Bacteriocins synthesized by *Bacillus thuringiensis*: generalities and potential applications

Elma Laura Salazar-Marroquín\textsuperscript{a,b}, Luis J. Galán-Wong\textsuperscript{a}, Víctor Ricardo Moreno-Medina\textsuperscript{b}, Miguel Ángel Reyes-López\textsuperscript{b} and Benito Pereyra-Alférrez\textsuperscript{a}

The members of the *Bacillus thuringiensis* group, commonly known as Bt, produce a huge number of metabolites, which show biocidal and antagonistic activity. *B. thuringiensis* is widely known for synthesizing Cry, Vip and Cyt proteins, active against insects and other parasporins with biocidal activity against certain types of cancerous cells. Nevertheless, *B. thuringiensis* also synthesizes compounds with antimicrobial activity, especially bacteriocins. Some *B. thuringiensis* bacteriocins resemble lantibiotics and other small linear peptides (class IIa) from the lactic acid bacteria bacteriocins classification system. Although many bacteriocins produced by Bt have been reported, there is no proper classification for them. In this work, we have grouped these based on molecular weight and functionality. Bacteriocins are small peptides synthesized by bacteria, presenting inhibitory activity against Gram-positive and Gram-negative bacteria and to a lesser extent against fungi. These molecules represent a good study model in the search for microbial control alternatives. Lactic acid bacteria produces a huge number of these types of molecules with great potential. Nonetheless, members of the *Bacillus, cereus* group, especially *B. thuringiensis*, emerge as an attractive alternative for obtaining bacteriocins showing novel activities. This review describes the potential applications of *B. thuringiensis* bacteriocins in the control of foodborne pathogens, environment and medical area.

Reviews in Medical Microbiology 2016, 27:95–101

**Keywords:** antimicrobial peptides, *Bacillus thuringiensis*, bacteriocins, biotherapy

Introduction

The steadily increasing use of antibiotics with the aim of controlling microorganisms which may damage food or infective agents for human, plants or animals led to the emergence of resistant microorganisms to a wide range of antimicrobial agents [1]. It is estimated that in Europe, approximately 25,000 persons are deceased on an annual basis because of infections caused by bacteria which are antibiotic resistant [2]. The emergence of drug-resistant bacteria requires us to search for and develop new antimicrobial agents. One viable alternative could be the use of bacteriocins [3–5]. Bacteriocins are small peptides (approximately between 12 and 70 amino acids) with antimicrobial activity, synthesized by prokaryotes. These peptides originally emerged as adaptation mechanisms [6], which allow them to compete for nutrients and space in their habitat, inhibiting growth within the members of the same producer species or members of different bacterial genera [4,7]. Lactic acid bacteria have been widely studied as bacteriocin producers [8]. For example, nisin, the most-commonly studied lantibiotic, has been approved as a food preservative in more than 50 countries [9]. In food, the addition of bacteriocins represents an...
excellent strategy to control pathogenic bacteria and/or food spoilers, such as Listeria monocytogenes, Clostridium botulinum, Yersinia enterocolitica, Staphylococcus aureus, Escherichia coli, Salmonella enterica subsp. enterica and Bacillus cereus, among others [10]. Dissemination of multidrug-resistant bacteria as S. aureus, Pseudomonas aeruginosa, and Enterococcus sp. represents a matter of great concern through an important increase in the hospital costs and morbimortality [11]. Although the 1970s another bacterium, Clostridium difficile, was found to be responsible for nosocomial diarrhoea [12]. Since then, the cases have increased in number and severity in many parts of the world. The main predisposing factor is broad-spectrum antibiotics, which eradicate beneficial bacteria, leading to C. difficile overgrowth [13].

