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تقييم التركيب الجيني للبكتيريا المنتجة للجسيمات الممغنطة في جينوم Magnetospirillum magneticum AMB-1

Ali Bin Thani [a,*], Essam Ghanem [a], Mohamed Bououdina [b,c], Salwa Al-Thawadi [a], Ahmed Al-Saie [b,c], Suad Rashdan [d]

[a] Department of Biology, College of Science, University of Bahrain, Bahrain
[b] Department of Physics, College of Science, University of Bahrain, Bahrain
[c] Nano-technology Center, University of Bahrain, Bahrain
[d] Department of Chemistry, College of Science, University of Bahrain, Bahrain

الملخص:

بعد استكمال الخريط الجينية للبكتريا المنتجة للجسيمات الممغنطة في جينوم Magnetospirillum magneticum AMB-1، فلقد تم الدمج بين التركيب الجيني للبكتريا والبروتينات المصاحبة لإنتاج الجسيمات الممغنطة في دراسات مقارنة لاستنتاج وظائف لأجزاء من المادة الوراثية للميكروب. الدراسة الحالية وضحت التباين في التركيب الجيني للأجزاء المسؤولة عن انتاج تلك الجسيمات وحددت العدد ب 100 "جينوم متغاير" باستخدام وظيفة (IslandPick). وقد خلصت الدراسة الى وجود جينوم متغاير مسؤول عن انتاج تلك الجسيمات الممغنطة وقدر حجمة ب 110 كيلو- نيكلوتيدة. و توصلت الدراسة الحالية الى مجموعة من الجينات التي تعتبر غير متغايرة "محافظة"، وعمدت الى اختيار احدى تلك الجينات واعتبار البروتين المصاحب "amb3135" كأداة للتصنيف بين مجموع البكتيريا المنتجة للجسيمات الممغنطة.

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ORIGINAL ARTICLE

Evaluation of the mobile content in *Magnetospirillum magneticum* AMB-1 genome using bioinformatical approaches reveals a new genome size for the magnetosome island

Ali Bin Thani [a,*], Essam Ghanem [a], Mohamed Bououdina [b,c], Salwa Al-Thawadi [a], Ahmed Al-Saie [b,c], Suad Rashdan [d]

[a] *Department of Biology, College of Science, University of Bahrain, Bahrain*
[b] *Department of Physics, College of Science, University of Bahrain, Bahrain*
[c] *Nano-technology Center, University of Bahrain, Bahrain*
[d] *Department of Chemistry, College of Science, University of Bahrain, Bahrain*

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Abstract After completing its sequence/annotation in 2005, *Magnetospirillum magneticum* AMB-1 had become one of the most important magnetotactic genomes used to facilitate analysis of the magnetosome formation process. In this paper we investigate the genome contents of AMB-1 and other magnetotactic bacteria to demonstrate the size of mobile genome and number of conserved genes in *M. magneticum* AMB-1. The preliminary analysis presented here shows the mosaic structure of these genomes. 100 genomic islands were identified in AMB-1 by IslandPick. Moreover, the size of AMB-1 magnetosome island (MAI), previously known to be 100 kb, was re-estimated to be in the size range of 110 kb. Thus more genes were included to be part of this GI. The investigation included the use of comparative approaches to elucidate conserved protein coding sequences. 13 CDS were identified to be conserved among three magnetotactic genomes. One CDS (amb3135) was conserved in five magnetotactic genomes. The amino acid sequence for this CDS (amb3135) was used to draw a phylogenetic tree among magnetotactic bacteria. The phylogeny based on amb3135 is in concordance with previous studies indicating a close relationship between strain AMB-1 and other *Magnetospirillum* species.

