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Research Article

Antimicrobial activity of bacteria isolated from *Leptinotarsa decemlineata* and *Solanum tuberosum*

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Abstract

From the intestinal microbiota of Colorado potato beetles and their larvae (*Leptinotarsa decemlineata*), as well as from their feed – potato leaves, 18 bacteria of different species exhibiting antimicrobial activity (56% of the total number of isolated strains) were isolated. The species of bacteria from all three sources of excretion are different. The following 12 species were described for the first time in the gut microbiota of *L. decemlineata* larvae and imago: *Micromonospora phytophila*, *Neobacillus drentensis*, *Pseudomonas gessardii*, *P. poae*, *P. rhizosphaerae*, *Pantoea agglomerans*, *Streptomyces chartreusis*, *S. clavifer*, *S. microflavus*, *S. rishiriensis*, *S. badius,* and *S. coelicoflavus*. Antimicrobial activity was not previously known for three species (*Staphylococcus argenteus*, *S. camponoticapitis*, *S. clavifer*). Antimicrobial activity against methicillin-resistant *Staphylococcus aureus* (MRSA), vancomycin-resistant *Leuconostoc mesenteroides*, multidrug-resistant *P. aeruginosa,* and *Mycobacterium smegmatis* was revealed. The gut microbiota of Colorado potato beetles can be considered an encouraging source of antibiotic–producing strains that overcome drug resistance of pathogenic bacteria, as well components of biopesticides.

Introduction

Our research is related to the study of microorganisms that form natural antibiotics. Based on Gause's theory, we consider antibiotics as an evolutionarily developed chemical weapon in the interspecific struggle for existence, therefore, complex multicomponent microbial communities are our main source of the search forantibiotic–producing microorganisms [1–4]. Several multifaceted studies show a variety of taxa of microorganisms that are inhabitants of such complex biocenoses, including the gut microbiota of invertebrates [5,6].

The objects of the work were bacteria – representatives of the gut microbiota of the Colorado potato beetle *Leptinotarsa decemlineata* (Say, 1824). Special interest in the study of the Colorado potato beetle in the world is since it is one of the most economically dangerous insect pests of agricultural crops, namely plants of the Solanaceae family. The main damage from the Colorado potato beetle is caused to a widespread potato crop, the leaves of which are the food of the Colorado potato beetle and its larvae, and the larvae can almost completely destroy the green mass of plants [7,8]. The first major outbreak of the Colorado potato beetle occurred in 1859 in potato fields in Nebraska, USA. Currently, the distribution area of *L. decemlineata* includes North America, Europe, and Asia, its further distribution to temperate zones is expected [9]. A few publications assessed the species diversity of the microbial world associated with the Colorado potato beetle. The results depended significantly on the range of the *L. decemlineata* population, as well as on the research method, especially after the introduction of methods based on DNA analysis into practice. For example, larvae of *L. decemlineata*

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were collected from private potato fields in the steppe zone of Western Siberia in July 2018. Based on the analysis of the 16S rRNA gene, the presence of intestinal bacteria belonging to 63 families, 21 classes, and 11 phyla in the samples of Colorado beetles was established. The predominant groups were Proteobacteria (*Enterobacteriaceae*) and *Spiroplasma* (Tenericutes, *Spiroplasmataceae*). The taxonomic composition differed in various samples. Some of them were dominated by *Enterobacter* and *Klebsiella*, others by *Citrobacter* strains. Also, a number of samples contained large amounts of *Serratia* (*Enterobacteriaceae*), *Acinetobacter* (*Moraxellaceae*), *Pseudomonas* (*Pseudomonadaceae*), and *Lactococcus* (*Streptococcaceae*). *Spiroplasma* (*Spiroplasma Leptinotarsa*) was presented in one of the samples, it is an obligate symbiont of the Colorado potato beetle [10,11]. The species *Spiroplasma Leptinotarsa* is a characteristic component of the intestinal microbiota of *L. decemlineata* and was first described in 1996 during the study of Colorado beetles collected in various regions of the USA and Eastern Europe [12]. In China, the Colorado potato beetle was first discovered in Xinjiang Uygur Autonomous Region in 1993. In 2021, microbial communities of *L. decemlineata* collected in 9 regions of China were examined using high-throughput sequencing technology. Bacteroidetes, Firmicutes, and Proteobacteria were the most dominant phyla, *Clostridia*, *Bacteroidetes*, and γ-Proteobacteria were the most dominant classes, *Enterobacterales*, *Lactobacillales*, *Clostridiales*, and *Bacteroidales* were the most dominant orders, and *Enterobacteriaceae*, *Streptococcidae*, *Verrucomicrobiaceae*, and *Rikenellaceae* were the most dominant families. A total of 383 genera were identified. Bacterial community diversity in *L. decemlineata* as well as the numbers of taxonomic groups were different depending on the areas where the beetles were collected [13].

Bacterial endosymbionts of *L. decemlineata* collected in potato fields in different regions of Poland were studied [14]. Ribosomal DNA analysis showed that of the 101 samples examined, 11.8% were infected with *Flavobacterium*. *The authors note the insecticidal effect of Flavobacterium on the imago and larvae of L. decemlineata.* Representatives of six genera of bacteria that were previously described as the most commonly present in arthropods were not found: *Wolbachia, Portiera, Hamiltonella, Rickettsia, Cardinium*, and *Arsenophonus*. The authors concluded that the level of infection rate and endosymbiont species composition for each insect species is variable and can be different even for the same insect species collected from various locations. The composition of the microbiota of *L. decemlineata* also depends on the stage of the life cycle. The beetles hibernate in the soil in the form of numb adults, but with the onset of the warm season, they come to the surface and lay their eggs on potato leaves. After 1–2 weeks, larvae hatch, which molts four times and, after the fourth molt, burrow into the soil, where pupae are formed. The transformation of a pupa into a sexually mature individual (adult) occurs approximately 1 month [7,8]. Analysis of the 16S rRNA gene showed that *L. decemlineata* pupae contain bacteria specific to this stage, namely *Blastococcus*, *Corynebacterium*, *Gordonia*, *Microbacterium*, *Nocardia*, *Nocardioides*, *Rhodococcus*, *Solirubrobacter*, *Tsukamurella*, *Enterococcus*, *Acinetobacter*, *Escherichia*, *Shigella*, *Lysobacter*, *Pseudomonas*, and *Stenotrophomonas*. Microbes from the types of Proteobacteria, Firmicutes, Actinobacteria, and Bacteroidetes were enriched in pupae, while microorganisms from the types of Proteobacteria, Tenericutes, Firmicutes, and Bacteroidetes prevailed in larvae and adult forms. In total, 34 types of bacteria were identified, representing 73 classes, 208 orders, 375 families, and 766 genera. The results show that the bacterial community switch occurs in the pupae since the pupae-specific bacteria are mainly derived from the soil and the bacterial biodiversity in the soil is favorable for the development of the pupae. These results provide new insight into the evolutionary adaptability of *L. decemlineata* to different environmental conditions at different stages of the life cycle [15].

