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Research article

INVESTIGATING THE IMPACT OF DIFFERENT *BACILLUS THURINGIENSIS* STRAINS ON *ASCARIS SUUM* INTESTINAL CHANGES

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The parasitic nematode *Ascaris suum* is an economically significant worm that infects pigs and causes health issues and economic losses in pig farming. The intestine of *A. suum* is a long, straight tube that runs from the mouth to the anus and can be colonized by bacteria. Several bacteria have been studied for their potential antinematocidal effects. *Bacillus thuringiensis* (Bt), a soil bacterium known to produce many toxic crystal proteins (Cry), is emerging as a promising candidate for nematode control. Treatment of *A. suum* with all tested Bt strains (SS_26.2, SS_29.2, SS_35.1, SS_37.7) resulted in histopathological changes in the parasite intestine. Our research highlights the anthelmintic effect of Cry proteins and emphasizes the potential of Bt as an alternative tool for controlling parasitic nematodes of domestic animals. The studied strains are promising for the eradication of *A. suum* as a novel, environmentally friendly and cost-effective One Health approach, but further testing in pigs is needed to confirm these findings.

Keywords: *Ascaris suum*, *Bacillus thuringiensis*, parasite intestine, Cry proteins

INTRODUCTION

Infections caused by soil-transmitted helminths are a major health challenge worldwide, affecting both human and animal populations. In the absence of effective vaccines and suboptimal sanitary conditions, the treatment of these infections relies heavily on anthelmintics [1]. *Ascaris suum* is a species of parasitic roundworm belonging to the phylum Nematoda. It is commonly known as porcine roundworm or large

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roundworm of pigs. *A. suum* primarily infects pigs, but can occasionally infect humans and cause a disease known as ascariasis. Husbandry and housing practices associated with pig farming contribute significantly to the release of organic matter into the environment, particularly in the form of animal feces. This environment favors the proliferation of various parasites, with *A. suum*, a soil-dwelling helminth, posing a particularly significant threat to human and animal welfare. The eggs of *A. suum* exhibit remarkable resilience and are capable of contaminating the soil, surface water and even wastewater treatment plants, leading to direct health risks through soil contact and indirect hazards via the consumption of contaminated products [2]. The economic impact of *A. suum* infestation in pig farming is considerable and has a negative impact on carcass composition, feed conversion and overall productivity, thereby affecting the profitability of the meat industry [3]. In addition, the zoonotic potential of *A. suum* highlights concerns regarding transmission between pigs and humans, especially in scenarios where pig manure serves as a fertilizer for crops intended for human consumption [4]. Therefore, understanding the biology, lifecycle, and control measures for this nematode is essential for effective management and prevention of infection in both animals and humans. *A. suum* is a relatively large nematode, with adult worms typically ranging from 15 to 35 centimeters (6 to 14 inches) in length. They have cylindrical bodies tapered at both ends, and the females are generally larger than the males. The life cycle of *A. suum* involves both definitive hosts (pigs) and intermediate hosts (soil). Pigs become infected by ingesting *Ascaris* eggs, which are passed in the feces of infected animals. The eggs hatch in the pig's intestine and release larvae which penetrate the intestinal wall and migrate through the liver and lungs before being coughed up and swallowed, thus returning to the intestine where they mature into adult worms. The adult worms then produce eggs, completing the cycle.

The foregut of *A. suum* is made up of the buccal cavity and the pharynx, both of which are lined with a cuticle reflecting their ectodermal origin. The pharynx, distinguished by its thick muscular walls, functions to draw food into the gut, overcoming the high hydrostatic pressure of the pseudocoel. In cross-section, the pharynx appears circular. The midgut or intestine begins immediately after the pharynx and takes the form of a flattened, ribbon-like tube [5]. The intestine is responsible for absorption and biochemical reactions. The worm primarily feeds on simple sugars and amino acids from the intestinal contents of its host. Monomers are absorbed by the microvilli of the midgut epithelium. The gut appears flattened dorsoventrally when observed in the middle region. Under high magnification, the intestinal walls are seen to consist of a simple columnar epithelium made up of very tall cells. Unlike the ectodermal foregut, the midgut wall is composed solely of this simple columnar epithelium and its basal membrane. The worm lacks associated muscles, connective tissue, and mesothelium. The basal membrane consists of basal ends and separates the pseudocoel from the epithelium. Externally, the pseudocoel is surrounded by somatic musculature derived from the mesoderm, while internally, it is lined by the midgut epithelium, which originates from the endoderm [5].

