RESEARCH ARTICLE

Whole-genome sequencing and key Cr(VI) reduction genes analysis of *Klebsiella* spp. Shm-1

Hongmei Sun, Guangchuan Shi, Ye Tao, Zhaoyang Wei, Yihan Wang, Changli Liang, Shilin Tian, Enzhong Li, Junhe Liu, Chaoying Liu, Lianbin Cao*

School of Biological Science and Food Engineering, Huanghuai University, Zhumadian, Henan, China.

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Hexavalent chromium (Cr(VI)), a prevalent heavy metal contaminant ubiquitous in industries such as metallurgy and chemistry, poses a significant threat to ecological security and human health. *Klebsiella* spp. Shm-1 has the ability to reduce Cr(VI) and was isolated from polluted river water. This research employed whole-genome sequencing technology to identify the Cr(VI) reducing gene and mechanism of *Klebsiella* spp. Shm-1. The full length *Klebsiella* spp. Shm-1 genome was 5,430,044 bp with 57.62% of GC content. By using GeneMarkS software to predict the coding genes of the newly sequenced genome, *Klebsiella* spp. Shm-1 had a total of 5,187 coding genes. The genes *cysAPUW*, *pstABCSU*, and *modABCEF* might play important roles in the intake of Cr(VI). The *chrA* gene might encode a chromate transporter, which was an efflux transporter that could expel Cr(VI) from the cell. The genes *chrR*, *ccmE*, *ccmF*, *ccmG*, and *ccmH* might be the key regulatory genes for intracellular Cr(VI) reduction. The genes *atpABCDEFGH*, *yrbG*, *galP*, *araE*, *nhaAB*, *citA*, and *ydjE* might be involved in intracellular and extracellular proton transport, providing the necessary conditions for extracellular Cr(VI) reduction. The genes *cyoABCD* and *cydABX* might play important roles in the extracellular export of electrons. The GO annotation results revealed that these genes were associated mainly with cell transmembrane transport, oxidoreductase activity, membrane activity, hydrogen ion transmembrane transporter activity, and oxidation–reduction processes. In addition, *Klebsiella* spp. Shm-1 had a high diversity of primary active transporters, electrochemical potential-driven transporters, and channels/pores in Transporter Classification Database (TCDB), which provided great potential for Cr(VI) transport and reduction. This study would provide a theoretical reference for optimizing the Cr(VI) reduction ability of chromium-resistant microorganisms at the genetic level, thereby advancing the development and widespread adoption of microbial heavy metal remediation technologies.

Keywords: *Klebsiella* spp.; whole-genome sequencing; Cr(VI); Cr(VI) reduction.

***Corresponding author:** Lianbin Cao, School of Biological Science and Food Engineering, Huanghuai University, No. 76 Kaiyuan Road, Zhumadian, Henan 463000, China. Email: caolianbin@163.com.

Introduction

Heavy metal contamination is a significant environmental issue that poses a threat to human health and ecosystems. Microorganisms play a crucial role in the bioremediation of heavy metals by reducing them to less toxic forms. Chromium (Cr) is one of the most toxic heavy metals and poses a threat to the health of millions of people worldwide. Hexavalent chromium (Cr(VI)) is a common heavy metal pollutant widely used in industries, such as metallurgy and chemistry, and can accumulate in aquatic biota, soil, and crops to severely impact

ecological security and human health [1]. Compared with Cr(VI), Cr(III) has lower toxicity, lower mobility, and tends to form precipitates [2]. Therefore, reducing highly toxic Cr(VI) effectively to less toxic Cr(III) *via* scientifically efficient heavy metal treatment techniques is a viable approach in contaminated environments. Many microorganisms have evolved various mechanisms to cope with Cr(VI) stress including the reduction of Cr(VI) to Cr(III) [3]. This process, known as metal reduction, is mediated by a variety of enzymes and metabolic pathways [4]. However, the mechanism of Cr(VI) reduction by reductases in chromate-resistant bacteria is not fully understood. Therefore, exploring chromium resistance genes in microorganisms is important for optimizing microbial Cr(VI) remediation techniques.

