High-quality-draft genomic sequence of *Paenibacillus ferrarius* CY1<sup>T</sup> with the potential to bioremediate Cd, Cr and Se contamination

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**Abstract**

*Paenibacillus ferrarius* CY1<sup>T</sup> (= KCTC 33419<sup>T</sup> = CCTCC AB2013369<sup>T</sup>) is a Gram-positive, aerobic, endospore-forming, motile and rod-shaped bacterium isolated from iron mineral soil. This bacterium reduces sulfate (SO<sub>4</sub><sup>2-</sup>) to S<sup>2-</sup>, which reacts with Cd(III) to generate precipitated CdS. It also reduces the toxic chromate [Cr(VI)] and selenite [Se(VI)] to the less bioavailable chromite [Cr(III)] and selenium (Se<sup>0</sup>), respectively. Thus, strain CY1<sup>T</sup> has the potential to bioremediate Cd, Cr and Se contamination, which is the main reason for the interest in sequencing its genome. Here we describe the features of strain CY1<sup>T</sup>, together with the draft genome sequence and its annotation. The 9,184,169 bp long genome exhibits a G + C content of 45.6%, 7,909 protein-coding genes and 81 RNA genes. Nine putative Se(IV)-reducing genes, five putative Cr(VI) reductase and nine putative sulfate-reducing genes were identified in the genome.

**Keywords:** *Paenibacillus ferrarius*, Genome sequence, Cadmium, Chromate-reducing bacterium, Selenite-reducing bacterium

**Introduction**

The genus *Paenibacillus* was established in 1993 with *Paenibacillus polymyxa* as the type species [1, 2]. The common characteristics of the *Paenibacillus* members are aerobic, Gram-positive, rod-shaped and endospore-forming [3]. Some *Paenibacillus* strains have the ability for plant growth promotion, biocontrol, manufacturing process and bioremediation, which making them very important in agricultural, industrial and medical applications [4]. A variety of industrial wastes including crude oil, diesel fuel, textile dyes, aliphatic and aromatic organic pollutants could be degraded by *Paenibacillus* strains [5–11]. However, the bioremediation of heavy metal(loids) contamination by *Paenibacillus* strains are rarely reported.

*Paenibacillus ferrarius* CY1<sup>T</sup> is a multi-metal(loids) resistant bacterium isolated from iron mineral soil in Hunan Province, China [12]. During cultivation, it could efficiently reduce sulfate (SO<sub>4</sub><sup>2-</sup>) to S<sup>2-</sup>, which could precipitate with cadmium [Cd(III)] to generate CdS [13]. In addition, it also reduces the more toxic chromate [Cr(VI)] and selenite [Se(VI)] to the much less toxic chromite [Cr(III)] and selenium (Se<sup>0</sup>), respectively. Based on these interesting features, we propose that strain CY1<sup>T</sup> represents a promising candidate for bioremediation of Cd, Cr and Se contamination. To gain insight into the molecular mechanisms involved in sulfate/chromate/selenite reduction and metal(loids) resistance, and to enhance its biotechnological applications, we analyze the high quality draft genome of this bacterium.

**Organism information**

**Classification and features**

*P. ferrarius* CY1<sup>T</sup> is a Gram-positive, endospore-forming, motile and aerobic bacterium. The rod-shaped cells are 0.5–0.8 mm in width and 4.2–5.7 mm in length with peritrichous flagella (Fig. 1). Colonies are yellowish to creamy-white, smooth and circular on NA agar plate [12]. Growth occurs at temperature and pH range of
4–37 °C and pH 5.0–8.0, respectively [12]. Optimal growth occurs at 28 °C and pH 6.0–7.0 (Table 1). Strain CY1 T grows on NA/R2A/LB and TSA media, but cannot grow on MacConkey agar [12]. The phylogenetic relationship of *P. ferrarius* CY1 T with other members within the genus *Paenibacillus* is shown in a 16S rRNA based neighbor-joining tree, and strain CY1 T is closely related to *Paenibacillus marchantiorum* R55 T (KP056549) (Fig. 2).