The emergence of its resistance to certain conventional antibiotics leads to research with a view to discovering novel therapeutic strategies. In addition to lactic acid bacteria, different members of the Bacillus sp. genus, particularly from the cereus group, such as Bacillus thuringiensis, have been studied because of their capability of producing bacteriocins. B. thuringiensis is a Gram-positive bacterium, which produces endospores and is well known for synthesizing an enormous ‘battery’ of compounds with biological activity, specially Cry, Cyt and Vip proteins, possessing biocidal activity against certain kinds of insects. Although B. thuringiensis also synthesizes proteins with antimicrobial activity [14]. In this regard, the knowledge relating to the mode of action of several B. thuringiensis antimicrobials is still limited. The application of B. thuringiensis antimicrobials is very important within different areas such as food biopreservation, medicine and environmental care. This review describes some of the most important aspects of bacteriocins synthesized by different strains of B. thuringiensis, such as activity spectrum, molecular mass and biological activity.

### Bacteriocins synthesized by B. thuringiensis

In the last few years, there has been a resurgence in interest with respect to the discovery of new treatments including the use of microorganisms as natural products. B. thuringiensis is considered a model organism for production of metabolites, which is currently employed in the biological control of plagues and agricultural crops. In 1989, Favret and Younsten [15] reported the detection of a peptide synthesized by a B. thuringiensis, which was subsequently named thuricin. So far, there is a report of 18 bacteriocins synthesized by different B. thuringiensis strains. Among these 18 bacteriocins are five inhibitory substances, which resemble bacteriocins known as bacteriocin-like inhibitory substance (BLIS) [16] (Table 1). Bacteriocins are peptides with a different molecular weight, varying from almost 1 kDa (thuricin, 0.950 kDa) to 12.4 kDa (entomocin 9). In terms of molecular weight, we propose to divide these bacteriocins, into groups A and B. Group A is composed of the bacteriocins weighing less than 5 kDa and group B which weigh more than 5 kDa. Although from a functional point of view, within group A, we can find two types: single peptide and two–component peptide. Almost all of them belong to type I and only thuricin CD and thuricin 439 belong to type II (Table 1). Another important aspect is that members of the serological subsp. entomocidus

**Table 1. Bacteriocins synthesized by different strains of Bacillus thuringiensis.**

| Bacteriocin | Molecular mass (kDa) | Producer strain (subsp.) | Reference |
|------------|----------------------|--------------------------|-----------|
| Al Thuricin | 0.950                | HD2 (thuringiensis)       | Favret and Younsten 1989 [15] |
| Thuricin S | 3.137                | HD198 (entomocidus)       | Chehimi et al. 2007 [29] |
|            | 9 (entomocidus)      |                          | Chehimi et al. 2012 [30] |
|            | HD110 (entomocidus)  |                          | Chehimi et al. 2012 [30] |
|            | HD125 (tolworthy)    |                          | Chehimi et al. 2012 [30] |
| Thuricin Bn1 | 3.139              | Bn1 (kurstaki)           | Ugras et al. 2013 [27] |
| Thuricin H | 3.140                | SF361                    | Lee et al. 2009 [37] |
| Bachuricin F4 | 3.160           | BUPM4 (kurstaki)         | Kamoun et al. 2005 [22] |
| Thuricin 17 | 3.172                | BT non-Bradyrhizobium    | Gray et al. 2006 [36] |
| Entomocin 110 | 4.800          | HD110 (entomocidus)      | Cherif et al. 2008 [31] |
| All Thuricin CD | Trm-a 2.760     | DPC 6431                 | Rea et al. 2010 [13] |
|              | Trm-B 2.860         |                          |           |
| Thuricin 439 | (A) 2.919           | B439                     | Ahern et al. 2003 [40] |
|              | (B) 2.803           |                          |           |
| Bl Morrnicin 269 | ~10.000     | LBIT269 (morrisoni)      | Barboza-Corona et al. 2007 [16] |
| Kurstacin 287 | ~10.000            | LBIT287 (kurstaki)       | Barboza-Corona et al. 2007 [16] |
| Kenyacin 404 | ~10.000            | LBIT404 (kenyae)         | Barboza-Corona et al. 2007 [16] |
| Entomocin 420 | ~10.000           | LBIT420(entoentomocidus) | Barboza-Corona et al. 2007 [16] |
| Tolworthcin 524 | ~10.000       | LBIT524 (tolworthy)      | Barboza-Corona et al. 2007 [16] |
| Tochicin    | 10.500              | HD868 (tochigienis)      | Paik et al. 1997 [39] |
| Bachuricin F103 | ~11.000         | BUMP103                  | Kamoun et al. 2011 [35] |
| Thuricin 7  | 11.600              | BMG1.7                   | Cherif et al. 2001 [21] |
| Entomocin 9 | 12.400              | HD9 (entomocidus)        | Cherif et al. 2003 [26] |
produce three different peptides, thuricin S, entomocin 110 and entomocin 9 (Table 1). On the other hand, the same peptide can be produced by different sub-species such as thuricin S, which is produced by the serological subsp. entomocidus and subsp. toworthy (Table 1).