1. Introduction

Magnetotactic bacteria (MTB) have become one of the most important bacterial agents used in different applications covering industry and medicine. They are involved in the formation of magnetic nano-particles such as magnetite (Fe_3O_4)

* Corresponding author. Tel.: +973 17437419.
E-mail address: abinthani@uob.edu.bh (A.B. Thani).
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or greigite (Fe_3S_4), (intracellular structures known as magnetosomes). These are responsible for the MTB's ability to orient along the magnetic field lines. Though, still the ability of these microorganisms to form magnetosomes is not fully understood (Arakaki et al., 2008). Different studies implemented that a cluster of genes forming large DNA fragments encode for proteins that control the synthesis of these magnetosomes (Grünberg et al., 2001; Schubbe et al., 2003; Matsunaga et al., 2005). These large DNA clusters are usually acquired into the bacterial chromosome from another bacteria living in the same habitat (Richter et al., 2007). Such foreign DNA fragments show some DNA signatures of the donor strain e.g., its GC contents. These large DNA segments are called genomic islands (GIs) and are usually inserted downstream of tRNA genes. Up to date two GIs were identified in two different magnetotactic bacteria *Magnetospirillum gryphiswaldense* and *Magnetospirillum magneticum* AMB-1 (Schubbe et al., 2003; Matsunaga et al., 2005; Ullrich et al., 2005). Both are considered α-proteobacteria. Because the two GIs identified in these two strains contain genes encoding magnetosome formation proteins, therefore, they were named magnetosome island (MAI) (Ullrich et al., 2005). In this study we are investigating the GI contents of *M. magneticum* AMB-1 using devised online application "IslandPick" developed by Langille and Brinkman (2009). The aim of this study is to evaluate the content and size of the mobile genome in *M. magneticum* AMB-1. Our investigation should provide better understanding for the mechanisms applied by AMB-1 in magnetosome formation.

2. Databases and *in silico* analysis tools

IslandPick from IslandViewer was used in this study to reassess the GI contents in *M. magneticum* AMB-1. IslandPick default parameters were applied except for the maximum distance (MD) changed to 0.48. Therefore, distantly related genomes *Rhodospirillum rubrum* ATCC 11170 (MD 0.471) and *Rhodospirillum centenum* SW (MD 0.475) could be included in the analysis. mGenomeSubtractor (default parameters: Matrix BLOSUM62 and *H*-value $\geqslant 0.64$ applied) an online application was used to verify the conserved protein coding sequences (CDS) among completely sequenced magnetotactic bacteria (Shao et al., 2010). Both ClustalX2 by Larkin et al. (2007) and tree-view by Page (2001) were used to draw phylogenetic tree between *M. magneticum* AMB-1 (NC_007626) and four other magnetotactic bacteria: *M. gryphiswaldense* MSR-1 (CU459003), *Magnetospirillum magnetotacticum* MS-1 (NZ_AAAP00000000), *Magnetococcus* sp. MC-1 (NC_008576), and *Desulfovibrio magneticus* RS-1 (NC_012796).

3. Results and discussion

3.1. Investigating the GI contents of *M. magneticum* AMB-1

Currently there are three online methods provided by IslandViewer for GI investigations: IslandPick, SIGI-HMM, and IslandPath-DIMOB.

In contrary to the other two, IslandPick provides the option of selecting the comparison genomes instead of applying the whole set of default genomes (Langille and Brinkman, 2009). Therefore, we used IslandPick in this study to reduce the number of compared genomes to only two non-MTB strains with some relatedness to *M. magneticum* AMB-1: *R. rubrum* ATCC 11170 (NC_007643) and *R. centenum* SW (NC_011420) (Richter et al., 2007). Using these two non-MTB strains should verify the differences between MTB and their distantly related relatives. This would enable proper investigation for the proposed genes involved in magnetosome formation and are unique to AMB-1.

100 GIs were identified by IslandPick, 21 of these were in the size range of 27–74 kb. The MAI previously identified as the 100 kb island in AMB-1 Matsunaga et al. (2005) was identified by IslandPick as 74 kb island and was the largest GI found by IslandPick (Table 1 and Fig. 1).

Table 1 shows that the total size of the mobile elements present in the genome of AMB-1 is about 1998 kb. Compared to other bacterial genomes the amount of unique DNA (proposed to be essential for magnetosome formation) in AMB-1 is considered high (about 40% of the AMB-1 genome – AMB-1 chromosome size is 5 Mb). For example, four *E. coli* strains had a unique DNA size between 65 and 1183 kb Ochman and Jones (2000).