Physiological and biochemical analyses were performed using the API 20NE test (bioMérieux, France), ID 32GN test (bioMérieux, France) and traditional classification methods. Strain CY1 T is positive for oxidase and catalase activities, hydrolysis of Tween 80 and aesculin and production of NH3 and H2S, but is negative for nitrate reduction, citrate utilization, egg yolk reaction, production of indole, and hydrolysis of starch, gelatin, casein, urea, L-tyrosine, arginine, Tween 20, DNA and CM-cellulose [12]. The carbon sources, which can be used by strain CY1 T, are shown in Table 1.

![Fig. 1 Scan electron microscope (SEM) image of *P. ferrarius* CY1 T cells. The bar scale represents 0.5 μm](image)

Table 1: Classification and general features of *Paenibacillus ferrarius* CY1 T

| MIGS ID | Property | Term | Evidence code |
|---------|----------|------|--------------|
| Classification | Domain | Bacteria | TAS [39] |
| | Phylum | Firmicutes | TAS [40–42] |
| | Class | Bacilli | TAS [43, 44] |
| | Order | Bacillales | TAS [45, 46] |
| | Family | Paenibacillaceae | TAS [44] |
| | Genus | *Paenibacillus* | TAS [1, 47–50] |
| | Species | *Paenibacillus ferrarius* | |
| | Strain | CY1 T | |
| Gram stain | | Positive | IDA |
| Cell shape | | Rod | IDA |
| Motility | | Motile | IDA |
| Sporulation | | Endospore | IDA |
| Temperature range | | 4–37 °C | IDA |
| Optimum temperature | | 28 °C | IDA |
| pH range; Optimum | | 5–8; 6–7 | IDA |
| Carbon source | | Rhamnose, glycogen, sucrose N-acetylglucosamine, maltose, mannitol, D-glucose, salicin, melibiose, D-sorbitol, L-arabinose, mannose, D-xylene, ammonium nitrate and L-proline | IDA |

The resistance levels of *P. ferrarius* CY1 T for multimetals(loids) were tested with the minimal inhibition concentration on NA agar plates using Na3AsO3, K2Sb2(C4H2O6)2, Na2SeO3, K2CrO4, CdCl2, PbCl2, CuCl2 and MnCl2. The results showed that the MICs for As(III), Sb(III), Se(IV), Cr(VI), Cd(II), Pb(II), Cu(II) and Mn(II) are 2, 1, 8, 4, 0.08, 1, 0.5 and 100 mmol/L, respectively. In addition, the abilities of strain CY1 T for Cd(II) removal, and Cr(VI) and Se(IV) reduction were tested. Strain CY1 T was incubated in LB medium for Cd(II) removal and in NA medium for Cr(VI) and Se(IV) reduction, since NA medium can absorb some of the Cd(II). When OD600 reach 0.6–0.7, CdCl2 (50 μmol/L), K2CrO4 (200 μmol/L) and Na2SeO3 (200 μmol/L) were each added to the culture. At designated times, culture samples were taken for measuring the residual concentrations of Cd(II), Cr(VI) and Se(IV). The concentration of Cd(II) was measured by the atomic absorption spectrometry [14]. The concentration of Cr(VI) was measured by the UV spectrophotometer (DU800, Beckman, CA, USA) with the colorimetric diphenylcarbazide method [15], and the concentration of Se(IV) was tested by HPLC-HG-AFS (Beijing Titan Instruments Co., Ltd., China) [16]. The results showed that strain CY1 T could
remove nearly 50 μmol/L Cd(II) in 72 h (Fig. 3a) and reduce 200 μmol/L Cr(VI) and Se(IV) in 5 h and 6 h, respectively (Fig. 3b, c). The removed Cd(II) is presented as pellets that is most probably by the reaction of Cd(II) with H₂S to produce precipitated CdS.

**Genome sequencing information**

**Genome project history**

Strain CY1ᵀ was selected for genome sequencing on the basis of its ability for Cd(II) removal, Cr(VI) and Se(IV) reduction, these characters made strain CY1ᵀ with great value for genetic study and for bioremediation of Cd, Cr and Se contamination. The draft genome sequence is deposited at DDBJ/EMBL/GenBank under the accession number MBTG00000000. The final genome consists of 73 scaffolds with 289.77 × coverage. A summary of the project information is shown in Table 2.

