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NEW STRAINS OF STREPTOMYCETES IN WHICH GENOMES CLUSTERS OF GENES FOR AGAROSE CATABOLISM WERE REVEALED

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Agarose is a polysaccharide found in the cell walls of red algae. Most of the detected agarolytic microorganisms are gram-negative bacteria from several taxonomically diverse groups, but a few gram-positive ones were also detected, for example — *Bacillus sp.* MK03, *Streptomyces coelicolor* A3(2). *S. coelicolor* A3(2) destroys agarose with 3 different hydrolases: two extracellular β-agarases (DagA and DagB), and an intracellular α-neoagarobiose hydrolase ScJC117. The aim of the work was to identify streptomycetes strains whose genomes contain sequences similar to genes encoding proteins of the agarolytic system of *S. coelicolor* A3(2). The objects of study were nucleotide sequences of streptomycetes deposited into databases of The National Center for Biotechnology Information (USA). Analysis of the primary structures of streptomycete DNAs was done using BLASTN programs on the NCBI server. BLASTN-analysis of information on databases NCBI revealed presence of five such strains (*Streptomyces sp.* SID7813, *Streptomyces sp.* NRRL B-16638, *Streptomyces sp.* ME02-6977A, *Streptomyces sp.* SM1, *Streptomyces sp.* S4.7). Their sequences contain fragments similar to *S. coelicolor* A3(2) genes that code agarolytic enzymes and a special NA2-transport system of neoagarobiose. Based on the similarity of the sequences of their «housekeeping genes» (*rpoB, rrnA, gyrB, atpB, trpB, recA*), conclusions were made about the closely related relationships of 4 strains (*Streptomyces sp.* SID7813, *Streptomyces sp.* NRRL B-16638, *Streptomyces sp.* ME02-6977A, *Streptomyces sp.* SM1) and *S. coelicolor* A3(2). The strain *Streptomyces sp.* S4.7 is related to the strains of other species (*S. niveus*).

Key words: *Streptomyces sp.,* agarase, hydrolysis, transport system, genetic affinity.

The vast majority of agarases are isolated from microorganisms that exist in the marine environment; however, some live in fresh water or soil. Most of the detected agarolytic microorganisms are gram-negative bacteria from several taxonomically diverse groups (*Alteromonas, Pseudomonas, Vibrio, Cytophaga, Agarivorans, Thalassomonas, Pseudoalteromonas, Acinetobacter*, etc.) [1—4], but a few gram-positive ones were also detected, for example — *Bacillus sp.* MK03, *Streptomyces coelicolor* A3(2) [5—10].

Agar is a polysaccharide found in the cell walls of red algae of the orders Gracilariales and Gelidiales. This polysaccharide consists of two different components, namely, agarose and agaropectin [8, 11, 12].

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It is known that *Streptomyces coelicolor* A3(2) is a unique streptomycete that can use agar as its sole carbon source [13, 14]. The streptomycete culture *S. coelicolor* (formerly *Actinomyces coelicolor*) was isolated from tap water as an agar-decomposing actinomycetes strain with the unique characteristic of producing colored pigments [13]. Later, *S. coelicolor* A3(2) were reisolated from a soil sample [14].

Agar depolymerization by *S. coelicolor* A3(2) can be carried out by 3 different hydrolases (EC 3.2.1.81): extracellular β-agarase DagA, which belongs to the hydrolase from the GH16 family, extracellular β-agarase DagB (GH50 family), alpha-neoagarobiose hydrolase ScJC117 (GH117 family) (Fig. 1) [11, 12].

The degradation pathway of agarose by *S. coelicolor* A3(2) consists of the upstream part, which includes the fermentation of agarose into its two monomers (D-galactose and 3,6-anhydro-α-L-galactose), and the downstream part, which includes monosaccharide decomposition reactions. The upstream part involves agarolytic enzymes such as β-agarase and α-neoagarobiose hydrolase. The downstream part includes the degradation pathways of D-galactose and 3,6-anhydro-α-L-galactose.

