytohormone better known as auxin, is of particular interest as it promotes plant growth (Batista et al., 2021). Vaca et al. (2020) noted the antimicrobial effects of indole alkaloids produced by *B. thuringiensis* and *Bacillus velezensis*. The authors hypothesised that the identified indole alkaloids could be used as building blocks to produce more complex molecules such as bacillamide known to display anti-alga activity (Jeong et al., 2003; Vaca et al., 2020).

Stilbenes are non-flavonoids phenolic molecules with a 14-carbon skeleton composed of two benzene rings connected by an ethylene bridge (Valletta et al., 2021). They are known as important plant metabolites (Dubrovina and Kiselev, 2017; Valletta et al., 2021) but the stilbene biosynthesis pathway has also been found in some bacteria (Joyce et al., 2008; Li et al., 2021; Mori et al., 2016). Stilbenes and their derivatives are major bioactive compounds known for their antimicrobial activity (De Filippis et al., 2019; Mattio et al., 2020) and two have been reported from *B. cereus* MTCC 5234 (Table 10) (Kumar and Nambisan, 2014; Kumar et al., 2012b).Table 10

## 6. Conclusion and perspectives

Because of their broad spectrum of lifestyles, members of the *B. cereus* group have developed an impressive repertoire of competitive molecules, including a large array of AMCs, designed to cope with the diversity and challenges of their ecological niches. Although the focus has long been set on strains of *B. anthracis*, *B. thuringiensis* or *B. cereus s.s.*, more recent studies have revealed the potentials of other members, including species such as *B. toyonensis*, *B. mycoides* or *B. pseudomycoides* as AMC producers (Fiedoruk et al., 2021). The present review gives an exhaustive list of these interesting AMC and their potential applications in the arms race against pathogenic bacteria and fungi. It also underlines

**Table 10**
Stilbene, indole alkaloid and benzenoid antimicrobial compounds from *B. cereus s.l.*

| Subclass | Name | Producer | Antimicrobial activity | | Reference |
|---|---|---|---|---|---|
| | | | Antibacterial | Antifungal | |
| Benzenoid | Methyl esters of p-hydroxybenzoic acid<br>Propyl esters of p-hydroxybenzoic acid | *B. cereus* RKHC-09 | **Gram** +: *S. aureus* | **Ascomycetes**: *S. cerevisiae* | Pinzón-Espinosa et al., (2017) |
| Indole alkaloid | Tryptamine | *B. thuringiensis* | **Gram** +: *L. monocytogenes, M. luteus*<br>**Gram** -: *S. choleraesuis, V. cholerae* | **Ascomycetes**: *Alternaria* sp., *F. oxysporum*<br>**Basidiomycetes**: *Moniliophthora roreri* | Vaca et al., (2020) |
| Indole alkaloid | N-acetyl tryptamine | *Ibid.* | **Gram** +: *L. monocytogenes, M. luteus, Staphylococcus saprophyticus, S. aureus, Streptococcus agalactiae*<br>**Gram** -: *E. coli, Serratia marcescens* | *Ibid.* | *Ibid.* |
| Indole alkaloid | Phenethylamine | *Ibid.* | **Gram** +: *M. luteus, S. saprophyticus, S. aureus*<br>**Gram** -: *S. marcescens, V. cholerae* | *Ibid.* | *Ibid.* |
| Indole alkaloid | Phenethyl acetamide | *Ibid.* | **Gram** -: *E. coli, P. aeruginosa, V. cholerae* | *Ibid.* | *Ibid.* |
| Stilbene | 3,4′,5-trihydroxystilbene (resveratrol) | *B. cereus* MTCC 5234* | **Gram** +: *B. subtilis, S. aureus*<br>**Gram** -: *E. coli, P. aeruginosa* | **Ascomycetes**: *A. flavus, B. cinerea, C. albicans, C. gloeosporioides, F. oxysporum*<br>**Basidiomycetes**: *R. solani*<br>**Oomycetes**: *P. capsici, P. expansum* | Kumar et al., (2012b); Kumar and Nambisan, (2014) |
| Stilbene | 3,5-dihydroxy-4-isopropylstilbene | *B. cereus* MTCC 5234* | **Gram** +: *B. subtilis, S. aureus* | **Ascomycetes**: *A. flavus, B. cinerea, C. albicans, C. gloeosporioides, F. oxysporum*<br>**Basidiomycetes**: *R. solani*<br>**Oomycetes**: P. *capsici, P. expansum* | *Ibid.* |