**Gram-positive bacteria inhibited by B. thuringiensis bacteriocins**

Most bacteriocins synthesized by B. thuringiensis are broad-spectrum, inhibiting several bacterial species. Some B. cereus strains synthesize toxins, which induce diarrhoea, whereas others may be responsible for causing nausea and vomiting [17]. Another important pathogen is L. monocytogenes, which may be inhibited by different bacteriocins, amongst which include: thuricin, thuricin S, thuricin Bn1, thuricin H, entomocin 110, bachuricin F103, thuricin 7, entomocin 9 and thuricin CD. Listeriosis is a zoonotic disease, which is rare in humans but is still extremely serious, presenting low morbility and high mortality. Generally, contamination takes place while consuming food containing L. monocytogenes, which are responsible of causing the disease [18]. Another bacterium, methicillin-resistant *Staphylococcus aureus*, has become immensely important in intrahospital as a causeative agent of wound infections [19,20]. Bacteriocins such as thuricin, thuricin H, bachuricin F4 and BLIS reported by Barboza-Corona et al. [16], morricin 269, kurstacin 287, kenyan 404, entomocin 420 and toworthycin 524 may represent the best option to control this problematic bacterium (Table 2).

### Table 2. *Bacillus thuringiensis* bacteriocins with biological activity against Gram-positive bacteria.

| Sensitive strain                                                                 | Reference                                |
|--------------------------------------------------------------------------------|------------------------------------------|
| *Bacillus thuringiensis*                                                        | Sensitive strain Reference               |
| *B. cereus, Bacillus polymyxa, Bacillus sphaericus, Corynebacterium xerosis*    | Favret and Younsten 1989 [15]           |
| *B. cereus, L. monocytogenes, B. subtilis, B. megaterium, Pediococcus acidilactis, Streptococcus thermophilus* | Chehimi et al. 2007 [29]                |
| *B. cereus, L. monocytogenes*                                                  | Ugras et al. 2013 [27]                  |
| *B. cereus, B. subtilis, B. megaterium, L. innocua, L. ivanovii, S. aureus, Carnobacterium psicola, Geobacillus stearothermophilus* | Lee et al. 2009 [37]                    |
| *B. cereus, B. subtilis, Bacillus licheniformis, S. aureus, Brevibacterium flavum* | Kamoun et al. 2005 [22]                |
| *B. cereus*                                                                    | Gray et al. 2006 [36]                   |
| *B. cereus, B. weihenstephanensis, C. difficile, Listeria innocua, S. aureus, Bacillus polymyxa, Bacillus sphaericus, Bacillus licheniformis, L. monocytogenes* | Cherif et al. 2008 [31]                |
| *B. cereus, Leuconostoc mesenteroides*                                         | Paik et al. 1997 [39]                   |
| *B. cereus, B. subtilis, B. licheniformis, L. monocytogenes*                   | Kamoun et al. 2011 [35]                 |
| *B. cereus, B. subtilis, B. pseudomycoides B. mycoides, Staphylococcus pyogenes* | Cherif et al. 2001 [21]                |
| *B. cereus, B. pseudomycoides, B. mycoides, B. weihenstephanensis*              | Cherif et al. 2003 [26]                 |
| *B. cereus, B. weihenstephanensis, C. difficile, Listeria innocua, S. aureus* | Barboza-Corona et al. 2007 [16]        |
| *Staphylococcus aureus, Carnobacterium psicola, Geobacillus stearothermophilus* | Rea et al. 2010 [13]                    |
| *B. cereus, Bacillus firmus, B. mycoides, C. difficile*                          | Ahern et al. 2003 [40]                  |