Agarose may be hydrolyzed mainly by DagA to neoagarotetraose and neoagarohexaose. The resulting neoagarosaccharides will be further hydrolyzed by DagB to form neoagarobiose. Additionally, agarose may be directly hydrolyzed by DagB to neoagarobiose. Neoagarobiose will be transported into the cytosol by a transporter and finally hydrolyzed into D-galactose and 3,6-anhydro-L-galactose by the enzyme ScJC117 (Fig. 1). *S. coelicolor* A3(2) transport system of neoagarobiose (encoded by the genes SCO3482, SCO3483 and SCO3484) was found (Fig. 1) [8, 11, 12].

The fairly close location of *S. coelicolor* A3(2) genes encoding proteins of agarolytic catabolism in the genome has been established. It is assumed that a number of these genes form a cluster (Fig. 2). The gene cluster encoding proteins required for agarose metabolism in *S. coelicolor* A3(2) contains both upstream and downstream genes (hereinafter denoted as agr-cluster) [12].

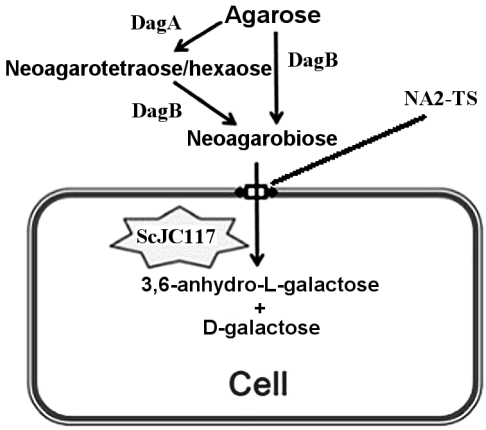

Fig. 1. Schematic representation of beta-agarose hydrolytic pathways: DagA — beta-agarose DagA, DagB — beta-agarose DagB, ScJC117 — alpha-neoagarobiose hydrolase, NA2-TS — neoagarobiose transport system [3, 4]

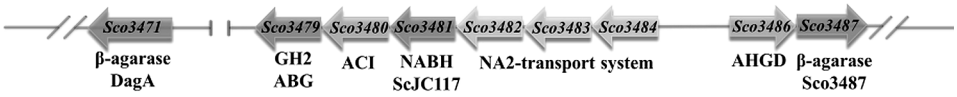

Fig. 2. Genomic context of the agr-cluster involved in agarose metabolism in *Streptomyces coelicolor* A3(2): ACI — 3,6-anhydrogalactonate cycloisomerase; NABH — α-neoagarobiose hydrolase; AHGD — 3,6-anhydro-L-galactose dehydrogenase; ABG — agarolytic β-galactosidase

The aim of the work was to identify streptomycetes strains whose genomes contain sequences similar to genes encoding proteins of the agr-cluster of *S. coelicolor* A3(2).

Materials and methods

The objects of the study were the nucleotide sequences of streptomycetes chromosomes deposited into the database (RefSeq Genome Database) of The National Center for Biotechnology Information (NCBI) server [www.ncbi.nlm.nih.gov/nucleotide/] (Table 1).

Analysis of the primary structures of streptomycete DNAs was done using BLAST (Basic Local Alignment Search Tool) programs on the NCBI server [www.ncbi.nlm.nih.gov/blast].

Results and discussion

The genes encoding proteins required for agarose metabolism in *S. coelicolor* A3(2) are located as a cluster on the chromosome sequence (3831705—3854645 bp). The presence of sequences similar to the fragment agr-cluster in the genomes of 5 streptomycete strains was determined by BLASTN-analysis of the database on the server of the NCBI (Fig. 3).

