UDK 579.69
DOI https://doi.org/10.32846/2306-9716/2021.eco.4-37.19

A MODERN VIEW AT SOME DIHYDROXYBENZOATE-CAPPED SIDEROPHORES: ECOLOGICAL, TECHNICAL AND MEDICAL ASPECTS

Tkachuk N.V.[1], Zelena L.B., Mazur P.D.
[1]T.H. Shevchenko National University "Chernihiv Colehium"
53, Getman Polubotok Str., 14013, Chernihiv
[2]Danylo Zabolotny Institute of Microbiology and Virology, NAS of Ukraine
154, Acad. Zabolotny Str., 03143, Kyiv
nataliia.smykun@gmail.com, MazurP@i.ua, zelenalyubov@gmail.com

Siderophores are non-toxic, environmentally unobjectionable compounds that exhibit a number of useful properties for solving some agriculture, environmental, technical problems and can determine the development of bacterial infections. Siderophores, in the chemical structure of which there is a dihydroxybenzoate fragment, effectively chelating iron, belong to dihydroxybenzoate-capped siderophores. Some dihydroxybenzoate-capped siderophores are acinetobactin, bacillibactin, enterobactin, petrobactin, salmochelins, trivanchrobactin, vanchrobactin, vibriobactin. The review article analyzes and summarizes information about microorganisms-producers such siderophores, the practical importance of these compounds for ecology, agriculture, technology, health. The considered dihydroxybenzoate-capped siderophores are represented in the group of catecholate siderophores and in the group of mixed siderophores. Their producers are both pathogenic and non-pathogenic microorganisms. It was determined that among the considered siderophores only bacillibactin is used in agriculture, perspective bioremediation agents are bacillibactin and petrobactin. Biological control in the industry for corrosion protection can be an alternative to the use of corrosion inhibitors to address environmental, safety and health concerns. Attention is paid to the use of siderophores as smart-green corrosion inhibitors to prevent corrosion, in particular, microbiologically influenced. It is noted that bacillilibactin and enterobactin should be considered as green smart-corrosion inhibitors. Intervention in the mechanisms of providing pathogens with iron by disrupting the biosynthesis of microbial siderophores, the use of siderophores as antimicrobial conjugates is discussed as a promising way to solve the problem of combating bacterial infections and maintaining human health. *Key words:* dihydroxybenzoate-capped siderophores, biological control, ecology, green smart-corrosion inhibitors, health, antimicrobials

Сучасний погляд на деякі дигідроксибензоат-кеповані сидерофори: екологічні, технічні та медичні аспекти. Ткачук Н., Зелена Л., Мазур П.
Сидерофори є нетоксичними, екодружніми сполуками, які проявляють низку корисних властивостей за вирішення деяких проблем сільського господарства, екологічних, технічних проблем і здатні визначати розвиток бактеріальних інфекцій. Сидерофори, в хімічній структурі яких є дигідроксибензоатний фрагмент, ефективно хелатуючий Ферум відносяться до дигідроксибензоат-кепованих сидерофорів. Деякими дигідроксибензоат-кепованими сидерофорами є акінетобактин, бацилібактин, ентеробактин, петробактин, сальмохелін, триванхробактин, ванхробактин, вібріобактин. В оглядовій статті проаналізовано й узагальнено інформацію про мікроорганізми-продуценти таких сидерофорів, практичне значення цих сполук для екології, сільського господарства, техніки, охорони здоров'я. Розглянуті дигідроксибензоат-кеповані сидерофори представлено у групі катехолатних сидерофорів і групі змішаних сидерофорів. Їхніми продуцентами є як патогенні, так і непатогенні мікроорганізми. Визначено, що серед розглянутих сидерофорів лише бацилібактин застосовується у сільському господарстві; перспективними агентами біоремедіації є бацилібактин і петробактин. Біологічний контроль у промисловості під час захисту від корозії може бути альтернативою використанню інгібіторів корозії задля вирішення проблем, пов'язаних із навколишнім середовищем, безпекою і здоров'ям. Приділено увагу використанню сидерофорів як розумних зелених інгібіторів для попередження корозії, зокрема мікробно індукованої. Зазначено, що в якості зелених розумних інгібіторів корозії слід розглядати бацилібактин та ентеробактин. Як перспективний напрямок розв'язання проблеми боротьби зі збудниками бактеріальних інфекцій і проблеми збереження здоров'я людини обговорено втручання у механізми забезпечення патогенів Ферумом шляхом порушення біосинтезу мікробних сидерофорів, використання сидерофорів як антимікробних кон'югатів. *Ключові слова:* дигідроксибензоат-кеповані сидерофори, біологічний контроль, екологія, зелені розумні інгібітори корозії, здоров'я, антимікробні сполуки.

Problem statement. Siderophores are low molecular weight compounds that chelate Fe (III) ions, convert insoluble Fe (III) to the bioavailable form of Fe (II), and are synthesized by some bacteria, fungus, and plants with iron ion deficiency in the medium [1-2]. Recent studies have also identified mammalian siderophore – like biomolecules, such as norepinephrine and 2,5-dihydroxybenzoic acid that also partake in iron transport and homeostasis [3]. Siderophores are non-toxic, environmentally unobjectionable compounds [4], which exhibit a number of useful properties to solve some agriculture, environmental, technical problems and can determine the development of bacterial infections [4-6].