**Growth conditions and genomic DNA preparation**

Overnight cultures of strain CY1ᵀ was inoculated into 50 mL of NA medium at 28 °C with 120 rpm shaking. After incubation for 36 h, the bacterial cells were harvested through centrifugation (13,400×g for 5 min at 4 °C). Genomic DNA was extracted using the QiAamp kit (Qiagen, Germany). The quality and quantity of the DNA were determined by a spectrophotometer (NanoDrop 2000, Thermo). Then, 10 μg of DNA was sent to Bio-broad Technology Co., Ltd., Wuhan, China for sequencing.

**Genome sequencing and assembly**

Genome sequencing and assembly were performed by Bio-broad Technology Co., Ltd., Wuhan, China, and all original sequence data can be found at the NCBI Sequence Read Archive. An Illumina standard shotgun library was constructed and sequenced using an Illumina
Hiseq2000 platform with pair-end sequencing strategy (300 bp insert size) [17]. The following quality control steps were performed for removing low quality reads: 1) removed the adapter sequences of reads; 2) trimmed the ambiguous bases (N) in 5′ end and the reads with a quality score lower than 20; and 3) filtered the reads which contain N more than 10% or have the length less than 50 bp (without adapters and N in 5′ end). The assembly of CY1T genome is based on 20,189,278 quality reads totaling 3,000,798,615 bp, which provides a coverage of 289.77×. Subsequently, the reads were assembled into 75 contigs (> 200 bp) using SOAPdenovo v2.04 [18], and the gaps between the contigs were closed by GapCloser v1.12 [19].

Table 2 Project information

| MIGS ID   | Property         | Term                                |
|-----------|------------------|-------------------------------------|
| MIGS-31   | Finishing quality| High-quality draft                  |
| MIGS-28   | Libraries used   | Illumina Paired-End library (300 bp insert size) |
| MIGS-29   | Sequencing platforms | Illumina Miseq 2000              |
| MIGS-31.2 | Fold coverage    | 289.77 x                           |
| MIGS-30   | Assemblers       | SOAPdenovo v2.04                   |
| MIGS-32   | Gene calling method | GeneMarkS+                      |
|           | Locus TAG        | BC351                               |
| Genbank ID|                  | MTBG000000000                      |
| Genbank Date of Release | Mar 16, 2017    |
| Bioproject|                 | PRJNA331076                         |
| MIGS-13   | Source material identifier | Strain KCTC 33419T (CCTCC AB2013369T) |
| Project relevance | Bioremediation |                      |

Table 3 Genome statistics

| Attribute            | Value     | % of total a |
|----------------------|-----------|--------------|
| Genome size (bp)     | 9,184,169 | 100.00       |
| DNA coding (bp)      | 7,828,640 | 85.24        |
| DNA G + C (bp)       | 4,205,829 | 45.79        |
| DNA scaffolds         | 73        | 100.00       |
| Contigs               | 75        | 100.00       |
| Total genes b         | 8260      |              |
| RNA genes             | 81        |              |
| Pseudo genes          | 209       |              |
| Protein-coding genes  | 7909      | 100.00       |
| Genes in internal clusters | 648       | 8.19         |
| Genes with function prediction | 4231 | 53.50 |
| Genes assigned to COGs | 6632 | 83.85 |
| Genes with Pfam domains | 6363 | 80.45 |
| Genes with signal peptides | 765 | 9.67 |
| Genes with transmembrane helices | 2251 | 28.46 |
| CRISPR repeats        | 24        | 0.30         |