Sequences similar to the full sequences of the *S. coelicolor* A3(2) agr-cluster were found in primary structures of 7 variants of *S. coelicolor* A3(2), 5 strains of *Streptomyces spp.,* and a lot of streptomycete fragments. The cluster sequence of *Streptomyces sp.* ME02-6977A is located on 2 contigs

TABLE 1. Studied strains of streptomycetes and some characteristics of their nucleotide sequences (GenBank)

Strains of *Streptomyces*	Accessions, GenBank	Accession length, bp	Sources of streptomycetes
S. coelicolor A3(2)	NC_003888.3	8667507	USA, tap water* GB, soil
Streptomyces sp. SID7813	NZ_WWHF01000001.1 (1 contig)	8667507	USA, insect
Streptomyces sp. ME02-6977A	NZ_JARAYD00000000.1 (496 contigs)	8853597	Canada, the lesion of potato
Streptomyces sp. SM1	NZ_NEUB00000000.1 (151 contigs)	8054772	Ireland, sea sponge
Streptomyces sp. NRRL B_16638	NZ_JARAWB00000000.1 (1057 contigs)	8873229	Canada, the lesion of potato
Streptomyces sp. S4.7	NC_CP048397.1	79200066	Germany, the rhizosphere of edelweiss

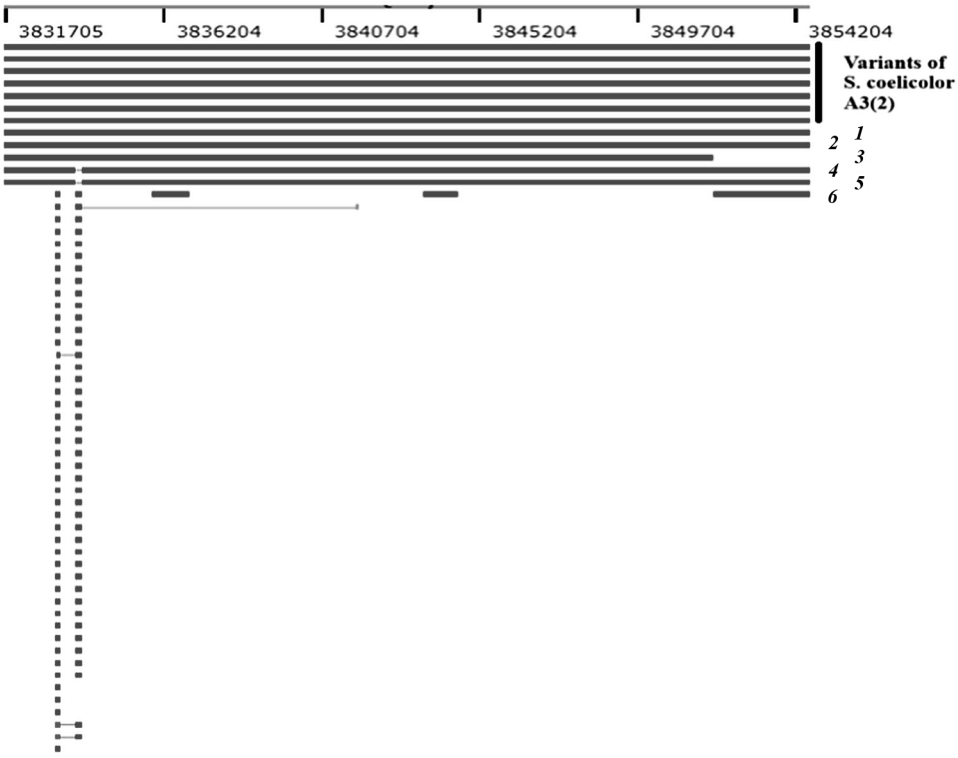

Fig. 3. Distribution of sequences similar to the agr-cluster sequence of *S. coelicolor* A3(2) (Query Sequence) in streptomycete genomes: *1 — Streptomyces sp.*SID7813; *2 — Streptomyces sp.* NRRL B_16638; *3, 6 — Streptomyces sp.* ME02-6977A; *4 — Streptomyces sp.* SM1; *5 — Streptomyces sp.* S4.7

due to the fact that the nucleotide sequence of its genome was deposited in the NCBI database as a set of 496 contigs. All identified sequences of 5 strepromycete strains had a high level of similarity to agr-cluster sequence of *S. coelicolor* A3(2) (Table 2).