Several bacteria have been studied for their potential antinematocidal effect, either by direct action on nematodes or indirectly by modulating the host's immune response. One of the notable bacteria with antinematocidal properties is *Bacillus thuringiensis* (Bt). In view of the continuing resistance of nematodes to conventional pharmacotherapy and the legal restrictions on chemical anthelmintics in organic farming, there is growing interest in research into natural alternatives to control parasitic nematodes. *B. thuringiensis*, a soil bacterium known to produce toxic crystal proteins (Cry), is considered a promising candidate for nematode control [6]. Cry proteins have been shown to be effective against insects and various nematode species by selectively targeting receptors in their gut, triggering the formation of pores and subsequent poisoning [7]. When ingested by insects or nematodes, these proteins (protoxins) dissolve in their midgut and are activated by proteases to form an active toxin. The toxin then binds to various membrane receptors, including glycopeptides [8,9], leading to final cell lysis [8]. The selective toxicity of Cry proteins is due to the fact that they are highly specific and only target invertebrates. Therefore, they are safe for vertebrates even in high concentrations, as vertebrates lack this glycoprotein receptor [3].

Despite the success of Cry proteins against certain nematodes, their efficacy against *A. suum* is still largely unexplored. The aim of this study is to find out whether *A. suum* possesses receptors for Cry proteins and to evaluate the *in vitro* intoxication of *A. suum* by Bt isolates. In this way, we aim not only to improve our understanding of the interactions between Cry proteins and parasitic nematodes but also to evaluate the potential of Bt as a therapeutic agent for *A. suum* infections, thereby addressing a critical need in veterinary and human medicine.

MATERIALS AND METHODS

Ethical approval

The conducted research is not related to animals use.

Isolation and visualization of bacterial inclusion bodies

The proteins from the parasporal inclusions were isolated to analyze the protein profile of the inclusions and the possible correlation of the profile with the phylogenetic relationship and nematocidal activity of the strains studied. The bacteria were cultivated in liquid Schaeffer medium at 30 °C and 180 rpm. After 5 days of incubation, the occurence of sporulation and the formation of parasporal inclusions were checked by Schaeffer-Fulton staining and observation of the preparations under immersion at 1000x magnification. Next, 2 mL of each culture was centrifuged (10000 rpm, 10 min) and washed twice with dH_2O. The suspension was then dissolved in 0.5 M NaOH and incubated at room temperature for 15 min, after which it was again washed twice with dH_2O. The culture was then resuspended in 0.2 mL crystal solubilization solution (1%

SDS, 0.01% β-mercaptoethanol) and incubated at 100 °C for 15 min. The supernatant containing the solubilized proteins from the parasporal inclusions was separated by centrifugation (13000 rpm, 30 min). The protein profiles of the extracts obtained were analyzed by SDS-PAGE electrophoresis on 10% acrylamide gel. Protein samples were mixed with 5X sample buffer (10% SDS, 10 mM β-mercaptoethanol, 20% glycerol, 0.2 M Tris pH 6.8, 0.05% bromophenol blue) and heated at 100 °C for 5 min, after which 30 µL of each sample was loaded onto the gel. The Bio-Rad Mini-PROTEAN® Vertical Electrophoresis System was used for electrophoresis. Gels were stained in 50% methanol, 10% acetic acid and 0.1% Coomassie Brilliant Blue R250 for 1 hour and then destained overnight in 50% methanol and 10% acetic acid. Protein size was determined relative to the PageRuler™ Plus Prestained_Protein Ladder (10 to 250 kDa, Thermo Fisher Scientific).

