

Evolutionary processes and environmental factors underlying the genetic diversity and lifestyles of *Bacillus cereus* group bacteria

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Abstract

Bacteria of the *Bacillus cereus* group are environmental Gram-positive spore-forming bacteria ubiquitously distributed. Despite the high degree of genetic similarity among the different strains, they show strong phenotypic variability, from mammal or entomopathogen strains to soil-dwelling saprophytes, and from psychrophilic to thermotolerant strains. Most of the phenotypes are linked to the presence of large plasmids that encode for diverse toxins. However, other processes, like mutation or recombination, also participate in shaping the evolution and population structure of these bacteria. Here we review different aspects of the evolution of this group.

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1. Introduction

The *Bacillus cereus* sensu lato complex, or *B. cereus* group, is a subdivision of the *Bacillus* genus that includes 8 validated and closely related species: *B. cereus* sensu stricto, *Bacillus thuringiensis*, *Bacillus mycoides*, *Bacillus pseudo-mycoides*, *Bacillus anthracis*, *Bacillus weihenstephanensis*, *Bacillus cytotoxicus* and *Bacillus toyonensis*. Members of this group have highly similar 16S and 23S rRNA sequences indicating that they have diverged from a common evolutionary lineage [1–3]. The full genome for at least 88 strains from the *B. cereus* group has been sequenced to date: *B. cereus* sensu stricto (27 genomes), *B. anthracis* (32 genomes), *B. thuringiensis* (30 genomes), *B. weihenstephanensis* (2 genomes) and *B. cytotoxicus* (2 genomes) and the draft sequence genomes of over 300 additional strains of the group [4] are also available. Comparisons of genome sequence similarity

between species have revealed enormous similarity in terms of nucleotide sequence identity and gene and operon organization, which highlights the very close relationships between the members of this bacterial group, making their identification at the species level difficult. The *Bacillus cereus* group is also characterized by an important extrachromosomal pool, which is largely responsible for the virulence specificities and adaptation properties of the different strains or species belonging to this group. However, there are still other virulence factors encoded in the chromosome and shared by all members of the *B. cereus* group, like the hemolytic and non-hemolytic enterotoxins [5]. Most of the strains usually contain one or more plasmids (up to 12), measuring between 2 and 600 Kb. Since a significant part of this extrachromosomal material is self-transmissible within the *B. cereus* group members, and since some of the main phenotypic traits of the *B. cereus* group species are carried on plasmids, the precise distinction of different strains of the *B. cereus* group, and the species definition of the *B. cereus* group members, is still unresolved and under debate.

Moreover, the pathogenic status of the *B. cereus* group members is not homogeneous as it contains strains used as

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probiotics, like *B. toyonensis* [6], and also the deadly dangerous pathogen *B. anthracis*, the agent of anthrax, a disease of domestic animals (cattle, sheep, etc.), that may be transmitted to humans. The *B. thuringiensis* strains are used commercially as biopesticides to combat insects that are damaging crops or are vectors of diseases such as malaria or yellow fever. The majority of *B. mycoides*, *B. pseudomycoides* and *B. weihenstephanensis* strains are mostly non-pathogenic saprophytes not or rarely associated with diseases in humans or other animals. On the other hand, many *B. cereus sensu stricto* strains are undesired food contaminants that cause foodborne poisoning. *B. cytotoxycus* is a new pathogenic specie of the *B. cereus* group established in 2013 that was responsible for a severe foodborne outbreak [7]. However, the severity of the infections caused by the different members of the *B. cereus* group varies enormously depending on the strain responsible for the disease. Also, the distinction between pathogenic and innocuous strains is far from clear regarding the entire *B. cereus* group.