The presence of high number of mobile elements in the chromosome of AMB-1 indicates a robust and highly dynamic genome acquiring foreign DNA fragments. This speculation is enforced by the findings of Hou (1999) and Williams (2002); in their studies they found that GIs are usually associated with island–encoded integrases capable of self excision/insertion by recognition of short sequences typically flanking the boundaries of these GIs. The dynamic mechanism applied by the mosaic DNA structure for AMB-1 could overcome stress conditions imposed by their environment. For example,

Table 1 21 GIs in the size range of 27–74 kb identified by IslandPick method in strain *M. magneticum* AMB-1[a].

No.	Start	End	Size (kb)[b]
1	64656	112973	48,317 (48)
2	116144	171326	55,182 (55)
3	403906	439081	35,175 (35)
4	492378	522384	30,006 (30)
5	987523	1061658	74,135 (74)[c]
6	1075584	1143180	67,596 (68)
7	1352548	1394957	42,409 (42)
8	1523909	1553799	29,890 (30)
9	1627216	1657770	30,554 (31)
10	1749453	1778090	28,637 (29)
11	1832297	1892486	60,189 (60)
12	1894691	1924393	29,702 (30)
13	2025274	2054484	29,210 (29)
14	2065014	2106668	41,654 (42)
15	2152512	2179581	27,069 (27)
16	2203373	2258854	55,481 (55)
17	3125031	3158087	33,056 (33)
18	3160859	3211078	50,219 (50)
19	3399857	3436053	36,196 (36)
20	3714652	3752680	38,028 (38)
21	4120182	4160540	40,358 (40)
Total			1998698 (2 Mb)[d]

[a] Numbers are written in bp.
[b] Numbers between two brackets are in kb.
[c] IslandPick predicted the size of MAI to be 74 kb.
[d] Total size of GIs present in the genome of AMB-1 is calculated in Mb.

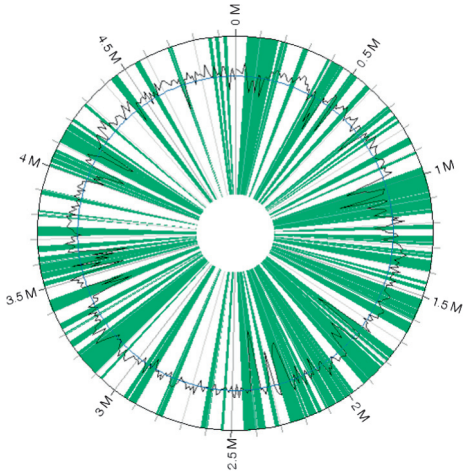

Figure 1 Circular representation of the AMB-1 genome and its associated GIs predicted by IslandPick. GIs are represented by green shaded areas (Image produced by the IslandPick application).

Richter et al. (2007) found that the function of additional genes outside the MAI is essential to coordinate both the magnetosome formation and the physiology of magnetotaxis, therefore, enabling the microbe to overcome the high iron environment.

3.2. Estimating the size of the MAI in AMB-1

This is the first report to propose a new size for the previously identified 100 kb MAI. The coordinates of the 100 kb MAI were 997403–1097027 (Matsunaga et al., 2005).

Both the 100 kb and 74 kb sizes of the MAI have different distal termini that are mapped to 9881 and 35370 bp distal extensions. The distal extension of 9881 bp identified by IslandPick maps to: diguanylate cyclase with hemerythrin-like metal-binding, transposases and putative integrase/recombinase proteins (Table 2). Presence of a metal-binding protein, transposases and integrase genes would suggest that this DNA fragment 9881 bp is part of the 100 kb MAI.

On the other hand, blastn search for the other distal extension 35370 bp missed by IslandPick corresponds to: parts of the *M. gryphiswaldense*/magnetosome island, magnetic particle proteins and the *MamAB* gene-one of the genes involved in magnetosome formation (Richter et al., 2007). Even that IslandPick did not recognize this DNA fragment as part of the MAI, the blastn result shows that this is still considered part of the MAI. Summing the whole DNA fragments all together would make the MAI size to be in the size range of 110 kb with the following new coordinates 987523–1097027 (Fig. 2).