Relevance of research. Currently, studies of siderophores for use in agriculture, industry, environmental protection [1; 6-7] and health [5-6; 8] are relevant. Their use is a biological control approach [1]. Currently, dihydroxybenzoate-capped (DHB-capped) siderophores deserve attention, which in the chemical structure contain a fragment that effectively chelates iron – 2,3-dihydroxybenzoate, and in the case of petrobactin 3,4-dihydroxybenzoate [9]. In the processes of biosynthesis of such siderophores there is a stage of dihydroxybenzoate adenylation, for which inhibitors are being developed [5]. In addition, there are reports that 2,3-dihydroxybenzoate and bacillibactin play an essential role in biofilm formation [10]. Therefore, in our review we paid attention to these compounds.

Analysis of recent research and publications. In agriculture, siderophores are used as promoters of plant growth, plant nutrition and control plant pathogens [1; 7-8; 11-12]. In industry, the biological method using siderophores is promising for the prevention of corrosion (smart-green corrosion inhibitors) [13], in particular microbiologically influenced [14]. However, this issue is currently controversial, as the use of a biological method to prevent corrosion has shown efficacy only in the laboratory [15]. Corrosion inhibitors used to protect against corrosion losses can lead to environmental, safety and health problems [16-17]. Siderophores as chelating compounds are involved in solving some environmental problems [1; 6-8; 11-12]. Some siderophores are factors of virulence of microorganisms, target in the development of modern antimicrobial agents and are considered in the future of new antimicrobial drugs, therapeutic compounds [1; 5-8; 11-12; 18-20].

The article is devoted to highlighting previously unsolved parts of the common problem. The available literature comprehensively characterizes the possibilities and prospects for the use of siderophores, but they do not define, do not separate information about DHB-capped siderophores. In addition, there is no generalized information on the use of siderophores as green smart-inhibitors. The outlined aspects confirm **the novelty** of the study.

Methodological or general scientific significance. The aim of this article is to analyze and summarize information on DHB-capped siderophores with a view to using them to address some practical issues of agriculture, ecology, technology, human and animal health. To achieve this aim in the research process formed and solved important scientific and practical tasks, namely:

– to characterize the essence of the concept of DHB-capped siderophores, to generalize information about microorganisms-producers of these siderophores;

– to analyze the use of some DHB-capped siderophores to address some practical issues of agriculture, ecology, technology, health;

– outline the prospects of using some DHB-capped siderophores to address practical issues in agriculture, ecology, technology, health.

Research methodology. The investigation used general scientific methods (methods of theoretical research of available information), analytical and generalized methods (for the analysis of scientific and literary sources on the problem); empirical (for the accumulation of facts); methods of argumentation (to prove ours own judgments).

Presentation of the main material

DHB-capped siderophores: structure and producers

DHB-capped siderophores are, in particular, acinetobactin, bacillibactin, enterobactin, petrobactin, salmochelins, trivanchrobactin, vanchrobactin, vibriobactin, the chemical structures of which are shown in Figure 1.

Acinetobactin is the siderophore which producing by *Acinetobacter baumannii* [21]. Bacillibactin is producing by the Gram-positive *Bacillus subtilis* [22-23] and related species such as human and/or animal pathogenic *Bacillus anthracis, B. cereus* and *B. thuringiensis* [9; 23], pathogenic *Paenibacillus larvae* [24], non-pathogenic bacteria *B. velezensis* [25-27]. Presence of gene cluster for producing bacillibactin in the genome *B. atrophaeus* GQJK17 has been reported [28]. Enterobactin, also known as enterochelin, is producing by a number of bacteria including bacteria of the family *Enterobacteriaceae* (*E. coli*) [29-31], some nitrogen-fixing bacteria, including *Klebsiella pneumoniae* and *K. terrigena* [31], some strains of streptomycetes (the nikkomycin-producing strain *Streptomyces tendae* Tü 901/8c and strain *Streptomyces* sp. Tü 6125) [30]. Salmochelins are C-glucosylated enterobactins [32]. These are excreted by *Salmonella enterica* and uropathogenic *Escherichia coli* [32-34]. Petrobactin is producing by *Bacillus anthracis* [35-36], oil-degrading marine bacterium *Marinobacter hydrocarbonoclasticus* [37]. Vanchrobactin and trivanchrobactin (a linear trimer of the vanchrobactin peptide formed through serine ester linkages) are producing by marine *Vibrio* species. [38-41]. Vibriobactin is producing by *Vibrio cholerae*, the pathogenic bacterium responsible for causing cholera [41-42].

Thus, DHB-capped siderophores are represented in the group of catecholate siderophores and the group of siderophores of mixed type. Their producers are both pathogenic and non-pathogenic microorganisms.

Some dihydroxybenzoate-capped siderophores in agriculture, ecology, technology

Agriculture

Siderophores are plant-growth-promoting agents [44]. Among the siderophores that are the subject of this article, only for bacillibactin are there reports of use in agriculture. Thus, inoculation of cells suspension of bacillibactin-producing *Bacillus* sp. promotes plant growth, plant nutrition and control plant pathogens [44-45]. Bacillibactin is considered an antimicrobial compound [46-47], in particular due to the fact that it chelates iron and limites access to iron that allows bacillibactin-producing bacteria to antagonize the growth of other surrounding microbes (for example, phytopatogenic *Fusarium oxysporum* f. sp. *capsici*) [47].