Species delineation relies mainly upon DNA–DNA relatedness studies, and guidelines for the delineation of a bacterial species require strains within a species to share more than 70% chromosomal DNA hybridization. Actually, *B. cereus* s.s., *B. anthracis* and *B. thuringiensis* hybridize beyond the 70% limit, suggesting that there is no taxonomic basis for separate species status [8]. In fact, these three species were classified as distinct because of the great relevance of their phenotypic differences (a phenotypic description is still a mandatory element of a valid species proposal), and most of their main distinguishing phenotypic features, especially their respective virulence properties, are directly associated with large plasmids. Indeed, the *cry* genes of *B. thuringiensis*, encoding the insecticidal toxins that form the crystalline inclusions, are located on plasmids [9] that may be lost during subculturing, making *B. thuringiensis* indistinguishable from *B. cereus sensu stricto* [10]. Similarly, the genes causing the lethal effect of anthrax are located on two large virulence plasmids, pXO1 and pXO2 [11,12]. Thus, in the *B. cereus* group, species are essentially primarily delineated on the basis of phenotypic traits of practical usefulness such as certain virulence properties (*B. cereus sensu stricto*, *B. anthracis*, *B. thuringiensis* and *B. cytotoxicus*), physiological properties conferring adaptation to low or high temperatures (*B. weihenstephanensis* and *B. cytotoxicus*), morphological properties (*B. mycoides* and *B. pseudomycoides*) and strains used as probiotics (*B. toyonensis*). Thus, the current taxonomy of the *B. cereus* group and the separate species status for the different bacteria that constitute the *B. cereus* group still relies on important phenotypes conferred by mobile genetic elements, as well as on the ability of certain strains to grow at low temperatures while other can grow at high temperatures.

The aim of this review is to provide an overview of the evolutionary mechanisms beneath the emergence and diversification of the *B. cereus* group from its last common ancestor to the extant strains. We will begin by presenting the main features of the *B. cereus* group and the phylogenetic

relationship within the *B. cereus* group members. We will then describe and discuss its genomic composition, focusing on the evolutionary mechanisms involved in the diversification, ecology and population structure among the *B. cereus* group. We will also describe the main genetic determinants of *B. cereus* lifestyles and discuss different aspects dealing with the role of plasmids in the evolution of *Bacillus cereus* group.

2. *B. cereus sensu lato* group features

B. cereus group bacteria belong to the genus *Bacillus* in the family Bacillaceae. Despite being of the same genera, it is difficult to draw a common evolutionary history between the different species of the *Bacillus* genus. Indeed, the genus *Bacillus* is the largest genus within the family Bacillaceae; it basically includes facultative anaerobic rod-shaped Gram-positive spore-forming bacteria, with a G + C content ranging between 32 and 69% [13]. Phylogenies of the Bacillaceae family obtained using the ribosomal ITR (internal transcribed spacer) identified up to 10 different groups, seven of which are members of the genus *Bacillus* [14]. Nevertheless, among the different clades described, only the *B. subtilis* and *B. cereus* groups possess specific molecular markers in the form of conserved signature indels (CSI) [15].

After the analysis of whole genome phylogenies, the relationships within this clade have been reassessed, dividing them into five different lineages: the basal group is formed by *Exiguobacterium*; then, there is a group formed by *Bacillus halodurans*, *Bacillus calusii* and other minor species; and finally, after the divergence of *Oceanobacillus*, there is a polytomy giving rise to the groups for *B. subtilis*, *Geobacillus* and the *B. cereus* group [16,17]. The topologies obtained through whole-genome phylogenies have also been replicated by MSLT, AFLP and MLEE genotyping [18].

The variety of environments and lifestyles that different members of the *B. cereus* group exhibit is reflected in their COG (cluster of orthologous genes) functional profile [19]. Indeed, the proportion of genes from the COG category G (carbohydrate transport and metabolism) is reduced, mainly due to the loss of genes involved in the degradation of plant-derived carbohydrates, as compared with other bacilli, while the COG V (defense mechanism) category is overrepresented [16]. On the other hand, the genes participating in the catabolism of glycogen, starch, chitin and chitosan are conserved within the *B. cereus* group members. This functional profile differentiates the *B. cereus* group from its close relative, soil-dwelling bacteria *B. subtilis* [20]. Another distinctive feature of these bacteria is the expansion of extracytoplasmic function sigma factors that appeared through a duplication process [17]. It has been proposed that ancestral sigma factors may control a large set of genes and that, after duplication occurred, each paralog will end controlling a subset of the previous gene set in a process known as subfunctionalization, resulting in a major specialization to respond and adapt to new environmental stresses [21].

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