Preparation of bacterial strains

B. thuringiensis SS-26.2, SS-29.2, SS-35.1 and SS-37.7 are part of a larger collection of isolates of *Bacillus* spp. from the isolate collection of the Department of Microbiology of the University of Belgrade – Faculty of Biology. The strains were selected based on their previous identification as Bt [9] and their nematocidal activity was demonstrated in a test for killing *Caenorhabditis elegans* [10]. The strains grown in Schaeffer's sporulation medium (peptone 5 g, Difco beef extract 3 g, $MgSO_4 \times 7H_2O$ 0.25 g, KCl 1 g, $MnCl_2 \times 4H_2O$ 1.98 mg, $FeSO_4 \times 7H_2O$ 0.28 mg, $CaNO_3 \times 4H_2O$ 0.118 g, thymidine 0.02 g, 1000 mL dH2O) were grown at 30 °C with shaking for aeration (180 rpm) for 5 days. The sporulated cultures were then harvested by centrifugation at 5000 rpm for 5 minutes, washed in phosphate-buffered saline pH 7.4 (PBS) and resuspended to a final concentration of 10^9 CFU/mL. These suspensions were further used for the nematocidal activity tests.

Treatment of A. suum with Bt.

Live adult forms of *Ascaris* were delivered to our laboratory from slaughterhouses in the vicinity of Belgrade. After removing the live worms from the intestines of the pigs, they were placed in a thermos flask with the prepared Lockes solution (155 mM NaCl, 5 mM KCl, 2 mM $CaCl_2$, 1.5 mM $NaHCO_3$ and 5 mM glucose), which was tempered to 37 °C. The worms were kept alive in a water bath in our laboratory for the next couple of days. On the second day after delivery of the live worms, an experiment was conducted with the application of the tested Bt strains. First, the tested strains were prepared for application, which we applied in a volume of 200 µL. In the test, we applied the volume of the strains through a plastic gastric tube, which is often used for application in laboratory mice. The entire procedure consisted of cutting off the head of the Ascaris cranially in front of the pharynx and then retracting and inserting the probe directly through the pharynx into the worm's intestine. Then, 200 µL of the suspension of the tested strains was applied. Then the front cranial part of the

worm's intestine and the caudal part of the exiting intestine were tied behind the anus to prevent leakage of the contents and leaking out of the suspension of the tested strains. The tested worms that were subjected to the application were then incubated in Lockes solution at 37 °C for the next 24 hours.

Histopathological assessment of Bt toxicity

After incubation for 24 hours at 37 °C, the anterior part of *A. suum*, which included the foregut (buccal cavity and pharynx) and the cranial part of the midgut, was fixed in 10% buffered formalin for 48 hours. After standard processing in an automated tissue processor, transverse sections of *A. suum* at the level of the midgut were embedded in paraffin blocks and 5 μm thick sections were stained with haematoxylin and eosin (HE). The results of histochemical staining were analyzed with a light microscope (BX51, Olympus Optical, Japan) and images were captured with an Olympus Colour View III® digital camera.

RESULTS

Characterization of Bt inclusion bodies

The Cry proteins produced by Bt are encapsulated in parasporal inclusion bodies, which are proteinaceous crystalline structures that form during sporulation and harbor the Cry toxins. The strains used in this study were previously characterized for their Cry content [10] and they contain several *cry* genes (Figure 1A). SS_29.2 and SS_26.2 are closely related and both contain *cry12*, while SS_26.2 also contains *cry1*, one of the most extensively studied Cry proteins known for its high insecticidal activity against lepidopteran larvae. SS_35.1 and SS_37.7 are also closely related and have the same Cry gene repertoire. Inclusion bodies were visible under the microscope in these two isolates (Figure 1B). Proteins of different sizes could be detected in these inclusion bodies, of which very few correspond to the expected sizes of the Cry proteins (65-145 kDa). SS_35.1 and SS_37.7, which have the same Cry protein content, also show the same pattern of bands in the SDS-PAGE gel, while SS_26.2 appears different.