Ecology

Siderophores can be involved in solving some environmental problems [8]. It is noted that enterobactin has been suggested to be involved in catalysis of gold nanoparticle formation by catechol redox cycling [48]. This is distinctive property of such siderophores and can be utilized for gold detection and extraction [8].

Bacillibactin produced by *B. subtillis* can bind Fe(III) at 1:1 ratio [49]. Possibilities of siderophores for complexation of heavy metal and use in bioremediation are discussed [6; 8; 50]. Egidi et al. were shown that *Bacillus cereus* LCR12 has genes encoding for siderophores (bacillibactin and petrobactin), that provides the genetic basis for its potential application to remediate contaminated soils in association with plants [51]. In our opinion, non-pathogenic bacteria *B. velezensis*, which produce bacillibactin, and siderophore itself can be considered as promising bioremediation agents. Currently, there are no reports on the use of bacillibactin and/or its non-pathogenic producers for bioremediation in the available scientific and methodological base. Most publications indicate that siderophore-producing microorganisms involved in bioremediation are bacteria of the genus *Pseudomonas* [4; 6].

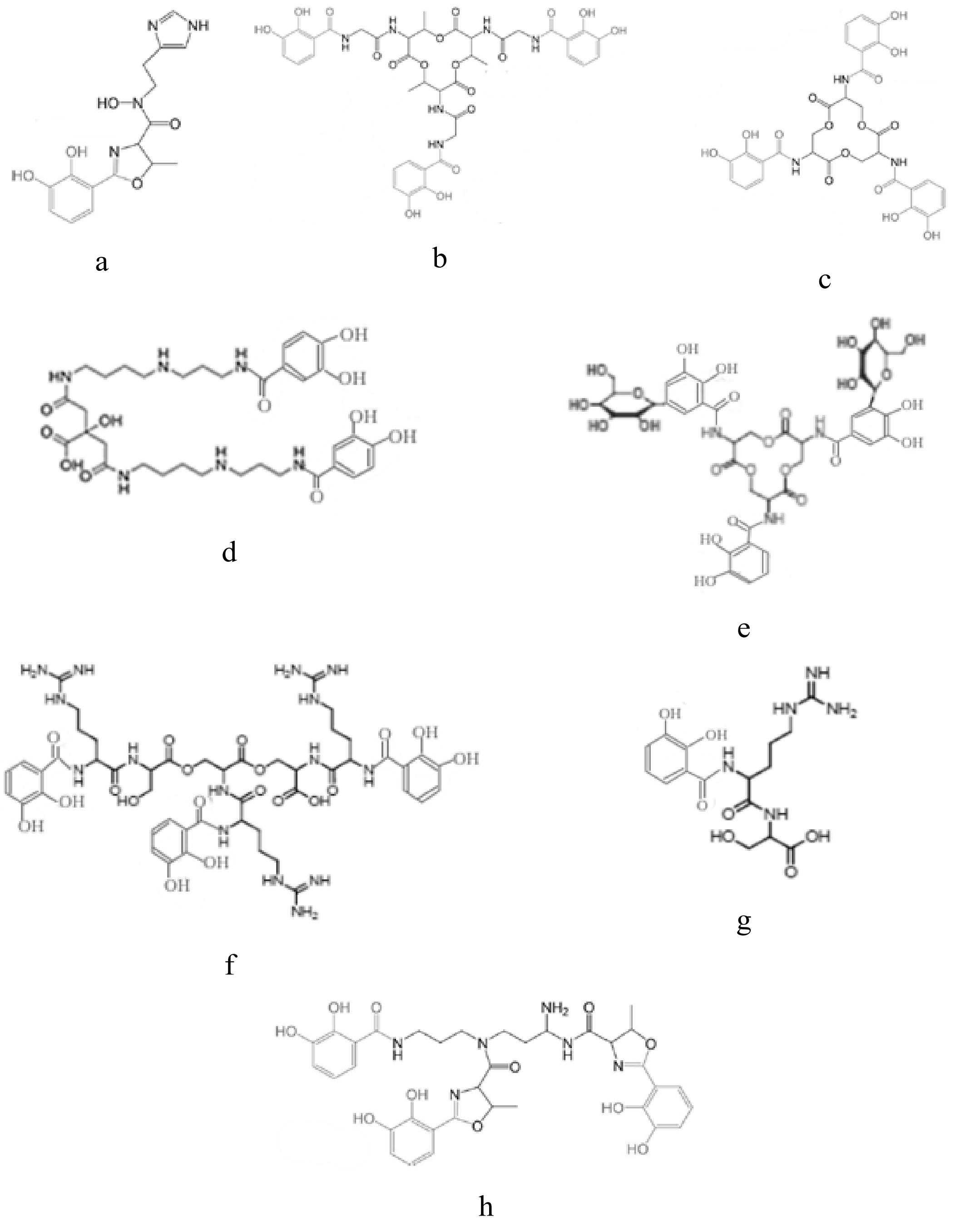

Fig. 1. Chemical structures of DHB-capped siderophores:

a – acinetobactin [5]; b – bacillibactin [5]; c – enterobactin [5]; d – petrobactin [41]; e – salmochelin-S4 [43]; f – trivanchrobactin [34]; g – vanchrobactin [41]; h – vibriobactin [41]

The involvement of some siderophores produced by marine bacteria (particularly petrobactin), in the biogeochemical cycling of Fe, in the remediation of petroleum hydrocarbons in the marine environment is discussed [4; 6].