TABLE 2. Similarity level of 5 streptomycete sequences to the agr-cluster sequence of S. coelicolor A3(2) sequence (Query Sequence)

Strains of *Streptomyces* (Subject Sequence)	Localization of clusters on sequences	Similarity indices to cluster *S. coelicolor*
Streptomyces sp. SID7813	WWHF01000001.1 3831705—3854645 bp	Q.c. = 100 % I = 100 %
Streptomyces sp. ME02-6977A	JARAYD010000020.1 1—20193 bp JARAYD010000024.1 1—2740 bp	Q.c. = 88 % I = 99.73 % Q.c. = 11 % I = 100 %
Streptomyces sp. SM1	NEUB01001033.1 3831705—3854645 bp	Q.c. = 99 % I = 98.36 %
Streptomyces sp. NRRL B_16638	JARAWB010000075.1 1071—24011 bp	Q.c. = 100 % I = 100 %
Streptomyces sp. S4.7	CP048397.1 786023—809597 bp	Q.c. = 99 % I = 98.36 %

Note. Q.c. — Query coverege, I — identity.

TABLE 3. Similarity level of streptomycete genes sequences to sequences of agr-genes S. coelicolor A3(2) (Query Sequence)

Strains	Similarity of streptomycete genes to referents genes of *S. coelicolor* A3(2)								
	Genes code agarolytic enzymes			Genes code transport system			Genes code the downstream part		
	SCO3471	SCO3481	SCO3487	SCO3482	SCO3483	SCO3484	SCO3479	SCO3480	SCO3486
S4.7	I = 99.78 % M = 2	I = 99.1 % M = 10	I = 98.37 % M = 38	I = 99.89 % M = 1	I = 99.59 % M = 4	I = 99.85 % M = 1	I = 99.81 % M = 6	I = 99.73 % M = 3	I = 98,5 % M = 21
SID7813	I = 100 %	I = 100 %	I = 100 %	I = 100 %	I = 100 %	I = 100 %	I = 100 %	I = 100 %	I = 100 %
NRRL B-16638	I = 100 %	I = 100 %	I = 100 %	I = 100 %	I = 100 %	I = 100 %	I = 100 %	I = 100 %	I = 100 %
ME02-6977A	I = 99.98 % M = 1	I = 100 %	I = 100 %	I = 100 %	I = 100 %	I = 100 %	I = 99.41 % M = 47	I = 100 %	I = 100 %
SM1	I = 99.78 % M = 2	I = 99.91 % M = 1	I = 98.41 % M = 39	I = 99.89 % M = 1	I = 100 %	I = 100 %	I = 99.93 % M = 2	I = 99.91 % M = 1	I = 98.89 % M = 15

Note. I — identity, M — mistake.

It was necessary to establish the similarity of the primary structure of individual genes of the streptomycetes agarolytic systems and the corresponding genes of *S. coelicolor* A3(2) (Table 3). The length of all identified fragments of streptomycetes were completely equal to the length of gene sequences in *S. coelicolor* A3(2) (Query Coverege = 100 %).

Analysis of the sequences of 5 streptomycete strains (both their entire agr-clusters and individual genes from the agr-clusters) showed that they have a high level of identity with the corresponding sequences of *S. coelicolor* A3(2) (Table 3). Their level of identity was, as a rule, greater than 99 %. However, the sequences of *Streptomyces sp.* S4.7 and *Streptomyces sp.* SM1 (both their entire agr-cluster and individual genes) are the least similar with the corresponding sequences of *S. coelicolor* A3(2) (Table 3). Interestingly, the most identical are the genes encoding proteins for the NA2-transport systems.

It was necessary to find out the genetic relationship between the identified strains. The International Committee on the Reconciliation of Approaches to Bacterial Systematics recommended the use of the primary structure of genomic DNA studies in the hierarchical classification, in addition to the results of traditional phenotypic and serological studies [15—17].