IslandPick uses a comparative genomic approach to predict the presence of GIs (Langille and Brinkman, 2009). Default parameters of the software apply the whole microbial genome set present in the database. However, users can select from the set of microbial genomes, more closely related strains for their comparative runs. One drawback of such approaches is that some strains with few closely related strains in the database e.g., AMB-1 would return IslandPick with large number of "false" predictions and limit the software ability to detect

Table 2 Blastx results for the 9881 bp DNA fragment (distal extension).

Sequence length (a.a)	Blastx hits of GI specific sequence	Blastx results	Product	NCBI accession No.
483	*Candidatus Accumulibacter* phosphatis clade IIA str	Bit score = 305 e-value = 9e80 ID = 153/35 (51%)	Diguanylate cyclase with hemerythrin-like metal-binding domain	YP_003168004
416	*Magnetospirillum magneticum* AMB-1	Bit score = 321 e-value = 5e-95 ID = 156/197 (80%)	Transposase	YP_420395
256	Alpha proteobacterium	Bit score = 352 e-value = 7e94I D = 182/23 (82%)	Putative integrase/recombinase protein	ZP_02186527
285	*Magnetospirillum magneticum* AMB-1	Bit score = 565 e-value = 2e161 ID = 285/25 (100%)	Integrase	YP_420289
110	*Magnetospirillum magneticum* AMB-1	Bit score = 208 e-value = 7e-54 ID = 106/110 (97%)	Nucleoid DNA binding protein	YP_420355
390	*Magnetospirillum magneticum* AMB-1	Bit score = 785 e-value = 0.0 ID = 389/390 (99%)	Putative transposase	YP_420290
174	*Magnetospirillum magneticum* AMB-1	Bit score = 297e-value = 2e-77ID = 146/146 (100%)	Hypothetical protein amb0929	YP_420292

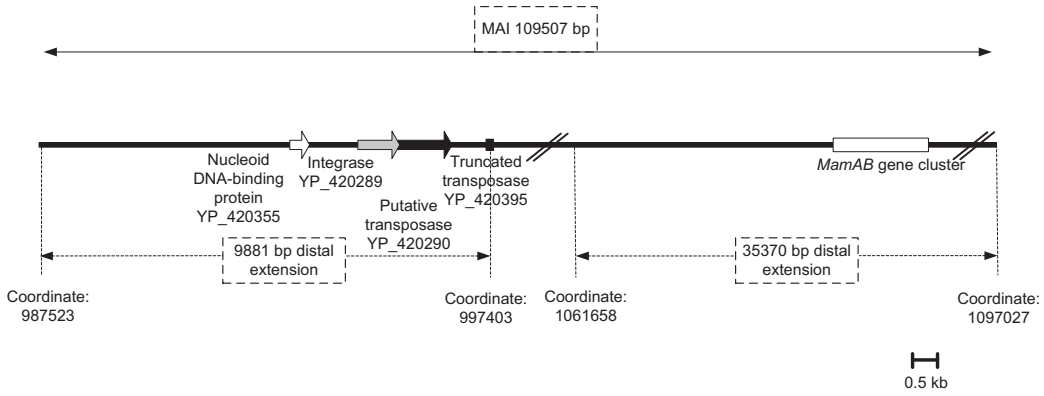

Figure 2 Distal extensions of the MAI in AMB-1.

Table 3 Conserved protein coding sequences obtained by mGenomeSubtractor/mpiBLASTP in three magnetotactic bacteria.