| Code | Value | % of total a | Description                                           |
|------|-------|--------------|-------------------------------------------------------|
| J    | 199   | 2.52         | Translation, ribosomal structure and biogenesis       |
| A    | 0     | 0.00         | RNA processing and modification                       |
| K    | 732   | 9.26         | Transcription                                         |
| L    | 213   | 2.69         | Replication, recombination and repair                  |
| B    | 1     | 0.01         | Chromatin structure and dynamics                       |
| D    | 55    | 0.70         | Cell cycle control, cell division, chromosome partitioning |
| Y    | 0     | 0.00         | Nuclear structure                                     |
| V    | 128   | 1.62         | Defense mechanisms                                    |
| T    | 694   | 8.77         | Signal transduction mechanisms                        |
| M    | 328   | 4.15         | Cell wall/membrane/envelope biogenesis                |
| N    | 107   | 1.35         | Cell motility                                         |
| Z    | 11    | 0.14         | Cytoskeleton                                          |
| U    | 63    | 0.80         | Intracellular trafficking, secretion, and vesicular transport |
| O    | 146   | 1.85         | Posttranslational modification, protein turnover, chaperones |
| C    | 268   | 3.39         | Energy production and conversion                      |
| G    | 1023  | 12.93        | Carbohydrate transport and metabolism                 |
| E    | 432   | 5.46         | Amino acid transport and metabolism                    |
| F    | 121   | 1.53         | Nucleotide transport and metabolism                    |
| H    | 194   | 2.45         | Coenzyme transport and metabolism                      |
| I    | 149   | 1.88         | Lipid transport and metabolism                        |
| P    | 361   | 4.56         | Inorganic ion transport and metabolism                 |
| Q    | 134   | 1.69         | Secondary metabolites biosynthesis, transport and catabolism |
| R    | 777   | 9.82         | General function prediction only                       |
| S    | 496   | 6.27         | Function unknown                                      |
| –    | 1277  | 16.15        | Not in COGs                                           |

| Code | Value | % of total a |
|------|-------|--------------|
| J    | 199   | 2.52         |
| A    | 0     | 0.00         |
| K    | 732   | 9.26         |
| L    | 213   | 2.69         |
| B    | 1     | 0.01         |
| D    | 55    | 0.70         |
| Y    | 0     | 0.00         |
| V    | 128   | 1.62         |
| T    | 694   | 8.77         |
| M    | 328   | 4.15         |
| N    | 107   | 1.35         |
| Z    | 11    | 0.14         |
| U    | 63    | 0.80         |
| O    | 146   | 1.85         |
| C    | 268   | 3.39         |
| G    | 1023  | 12.93        |
| E    | 432   | 5.46         |
| F    | 121   | 1.53         |
| H    | 194   | 2.45         |
| I    | 149   | 1.88         |
| P    | 361   | 4.56         |
| Q    | 134   | 1.69         |
| R    | 777   | 9.82         |
| S    | 496   | 6.27         |
| –    | 1277  | 16.15        |

The COGs functional categories were assigned by WebMGA server [23] with E-value cutoff of 1-e10. The
Table 5 Putative proteins involved in selenite, chromate and sulfate reduction

| Metal(loids) | Putative function                        | Locus_tag of the predicted protein |
|--------------|------------------------------------------|-----------------------------------|
| Selenite     | Thioredoxin reductase                     | BC351_25440                       |
|              | Thioredoxin reductase                     | BC351_17745                       |
|              | Thioredoxin reductase                     | BC351_21345                       |
|              | Thioredoxin reductase                     | BC351_06135                       |
|              | Thioredoxin reductase                     | BC351_33000                       |
|              | Thioredoxin reductase                     | BC351_13625                       |
|              | Thioredoxin disulfide reductase           | BC351_19150                       |
|              | NADH-dependent flavin oxidoreductase      | BC351_22155                       |
|              | NADH-dependent flavin oxidoreductase      | BC351_12795                       |
| Chromate     | NADPH-dependent FMN reductase             | BC351_21415                       |
|              | NADPH-dependent FMN reductase             | BC351_05445                       |
|              | NADPH-dependent FMN reductase             | BC351_40245                       |
|              | NADPH-dependent FMN reductase             | BC351_15505                       |
|              | NADPH-dependent FMN reductase             | BC351_15285                       |
| Sulfate      | Sulfate adenylyltransferase small subunit | BC351_30725                       |
|              | CysD                                     | BC351_31925                       |
|              | Adenylyl-sulfate kinase CysC              | BC351_32075                       |
|              | Adenylyl-sulfate kinase CysC              | BC351_32075                       |
|              | Phosphoadenosine phosphosulfate reductase | BC351_36025                       |
|              | CysH                                     | BC351_12315                       |
|              | Sulfate ABC transporter substrate-binding protein | BC351_31155                   |
|              | CysP                                     | BC351_12325                       |
|              | CysA                                     | BC351_12330                       |
|              | Sulfite reductase alpha component         | BC351_31155                       |
|              | Sulfite reductase beta subunit            | BC351_31160                       |
translations of the predicted CDSs were used to search against the Pfam protein family database [24] and the KEGG database [25]. The transmembrane helices and signal peptides were predicted by TMHMM v. 2.0 [26] and SignalP 4.1 [27], respectively.