**Gram-negative bacteria inhibited by B. thuringiensis bacteriocins**

Bacteriocins including bachuricin F4, thuricin 7, morricin 269, kurstacin 287, kenyan 404, entomocin 420 and toworthycin 524 have the potential to control *Klebsiella pneumoniae*, a Gram-negative bacillus, which lives in the human intestine as part of its microbiota [16,21,22], considered one of the most important agents in relation to nosocomial infections, producing septicaemia and urinary and respiratory tract infections [23]. Another important microorganism is *P. aeruginosa*, which may be found in hospitals. This opportunistic pathogen is frequently present in extra intestinal infections, mainly in immunocompromised and malnourished patients [24]. This microorganism shows resistance to almost all conventional antimicrobials [25], even though it is susceptible to entomocin 110 and entomocin 9 (Table 3). Some members of the BLIS group showed inhibitory activity against *Vibrio cholerae*. Since ancient times, cholera has been the cause of deadly epidemics; however, nowadays its morbimortality has diminished. Nonetheless, there are certain endemic zones presenting with a high percentage of this disease, which causes acute
gastroenteritis. If the disease is not correctly treated, it may even cause death [19] (Table 4).

**Fungi inhibited by B. thuringiensis bacteriocins**

Fungi may also be targeted by some bacteriocins. For instance, Bn1 bacteriocin and entomocin nine inhibit *Aspergillus* growth [26,27]. Food containing starch (as in the case of potatoes and bread) may stimulate its growth. In addition, it may grow within dirty air conditioning units located in buildings and houses, representing a serious problem, including in hospitals. Frequently, *Aspergillus niger* is present in human ear infections and in certain instances it can even infect the lungs of people who present with a weak immune system. *A. niger* may be toxic if ingested through infected fruits, vegetables or grains; it can produce food poisoning (single ingestion) or cancer (chronic consumption) [28].

**Potential applications of B. thuringiensis bacteriocins**

**Thuricin S:** This bacteriocin is heat resistant and stable in a wide range of pH conditions and inhibits not only the pathogens that are transmitted through food causing poisoning such as *L. monocytogenes* and *B. cereus*, but also a great number of Gram-negative pathogens such as *S. enterica* subsp. *enterica* and *P. aeruginosa*. The use of *B. thuringiensis* as a biological insecticide, as well as the information about the bacteriocins, like thuricin S, empower its practical use as an antagonistic agent towards phytopathogenic bacteria such as *Pseudomonas syringae* [29,30].

**Thuricin Bn1:** This peptide is synthesized by *B. thuringiensis* subsp. *kurstaki* Bn1, which presents bifunctional properties in agriculture. This strain is active against insects through a crystalline protein [31] and active against plant pathogenic bacteria through a bacteriocin. On the other hand, the *Bacillus* genus includes a great variety of species that may be safely used within industry. Example, *B. thuringiensis* Bn1 produces Bacteriocin Bn1, which as proteinaceous nature, can be used as a natural food preservative [32]. Besides, bacteriocins have gained importance as natural biopreservatives for degradation control and against pathogenic bacteria transmitted by food [6].

**Thuricin 17:** This bacteriocin inhibits the growth of *B. cereus*, *L. monocytogenes*, *Listeria innocua* and *Listeria ivanovii* [33]. All of these bacteria seem to affect both animals and humans [18]. An example includes the fatal case where *L. innocua* was found on a hemoculture. In this situation, the patient died because of septic shock caused by cholangitis [34].