Activity of Bt isolates on the intestine

The intestine of the *A. suum* is a long, straight tube that runs from the mouth to the anus. It consists of three parts: an anterior, ectodermal foregut, an endodermal midgut and an ectodermal hindgut. The anterior, ectodermal foregut is lined with a cuticle and consists of the oral cavity and the pharynx, the wall of which is muscular. The endodermal midgut is flattened dorsoventrally and is located in the middle region. It consists of very large columnar epithelial cells. The basal part of these epithelial cells lies on the thick basement membrane and the cell nucleus is located in this end of the cell. The opposite, apical part of the epithelial cells is microvillated and forms

a brush border, which is responsible for the uptake of nutrients. The ectodermal hindgut or rectum is lined with a cuticle [5]. This normal intestinal morphology can be seen in in the control group (Figure 1C), where *A. suum* was treated with sterile PBS containing no bacterial cells. The endodermal epithelium of the midgut consisted of large columnar epithelial cells lying on the thick basal membrane. The nuclei of the epithelial cells were located at the basal end of the cell, while an intact brush border was observed at the apical end of the cell.

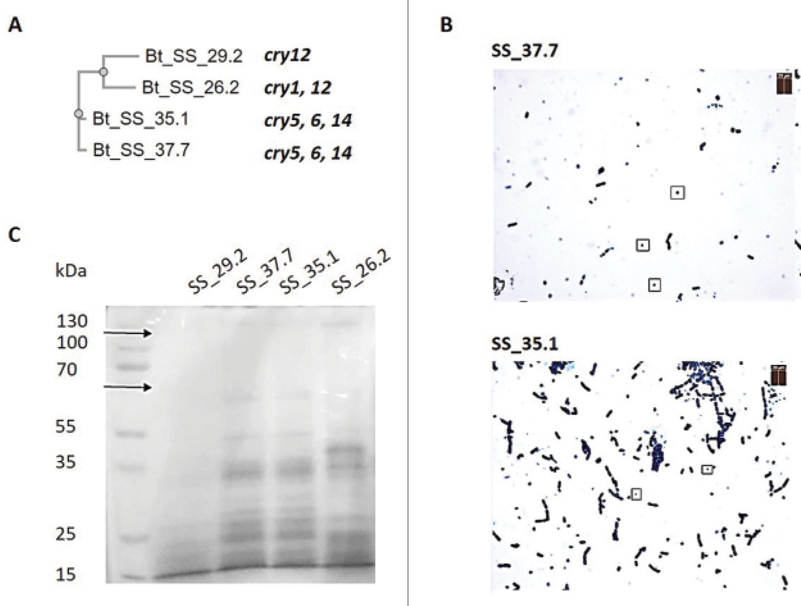

Figure 1. A – Phylogenetic relationship between the tested Bt isolates and their *cry* gene content. **B** – Bt spores and inclusion bodies (labeled with a box) under light microscope (magnification 1000×). **C** – SDS-PAGE gel (10%) of the parasporal inclusion bodies. 10-250 kDa protein ruler was used and the size range of the Cry proteins is indicated by arrows.

Treatment of *A. suum* with all tested Bt strains led to morphological and histological changes in the intestine (Figure 2).