No	Synonym	Length (aa)	Gene	Product
1	amb0034	49	–	Hypothetical protein
2	amb0203	552	*groEL*	Chaperonin GroEL
3	amb1077	290	–	GDP-D-mannose dehydratase
4	amb3109	131	–	30S ribosomal protein S11
5	amb3120	122	–	Ribosomal protein L14
6	amb3131	102	*rpsj*	30S ribosomal protein S10
7	amb3132	396	–	Elongation factor Tu
8	amb3135	123	*rpsL*	30S ribosomal protein S12
9	amb3148	396	–	Elongation factor Tu
10	amb3206	546	–	ATP-dependent Zn protease
11	amb4139	474	–	F0F1 ATP Synthase subunit beta
12	amb4440	642	dnaK	Chaperone DnaK
13	amb4553	418	*rho*	Transcription termination factor Rho

the "correct" boundaries of these GIs (Langille and Brinkman, 2009).

3.3. Estimating the number of conserved protein coding sequences among completely sequenced magnetotactic bacterial genomes using mGenomeSubtractor

mGenomeSubtractor uses mpiBLAST-based procedure to generate a list of conserved protein coding sequences by comparing closely related genomes (Shao et al., 2010). Thus, the online application is able to perform a subtractive hybridization among the user-selected genomes. We used mGenomeSubtractor to generate a list of conserved protein coding sequences. The application was compared using mpiBLASTp search between AMB-1 genome and two other completely sequenced magnetotactic genomes: *Magnetococcus* sp. MC-1 and *D. magneticus* RS-1.

The results obtained are shown in Table 3. 13 different CDS were obtained as the conserved part among the three magnetotactic bacteria. The DNA sequences of these 13 conserved CDS were extracted and used in blastx search to verify if these sequences were also conserved among in-progress magnetotactic genomes.

The blastx results are not shown but one CDS (amb3135, the 30S ribosomal protein S12) of the 13 conserved proteins had high similarity hits to two more in-progress magnetotactic genomes: *M. gryphiswaldense* MSR-1 (e-value 3e-64, ID 119/123, 97%) and *M. magnetotacticum* MS-1 (e-value 9e-65, ID 121/123, 99%).

3.4. Classifying the 13 CDS into MTB and non-MTB

To classify the identified 13 CDS into MTB specific and non-MTB proteins, the mGenomeSubtractor mpiBLASTp search was repeated for the MTB genomes (AMB-1, MC-1 and RS-1) and a fourth genome: *R. rubrum* ATCC 11170 (NC_007643). *R. rubrum* is a non-MTB close relative to the *Magnetospirillum* strains (Richter et al., 2007). *R. rubrum* was used as control to identify MTB specific proteins among the 13 CDS.

All 13 CDS were identified as non-MTB proteins (12 CDS were represented in the genome of *R. rubrum*) except for amb0034. The DNA sequence for amb0034 was used in NCBI-blastn to find if it is part of the MAI in the three MTB genomes (AMB-1, MC-1, and RS-1). The results retrieved for amb0034 blastn indicated that it is located outside the MAI (Table 4).

The obtained results suggest that amb0034 is MTB-associated gene and it could be postulated that the genomes of magnetotactic bacteria had once evolved from the same habitat. However, further investigations are required to elucidate possible functions for the amb0034 protein.

Table 4 Location of the amb0034 in the three MTB genomes.

Genome	Orthologous genes	Gene locus (bp)	MAI location (bp)[a]	MAI size (kb)[a]
AMB-1	amb0034	38999–39148	997403–1097027	100
MC-1	Mmc1–0763	944923–945072	2.80–2.93 Mb[b]	102
RS-1	DMR-44360	5029207–5029356	4605425–4677646	71

[a] The MAI locations and sizes were obtained from Matsunaga et al. (2005), Scubbe et al. (2009) and Nakazawa et al. (2009) respectively.
[b] Authors had only indicated the coordinates in Mb.