**Bacthuricin F4:** This bacteriocin is stable at a wide pH range and heat treatment, which indicates that the bactericidal function can be preserved even in extreme conditions. This presents an extremely interesting characteristic for its use in the agro-industry. The study of the bacteriocin

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### Table 3. *Bacillus thuringiensis* bacteriocins with biological activity against Gram-negative bacteria.

| Sensitive strain | Reference |
|------------------|-----------|
| *Enterobacter cloacae*, *Pseudomonas syringae*. | Chehimi et al. 2007 [29] |
| *S. enterica* ser. *Cholerae*. | Ugras et al. 2013 [27] |
| *Pseudomonas lorenzii*, *Pseudomonas savastanoi* | Kamoun et al. 2005 [22] |
| *K. pneumoniae* | Gray et al. 2006 [36] |
| *E. coli MM294* | Cherif et al. 2008 [31] |
| *P. aeruginosa* | Kamoun et al. 2011 [35] |
| *A. tumefaciens* | Cherif et al. 2003 [26] |
| *V. cholerae*, *Shigella flexneri*, *Salmonella sp.*, *E. coli*, *K. pneumoniae*, *Enterobacter cloacae*, *Proteus vulgaris* | Barboza-Corona et al. 2007 [16] |

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### Table 4. *Bacillus thuringiensis* bacteriocins with biological activity against fungi.

| Sensitive strain | Reference |
|------------------|-----------|
| *Aspergillus nidulans*, *Fusarium graminis* | Cherif et al. 2003 [26] |
| *Rizopus sp.*, *Fusarium oxysporum*, *Mucor rouxii IM80*, Trichoderma sp. SH1, Trichoderma sp. SD3. | De la Fuente-Salcido et al. 2008 [10] |
| *Entomocin 9* | |
| *Morricin 269* | |
| *Kurstacin 287* | |
| *Kenycacin 404* | |
| *Entomocin 420* | |
| *Tolworthcin 524* | |
inhibition spectrum against indicator strains revealed that this bacteriocin presents a bactericidal effect against bacterial strains highly linked to *B. thuringiensis* and other Gram-positive bacteria. Importantly, it is highly active against *B. cereus*, which is one of the most virulent bacteria that may be found in agro-industrial products [22]. Although this bacteriocin is less active against Gram-negative bacteria [35]. It is the only bacteriocin produced by *B. thuringiensis*, which displays activity against *K. pneumoniae*. **Thuricin 7:** This peptide was isolated from a bacterium, which promotes plant growth [36], and has been demonstrated to increase plant growth [37]. This peptide is stable in a wide range of temperatures and is biologically active between pH 1.00 and 9.25. In addition, thuricin 17 is the only *B. thuringiensis* bacteriocin which shows activity against *E. coli* [36].

**Entomocin 110:** This bacteriocin has been demonstrated to be inhibitory to several Gram-positive bacteria, including *L. monocytogenes*, *Paenibacillus larvae* and other *Bacillus* species [31]. *P. larvae* are extremely important bacteria within the apiculture sector, as they produce the American foulbrood disease, which affects bee larvae [38]. **Tochicin:** This bacteriocin exhibits activity against *B. cereus* and certain *B. thuringiensis* subspecies [39]. Although its spectrum of activity is unclear as it has not been tested against *L. monocytogenes*, as is the case of bacthuricin F4 it has not been tested in *L. monocytogenes* or *S. aureus*, as it happens in the case of thuricin S. For this reason, its application and potential use in biomedical treatments has not been completely defined.