A few publications on the microbiota of *L. decemlineata* are related to the development of biopesticides, i.e., organisms and substances derived from them that can fight pests without causing damage to nature [16]. The disadvantage of chemical insecticides is their toxicity, in addition, has developed resistance to all major classes of these agents, which also makes the development of biopesticides an even more urgent task [9,17]. The most famous example of a biopesticide is the bacterium *Bacillus thuringiensis*, which forms the Cry toxin. This toxin suppresses the activity of phenol oxidase and acetylcholinesterase in the hemolymph of beetles, which leads to their death. *B. thuringiensis* is widespread in nature, and it has been isolated from both insects and their host plants [18-22]. Biopesticides have been developed, for example, based on the selection strain *Bacillus thuringiensis* var. *darmstadiensis* 56 (BtH_{10} 56), which in field tests against the Colorado potato beetle showed an efficiency of more than 80%, which was equal in effect to the chemical standard [23]. Work with *B. thuringiensis* toxin has been carried out for a long time, including by genetic methods, namely the creation of genetically modified plant varieties [24].

In addition to *B. thuringiensis*, other endobionts of the Colorado potato beetle have also been developed as biopesticides. The bacteria *Leclercia adecarboxylata*, *Acinetobacter* sp., *P. putida*, and *Acinetobacter haemolyticus* were identified. Of these, *Leclercia adecarboxylata* and *P. putida* suppressed 100% of the Colorado potato beetle population and were considered by the authors as promising bacteria for the development of biopesticides [25]. Another candidate recommended for use as a biopesticide is the fungus *Beauveria bassiana*, a natural insect pathogen. The strain was isolated from a naturally infected Colorado potato beetle taken from a potato field in the Czech Republic. The effectiveness of beetle destruction was almost total [26].

The dependence on species' survival may have a more complex multi-component character. An example of the relationship of organisms of different taxonomic groups is the relationship of the nematode *Caenorhabditis elegans*, parasitic in insects, with the strain *Bacillus nematocida* B16, resulting in a change in the number and composition of the intestinal microbiota of *C. elegans*, in particular, an increase in the proportion of Firmicutes bacteria and a decrease in the proportion of bacteria from the classes Proteobacteria, Actinobacteria, Cyanobacteria and Acidobacteria [27]. The

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bacterium *Photorhabdus luminescens* is a symbiont of the entomopathogenic nematode *Heterorhabditis bacteriophora*, which lives in insect larvae, including *L. decemlineata*. Nematodes do not grow or reproduce in the host insect or on artificial media in the absence of viable *Ph. luminescens* cells. With the help of mutant analysis, it is shown that the production of siderophore and antibiotic activities by the bacterium is important for the existence of a nematode [28].

Despite the description of bacterial complexes associated with the Colorado potato beetle, the antibiotic activity of microorganisms of these complexes has not been studied before. Our task was to study the antibiotic properties of bacteria associated with the Colorado potato beetle and its food. The description of the microbial diversity of the intestines of Colorado beetles was not a special purpose of the study, and the species identification of isolated bacteria was carried out in parallel with the analysis of the literature on antibiotics formed by representatives of these species.

Materials and methods

Sampling

Samples for research, namely potato leaves (*Solanum tuberosum*), larvae of the third instar living on them, and adults of the Colorado potato beetle (*Leptinotarsa decemlineata*) were manually collected in July 2020 on the experimental fields of the Chashnikovo Biological Station of Lomonosov Moscow State University (Moscow region, Russia) and studied. The fields were not treated with biopesticides or any chemicals.

Isolation of microorganisms from selected samples

Isolation of microorganisms from the studied samples as potential antibiotic producers was carried out by microbiological inoculation of intestinal homogenates of larvae and adults of Colorado beetles, as well as homogenates of potato leaves. Sowing was carried out on an agarized medium of the following composition (g/L): glucose – 0.3, peptone – 0.3, yeast extract – 0.3, and agar – 15. The samples were incubated at 28 °C for 14 days.

Media and culture conditions

Four agarized media were used for surface cultivation of the studied strains (%): medium No. 1 Gause: starch 2.0, K_2HPO_4 0.05, $MgSO_4$ 0.05, NaCl 0.05, $FeSO_4$ 0.001, agar 2.0, pH 7.2–7.4; modified medium No. 2 Gause: glucose 1.0, peptone 0.5, tryptone 0.3, NaCl 0.5, agar 2.0, tap water, pH 7.2–7.4; oatmeal agar (ISP3): oatmeal 2.0, agar 2.0, tap water, pH 7.2; soy medium: glucose 1.0, soybean flour 2.0, NaCl 0.5, agar 2.0, tap water; pH 6.9 [29,30].

The submerged cultivation of actinobacteria was carried out in eight liquid nutrient media developed for antibiotic producers at the Gause Institute of New Antibiotics (%):

STR: glucose 1.0, peptone 0.5, tryptone 0.3, NaCl 0.5, pH 7.2–7.4;

A4: glucose 1.0, soybean flour 1.0, NaCl 0.5, chalk 0.25, pH 6.8;

6613: starch 2.0, corn extract 0.3, KNO_3 0.4, NaCl 0.5, chalk 0.5, pH 7.0–7.2;

2663: glycerin 3.0, soybean flour 1.5, NaCl 0.3, chalk 0.3, pH 7.0;

5539: glycerin 2.0, soybean flour 0.5, $(NH_4)_2SO_4$ 0.15, NaCl 0.3, chalk 0.3, pH 6.8;

Suc: sucrose 2.0, soybean flour 1.0, NaCl 0.3, chalk 0.3, pH 6.8–7.0;

330: sucrose 2.1, starch 0.85, pea flour 1.5, chalk 0.5, NaCl 0.5, $NaNO_3$ 0.5, pH 7.0;

Am: sucrose 4.0, yeast extract 0.25, K_2HPO_4 0.1, Na_2SO_4 0.1, NaCl 0.1, $(NH_4)_2SO_4$ 0.2, $FeSO_4 \cdot 7H_2O$ 0.0001, $MnCl_2 \cdot 4H_2O$ 0.0001, NaI 0.00005, chalk 0.2, pH 6.5–6.7.

Test strains of fungi and *L. mesenteroides* were cultured on agar medium No. 2 Gause at 28 °C, the remaining bacterial strains – at 37 °C. Submerged cultivation of potential producers was carried out in 750 mL Erlenmeyer flasks with 150 mL of the medium on a rotary shaker at 200 rpm at 28 °C. Actinobacteria were fermented in two stages. In the first stage, the strains were incubated for four days in an STR medium, and the resulting seed material was injected 5 mL into flasks with the abovementioned media; antimicrobial activity was determined on the sixth day of incubation at the second stage. Bacteria of other taxonomic groups, as well as actinobacteria *Gordonia* sp. and *Micrococcus aloe vera*, grown in one stage in the medium of STR, the antimicrobial activity of the culture liquid was determined on the 1st, 2nd, and 4th days of incubation. Each strain was cultured and the activity was determined at least three times.