The primary structure of 16S rRNA was considered the «gold standard» in determining the genetic affinity of streptomycetes, but the Committee

later recommended the use of a number of essential genes for the hierarchical classification of a number of «housekeeping genes» (*rpo*B, *atp*D, *trp*B, *ric*A, *hrp*A) [16, 17].

Determination of the genetic relationship between the 5 identified strains was carried out in 2 stages. Determination of the genetic relationship of the 5 strains based on similarity of their 16S RNAs sequences were made at first. In our experiment, the *rrn*A-gene sequence of *S. coelicolor* A3(2) was used as a reference sequence (Table 4). The length of all identified fragments of streptomycetes is completely equal to the length of gene sequence of *S. coelicolor* A3(2) (Query Coverege = 100 %).

Levels of similarity in the sequences of 16S RNA genes of four streptomycetes strains demonstrated that streptomycetes are related to *S. coelicolor* A3(2). However, the 16S RNA gene sequence of *Streptomyces sp.* S4.7 had an identity index (I = 97.3 %) less than the required level (98.7 %) [15].

Then the tree of genetic consanguinity of 6 strains was constructed on the basis of the similarity of their «housekeeping genes» sequences. The summary sequence of 6 «housekeeping genes» (*rpoB, rrnA, gyrB, atpB, trpB, recA*) of *S. coelicolor* A3(2) was used as Query Sequence (Fig. 4).

The strain *S. coelicolor* A3(2) was reportedly isolated twice from different sources on different continents [13, 14]. It is possible that the strain *Streptomyces sp.* SID7813 is the next isolation of *S. coelicolor* A3(2), since complete similarity of the sequences of their 16S RNAs, agr-clusters, and 6 «housekeeping genes» was revealed (Tables 3 and 4, Fig. 4). In addition, the complete identity (Q.c. = 100 %, I = 100 %, M = 0, G = 0) of the

TABLE 4. Levels of identity of 16S RNA-genes sequences of streptomycetes to rrnA-gene of S. coelicolor A3(2) (Query Sequence)

Strain of streptomycetes (Subject Sequence)	16S RNA-genes and their levels of identity to *rrnA*-gene of *S. coelicolor* A3(2)	
Streptomyces sp. S4.7	SSPS47_04185	I = 97.3 % (M/G = 42/3)
Streptomyces sp. SID7813	GTY87_06950	I = 100 %
Streptomyces sp. NRRL B-16638	PV411_40795	I = 99.9 % (M/G = 1/0)
Streptomyces sp. ME02-6977A	PV708_41240	I = 99.9 % (M/G = 1/0)
Streptomyces sp. SM1	B9S61_19200	I = 99.3 % (M/G = 11/0)

Note. I — identity, M — mistake, G — gate.

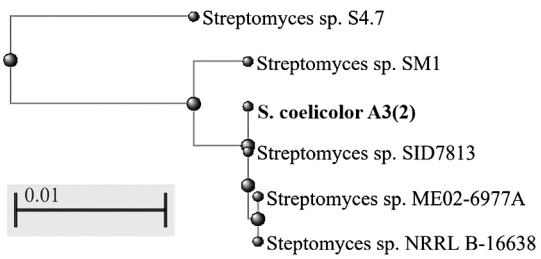

Fig. 4. The tree of genetic consanguinity of *Streptomyces* species built on the basis of similarity to *S. coelicolor* A3(2) sequences of 6 genes that coding conservative proteins

chromosome sequences of *S. coelicolor* A3(2) and *Streptomyces sp.* SID 7813 was established. However, there is no mention of the presence of plasmids in the *Streptomyces sp.* SID7813 cells, while the strain *S. coelicolor* A3(2) contains 2 plasmids (SCP1, SCP2).