**Genome properties**

The whole genome of strain CY1T reveals a genome size of 9,184,169 bp and a G + C content of 45.6% (Table 3). The genome contains 8260 coding sequences, 19 rRNA, 58 tRNA, and 4 ncRNA. Among 7909 protein-coding genes, 4231 were assigned as putative function, while the other 3678 were designated as hypothetical proteins. In addition, 6632 genes were categorized into COGs functional groups. Information about the genome statistics is shown in Table 3 and the classification of genes into COGs functional categories is summarized in Table 4.

**Insights from the genome sequence**

*P. ferrarius* CY1T is a multi-metal(loids) resistant bacterium with the capability of SO$_4^{2-}$, Cr(VI) and Se(IV) reduction, suggesting that it has developed a number of evolutionary strategies to adapt to heavy metal (or metalloids) contaminated environments. To identify pathways and enzymes involved in SO$_4^{2-}$, Cr(VI) and Se(IV) reduction, high quality draft genome sequence of strain CY1T was generated. The map of the *P. ferrarius* CY1T genome is shown in Fig. 4.

KEGG analysis showed that strain CY1T contains a complete SO$_4^{2-}$ reduction pathway, which is consistent with the phenotype of H$_2$S production. The genes responsible for SO$_4^{2-}$ reduction include sulfate ABC transporter CysPWA, sulfate adenylyltransferase CysD, adenylylsulfate kinase CysC, adenylylsulfate reductase CysH and sulfite reductase CysJI (Table 5). The S$^{2-}$ generated from SO$_4^{2-}$ reduction could react with Cd(II) to form the participated CdS [13], which may contribute to the

### Table 6

| Heavy metal | Putative protein | Locus_tag of the predicted protein |
|-------------|------------------|-----------------------------------|
| Arsenic     | Arsenic transporter | BC351_03410                       |
|             | Arsenical efflux pump membrane protein ArsB | BC351_32265                      |
|             | Arsenic ABC transporter ATPase | BC351_35545                     |
|             | ArsR family transcriptional regulator | BC351_32260                     |
|             | ArsR family transcriptional regulator | BC351_02635                     |
|             | ArsC reductase | BC351_15540                       |
| Antimony    | Oxidoreductase (putative AnoA) | BC351_17295                      |
|             | Catalase | BC351_40130                       |
|             | Catalase | BC351_06195                       |
|             | Catalase | BC351_15905                       |
|             | Catalase | BC351_07965                       |
|             | Catalase | BC351_29865                       |
| Chromate    | ChrA protein | BC351_26450                       |
|             | Chromate transporter | BC351_15935                     |
|             | Chromate transporter | BC351_29720                     |
|             | Chromate transporter | BC351_29725                     |
| Cadmium, lead and zinc | Cobalt-zinc-cadmium resistance protein | BC351_15845                     |
|             | Cobalt-zinc-cadmium efflux system protein | BC351_17600                     |
|             | Cation diffusion facilitator family transporter | BC351_20420                     |
|             | Cation diffusion facilitator family transporter | BC351_03295                     |
|             | RND family efflux transporter | BC351_25240                     |
|             | RND family efflux transporter/MFP transporter | BC351_17480                     |
|             | RND family efflux transporter, MFP subunit | BC351_10185                     |
|             | Efflux transporter periplasmic adaptor subunit | BC351_04820                     |
|             | Efflux transporter periplasmic adaptor subunit | BC351_25355                     |
|             | Cd$^{2+}$/Zn$^{2+}$-exporting ATPase | BC351_28470                     |
|             | Cd$^{2+}$/Zn$^{2+}$-exporting ATPase | BC351_14640                     |
|             | Hyd family secretion protein | BC351_33510                     |
|             | Hyd family secretion protein/MFP transporter | BC351_35605                     |
|             | Multidrug efflux pump subunit AcrA | BC351_02380                     |
|             | Efflux transporter periplasmic adaptor subunit | BC351_37435                     |
|             | Cation transporter | BC351_08750                       |
|             | Zinc transporter ZitB | BC351_12865                       |
|             | Cadmium transporter | BC351_35590                       |
|             | Cadmium-transporting P-type ATPase | BC351_14640                     |
| Copper      | Bct/Cfr family drug resistance efflux transporter | BC351_19565                     |
|             | Multidrug resistance transporter, Bct/Cfr family | BC351_07275                     |
|             | Copper transport protein | BC351_15720                       |
|             | Copper-translocating P-type ATPase | BC351_26145                     |
|             | Copper-translocating P-type ATPase | BC351_38485                     |
|             | Copper-transporting P-type ATPase/CopZ | BC351_38480                     |
| Manganese   | Manganese transport protein MntH | BC351_25600                     |
|             | Manganese transport protein MntH | BC351_14100                     |