Species identification of bacteria

Morphological characteristics: For the description of the actinomycetes' cultural and morphological characteristics, medium No. 1 Gause, glycerin-nitrate agar, and media ISP3, ISP4, and ISP5 were additionally used [29,30]. To describe the bacteria, the morphology of cells and spores was examined using a Micmed-6 light microscope (LOMO, Saint-Petersburg, Russia). For actinomycete species identification, characteristics such as the structure of the sporophores, the spore surface, the pigmentation of the air mycelium and substrate mycelium, and the pigment released into the medium were considered.

Molecular characteristics: The species identification of actinobacteria was carried out by morphological features, as well as based on the analysis of the sequence of the 16S rRNA gene. Biomass for DNA isolation was provided from culture liquid obtained after three days of growth in the STR medium. Genomic DNA from the bacterial biomass was isolated using the PowerSoil DNA Kit (MO BIO, Carlsbad, CA, USA). PCR of the 16S rRNA gene was performed using a set of BioMaster HS-Taq PCR-Sp (Biolabmix, Novosibirsk, Russia) with universal bacterial primers: 27F (AGA GTT TGA TCC TGG CTCAG), and 1492R (TAC GGY TAC CTT GTT ACG ACT T) [31].

PCR was performed on a Thermal Cycler 2720 (Applied Biosystems, Foster City, USA) according to the following program: (1) 94 °C for 5 min; (2) 30 cycles with temperature intervals of 94 °C for 1 min, 51 °C for 1 min, and 72 °C for 2 min; (3) 72 °C for 7 min. The nucleotide sequences were determined by the Sanger method on a Genetic Analyzer 3500 (Applied Biosystems, Beverly, MA, USA) using universal bacterial

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primers: 27f, 341f (CCT ACG GGA GGC AGC AG), 785f (GGM TTA GAT ACC TGG TAG TCC), 1114f (GCA ACG AGC GCA ACC C), 519r (GTA TTA CCG CGG CTG CTG), 907r (CCG TCA ATT CCT TTG AGT TT), 1100r (GGG TTG CGC TCG TTG), 1392r (ACG GGC GGT GTG TRC), and 1492r. The Mega 7 program and 16S rRNA gene reference sequences obtained from the GenBank databases (blast.ncbi.nlm.nih.gov/Blast.cgi) and the Ribosomal Database Project (rdp.cme.msu.edu/) were used to assemble the nucleotide sequences [32].

Test strains

Gram-positive bacteria: *Bacillus subtilis* ATCC 6633, *B. pumilus* NCTC 8241, *B. mycoides* 537, methicillin-resistant *Staphylococcus aureus* INA 00761 (MRSA), methicillin-sensitive *St. aureus* FDA 209P (MSSA), *Micrococcus luteus* NCTC 8340, *Leuconostoc mesenteroides* VKPM B-4177 (resistant strain to glycopeptide antibiotics of the vancomycin group – vancomycin-resistant *Leuconostoc mesenteroides*, VRLM), and two strains of *Mycobacterium smegmatis* VKPM Ac 1339 and *Myc. smegmatis* 155 mc²; Gram-negative bacteria: *Escherichia coli* ATCC 25922, *Pseudomonas aeruginosa* ATCC 27853 with multidrug-resistance (MDR); and fungi: *Aspergillus niger* INA 00760, *Saccharomyces cerevisiae* RIA 259 were used as test strains to determine antibiotic activity. Most of the test strains were incubated for 24 hours at 37; mycobacteria were incubated for 2 days. *L. mesenteroides* VKPM B-4177, *A. niger* INA 00760 and *Sac. cerevisiae* RIA 259 were incubated at 28 for 24 hours.

Determination of antimicrobial activity by agar diffusion method

To determine the antibiotic activity in Petri dishes on a balanced platform was poured agar medium No. 2 Gause in the amount of 15 ml/dish. An aqueous suspension of test bacteria was applied to the frozen surface of the medium at the rate of 10^7 cells/cm². Wells 9 mm in diameter were made in the medium, with 6 holes per dish. The culture liquid to be analyzed was centrifuged in an Eppendorf (MiniSpin®, Eppendorf AG, Germany) and sterilized by filtration through a 0.20 µm membrane (Corning®, NY 14831). 100 µl of the culture liquid filtrate was added to the wells. The dishes were incubated for 20 h at a temperature corresponding to the needs of the test strain. After incubation, the evaluation of antibiotic activity in the culture liquid was carried out by the diameter of the growth retardation zones of the tested strains (mm).

Results

Identification of microorganisms from the Colorado potato beetle and its feed (potato leaves)

32 strains of bacteria were isolated from the intestines of imago (11) and larvae (10) of *Leptinotarsa decemlineata*, as well as its feed – *Solanum tuberosum* leaves (11). Of the 32 strains, antimicrobial activity was detected for 18, which indicates a high percentage of active strains (56%). These strains were identified as a species or genus by analysis of the 16S rRNA gene, considering the coincidence of morphological characteristics of the strain with the description of the corresponding taxa. Alignment of the obtained nucleotide sequences of the 16S rRNA gene was performed with sequences of type strains from the RDP database. The sequences were deposited into the GenBank database (Table 1). The phylogenetic position of the four strains in which the sequence of the 16S rRNA gene was less than 97% (from 94.2 to 96.8%) is shown in Figures S1-4. Species identification of the studied bacteria showed that the bacterial intestinal complex of the Colorado potato beetle includes both known resident animal-associated bacteria (*Bacillus thuringiensis, Staphylococcus argenteus, Gordonia* sp.) and transient bacteria from feed associated with plants (*Micrococcus aloe vera, Neobacillus drentensis, Pantoea agglomerans, P. poae, P. rhizosphaerae*). Streptomycetes prevailed among *Actinobacteria*, but representatives of other genera of actinobacteria, namely *Gordonia, Micrococcus, Micromonospora, and Nocardia*, were also isolated.

Antimicrobial activity of the bacterial isolates

Antimicrobial spectra of these strains in relation to collection test microorganisms are presented in Table 2: 7 strains from imago, 6 from the third generation of larvae, and 3 from potato leaves. Data on the antimicrobial activity of actinobacteria *Micromonospora phytophila* INA 01405 (from imago) and *Micrococcus aloe vera* INA 01419 (from potato leaves) were obtained only during growth on agar medium; both strains exhibit antifungal activity against *Aspergillus niger* INA 00760.

All the studied bacteria of the genera *Bacillus*, *Gordonia*, *Neobacillus*, *Pantoea*, and *Pseudomonas* form antimicrobial substances on the first day of growth, but on a later day, the activity shown in many has a different focus. For example, the daily culture liquid of *P. gessardii* INA 01409 shows activity recorded against *Myc. smegmatis* VKPM Ac 1339 and *E. coli* ATCC

Table 1: The results of the identification of isolated promising bacterial strains based on the analysis of the 16S rRNA gene sequence.