Technology

Siderophores are environmentally unobjectionable compounds with high corrosion inhibitory properties of steel [13-14; 52-53], promoting passivation of metals [54-56].

They are classified as green corrosion inhibitors along with macromolecules, bacteria, alkaloids, polyphenols [13]. In the last decade, the research on green corrosion inhibitors has been booming because they do not pose problems of toxicity, bioaccumulation and biodegradation [13]. However, there is an opinion that stable corrosion layers could be broken down by siderophore action – changing Fe(III)ions into Fe(II)ions [57].

Enterobactin has now been shown to be one of the most effective (among siderophores studied by McCafferty and McArdle in 1995 [52]) corrosion inhibitors against Ferrovac E iron in 1N HCl because it has the optimal combination of relatively high pK_{a1} value and the largest molecular cross-sectional areas [52]. Enterobactin was also identified in a study by Zanna et al. [56], which shows modifications of the passive film on stainless steel (316 L) after *E. coli* adhesion in the early stage of biofilm formation.

In general, microbiologically influenced corrosion processes occur in the biofilm that forms on the surface of the damaged material [58]. From the end of the 20th to the beginning of the 21st century the prospect of preventing corrosion damage to materials by forming protective aerobic bacterial biofilms capable of producing siderophores has been discussed [59]. At the same time, siderophores are able to prevent the formation of biofilms of microorganisms on surfaces [27]. Kostakioti et al. note [60] that chelating agents inhibit and/or disrupt the formation of the biofilm in stages 2 and 3 of the formation of the biofilm – the formation of microcolonies and the maturation of the biofilm, respectively [60]. We found that bacillibactin-producing strains of *B. velezensis* inhibit the formation of sulfate-reducing bacteria (the main agents of microbiologically influenced corrosion) biofilms on the polymeric material poly(ethylene terephthalate) during its long-term exposure (50 days) under conditions of sufficient iron supply [27]. This may be one of the reasons for slowing down the degradation of this polymer [27]. It is likely that bacillibactin-producing strains or bacillibactin will inhibit the process of microbiologically influenced corrosion of steel, which is a prospect for further research.

Table 1

Practical meaning/application some dihydroxybenzoate-capped siderophores

Dihydroxybenzoate-capped siderophore	Practical meaning/application	References
Acinetobactin	Chelator of Fe (III), virulence factor	[21]
	Target for new generation antimicrobials	[5]
Bacillibactin	Chelator of Fe (III)	[9]
	Promoter of plant growth, plant nutrition and control plant pathogens	[44-45]
	Target for new generation antimicrobials	[5]
	Perspective bioremediation agent	[51], this article
	Perspective environmentally friendly corrosion/ microbiologically influenced corrosion inhibitor	this article
Enterobactin	Chelator of Fe (III), virulence factor	[29-31]
	Target for new generation antimicrobials	[5]
	Perspective environmentally friendly corrosion/ microbiologically influenced corrosion inhibitor	[5; 56]
Petrobactin	Chelator of Fe (III), virulence factor	[35-36]
	Target for new generation antimicrobial	[5]
	Perspective bioremediation agent	[4; 6]
Salmochelin	Chelator of Fe (III), virulence factor	[32-34]
	Target for new generation antimicrobials	[5]
Trivanchrobactin	Chelator of Fe (III), virulence factor	[38-40]
	Target for new generation antimicrobials	[5]
Vanchrobactin	Chelator of Fe (III), virulence factor	[38-40]
	Target for new generation antimicrobials	[5]
	Antimicrobial conjugate	[65]
Vibriobactin	Chelator of Fe (III), virulence factor	[42]
	Target for new generation antimicrobials	[5]

Some dihydroxybenzoate–capped siderophores for medicine

Information about siderophores important for medicine and veterinary medicine has been summarized in reviews [5; 61]. The siderophores considered by us provide cells of pathogenic bacteria with Ferrum and are a factor of virulence (except for bacillibactin) [62].

Gaddy et al. [63] was showed that the ability of *A. baumannii* ATCC 19606^{T} to persist inside A549 human alveolar epithelial cells and cause their apoptosis depends on the expression of active acinetobactin-mediated iron utilization functions, the production of the acinetobactin siderophore. The ability of *A. baumannii* ATCC 19606^{T} cells to express active acinetobactin biosynthesis and transport functions визначає the infection and killing of mice and *G. mellonella* larvae. Also the observation suggests that acinetobactin intermediates or precursors play a virulence role, although their contribution to iron acquisition is less relevant than that of mature acinetobactin [63].

Vanchrobactin is one key virulence factor for the fish pathogen *V. anguillarum* [38-39].

Yeremenko notes [9] that bacillibactin and petrobactin functions are realized on different stages of *B. anthracis* growth *in vivo,* whereas petrobactin synthesis is also necessary for manifestation of bacteria virulence. Enterobactin is considered as an oxidative stress protector for *E. coli* colony development [64].

In the literature it is noted that siderophor-mediated iron acquisition could be used as a target for therapeutic purposes [5; 63] highlight in the review the recent work toward exploiting the biosynthetic enzymes of siderophore production for the design of next generation antimicrobials [5].