(Continued)
Cd(II) removal. For Cr(VI) reduction, five NADPH-dependent FMN reductase which have the same conserved domain as the Cr(VI) reductases ChrR (from Pseudomonas putida) and YieF (from Escherichia coli) [28], were identified in the genome of strain CY1T (Table 5). It has been reported that thioredoxin reductase ThXR and NADH:flavin oxidoreductase could reduce Se(IV) in Pseudomonas sele-
niipracepsitans and Rhizobium selenitireducens, respectively [29–31]. According to the NCBI and RAST annotation, seven thioredoxin reductases and two NADH-dependent flavin oxidoreductases were found in the genome of strain CY1T (Table 5), and some of these proteins may responsible for Se(IV) reduction in strain CY1T.

Strain CY1T could tolerant multi-metal(loid)s, such as As(III), Pb(II), Cr(VI), Cd(II), Pb(II), Cu(II) and Mn(II). Expectably, various metal resistant genes were identified in its genome (Table 6). Several transporters were found to responsible for the efflux of these metal(loid)s. In addition, the transcriptional regulator ArsR and arsenite reductase ArsC were also found to be involved in the As(III)/Sb(III) resistance (Table 6) [32–34]. Recently, it has been reported that an oxidoreductase AnoA, which belongs to the short-chain dehydrogenase/reductase family, and catalase KatA, which is responsible for H2O2 degradation, are all involved in bacterial Sb(III) oxidation/resistance in Agrobacterium tumefaciens GW4 [35–38]. One AnoA homologue oxidore-
ductase gene and five catalase genes were identified in the genome of strain CY1T (Table 6), which may associate with Sb(III) oxidation/resistance.

Conclusions
The genome of P. ferrarius CY1T harbors various genes responsible for sulfate transport and reduction, chromatate and selenite reduction and resistance of multi-metal(loids), which is consistent with its phenotypes. To date, the utilization of Paenibacillus species in immobilization of heavy-metals (or metalloids) is still limited and the genes and enzymes involves in Cr(VI) and Se(IV) reduction were poorly understood in Paenibacillus members. The genomic sequence of strain CY1T enriches the genome information of Paenibacillus strains. More importantly, the genome information provides basis for understanding molecular mechanisms of microbial redox transformations of metal(loids).

Acknowledgements
We thank Mr. Xian Xia and Dr. Jing Huang for technical assistance. This study was supported by National key research and development program of China (2016YFD0800702).

Authors’ contributions
JL, WG, MS and YC conducted the study. JL performed the data analyses and wrote the manuscript. GW participated in research design and revised the manuscript. All authors read and approved the final manuscript.

Competing interests
The authors declare that they have no competing interests.

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Received: 5 April 2017 Accepted: 21 September 2017
Published online: 10 October 2017

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