Source	Genus, species, strain	Length (bp)	Identity (%)	GenBank accession number
Imago	*Gordonia* sp. INA 01411	1365	94.8*	ON763831
	Micromonospora phytophila INA 01405	1374	96.8*	ON763823
	Neobacillus drentensis INA 01404	1357	100	ON763829
	Pseudomonas gessardii INA 01409	1343	96.4*	ON763830
	Streptomyces chartreusis INA 01406	1207	97.9	ON763824
	S. clavifer INA 01407	1375	99.7	ON763822
	S. microflavus INA 01408	783	98.8	ON763820
	S. rishiriensis INA 01410	1373	98.8	ON763821
Larvae	*Bacillus thuringiensis* INA 01412	1367	100	ON763835
	Pantoea agglomerans INA 01413	1422	99.5	ON763834
	Pseudomonas poae INA 01414	1361	99.0	ON763833
	P. rhizosphaerae INA 01417	1365	94.2*	ON763832
	S. badius INA 01416	1294	100	ON763825
	S. coelicoflavus INA 01415	1387	100	ON763826
Potato leaves	*Micrococcus aloe vera* INA 01419	1335	98.6	ON763837
	Nocardia salmonicida subsp. *cummidelens* INA 01418	1366	100	ON763827
	Staphylococcus argenteus INA 01420	1423	99.5	ON763836
	S. camponoticapitis INA 01421	1361	97.8	ON763828

* The phylogenetic position of these strains is shown in Figures S1-4.

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Table 2: Spectra of antimicrobial activity of bacterial strains isolated from imago and larvae of the Colorado potato beetle, as well as from potato leaves.

Source	Strains showing antimicrobial activity	Culture medium (Day of growth) *	Growth inhibition zones, mm												
			Bacillus subtilis ATCC 6633	*B. mycoides* 537	*B. pumilus* NCTC 8241		*St. aureus* INA 00761 (MRSA)	*Micrococcus luteus* NCTC 8340	*Leuconostoc mesenteroides* VKPM B-4177 (VRLM)	*Mycobacterium smegmatis* VKPM Ac 1339	*Myc. smegmatis* 155 mc²	*Escherichia coli* ATCC 25922	*Pseudomonas aeruginosa* ATCC 27853 (MDR)	*Saccharomyces cerevisiae* RIA 259	*Aspergillus niger* INA 00760
Imago	*Gordonia* sp. INA 01411	STR (1)	0	0	0	0	0	0	0	0	27.67 ± 0.58	0	0	0	0
	Neobacillus drentensis INA 01404	STR (1)	0	0	0	0	0	0	0	19.33 ± 0.47	0	23.0 ± 1.41	0	0	0
	Pseudomonas gessardii INA 01409	STR (1)	0	0	0	0	0	0	0	20.67 ± 1.25	0	24.67 ± 0.47	0	0	0
		STR (4)	0	14.67 ± 0.47	0	0	12.33 ± 1.25	0	0	0	0	0	0	0	0
	Streptomyces chartreusis INA 01406	6613	0	0	0	11.33 ± 0.94	0	0	0	nd	0	0	0	11.67 ± 0.47	0
		Suc	0	0	0	0	12.0 ± 0.47	12.67 ± 0.94	0	nd	0	0	0	0	0
		330	0	0	0	0	0	0	0	nd	19.67 ± 1.70	0	0	0	17.33 ± 0.94
	S. clavifer INA 01407	6613	0	0	0	0	0	13.33 ± 0.47	0	nd	0	0	0	0	0
	S. microflavus INA 01408	A4	14.0 ± 0.00	14.0 ± .82	13.33 ± 0.47	19.33 ± 0.47	16.67 ± 0.47	16.67 ± 1.70	12.33 ± 1.25	nd	14.33 ± 0.94	0	0	0	0
		6613	0	0	0	0	0	0	0	nd	18.67 ± 0.47	0	0	0	0
		2663	0	0	0	0	15.0 ± 0.47	18.33 ± 1.25	0	nd	0	0	17.33 ± 0.47	0	0
		5339	0	0	0	12.33 ± 0.47	0	17.33 ± 0.47	0	nd	20.33 ± 1.25	0	0	0	0
		Suc	0	0	0	0	0	0	0	nd	0	0	0	0	14.0 ± 0.00
		330	0	12.33 ± 1.25	12.0 ± 0.82	16.67 ± 0.47	0	16.0 ± 0.82	15.67 ± 0.94	nd	23.33 ± 1.25	0	0	0	16.0 ± 0.82
		Am	12.0 ± 0.82	0	0	0	0	15.33 ± 0.47	15.67 ± 0.47	nd	17.33 ± 0.47	0	0	0	0
	S. rishiriensis INA 01410	6613	0	0	0	0	0	13.0 ± 0.82	0	nd	16.67 ± 0.47	0	0	0	0
		Suc	0	0	0	0	0	0	16.0 ± 0.82	nd	0	0	0	0	0
		330	0	20.67 ± 0.47	0	0	0	0	0	nd	0	0	0	16.33 ± 0.94	0