Another use of siderophores is antimicrobial conjugates – siderophore is attached to an antibiotic and used to serve as a drug delivery agent (“Trojan horse”) [6]. Now vanchrobactin-norfloxacin conjugate showed antimicrobial activity against *V. anguillarum* and its mutants [65].

Therefore, generalizations about the practical significance of the siderophores considered by us can be presented in the form of Table 1.

Conclusions. Thus, dihydroxybenzoate-containing siderophores acinetobactin, bacillibactin, enterobactin, petrobactin, salmochelins, trivanchrobactin, vanchrobactin, vibriobactin are produced by some pathogenic and non-patogenic bacteria and used by them to provide iron, are a factor of virulence (except bacillibactin). Interference in the mechanisms of providing pathogens with iron by disrupting the biosynthesis of siderophores is a promising way to solve the problem of combating bacterial infections and maintaining health. Among the considered siderophores only bacillibactin is used in agriculture. Perspective bioremediation agents are bacillibactin and petrobactin. Bacillibactin and enterobactin should be considered as promising green smart-corrosion inhibitors.

References

1. Saha M., Sarkar S., Sarkar B. et al. Microbial siderophores and their potential applications: a review. *Environ. Sci. Pollut. Res.* 2015. Issue 23. P. 39840-3999. DOI: 10.1007/s11356-015-4294-0.
2. Leonov V.V., Mironov A.Yu., Anan′ina I.V., Rubal′skaya E.E., Sentyurova L.G. Mikrobnye siderofory: struktura, svojstva, funkcii [Siderophores of microbes: structure, properties and functions]. *Astrakhan Medical Journal*. 2016. Vol. 11, No 4. C. 24-37 (in Russian).
3. Golonka R., Yeoh B.S., Vijay-Kumar M. The Iron Tug-of-War between Bacterial Siderophores and Innate Immunity. *J. Innate. Immun.* 2019. Issue 11. P. 249-262. DOI: 10.1159/000494627.
4. Ahmed E., Holmström S.J.M. Siderophores in environmental research: roles and applications. *Microbial Biotechnology.* 2014. Vol. 7, Issue 3. P. 196-208. DOI: 10.1111/1751-7915.12117.
5. Lamb A.L. Breaking a pathogen’s iron will: Inhibiting siderophore production as an antimicrobial strategy. *Biochimica et Biophysica Acta*. 2015. Issue 1854. P. 1054-1070. DOI: 10.1016/j.bbapap.2015.05.001.
6. De Serrano L.O. Biotechnology of siderophores in high-impact scientific fields. *Biomolecular concepts*. 2017. Vol. 8, Issue 3-4. P. 169-178.
7. Saha R., Saha N., Donofrio R.S., Bestervelt L.L. Microbial siderophores: a mini review. *J. Basic. Microbiol.* 2012. Issue 52. P. 1-15. DOI: 10.1002/jobm.201100552.
8. Khan A., Singh P., Srivastava A. Synthesis, nature and utility of universal iron chelator – siderophore: a review. *Microbiological Research*. 2018. Vol. 212–213. P. 103-111. DOI: 10.1016/j.micres.2017.10.012.
9. Yeremenko E.I. Siderofory *Bacillus anthracis* [Siderophores *Bacillus anthracis*]. *Problems of especially dangerous infections*. 2016. No 1. C. 68074 (in Russian). DOI: 10.21055/0370-1069-2016-1-68-74.
10. Rizzi A., Roy S., Bellenger J.P., Beauregard P.B. Iron homeostasis in *Bacillus subtilis* requires siderophore production and biofilm formation. *Appl. Environ. Microbiol.* 2019. Issue 85. e02439-02418.
11. Kramer J., Özkaya Ö., Kümmerli R. Bacterial siderophores in community and host interactions. *Nat. Rev. Microbiol.* 2020. Issue 18. P. 152-163. DOI: 10.1038/s41579-019-0284-4.
12. Prabhakar P.K. Bacterial Siderophores and Their Potential Applications: A Review. *Current Molecular Pharmacology*. 2020. Vol. 13, Issue 4. DOI: 10.2174/1874467213666200518094445.
13. Pérez-Miranda S., Zamudio-Rivera L.S., Cisneros-Dévora R., George-Téllez R., Fernández F.J. Theoretical insight and experimental elucidation of desferrioxamine B from *Bacillus* sp. AS7 as a green corrosion inhibitor. *Corros. Eng. Sci. Technol.* 2020. Vol. 56, Issue 1. P. 93-101. DOI: 10.1080/1478422X.2020.1824441.
14. Little B., Mansfeld F. Passivity of stainless steels in natural seawater. In Uhlig, H.H. *Memorial Symposium: Corrosion monograph series. Proceeding.* Mansfeld F., Asphahani A., Bohni H., Latansion R., Eds. New Jersey: The Electrochemical Society, Inc., 1995. Vol. 94-26. P. 42-52.