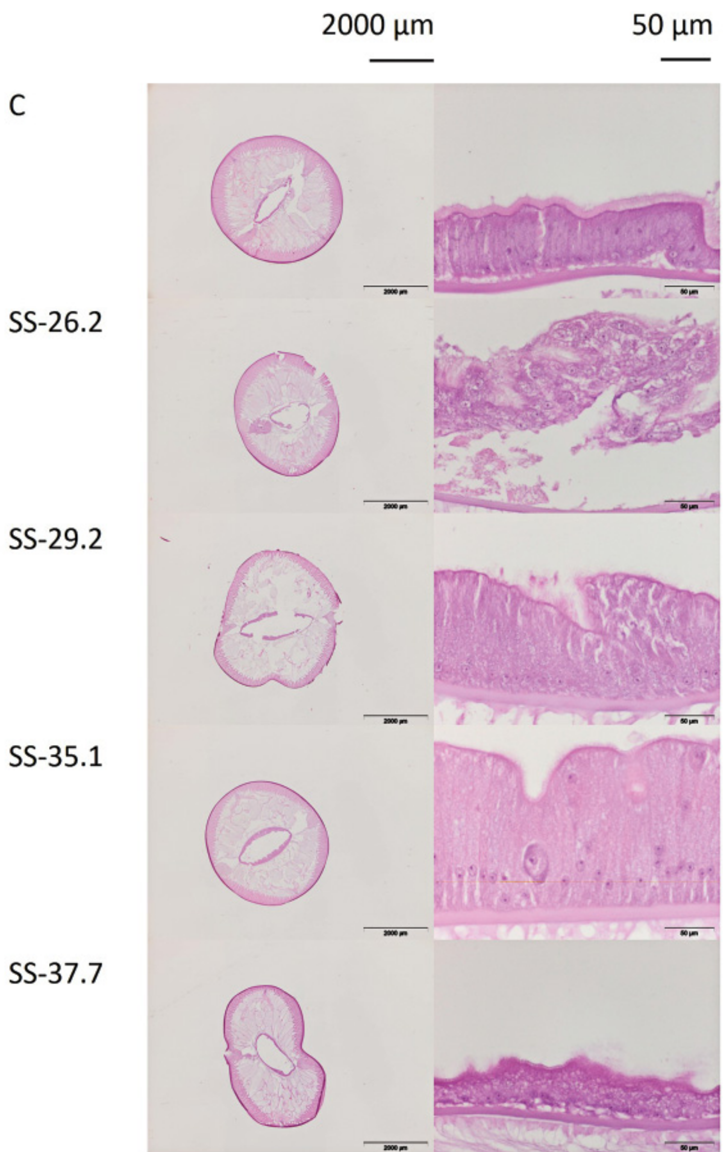

Figure 2. Morphological and histological changes in the *A. suum* intestine. **C** is the control group that was not treated with bacteria. SS-26.2, 29.2, 35.1 and 37.7 indicate treatments with spores and inclusion bodies of different Bt strains. **C** – intestinal simple columnar epithelium of very tall microvillated cells that rests on the basal membrane. The absorptive brush border is clearly visible (HEx20 and HEx600). **SS – 26.2** – necrotic intestinal epithelium cells detached from the basal membrane, with loss of cellular structure and brush border. **SS – 29.2** – intestinal epithelial cells with partial loss of brush border, degenerative changes and cracks in the epithelium. **SS – 35.1** – edematous intestinal cells with partial loss of brush border and macronuclei. **SS – 37.7** – necrotic intestinal epithelium cells with complete loss cellular structure.

The epithelial layer of the midgut was destroyed, with degenerated and necrotic epithelial cells without brush border that had detached from the basal membrane (Figure 3).