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Larvae	*Bacillus thuringiensis* INA 01412	STR (1)	0	0	0	14.67 ± 0.47	0	0	0	26.33 ± 0.94	13.33 ± 0.47	0	0	0	0
		STR (2)	0	0	0	0	16.67 ± 1.70	14.0 ± 0.47	0	0	0	0	0	0	0
		STR (4)	0	0	0	0	0	14.0 ± 0.47	0	0	0	0	0	0	0
	Pantoea agglomerans INA 01413	STR (1)	0	0	0	0	0	0	0	0	0	24.67 ± 1.25	12.0 ± 0.82	0	0
		STR (4)	14.67 ± 0.47	15.67 ± 1.25	16.67 ± 0.47	18.0 ± 1.63	17.33 ± 0.94	20.33 ± 1.25	0	0	18.0 ± 1.63	0	0	0	0
	P. poae INA 01414	STR (1)	0	0	0	0	0	0	0	0	0	25.33 ± 0.94	0	0	0
		STR (2)	0	0	0	0	14.33 ± 1.25	15.0 ± 0.82	0	0	16.67 ± 0.47	0	0	0	0
		STR (4)	13.33 ± 0.47	13.67 ± 0.47	0	0	14.33 ± 1.25	15.0 ± 0.82	0	0	16.67 ± 0.47	0	0	0	0
	P. rhizosphaerae INA 01417	STR (1)	0	0	0	0	0	0	0	0	0	18.67 ± 0.47	0	0	0
	S. badius INA 01416	A4	15.0 ± 0.82	17.33 ± 0.94	15.33 ± 0.47	17.67 ± 0.47	17.67 ± 0.94	23.0 ± 0.47	0	nd	21.67 ± 0.82	0	0	0	0
		6613	17.0 ± 0.47	22.33 ± 0.94	0	18.33 ± 0.94	19.67 ± 1.25	26.0 ± 0.47	16.0 ± 0.82	nd	21.33 ± 0.82	0	0	0	13.67 ± 0.47
		2663	17.33 ± 0.47	19.67 ± 1.25	16.33 ± 0.82	0	20.0 ± 0.82	23.67 ± 1.25	20.0 ± 0.82	nd	20.0 ± 1.63	0	0	15.33 ± 0.94	0
		Suc	0	12.67 ± 0.47	12.0 ± 0.82	19.33 ± 0.47	14.0 ± 0.94	17.33 ± 0.94	0	nd	0	0	0	0	0
		330	13.0 ± 0.82	15.33 ± .47	15.67 ± 0.94	15.0 ± 0.82	0	20.33 ± 0.47	16.33 ± 0.94	nd	18.33 ± 0.94	0	0	0	0
		Am	0	0	0	0	0	16.33 ± 0.47	16.67 ± 1.25	nd	15.0 ± 0.94	0	0	0	0
	S. coelicoflavus INA 01415	A4, 6613	0	0	0	0	0	25.0 ± 0.82	0	nd	0	0	0	0	0
		2663	16.67 ± 0.47	14.33 ± 0.82	0	0	0	19.67 ± 0.47	13.0 ± 0.00	nd	0	0	0	0	0
		5339	14.67 ± 0.47	15.0 ± 0.00	13.33 ± 0.94	0	0	15.33 ± 0.94	12.33 ± 0.47	nd	0	0	0	0	0
		330, Am	0	0	0	0	0	25.33 ± 0.47	13.67 ± 1.25	nd	0	0	0	0	0
Potato leaves	*Nocardia salmonicida* subsp. *cummidelens* INA 01418	A4	15.0 ± 0.94	0	0	0	0	0	0	nd	0	0	0	0	0
		2663	12.67 ± 0.47	13.0 ± 0.82	12.33 ± 0.47	20.0 ± 1.63	21.0 ± 0.82	19.0 ± 0.82	12.33 ± 0.47	nd	0	0	0	0	0
		330	0	0	0	0	0	0	14.67 ± 0.94	nd	0	0	0	0	0
		Am	0	0	0	0	0	0	0	nd	0	18.33 ± 0.94	0	0	0
	St. argenteus INA 01420	STR (1)	0	0	0	0	0	0	0	0	0	0	0	0	16.67 ± 0.47
	S. camponoticapitis INA 01421	A4, 5339	25.67 ± 0.47	23.0 ± 0.82	19.67 ± 0.47	31.67 ± 0.47	32.0 ± 0.82	42.0 ± 0.82	0	nd	0	0	0	0	0
		6613	22.0 ± 0.47	20.33 ± 0.47	17.67 ± 0.94	31.67 ± 0.47	30.0 ± 0.82	37.33 ± 0.47	0	nd	0	0	0	22.67 ± 0.47	16.0 ± 0.82
		2663	23.33 ± 0.47	20.0 ± ©1.63	18.33 ± 0.94	31.67 ± 0.47	28.67 ± 0.47	34.33 ± 0.94	26.67 ± 0.47	nd	0	0	0	0	0
		Suc	20.33 ± 0.94	17.0 ± 0.82	0	27.0 ± 0.47	27.33 ± 0.47	35.33 ± 0.94	0	nd	0	0	0	0	0
		330	21.33 ± 0.47	21.0 ± 0.82	14.0 ± 0.82	32.33 ± 0.47	28.67 ± 0.82	35.67 ± 0.82	0	nd	0	0	0	21.33 ± 0.94	0

Note: nd: no data.

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25922, but on the fourth day with partial lysis of the culture – against *B. mycoides* 537 and *St. aureus* INA 00761 (MRSA), i.e., this strain presumably forms at least two antimicrobial substances at different times and with different antibiotic activity. *P. poae* INA 01414 on the first day of growth is active only against *E. coli* ATCC 25922, and on the second day – against two strains of *St. aureus* and *Myc. smegmatis* 155 mc², and on the fourth day additionally against two bacilli strains (*B. subtilis* ATCC 6633 and *B. mycoides* 537). *St. argenteus* INA 01420 is active only against *Aspergillus niger* INA 00760 on the first day of growth (Table 2).

Actinobacteria of the genera *Streptomyces* and *Nocardia* have a different antimicrobial spectrum depending on the culture medium. For example, *S. microflavus* INA 01408 exhibits antimicrobial activity on all seven media, but the spectrum of antimicrobial activity is different, that is, it corresponds to at least seven different substances. In contrast, *S. clavifer* INA 01407 is active only against *St. aureus* INA 00761 on the single medium (6613). *S. camponoticapitis* INA 01421 exhibits antimicrobial activity against various Gram-positive bacteria regardless of the composition of the medium, however, against *L. mesenteroides* VKPM B-4177 is active only on medium 2663, against *Saccharomyces cerevisiae* RIA 259 – only on medium 330, and against *Sac. cerevisiae* RIA 259 and *Aspergillus niger* INA 00760 - only on medium 6613. Accordingly, it can be assumed that *S. camponoticapitis* INA 01421 produces at least 4 antimicrobial substances in the culture liquid (Table 2).

It follows from Table 2 that the studied producers produce antimicrobial substances active against various groups of microorganisms. In particular, activity was shown against antibiotic-resistant test strains: 9 producers were active against methicillin-resistant *Staphylococcus aureus* INA 00761 (MRSA), 6 – against *Leuconostoc mesenteroides* VKPM B-4177 (vancomycin-resistant *Leuconostoc mesenteroides*, VRLM), 10 – against *Mycobacterium smegmatis* VKPM Ac 1339 and/or *Myc. smegmatis* 155 mc², 2 – against *P. aeruginosa* ATCC 27853 (multidrug-resistant, MDR), and 6 – against fungi. Thus, the strains associated with the Colorado potato beetle and its feed represent an encouraging object for the search for antibiotics that overcome bacterial resistance.

Comparative evaluation of the antimicrobial activity of isolates obtained during the experiment with the data published in the literature

Table 3 presents a comparative analysis of our results from Table 2 with the literature data. Of the 18 bacteria, 12 showed for the first time antimicrobial activity as such or against certain test microorganisms (Table 3, marked "▲"). A more detailed comparison with previously described antibiotics in these species can be found in Table S1 and in the Discussion section.

Discussion

In this study, the species identity was determined for 17 of the 18 isolated strains exhibiting antimicrobial activity; for the strain, INA 01411, belonging to the genus *Gordonia* was established (Table 1). It should be noted that the strains of each of the three groups, namely, isolated from imago, larvae, and potato leaves, belong to different species and are not repeated. Since the Colorado potato beetle feeds exclusively on *Solanaceae*, in this case, potatoes, one would expect the presence of microorganisms isolated from potato

Table 3: Summary of antimicrobial activity results and their comparison with published data on the corresponding species.