15. Little B.J., Blackwood D.J., Hinks J., Lauro F.M., Marsili E., Okamoto A., Rice S.A., Wade, S.A., Flemming, H.-C. Microbially influenced corrosion – Any progress? *Corros. Sci.* 2020. Issue 170. P. 108641. DOI: 10.1016/j.corsci.2020.108641.
16. Scarascia G., Wang T., Hong P.-Y. Quorum sensing and the use of quorum quenchers as natural biocides to inhibit sulfate-reducing bacteria. *Antibiotics*. 2016. Vol. 5(4), Issue 39. P. 1-20. DOI: 10.3390/antibiotics5040039.
17. Smykun N.V. Rozvytok koroziino-nebezpechnoi mikroflory gruntu pid vplyvom deiakykh pestytsydiv [Development of corrosion-dangerous microflora of soil under the influence of some pesticides]. *Mikrobiol. Z.* 2008. Vol. 70, No 6. C. 74-87 (in Ukrainian).
18. Patel K., Butala S., Khan T., Suvarna V., Sherje A., Dravyakar B. Mycobacterial siderophore: A review on chemistry and biology of siderophore and its potential as a target for tuberculosis. *Eur. J. Med. Chem.* 2018. Issue 157. P.783-790. DOI: 10.1016/j.ejmech.2018.08.030.
19. Wilson B.R., Bogdan A.R., Miyazawa M., Hashimoto K., Tsuji Y. Siderophores in Iron Metabolism: From Mechanism to Therapy Potential. *Trends in Molecular Medicine.* 2016. Vol. 22, Issue 12. P. 1077-1090. DOI: 10.1016/j.molmed.2016.10.005.
20. Butler A., Harder T., Ostrowski A.D., Carrano C.J. Photoactive siderophores: Structure, function and biology. *Journal of Inorganic Biochemistry.* 2021. Issue 221. P. 111457.
21. Penwell W.F., Actis L.A. Isolation and Characterization of the Acinetobactin and Baumannoferrin Siderophores Produced by *Acinetobacter baumannii*. *Methods Mol. Biol.* 2019. Issue 1946. P. 259-270. DOI: 10.1007/978-1-4939-9118-1_24.
22. Raza W., Hussain Q., Shen Q. Production, regulation and transportation of bacillibactin in bacillus subtilis. *Journal of the Chemical Society of Pakistan*. 2012. Vol. 34, Issue 4. P. 996-1002.
23. Miethke M., Klotz O., Linne U., May J.J., Beckering C.L., Marahiel M.A. Ferri-bacillibactin uptake and hydrolysis in *Bacillus subtilis. Molecular Microbiology*. 2006. Vol. 61, Issue 6. P. 1413-1427. DOI: 0.1111/j.1365-2958.2006.05321.x.
24. Hertlein G., Müller S., Garcia-Gonzalez E., Poppinga L., Süssmuth R.D. et al. Production of the Catechol Type Siderophore Bacillibactin by the Honey Bee Pathogen *Paenibacillus larvae*. *PLoS ONE*. 2014. Vol. 9, Issue 9. e108272. DOI:10.1371/journal.pone.0108272.
25. Harwood C.R., Mouillon J.M., Pohl S., Arnau J. Secondary metabolite production and the safety of industrially important members of the *Bacillus subtilis* group. *FEMS Microbiol. Rev.* 2018. Vol. 42, Issue 6. P. 721-738. DOI: 10.1093/femsre/fuy028.
26. Rabbee M.F., Ali Md.S., Choi J., Hwang B.S., Jeong S.Ch., Baek K.-h. *Bacillus velezensis*: A Valuable Member of Bioactive Molecules within Plant Microbiomes. Molecules. 2019. Issue 24. P. 1046. DOI: 10.3390/molecules24061046.
27. Tkachuk N., Zelena L., Lukash O., Mazur P. Microbiological and genetic characteristics of *Bacillus velezensis* bacillibactin-producing strains and their effect on the sulfate-reducing bacteria biofilms on the poly(ethylene terephthalate) surface. *Ecological Questions*. 2021. Vol. 32, Issue 2. P.119-129.
28. Ma J., Wang Ch., Wang H., Liu K., Zhang T., Yao L., Zhao Z., Du B., Ding Y. Analysis of the Complete Genome Sequence of *Bacillus atrophaeus* GQJK17 Reveals Its Biocontrol Characteristics as a Plant Growth-Promoting *Rhizobacterium*. *BioMed Research International.* 2018. Article ID 9473542. P.1-9. DOI: https://doi.org/10.1155/2018/9473542.