*This strain is also called *Bacillus* sp. N strain which was identified as a *B. cereus* according to the sequence of the 16 S rDNA. The strain was deposited under the accession number MTCC 5234 in IMTECH (Institute of Microbial Technology, Chandigarh, India) (Kumar et al., 2012b).

the immense "still-to-be-discovered" reservoir of antagonism molecules suggested by recent bioinformatic studies (Xia et al., 2022).

Yet, it is undeniable that the current taxonomy of the *B. cereus* group has blurred the frontiers between pathogenic and commensal species. For instance, the genetic determinants of some potential enterotoxins are found among different members of the *B. cereus* group, including those considered non-pathogenic such as *B. thuringiensis*. Although the role of these potential enterotoxins in the pathogenicity of diarrhoeal syndromes has not yet been fully elucidated (Dietrich et al., 2021), their presence constitutes an obstacle to the valorisation *B. cereus s.l.* strains as AMCs producers, compared to more practical GRAS (Generally Recognised as Safe) or QPS-accredited (Qualified Presumption of Safety) bacteria. This safety consideration is well-illustrated by the *B. cereus s.s.* member, that comprises mainly commensal strains, some of which are even used as probiotics (Cui et al., 2019), but also emetic and/or diarrhoeal strains. A clear and consensual taxonomy of the group could help the safety of the different strains to be distinctly defined, and would certainly increase the interest in the *B. cereus* group for the development of antimicrobial applications. Along the same lines, combination of genome mining (Vater et al., 2023) and genetic engineering could enable the use of AMCs from opportunistic/pathogenic *B. cereus s.l.* by cloning and expressing their biosynthetic genetic determinants in safer microbes.

Because distinct AMCs can be produced by the same *B. cereus* strain, it is essential to identify the biosynthetic gene cluster responsible for the production of each compound, and confirm its *bona fide* involvement through genetic approaches such as gene knockouts. Unfortunately, these confirmations have rarely been done so far. Similarly, the modes of action of AMCs are often not well-understood (Tran et al., 2022) although their knowledge remains crucial for preventing the emergence of resistance. It is also crucial to determine the appropriate concentration needed to exert the antimicrobial effects while ensuring its biological innocuity. Regrettably, such information often lacks in the case of *B. cereus s.l.* AMCs. Finally, beside their antibacterial and antifungal arsenal, members of the *B. cereus* group are also a reservoir of other metabolites exerting potential antiviral or nematicide activities, alongside with probiotic or plant growth promotion features (Azizoglu et al., 2023; Cui et al., 2019; Cutting, 2011; Engelbrecht et al., 2018; Kulkova et al., 2023; Zhou, and Niu, 2009; Gomis-Cebolla and Berry, 2023). Altogether, these valuable traits make *B. cereus s.l.* a very attractive territory for the discovery and application of highly desired and awaited compounds as valid and safe alternatives to chemical antimicrobial molecules. This clearly calls for further research on *B. cereus s.l.* AMCs and their potential applications.

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## Declarations of interest

None.

## Author contributions

Conceptualization: LM, SC, JM; Data curation: LM, JM; Formal analysis: LM, JM; Funding acquisition: CB, JM; Investigation: LM, JM; Methodology: LM, JM; Project administration: JM; Resources: CB, JM; Supervision: JM; Validation: JM; Writing - original draft; and Writing - review & editing: LM, SC, CB, JM.

## CRediT authorship contribution statement

**Jacques Mahillon:** Writing – review & editing, Writing – original draft, Validation, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Claude Bragard:** Writing – review & editing, Resources, Funding acquisition. **Simon Caulier:** Writing – review & editing, Conceptualization. **Louis Morandini:** Writing – review & editing, Writing – original draft, Methodology, Investigation, Formal analysis, Data curation, Conceptualization.

## Data Availability

No data was used for the research described in the article.

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## Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.micres.2024.127697.

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