Species, strain	Activity against different groups of microorganisms (obtained during the experiment)				Activity against different groups of microorganisms (according to literature data)				
	Gram-positive	Gram-negative	*Myc. smegmatis**	Fungi	Gram-positive	Gram-negative	*Myc. smegmatis**	Fungi	References
Bacillus thuringiensis INA 01412	●	○	▲	○	●	●	nd	●	[18,23,33–42]
Gordonia sp. INA 01411	○	○	▲	○	●	●	nd	●	[43–50]
Neobacillus drentensis INA 01404	○	▲	●	○	○	○	nd	●	[51,52]
Nocardia salmonicida subsp. *cummidelens* INA 01418	▲	●	○	○	○	●	nd	●	[53]
Pantoea agglomerans INA 01413	●	●	▲	○	●	●	nd	○	[54–60]
Pseudomonas gessardii INA 01409	●	●	▲	○	●	●	nd	○	[61]
P. poae INA 01414	●	●	▲	○	●	●	nd	●	[62–65]
P. rhizosphaerae INA 01417	○	●	○	○	●	●	nd	○	[67]
Staphylococcus argenteus INA 01420	○	○	○	▲	nd	nd	nd	nd	–
Streptomyces badius INA 01416	▲	○	▲	●	○	○	nd	●	[68,69]
S. camponoticapitis INA 01421	▲	○	○	▲	nd	nd	nd	nd	–
S. chartreusis INA 01406	●	○	●	●	●	○	●**	●	[70–73]
S. clavifer INA 01407	▲	○	○	○	nd	nd	nd	nd	–
S. coelicoflavus INA 01415	●	○	○	○	●	●	nd	●	[76–77]
S. microflavus INA 01408	●	●	▲	●	●	●	nd	●	[78–83]
S. rishiriensis INA 01410	●	○	●	●	●	●	●**	●	[84–91]

Note. «●» – antimicrobial activity has been evaluated against at least one tested strain of the given species; «○» – antimicrobial activity was not detected against any of the studied strains of the given species; «▲» – the antimicrobial activity of the species was first established against at least one of the tested strains during this experiment; (nd) – no data; * – two *Myc. smegmatis* test strains belong to actinobacteria, but are allocated to a separate group as a significant model that allows searching for antibiotics presumably active against tuberculosis; ** – activity was detected against *Mycobacterium tuberculosis*.

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leaves in the intestinal microbiota, but this was not detected. Previously, the specificity of the species composition of the microbiota of the Colorado potato beetle and its change during the transition from the larval stage to the pupal stage, and then to the imago stage were noted [15]. Presumably, with an increase in the number of isolated microorganisms, it would be possible to detect in the Colorado potato beetle bacteria of those species that are contained in potato leaves, which would give reason to attribute them to transitional species that enter the body with feed and remain viable as part of the microbiota for some time. For example, a strain of *Micrococcus aloeverae* (strain INA 01419), a representative of the endobiont species previously isolated from *Aloe vera*, was isolated from potato leaves [92], but we have not found this species in the larvae and image of the Colorado beetle. Alternatively, the endophytes of *Micromonospora phytophila* and *Neob. drentensis* previously isolated from a root nodule of peas (*Pisum sativum*) and nightshade (*Physalis ixocarpa) [52,93],* we isolated from imago, but we did not find it in potato leaves (Table 1). Despite the description of representatives of a large number of taxa mentioned above in the introduction, we were the first to isolate and identify strains in the microbiota of Colorado beetles: *Micromonospora phytophila, Neobacillus drentensis, Pseudomonas gessardii, P. poae, P. rhizosphaerae, Pan. agglomerans, Streptomyces chartreusis, S. clavifer, S. microflavus, S. rishiriensis, S. badius*, and *S. coelicoflavus*. Of the bacteria listed in Table 1, only *Bacillus thuringiensis* and *Gordonia* sp. were previously isolated from Colorado beetles [15,18,22].

The predominant part of currently known antibiotics of microbial origin has been isolated from actinobacteria and the leader in the production of antibiotics is the genus *Streptomyces* [94-96]. In addition to streptomycetes among actinobacteria, the "rare" genera *Actinomadura*, *Actinoplanes*, *Micromonospora*, *Nocardia*, *Saccharopolyspora*, *Streptosporangium*, *Streptoverticillium* are important and currently actively studied potential producers [94,97-101].

Three antifungal antibiotics have been isolated from *S. badius*, effective against the phytopathogenic fungus *Colletotrichum gloeosporioides* – the causative agent of rubber anthracnose, antimicrobial activity against other microorganisms has not been studied [68]. The antibiotic marilone C with antioxidant, anticancer, and antiviral activities has also been isolated in this species, but no research has been conducted against bacteria and fungi [69]. In addition, six new compounds were also isolated from *S. badius*, however, against two Gram positive bacteria (*B. subtilis* ATCC 6633, *St. aureus* ATCC 25923), three pathogenic yeasts (*Candida albicans* MYA 2867, *Candida parapsilosis* ATCC 22019, and *Cryptococcus neoformans* ATCC 208821), and tumor cells, there was no biological activity detected [102]. Strain *S. badius* B192 UFL isolated from Algerian Sahara soil exhibited antimicrobial activity against Gram-positive and Gram-negative bacteria, as well as fungi, including phytopathogens. The authors note that extreme ecosystems can be a source of untapped microorganisms to produce novel bioactive compounds of industrial interest [103]. The strain of *S. badius* INA 01416 studied by us is active against Gram-positive bacteria and fungi. Since the antimicrobial spectrum varies on different media, and activity is exhibited against resistant forms (MRSA, VRLM, *Myc. smegmatis* 155 mc^2), it can be assumed that different substances are formed, including those overcoming antibiotic resistance, and therefore it is advisable to investigate the chemical structure of the substances formed by *S. badius* INA 01416.

Strain INA 01421 belongs to the species *S. camponoticapitis*, described relatively recently, in 2016 [104]. It was isolated from the head of the ant *Camponotus japonicus*. We have not found any information about the antimicrobial activity of this strain in the literature. This strain as a producer is certainly of interest since it forms at least five antimicrobial substances (Table 2).

Streptomyces chartreusis is known as a producer of one of the first discovered antibiotics – chartreusin. Chartreusin is active against Gram-positive bacteria, including the causative agent of tuberculosis. It was later shown to inhibit RNA synthesis and cause single-strand scission of DNA via the formation of free radicals, which allowed it to be evaluated as an antitumor antibiotic. This species also forms the antibiotics tunicamycins, cephalosporins, holomycins, N-deacyltunicamycin, elsamicin A, and calcimycin [70-74]. It is possible that the strain *Streptomyces chartreusis* INA 01406 forms antibiotics previously described in this species.

S. clavifer is known as a producer of biologically active substances melanostatin and α-amylase, but no antibiotics have been described in this species [105,106]. Therefore, we consider the strain *S. clavifer* INA 01407 as a potential producer of an antibiotic, the study of which is advisable to continue.

The *S. coelicoflavus* INA 01415 strain has activity only against Gram-positive bacteria but is not active against Gram-negative bacteria and fungi. Presumably, this strain forms at least two antibiotics (Table 2). Previously, a broad range of antimicrobial activity was described in representatives of this species isolated from bottom sediments of the Chukchi Sea and mangrove soil [76,77]. The activity of the INA 01415 strain is of interest because the spectrum of antimicrobial activity is limited, activity exhibited against the vancomycin-resistant *L. mesenteroides* VKPM B-4177 (VRLM) and in chemical terms, antibiotics of this type have not been sufficiently studied.