29. Rajendran N., Marahiel M.A. Multifunctional Peptide Synthetases Required for Nonribosomal Biosynthesis of Peptide Antibiotics. In: Chemistry, Molecular Sciences and Chemical Engineering. Comprehensive Natural Products Chemistry. Editor(s): Sir Derek Barton, Koji Nakanishi, Otto Meth–Cohn, Comprehensive Natural Products Chemistry, Pergamon, 1999. Vol. 4. P. 195-220. DOI: 10.1016/B978-0-08-091283-7.00094-1.
30. Fiedler H.-P., Krastel Ph., Müller J., Gebhardt K., Zeeck A. Enterobactin: the characteristic catecholate siderophore of *Enterobacteriaceae* is produced by Streptomyces species, FEMS Microbiology Letters. 2001. Vol. 196, Issue 2. P. 147-151. DOI: 10.1111/j.1574-6968.2001.tb10556.x.
31. Clark B.L. Characterization of a Catechol-Type Siderophore and the Detection of a Possible Outer Membrane Receptor Protein from *Rhizobium leguminosarum* strain IARI 312. *Electronic Theses and Dissertations.* 2004. Paper 922. URL: https://dc.etsu.edu/etd/922 (дата звернення 10.07.2021).
32. Bister B., Bischoff D., Nicholson G.J., Valdebenito M., Schneider K., Winkelmann G., Hantke K., Süssmuth R.D. The structure of salmochelins: C–glucosylated enterobactins of *Salmonella enterica*. *Biometals*. 2004. Vol. 17, Issue 4. P.471-481. DOI: 10.1023/b:biom.0000029432.69418.6a.
33. Hantke K., Nicholson G., Rabsch W., Winkelmann G. Salmochelins, siderophores of *Salmonella enterica* and uropathogenic *Escherichia coli* strains, are recognized by the outer membrane receptor IroN. *Proceedings of the National Academy of Sciences.* 2003. Vol. 100, Issue 7. P. 3677-3682. DOI: 10.1073/pnas.0737682100.
34. Valdebenito M., Crumbliss A. L., Winkelmann G., Hantke K. Environmental factors influence the production of enterobactin, salmochelin, aerobactin, and yersiniabactin in Escherichia coli strain Nissle 1917. *International Journal of Medical Microbiology*. 2006. Vol. 296, Issue 8. P. 513-520. DOI: 10.1016/j.ijmm.2006.06.003.
35. Koppisch A.T., Browder C.C., Moe A.L. et al. Petrobactin is the Primary Siderophore Synthesized by *Bacillus anthracis* Str. *Sterne* under Conditions of Iron Starvation. *Biometals*. 2005. Issue 18. P. 577-585. DOI: 10.1007/s10534-005-1782-6.
36. Lee J.Y., Janes B.K., Passalacqua K.D., Pfleger B.F., Bergman N.H., Liu H., Håkansson K., Somu R.V., Aldrich C.C., Cendrowski S., Hanna P.C., Sherman D.H. Biosynthetic analysis of the petrobactin siderophore pathway from *Bacillus anthracis*. *J. Bacteriol.* 2007. Vol. 189, Issue 5. P.1698-710. DOI: 10.1128/JB.01526-06.
37. Barbeau K., Zhang G., Live D.H., Butler A. Petrobactin, a photoreactive siderophore produced by the oil-degrading marine bacterium *Marinobacter hydrocarbonoclasticus*. *J. Am. Chem. Soc.* 2002. Vol. 124, Issue 3. P. 378-379. DOI: 10.1021/ja0119088.
38. Jalal M.A.F., Hossain M.B., van der Helm D., Sanders-Loehr J., Actis L.A., Crosa J.H. Structure of anguibactin, a unique plasmid-related bacterial siderophore from the fish pathogen *Vibrio anguillarum*. *J. Am. Chem. Soc.* 1989. Issue 111. P. 292-296.
39. Soengas R.G., Anta C., Espada A., Paz V., Ares I.R., Balado M., Rodriguez J., Lemos M.L., Jimenez C. Structural characterization of vanchrobactin, a new catechol siderophore produced by the fish pathogen *Vibrio anguillarum* serotype O2. *Tetrahedron Lett.* 2006. Issue 47. P. 7113-7116.