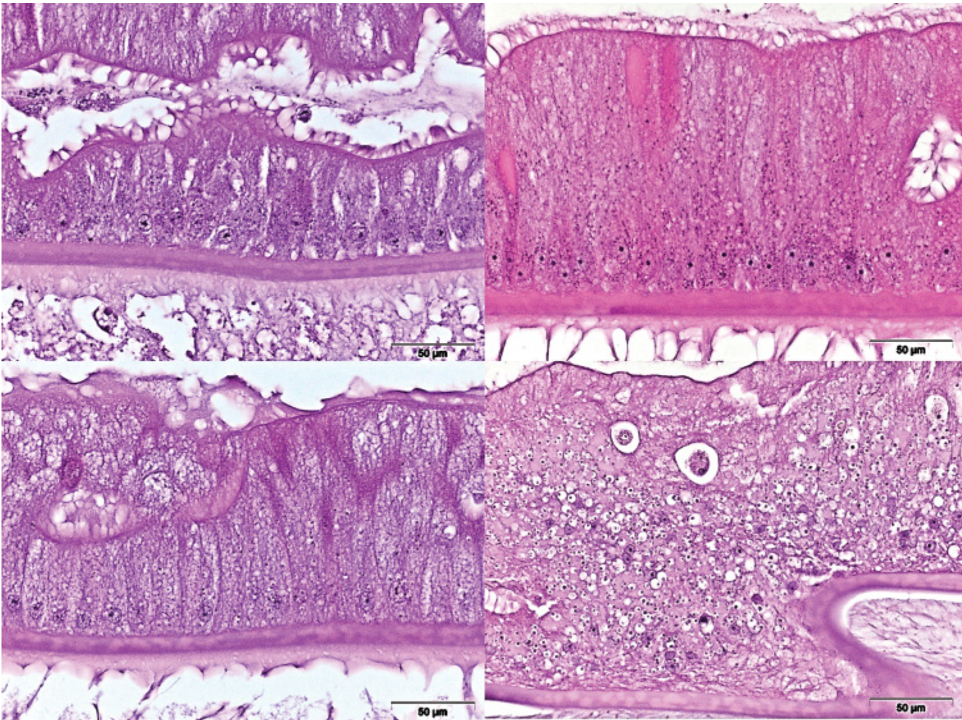

Figure 3. Histopathological changes with degenerated and necrotic epithelial cells without brush border. All four panels represent histopathological changes obtained after treatment with Bt 29.2. **Upper left –** degenerative changes and partial loss of brush border on intestinal epithelial cells. **Upper right –** degenerative changes, numerous intracellular microorganisms, epithelial cysts and partial loss of brush border on intestinal epithelial cells. **Down left –** degenerative changes and complete loss of brush border on intestinal epithelial cells. **Down right –** degenerative and necrotic changes of intestinal epithelial cells, numerous intracellular microorganisms and complete loss of brush border.

DISCUSSION

The development of new antiparasitic drugs with novel mechanisms of action is essential to ensure both efficacy and host safety. Current antiparasitic treatments are facing major challenges as resistance is increasingly reported in various parasitic nematodes. In addition, the need for higher drug doses to maintain efficacy raises toxicity concerns [11]. Bacteria, particularly probiotics, represent a promising avenue in the ongoing fight against helminth infections, which pose a significant global health threat affecting people and livestock worldwide. Despite ongoing efforts, the lack of

an effective vaccine against helminths remains a formidable challenge. Conventional anthelmintics, including benzimidazoles and macrocyclic lactones, are increasingly encountering resistance, particularly in livestock, jeopardizing both economic sustainability and public health [12]. In response to this urgent need, alternative treatments such as probiotics have attracted considerable attention. Probiotics are known for their multiple health benefits, including modulation of the immune system and improvement of gut health, and show promising potential in the containment of helminth infections. In the field of probiotics, the genus *Bacillus* is emerging as a significant contender due to its considerable probiotic potential [13]. Commercially available probiotic *Bacillus* strains include *B. cereus*, *B. clausii*, *B. coagulans*, *B. licheniformis*, *B. polyfermenticus*, *B. pumilus* and *B. subtilis*. However, the potential of *B. thuringiensis* (Bt) as a probiotic is still largely unexplored, despite its commercial use as a biological pesticide due to the production of Cry proteins that are toxic to insects. Bt strains produce a variety of insecticidal and nematocidal proteins, including Cry and Cyt proteins, β-exotoxin, vegetative insecticidal proteins, secreted insecticidal protein, Zwittermicin A, Mtx-like toxin and Bin-like toxin. The production, secretion and activity of these metabolites depend on the bacterial growth phase [6]. Recent research highlighting the anthelmintic activity of these proteins emphasizes the potential utility of Bt as a probiotic veterinary drug that offers a promising approach to controlling the spread of parasitic nematodes.