**Thuricin F103:** This bacteriocin presents a wide spectrum of inhibition against the related bacteria and different pathogens transmitted through food such as *L. monocytogenes*, *B. cereus* and the phytopatogenic bacterium *Agrobacterium tumefaciens*. Subsequently, Kaumon and his colleagues [35] demonstrated that bacthuricin F103 may be applied to raw beef meat with the purpose of avoiding contamination by *L. monocytogenes* [35]. **Thuricin 7:** The action and inhibitory spectrum of this bacteriocin includes *B. cereus* and *Bacillus weihenstephanensis* strains (commonly associated with the deterioration of dairy products and raw milk). Such properties make thuricin 7 the perfect candidate to be used as a food antimicrobial agent in order to control Gram-positive bacterial contaminants, without interfering with lactic acid bacteria growth [21]. **Entomocin 9:** This bacteriocin displays antimicrobial activity against *L. monocytogenes*, *P. aeruginosa* and several fungi. Entomocin 9 is a new bacteriocin produced by *B. thuringiensis* HD9 characterized as being heat stable. Lack of toxicity against Vero cells renders strain HD9 as being suitable for a safe application in antimicrobial treatments. The importance and impact of entomocin 9 makes *B. thuringiensis* strain HD9 an attractive microorganism in biotechnological applications as an antimicrobial agent in the food and agricultural industry [26]. **Thuricin CD:** The effectiveness of thuricin CD against the clinical *C. difficile* isolates, especially hypervirulent PCR R027 strains, makes it extremely interesting because of its structural characteristics and potential as a therapeutic agent. The isolation and characterization of thuricin CD may represent a structural class of bacteriocins as well as potentially providing a treatment for *C. difficile*-associated disease [13]. **Thuricin 439:** *B. thuringiensis* strain B439 produces thuricin 439, a small substance like bacteriocin produced as two active peptides with different molecular mass. Thuricin 439 is active against *B. cereus* and *B. thuringiensis* strains, while at the same time showing activity against *L. innocua* 4202 [40]. This bacteriocin could be used to control *B. cereus*, which can cause diarrhoea and vomiting. **Bt-BLIS:** The *B. thuringiensis* BLIS include morricin 269, kurstacin 287, kenycin 404, entomocin 420 and tolworthcin 524, produced by *B. thuringiensis* strains isolated in Mexico. These BLIS have been shown effective against Gram-positive and Gram-negative bacteria, including aetiologic agents of human diseases such as throat infections, scarlet fever, septicemia, pneumonia, urinary tract infections, emetic and gastrointestinal syndromes and different types of fungal infections. Furthermore, activity of the five BLIS mentioned earlier was tested against isolates of *S. aureus* associated with bovine mastitis. All the *S. aureus* isolates were shown to be susceptible to the five bacteriocins synthesized by *B. thuringiensis*, mainly to morricin 269 and kurstacin 287, followed by kenycin 404, entomocin 420 and tolworthcin 524 [16].

**Conclusion**

In this report, we propose a classification of Bt based on molecular weight, and functionality in single peptide and two-component peptide bacteriocins.

Because of the broad-spectrum nature of some *B. thuringiensis* bacteriocins, some may be included in antimicrobial strategies against virus, fungi, parasitic diseases and cancer, as well as in the immune system modulation [41]. The potential applications of these peptides reinforce the importance of studying their biological properties.

As previously mentioned, nisin, a bacteriocin approved by the Food and Drug Administration, is employed to inhibit bacterial growth in processed food. Although the potential application can be quite diverse and requires greater knowledge and tests that may be used in different health sectors as pathogen control in hospitals, environment and new antibiotics for controlling human and animal diseases.

For decades, *B. thuringiensis* has been one of the best options, as it has been safely employed as a bioinsecticide and applied in different human consumption crops without showing adverse effects. In particular, thuricin CD is a good example as it displays specific activity against...
C. difficile and it has no effect on the good flora living in the intestine, as is the case with most traditional antibiotics [42].

Acknowledgements

E.L.S.M. was a recipient of a fellowship from the Consejo Nacional de Ciencia y Tecnología (CONACyT) México. M.A.R.L. is SNI member. The authors thank Secretaría de Investigación y Posgrado, Instituto Politécnico Nacional; Grant: 20151437.

Conflicts of interest

There are no conflicts of interest.

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