Antiviral and anthelmintic antibiotics, including avermectin group antibiotics with veterinary use, have been described for *S. microflavus* [78-80]. In addition, marine bacterium strain *S. microflavus* MBTI36 produces four antibiotics of the aureolic acid family named chromomycins. These antibiotics exhibit antibiotic activity against Gram-positive bacteria with a MIC of fewer than 0.5 μg/mL. It is interesting to note that activity against Gram-negative bacteria has been established only against *Salmonella enterica* ATCC14028 (MIC 0.5 μg/mL - 1 μg/mL) [81]. Another antibacterial compound reported for *S. microflavus*, as well as in some other streptomycetes, is the cyclic peptide valinomycin – potassium ionophore [82]. In addition, *S. microflavus* produces antibiotic close to macrocyclic lactone antibiotic nemadectin with acaricidal and nematocidal activities and macrolide antibiotic irumamycin

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which is practicable as an agricultural antifungal agent [78,83]. The strain *S. microflavus* INA 01408 described by us exhibited antimicrobial activity specific to each of the media on all seven fermentation media. It can be assumed that the antibiotics formed by the INA 01408 strain are already described for this species, but considering its genetic reserve, we can expect the detection of new substances.

Hexacyclic antibiotic lactonamycin was isolated from the culture broth of *S. rishiriensis* MJ773-88K4. The antibiotic exhibited antimicrobial activities against Gram-positive bacteria including methicillin-resistant *Staphylococcus aureus* (MRSA) and vancomycin-resistant *Enterococcus* (VRE) [84]. Another antibiotic coumermycin A1 which is of aminocoumarin nature was first isolated from the fermentation broths of *Streptomyces rishiriensis* in 1965 [85]. *In vitro* coumermycin, A1 was active against some cell lines and Gram-positive bacteria (*Streptococcus*, *Bacillus*, and three *Mycobacterium* species), as well as a number of *Enterobacteriaceae* strains [86-89].

Previous studies have also shown the activity of purified *S. rishiriensis* extract against Gram-positive bacteria *St. aureus* and *Ent. faecium*, Gram-negative bacteria *E. coli* and *P. aeruginosa*, and against yeast *C. albicans* [91]. The strain of *S. rishiriensis* INA 01410 described by us exhibits antimicrobial activity against Gram-positive test bacteria, including the vancomycin-resistant strain, and *Mycobacterium*. Antifungal activity is also shown. Based on the results in Table 2 it can be assumed that at least three antibiotics are formed, possibly those described above.

Actinobacteria of the genus *Gordonia* are found in association with animals of different taxa, including beetles. Their biologically active substances are known to cause antimicrobial effects, such as enzymes and organic acids [107]. The strain *Gordonia* sp. INA 01411 isolated by us under these experimental conditions shows activity only against *Myc. smegmatis* 155 mc^2 in the initial stage of growth. It can be assumed that, as in the case of many other bacteria (Table 2), cells in the initial stage of growth on the first day of incubation (lag phase and growth delay phase) secrete enzymes into the medium, mainly hydrolases, causing an antimicrobial effect [108].

The type strain *Micrococcus aloeverae* AE-6^T(=MCC 2184^T=DSM 27472^T) was isolated from the internal tissues of the leaves of *Aloe barbadensis* (*Aloe vera*) collected in Pune, Maharashtra, India [92]. Representatives of this species are widely spread and isolated from a variety of sources: sea cocktails [109]; cow cheese samples [110]; caves [111]; sea sponges [112], and others. It is known that *M. aloeverae* is a producer of siderophores [113]. Antifungal activity against *A. niger* ATCC 16888 has been described for *Micrococcus aloeverae* [114]. We also noted the activity of *Micrococcus aloeverae* INA 01419 against *A. niger* when growing on an agar medium. Since antibiotics have not been identified in this species, we plan to develop biosynthesis conditions to isolate and identify an antifungal antibiotic.

Micromonospora is the second largest genus among actinobacteria. Basically, micromonospores form aminoglycoside antibiotics, among which gentamicin is widely used in medicine. *Micromonospora phytophila* was described 4 years ago, and in the literature, we have found no information about antimicrobial activity for this species [93]. The strain *Mic. phytophila* INA 01405 isolated by us is active against *Aspergillus niger* INA 00760 when growing on an agar medium, and work with it will continue.

Representatives of the genus *Nocardia* have been studied for a long time, but most studies have focused on the characterization and taxonomic classification of new isolates, as well as the pathophysiology of the host. Due to their clinical importance, many *Nocardia* genomes have been sequenced over the past decade. And only recently, some *Nocardia* species (*N. brasiliensis, N. abscessus, N. transvalensis, N. terpenica,* and *N. pseudobrasiliensis*) have been in the spotlight as producers of compounds with a diverse chemical structure, such as beta-lactams, polyketides, terpenoids, and siderophores, which have pharmaceutical value due to their immunosuppressive, antibacterial, cytotoxic, or antifungal biological activities [115,116]. In a study by Seratnahaei et al. strain *N. soli* N4 was isolated from a soil sample in Tehran, and its antimicrobial activity against *E. coli* ATCC 25922, *P. aeruginosa* ATCC 27853, *K. pneumoniae* ATCC 700603, fungi *A. niger* ATCC 1015 and *A. fumigatus* ATCC 1022 was described [53]. In our study, the nucleotide sequence of the 16S rRNA gene of the INA 01418 strain has a 100% match with the gene of *N. salmonicida* subsp. *cummidelens* (synonym *N. soli*) [117]. The antimicrobial activity of the culture liquid of the studied strain INA 01418 differs from that described by the authors Seratnahaei et al.: strain INA 01418 inhibits the growth of all used Gram-positive test cultures (excluding both strains of *M. smegmatis*) and *E. coli* ATCC 25922; antifungal activity is absent. It can be assumed that the strain of *N. salmonicida* subsp. *cummidelens* INA 01418 produces a compound(s) different from the described one, and it is advisable to carry out further research to determine the structure and properties of antimicrobial substances.

In addition to actinobacteria, the most common bacterial producers are representatives of genera such as *Bacillus* (about 800 compounds) and *Pseudomonas* (about 600 compounds), followed by entero- and lactobacilli and streptococci. Bacteria usually produce peptides, simple heterocycles (phenazines), and aliphatic compounds (fatty acid derivatives) [94]. One of the antibiotics actively used in medicine is mupirocin ($C_{26}H_{44}O_9$) isolated from *P. fluorescens*, and peptide antibiotics polymyxin and bacitracin isolated from bacilli [118,119].

In agriculture, biopesticides based on *Bacillus thuringiensis*, *B. subtilis*, and *P. fluorescens* are most widely used [120–123]. *B. thuringiensis* is known as a producer of peptide toxins with insecticidal action. Due to this, this bacterium is widely used as a biopesticide. The formed toxins also have a wide spectrum of antibacterial action [34-36]. For *B. thuringiensis*, antibiotics of a different chemical nature with both a broad antibacterial spectrum and antifungal action are also described (Table 3). The strain INA 01412 isolated by us presumably produces at least three antibiotics acting on Gram-positive bacteria and formed at different times of cultivation (Table 2). Activity against

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Gram-negative test bacteria and fungi was not detected. The isolated strain INA 01412 also does not inhibit the growth of bacillary test strains of three types, so the substances formed cannot be attributed to bacteriocins (Table 2). Since the activity shown on the antimicrobial spectrum does not correspond to the antimicrobial compounds described earlier and taking into account that the secreted substances inhibit the growth of mycobacteria and MRSA, we assess the strain INA 01412 as promising for chemical analysis.