40. Sandy M., Han A., Blunt J., Munro M., Haygood M., Butler A. Vanchrobactin and anguibactin siderophores produced by *Vibrio* sp. DS40M4. *J. Nat. Prod.* 2010. Issue 73. P. 1038-1043.
41. Timmermans M.L., Paudel Y.P., Ross A.C. Investigating the Biosynthesis of Natural Products from Marine Proteobacteria: A Survey of Molecules and Strategies. *Marine Drugs*. 2017. Vol. 15, Issue 8. P. 235. DOI: 10.3390/md15080235.
42. Griffiths G.L., Sigel S.P., Payne S.M., Neilands J.B. Vibriobactin, a siderophore from *Vibrio cholerae*. *J. Biol. Chem.* 1984. Issue 259. P. 383-385.
43. Lee J.Y., Passalacqua K.D., Hanna P.C., Sherman D.H. Regulation of Petrobactin and Bacillibactin Biosynthesis in *Bacillus anthracis* under Iron and Oxygen Variation. *PLoS ONE*. 2011. Vol. 6, Issue 6. e20777. DOI: 10.1371/journal.pone.0020777.
44. Zope V., El Enshasy H., Sayyed R.Z. Plant growth-promoting rhizobacteria: An overview in agricultural perspectives. In: Plant Growth-Promoting Rhizobacteria for Sustainable Stress Management. Vol. II. Rhizobacteria in Biotic Stress Management; Sayyed, R.Z., Ed. Singapore: Springer, 2019. P. 345-362.
45. Nithyapriya S., Lalitha S., Sayyed R.Z., Reddy M.S., Dailin D.J., El Enshasy H.A., Luh Suriani N., Herlambang S. Production, Purification, and Characterization of Bacillibactin Siderophore of *Bacillus subtilis* and Its Application for Improvement in Plant Growth and Oil Content in Sesame. *Sustainability*. 2021. Issue 13. P. 5394. DOI: 10.3390/su13105394.
46. Li B., Li Q., Xu Z., Zhang N., Shen Q., Zhang R. Responses of beneficial *Bacillus amyloliquefaciens* SQR9 to different soilborne fungal pathogens through the alteration of antifungal compounds production. *Front. Microbiol.* 2014. Issue 5. P. 636. DOI: 10.3389/fmicb.2014.00636.
47. Yu X., Ai C., Xin L., Zhou G. The siderophore-producing bacterium, *Bacillus subtilis* CAS15, has a biocontrol effect on *Fusarium* wilt and promotes the growth of pepper. *Eur. J. Soil Biol.* 2011. Issue 47. P. 138-145. DOI: 10.1016/j.ejsobi.2010.11.001.
48. Wyatt M., Johnston C., Magarvey N. Gold nanoparticle formation via microbial metallophore chemistries. *J. Nanopart. Res.* 2014. Vol. 16, Issue 3.
49. Dertz E.A., Stintzi A., Stintzi A., Raymond K.N. Siderophore-mediated iron transport in *Bacillus subtillis* and *Corynebacterium glutamicum*. J. *Biol. Inorg. Chem.* 2006. Issue 11: P. 1087-1097. DOI: 10.1007/s00775-006-0151-4.
50. Rajkumar M., Ae N., Prasad M.N.V., Freitas H. Potential of siderophore-producing bacteria for improving heavy metal phytoextraction. *Trends in Biotechnology*. 2010. Vol. 28, Issue 3. P. 142-149. DOI: 10.1016/j.tibtech.2009.12.002.
51. Egidi E., Wood J.L., Mathews E., Fox E., Liu W., Franks A.E. Draft Genome Sequence of *Bacillus cereus* LCR12, a Plant Growth–Promoting Rhizobacterium Isolated from a Heavy Metal–Contaminated Environment. *Genome Announcements*. 2016. Vol. 4, Issue 5, e01041-16. DOI: 10.1128/genomeA.01041-16
52. McCafferty E., McArdle J.V. Corrosion inhibition of iron in acid solutions by biological siderophores. J. Electrochem. Soc. 1995. Issue 142. P. 1447-1453.
53. Rajala P. Microbially-induced corrosion of carbon steel in a geological repository environment. Helsinki: Julkaisija – Utgivare Publisher, 2017. 83 p.
54. Little B.J., Lee J.S., Ray R.I. The influence of marine biofilms on corrosion: A concise review. *Electrochim. Acta.* 2008. Issue 54. P. 2-7. DOI: 10.1016/j.electacta.2008.02.071.
55. Javaherdashti R., Alasvand K. *Biological Treatment of Microbial Corrosion: Opportunities and Challenges*. Saint Louis, Missouri: Elsevier Science, 2019. 156 p.
56. Zanna S., Seyeux A., Allion-Maurer A., Marcus Ph. *Escherichia coli* siderophore-induced modification of passive films on stainless steel. *Corros. Sci.* 2020. Issue 175. P. 1-11. DOI: 10.1016/j.corsci.2020.108872.
57. Lewicka D., Pfennig A. Abiotic and microbially influenced corrosion on buried iron artefacts. In: Structural Studies, Repairs and Maintenance of Heritage Architecture XIII. Edited By: C.A. Brebbia, Wessex Institute of Technology, UK, 2013. Vol. 131. P. 379-388. DOI: 10.2495/STR130321.
58. Andreiuk K.I., Kozlova I.P., Koptieva Zh.P., Piliashenko-Novokhatnyi A.I., Zanina V.V., Purish L.M. Mikrobna koroziia pidzemnykh sporud [Microbial Corrosion of Underground Structures], Kyiv: Nauk. Dumka, 2005. 258 c. (in Ukrainian).
59. Little B., Ray R. A Perspective on Corrosion Inhibition by Biofilms. Corrosion. 2002. Vol. 58, Issue 5. P. 424-428. DOI: 10.5006/1.3277632.
60. Kostakioti M., Hadjifrangiskou M., Hultgren S.J. Bacterial biofilms: development, dispersal, and therapeutic strategies in the dawn of the postantibiotic era. *Cold Spring Harb. Perspect. Med.* 2013. 3(a010306). P. 1-23. DOI: 10.1101/cshperspect.a010306.
61. Kurth C., Kage H., Nett M. Siderophores as molecular tools in medical and environmental applications. *Org. Biomol. Chem.* 2016. Issue 14**.** P. 8212-8227. DOI: 10.1039/c6ob01400c.
62. Cendrowski S., MacArthur W., Hanna P. *Bacillus anthracis* requires siderophore biosynthesis for growth in macrophages and mouse virulence. *Mol. Microbiol.* 2004. Issue 51. P. 407-417.
63. Gaddy J.A., Arivett B.A., McConnell M.J., López-Rojas R., Pachón J., Actis L.A. Role of acinetobactin–mediated iron acquisition functions in the interaction of *Acinetobacter baumannii* strain ATCC 19606T with human lung epithelial cells, *Galleria mellonella* caterpillars, and mice. *Infection and immunity*. 2012. Vol.80. Issue 3. P. 1015-1024. DOI: 10.1128/IAI.06279-11.
64. Adler C., Corbalan N.S., Peralta D.R., Pomares M.F., de Cristóbal R.E., Vincent P.A. The alternative role of enterobactin as an oxidative stress protector allows *Escherichia coli* colony development. *PLoS One*. 2014. Vol. 9, No 1. e84734. DOI: 10.1371/journal.pone.0084734.
65. Souto A., Montaos M.A., Balado M., Osorio C.R., Rodriguez J., Lemos M.L., Jiménez C. Synthesis and antibacterial activity of conjugates between norfloxacin and analogues of the siderophore vanchrobactin. *Bioorg. Med. Chem.* 2013. Issue 21. P. 295-302.