It should be noted that the sequences of 5 contigs of the *Streptomyces sp.* NRRL B-16638 (NZ_JARAWB010000039, NZ_JARAWB010000046, NZ_JARAWB010000049, NZ_JARAWB010000059, NZ_JARAWB010000069) contain 97 % (I = 99.99 %) of the plasmid SCP1 sequence. In addition, there are 2 *Streptomyces sp.* S4.7 plasmids (pSSPS4.7a, pSSPS4.7b) in the database, but their sequences are completely different from the plasmid sequences (SCP2 and SCP1) of *S. coelicolor* A3(2).

It was interesting to determine the close relationship of the *Streptomyces sp.* S4.7 strain. The sequence of the 16S RNA gene of the *Streptomyces sp.* S4.7 strain has the greatest affinity for sequences of 16S RNA genes of strains SCSIO 3406 (I = 99.93 %), NRRL2449 (I = 99.74 %), NRRL2466 (I = 99.03 %) of *S. niveus.*

Thus, the existence of 5 streptomycetes strains (*Streptomyces sp.* SID7813, *Streptomyces sp.* NRRL B-16638, *Streptomyces sp.* ME02-6977A, *Streptomyces sp.* SM1, *Streptomyces sp.* S4.7) the genomes of which contain genes that determine agarolytic enzymes and the NA2-transport system was found. It has been established that the strains (*Streptomyces sp.* SID7813, *Streptomyces sp.* NRRL B-16638, *Streptomyces sp.* ME02-6977A, *Streptomyces sp.* SM1) are closely related *S. coelicolor* A3(2). It is very interesting that the strain *Streptomyces sp.* S4.7 is related to the strains of other species (*S. niveus*).

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НОВІ ШТАМИ СТРЕПТОМІЦЕТІВ, В ГЕНОМАХ ЯКИХ ВИЯВЛЕНО КЛАСТЕРИ ГЕНІВ КАТАБОЛІЗМУ АГАРОЗИ

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Агароза — полісахарид, що міститься в клітинних стінках червоних водоростей. Більшість виявлених агаролітичних мікроорганізмів є грам-негативними бактеріями з кількох таксономічно різноманітних груп, але було виявлено також кілька грам-позитивних, наприклад, *Bacillus sp.* MK03, *Streptomyces coelicolor* A3(2). *S. coelicolor* A3(2) ферментує агарозу за допомогою 3 різних гідролаз: двох позаклітинних β-агараз (DagA і DagB) і внутрішньоклітинної α-неоагаробіозної гідролази ScJC117. Мета роботи полягала в ідентифікуванні штамів стрептоміцетів, геноми яких містять послідовності, подібні до генів, що кодують білки агаролітичної системи *S. coelicolor* A3(2). Об'єктами дослідження були нуклеотидні послідовності стрептоміцетів, депоновані в базах даних Національного центру біотехнологічної інформації (NCBI, США). Аналіз первинних структур ДНК стрептоміцетів проводили за допомогою програм BLASTN на сервері NCBI. BLASTN-аналіз інформації в базах даних NCBI виявив наявність у

них 5 таких штамів (*Streptomyces sp*. SID7813, *Streptomyces sp*. NRRL B-16638, *Streptomyces sp.* ME02-6977A, *Streptomyces sp*. SM1, *Streptomyces sp*. S4.7). Їх послідовності містять фрагменти, подібні генам *S. coelicolor* A3(2), які кодують агаролітичні ферменти та особливу NA2-транспортну систему неоагаробіози. На підставі схожості послідовностей їхніх «генів господарювання» *(rpoB, rrnA, gyrB, atpB, trpB, recA*) зроблено висновки про близьке споріднення 4 штамів (*Streptomyces sp*. SID7813, *Streptomyces sp*. NRRL B-16638, *Streptomyces sp*. ME02-6977A, *Streptomyces sp*. SM1) і *S. coelicolor* A3(2). Штам *Streptomyces sp*. S4.7 належить до штамів іншого виду (*S. niveus*).

Ключові слова: *Streptomyces sp.,* агараза, гідроліз, транспортна система, генетична спорідненість.

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