During sporulation, Bt strains produce Cry proteins, whereby the content of *cry* genes is strain-specific. While some Cry proteins have specific activity against certain insect or nematode species, others have a broader spectrum of activity. In our study, all tested Bt isolates showed toxic activity against *A. suum*, whereas their efficacy against the model nematode *C. elegans* has already been described [10]. In addition, the Cry content of the isolates shows different profiles as characterized by Atanasković et al. (2020): SS-26.2 harbors Cry1 and Cry12, SS-29.2 contains Cry12, while SS-35.1 and 37.7 possess Cry5, 6 and 14. These Cry proteins have previously been associated with nematocidal Bt activity against various plant-parasitic nematodes. For example, Cry12 shows activity against the pine nematode *Bursaphelenchus xylophilus* [8], Cry5 targets plant root-knot nematodes [14] and Cry14 is effective against soya cyst nematodes [6]. However, the anthelminthic activity of Bt against animal parasitic nematodes is still poorly understood. Urban at al. [8] demonstrated that the Cry5B protein is active against *A. suum*, but our data provides initial evidence that other Cry proteins may also be active against this nematode, as only two of the four strains tested contained Cry5. Future studies should address the anthelmintic activity of other purified Cry proteins, such as Cry12, 6 and 14, which are common among the strains tested in our study.

The potential of Bt strains as probiotics to protect pigs against *A. suum* infections is underlined by convincing evidence of their antihelminthic effect. In our study, remarkable changes in the intestinal architecture of *A. suum* were observed after treatment with a single dose of sporulated Bt cells (10^6 CFUs), indicating an effective intervention. In addition, confirmatory results from a separate study show a remarkable

96% reduction in parasite burden in *A. suum* infections in pigs after administration of a single oral dose of a Bt paraprobiotic consisting of inactivated Bt cells [8]. Furthermore, the resilience of Bt strains in soil environments is remarkable, as *A. suum* eggs often remain in the soil despite conventional anthelmintic treatments and lead to recurrent infections in pigs. The use of Bt as a probiotic is promising to mitigate this problem, as Bt spores released via pig feces can persist in the soil of the farm and thus potentially contain reinfections. To fully harness this potential, further research is needed to understand the survival and activity of Bt cells in the intestine. While this aspect has not yet been explored in pigs, studies in rats have shown that Bt spores can persist and germinate in the gastrointestinal tract without causing significant changes to the gut microbiome or showing toxicity [15]. The strains analyzed in our study show promising potential for the eradication of *A. suum* infections and represent a novel One Health approach that is environmentally safe, effective and inexpensive to produce and can even be used in developing regions worldwide. Nevertheless, comprehensive testing in pigs is mandatory to validate these results and will be the focus of our future studies.

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Authors' contributions

IA was involved in the conceptualization, and investigation of molecular genetic studies, and took part in writing the original paper. ST reviewed and edited of research paper. DM was in charge of visualization and writing the original draft. SS was involved in the supervision and methodology of work. JL reviewed and edited the original idea and conceptualization, and performed the main investigation. DrM created a visualization and made part of the review. DjM was in charge of the original idea and conceptualization, performed the main investigation, and took part in writing the original paper. All authors read and approved the final manuscript.

Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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ISTRAŽIVANJE UTICAJA RAZLIČITIH SOJEVA *BACILLUS THURINGIENSIS* NA CREVNE PROMENE *ASCARIS SUUM*

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Parazitska nematoda *Ascaris suum* je ekonomski značajan crv koji inficira svinje i izaziva zdravstvene probleme i ekonomske gubitke u proizvodnji svinja. Crevo *Ascaris suum* je duga, ravna cev koja ide od usta do anusa i može biti kolonizovana bakterijama. Nekoliko bakterija je proučavano zbog njihovog potencijalnog antinematodnog efekta. *Bacillus thuringiensis* (Bt) bakterija iz zemljišta za koju se zna da proizvodi mnogo toksičnih kristalnih proteina (*Cry*), pojavljuje se kao obećavajući kandidat za kontrolu nematoda. Tretman *Ascaris suum* sa svim testiranim sojevima Bt (SS_26.2, SS_29.2, SS_35.1, SS_37.7) rezultirali su histopatološkim promenama u crevima parazita. Naše istraživanje naglašava antihelmintički efekat *Cry* proteina i naglašava potencijal Bt kao alternativno sredstvo za suzbijanje parazitskih nematoda domaćih životinja. Proučavani sojevi bakterija obećavajući su faktor za iskorenjivanje *Ascaris suum* kao novi, ekološki prihvatljiv i isplativ pristup koji se naziva „Jedno Zdravlje“, ali je potrebno dalje testiranje na svinjama da bi se naši nalazi potvrdili.