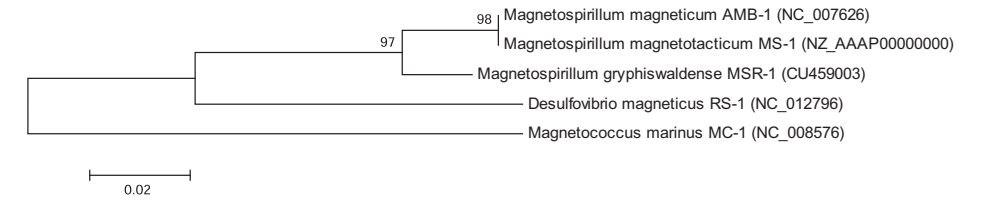

Figure 3 Phylogenetic tree of the 30S ribosomal protein S12 orthologous proteins. The evolutionary history was inferred using the Neighbor-Joining method. The optimal tree with the sum of branch length = 0.27141455 is shown. The percentage of replicate trees in which the associated taxa clustered together in the bootstrap test (500 replicates) are shown next to the branches. The tree is drawn to scale, with branch lengths in the same units as those of the evolutionary distances used to infer the phylogenetic tree. The evolutionary distances were computed using the Poisson correction method, and are in the units of the number of amino acid substitutions per site. The analysis involved 5 amino acid sequences. All positions containing gaps and missing data were eliminated. There were a total of 123 positions in the final dataset.

As suggested by previous studies (Richter et al., 2007; Rioux et al., 2010) the number of strain specific genes obtained by mpiBLASTp for MC-1 and RS-1 (data not shown) indicates that both genomes are remote in the sense of their mechanism of magnetosome formation (magnetotaxis) compared to other strains such as *M. magnetotacticum* MS-1 and *M. gryphiswaldense* MSR-1. The cut-off used by mGenomeSubtractor to identify the 13 CDS was e-value 0.01. This cut-off is less stringent compared to those implemented by Richter et al. (2007) $>$ 1e-50. We applied the auto cut-off of mGenomeSubtractor to obtain the maximum number of genes related to the magnetosome formation.

3.5. Drawing a phylogenetic relationship between the magnetotactic bacteria

Heterogeneity was previously observed among magnetotactic bacteria and that they represent different phylogenetic groups (Arakaki et al., 2008; Lefevre and Bazylinski, 2013). However, we have analyzed the phylogenetic relationship among a few magnetotactic bacteria based on the conserved 30S ribosomal protein S12 to verify the possible evolutionary pathways for the magnetotactic trait.

The amino acid sequence of the amb3135 30S ribosomal protein S12 shown to be conserved among the five different magnetotactic bacteria was obtained from the 5 bacterial genomes: *M. magneticum* AMB-1, *M. gryphiswaldense* MSR-1, *M. magnetotacticum* MS-1, *Magnetococcus* sp. MC-1 and *D. magneticus* RS-1.

Because the protein sequence of amb3135 was conserved in five magnetotactic genomes, it was used to draw a phylogenetic tree using the ClustlX2 Larkin et al. (2007) and tree-view Page (2001) software. The preview of the phylogenetic tree indicates that AMB-1 is more closely related to MS-1 and MSR-1 than it is to RS-1 and MC-1 (Fig. 3). Moreover, both RS-1 and MC-1 are clustered together indicating that they too represent a smaller subgroup within the magnetotactic bacteria.

Our phylogenetic results are in concordance with similar phylogenetic studies done by other groups Richter et al. (2007). However, our study was the first and unique in using novel approaches such as mGenomeSubtractor to deduce the conserved CDS before using them in drawing phylogenetic trees.

4. Conclusion and future work

We investigated the heterogeneity of the magnetotactic chromosomes and the highly mosaic structure of the AMB-1 genome. This heterogeneity has limited the selection of possible genomes used in comparative approaches to elucidate functional genes in the magnetosome formation. To overcome such limitations we would investigate the contents of the 100 AMB-1 GIs obtained by the IslandPick individually using GeneSpring software and COG database to predict possible functions for the different obtained GIs.

In summary, the bioinformatic approaches applied in this paper elucidate a new genome size for the MAI in AMB-1. Moreover, our investigation revealed 13 CDS conserved in three magnetotactic genomes. One of these CDS termed amb3135 encodes for the 30S ribosomal protein S12 which is conserved in different bacterial strains. Therefore, the amino acid sequence for the amb3135 was used to illustrate the phylogenic relatedness among magnetotatic bacteria. The obtained phylogeny indicated a close relationship between strain AMB-1 and two more magnetotactic bacteria (RS-1 and MC-1).

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