Bioactive cyclic peptides with antifungal activity against *C. albicans*, including azole-sensitive strains, have been described for *Neobacillus drentensis* isolated from seawater [51]. Antifungal activity is also described for *Neob. drentensis* – endobionts of *Physalis ixocarpa*, demonstrated against phytopathogenic fungi *Botrytis cinerea*, *Fusarium solani*, *F. oxysporum*, *Rhizoctonia solani* [52]. The strain described by us did not show antifungal activity but demonstrated antimycobacterial activity and activity against *E. coli* ATCC 25922 and so is of interest as a potential producer of new antimicrobial compounds.

Previously, it was found that in the rhizosphere of sphagnum mosses, many isolated bacteria, including *P. poae*, exhibit antimicrobial activity against phytopathogenic fungi (*F. graminearum*, *F. sporotrichioides*, *F. culmorum*, *Alternaria alternata*) and bacteria, both Gram-positive and Gram-negative (actinobacteria *Clavibacter michiganensis* subsp. *sepedonicum*, as well as *Erwinia carotovora* (syn. *Pectobacterium carotovorum*) var. *atroceptica*) [62-64]. Endophytic *P. poae* strain RE*1-1-14 was originally isolated from the internal root tissue of sugar beet plants and produced lipopeptide poaeamide which is a structurally new member of the famine family. Poaeamide inhibits the growth of different oomycetes, including *Phytophthora capsici*, *Phytophthora infestans*, and *Pythium ultimum* [66]. In our study, the strain *Pseudomonas poae* INA 01414 produces at least three antimicrobial substances: on the first day of growth against *E. coli*, on the second and fourth days – against staphylococci and *Myc. smegmatis* 155 mc², on the fourth-day activity against bacilli, is also shown (Table 2). Antifungal activity was not detected. The strain is planned for further study of the chemical structure of the substances formed.

P. rhizosphaerae is found in various natural sources. The antibacterial and antilarval diketopiperazine and benzene-type secondary metabolites have been described in the strain isolated from deep-sea sediments. The antibacterial activity of these compounds was established against five marine Gram-negative (*Loktanella hongkongensis*, *Ruegeria* sp., *Pseudoalteromona* sp.) and Gram-positive bacteria (*Micrococcus luteus*, *Bacillus cereus*), as well as antilarval action against the larvae of *Balanus amphitrite* and *Bugula neritina*. The results suggested that the marine bacterium *Pseudomonas rhizosphaerae* could produce potent antibacterial and antilarval diketopiperazine and benzene-type secondary metabolites [67]. The strain of *P. rhizosphaerae* INA 01417, isolated by us from the larvae of the Colorado potato beetle, showed activity only against *E. coli* ATCC 25922. It can be assumed that the test strain of *E. coli* ATCC 25922 is most sensitive to compounds from the culture liquid, and when they are isolated and concentrated, the activity can be recorded against other bacteria.

P. gessardii was first isolated in France from mineral waters [126]. Later based on the analysis of the 16S rRNA gene, it was assigned to the *P. fluorescens* group [127]. It has been established that this bacterium is dangerous to humans and can cause blindness [128]. An antibiotic active against *Listeria monocytogenes* and *Stenotrophomonas maltophilia* has been described in this species [61].

In 2015, *St. argenteus* was isolated into a new species related to *St. aureus* and causing similar clinical syndromes, including skin and soft tissue infections, bone and joint infections, sepsis, and enterotoxin-induced gastroenteritis. Research on the study of this species is currently focused on phylogenetic divergence, virulence factors, and antibiotic resistance [124,125]. We have not found any antibiotics described for this species. Our study shows activity against *Myc. smegmatis* mc² 155 and *Aspergillus niger* INA 00760. Thus, the strain *Staphylococcus argenteus* INA 01420 is promising for further study of the antibiotic it forms.

Representatives of the species *Pan. agglomerans* are opportunistic microorganisms for humans and plants, but they are also known to produce antibiotics such as phenazine, pantocin, herbicolin, microcins, and dapdiamide antibiotics effective against phytomycosis caused by *Erwinia amylovora* (fire blight) [54-58]. In 2020, a group of scientists showed that the strain *Pan. agglomerans* Tx10 carries the predicted biosynthetic cluster, which is involved in the synthesis of PNP-2 (*Pantoea* Natural Product 2), and with the help of mutant strains were able to show its broad antimicrobial spectrum against clinically significant strains of Gram-positive genera *Staphylococcus* sp. and *Streptococcus* sp., as well as Gram-negative *Aeromonas* sp., *Enterobacter* sp., *E. coli*, *Klebsiella* sp., *Kosakonia* sp., *Pseudocitrobacter* sp., and *Salmonella* sp. [60,129]. In addition, the authors show that the cluster is limited in distribution among their diverse collection of *Pantoea* strains. In our study, the strain *Pan. agglomerans* INA 01413 also has a broad spectrum of antimicrobial action and inhibits the growth of resistant Gram-positive bacteria, including *Staphylococcus aureus* and *Mycobacterium*, and Gram-negative bacteria. Probably, the strain INA 01413 is a producer of the described compound. However, the study by Robinson et al. detected an absence of activity against *Pseudomonas aeruginosa* and *Acinetobacter baumannii*, while the strain INA 01413 has moderate activity against *P. aeruginosa* ATCC 27853 with multidrug resistance. In this regard, it can be assumed that at least two compounds are produced.

Conclusion

Bacterial species isolated from the intestinal microbiota of Colorado potato beetles, their larvae, and their food, potato leaves, differ, which may indicate the species-specific composition of the microbiota of adults and larvae.

As components of the intestinal microbiota *Leptinotarsa decemlineata* have been described for the first time: *Micromonospora phytophila*, *Neobacillus drentensis*, *Pseudomonas gessardii*, *P. poae*, *P. rhizosphaerae*, *Pantoea agglomerans*, *Streptomyces chartreusis*, *S. clavifer*, *S. microflavus*, *S. rishiriensis*, *S. badius*, and *S. coelicoflavus*.

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Strains produced antimicrobial compounds were selected for the subsequent chemical study based on the activity first described in the respective species, including against methicillin-resistant *Staphylococcus aureus* (MRSA), vancomycin-resistant *Leuconostoc mesenteroides*, multidrug-resistant *Pseudomonas aeruginosa*, and *Mycobacterium smegmatis*. A high percentage of bacteria exhibiting antimicrobial activity confirms the expediency of searching for antibiotic producers among representatives of complex microbial biocenoses.

Author contributions

A.V.Ya., V.S.S., and O.V.E. conceived and designed the experiments; T.A.E., A.V.Ya., M.V.D., T.I.K., A.A.G., O.V.E. performed the experiments; T.A.E., A.V.Ya., and O.V.E. analyzed the data; T.A.E., A.V.Ya., M.V.D., V.S.S., and O.V.E. wrote the paper. All authors have read and agreed to the published version of the manuscript.

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Supplementary Materials

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