In recent years, interest in the use of whole-genome analysis to study the microbial mechanisms of heavy metal reduction has increased. Whole-genome sequencing and analysis can provide valuable insights into the genetic basis of heavy metal reduction mechanisms in microorganisms [5]. By sequencing and analyzing the entire genome of a metal-reducing microorganism, researchers can identify the genes and pathways involved in heavy metal reduction and gain a deeper understanding of the molecular mechanisms underlying this process. Huang *et al*. reported that *Exiguobacterium* sp. PY14 contained the gene *chrR*, which coded for chromate reductase and might be a key gene in the metabolism of Cr(VI) through genome sequencing analysis [6]. Wang *et al*. analyzed the omics data of *Alicycliphilus denitrificans* Ylb10 and reported that *CysJ*, *TsdA*, *NrfA*, *NorB*, and *ChrR* genes played important roles in the reduction of Cr(VI) [7]. Sedláček *et al*. reported that *Paracoccus denitrificans* contained the gene *ferB*, which could encode ferric reductase B with a structure similar to that of chromate reductase [8]. These genes play crucial roles in the detoxification and sequestration of heavy metals, thereby reducing their toxicity to the environment. Therefore, the study of microbial Cr(VI) reduction mechanisms *via* whole-genome analysis holds great promise for advancing understanding of how microorganisms interact with Cr(VI) in the environment and may ultimately lead to the development of novel strategies for mitigating the environmental impact of Cr(VI) pollution. *Klebsiella* has attracted much attention because of its ability to reduce Cr(VI). Hossan *et al*. successfully isolated chromate-resistant bacteria from tannery wastewater and identified them as *Klebsiella* species [9]. Yu *et al*. prepared *Klebsiella variicola* H12-CMC-FeS@biochar, which was based on the Cr(VI) reduction capacity of *Klebsiella variicola* H12 and could efficiently remove Cr(VI) from sewage [10]. Through transcriptomic analysis, Lara *et al*. elucidated the mechanism of the chromium stress response in the *Klebsiella* strain AqSCr. However, the key genes involved in Cr(VI) reduction in *Klebsiella* still need to be further explored [11].

Klebsiella spp. Shm-1 demonstrates the ability to reduce Cr(VI). However, the key genes and mechanisms of Cr(VI) reduction need to be further elucidated. This study used whole-genome sequencing technology to identify the Cr(VI) resistance gene(s) of *Klebsiella* spp. Shm-1 and investigate Cr(VI) reduction mechanism. The study would provide a theoretical reference for optimizing the Cr(VI) reduction ability of chromium-resistant microorganisms at the genetic level. In addition, the findings could have important implications for the development of novel biotechnological strategies for chromium detoxification and environmental remediation.

Materials and methods

Medium preparation

The growth medium was prepared by mixing 0.6 g of KCl, 1.5 g of NH_4Cl, 0.3 g of KH_2PO_4, 0.1 g of $MgCl_2$, 0.1 g of $CaCl_2$, 10 mL of trace mineral solution, and 10 mL of vitamin solution in 1 L of Luria–Bertani (LB) medium made by mixing 1 g of tryptone, 0.5 g of yeast extract, and 1 g of NaCl in 100 mL of distill water [12]. The trace mineral solution contained 0.1 g of $MnCl_2{\cdot}4H_2O$, 0.5 g of

$FeSO_4 \cdot 7H_2O$, 0.17 g of $CoCl_2 \cdot 6H_2O$, 0.1 g of $ZnCl_2$, 0.05 g of $NiCl_2$, 1.5 g of $N(CH_2COOH)_3$, 0.03 g of $CuSO_4 \cdot 5H_2O$, 0.1 g of Na_2SeO_4, 0.005 g of H_3PO_3, 0.09 g of Na_2MoO_4, and 0.02 g of $Na_2WO_4 \cdot 2H_2O$. The vitamin solution contained 0.002 g of folic acid, 0.01 g of pyridoxine HCl, 0.005 g of riboflavin, 0.002 g of biotin, 0.005 g of thiamine, 0.005 g of nicotinic acid, 0.005 g of pantothenic acid, 0.0001 g of vitamin B12, 0.005 g of P-aminobenzoic acid, and 0.005 g of thioctic acid. All reagents were purchased from Sinopharm Chemical Reagent Co., Shanghai, China. All media were adjusted to pH 7.2 prior to sterilization,

Isolation and identification of single purified bacterial species

5 mL of water from Lianjiang River (33.00 N, 114.00E) (Zhumadian, Henan, China) was added to 40 mL of growth medium supplemented with 0.2 mM Cr(VI) ($K_2Cr_2O_7$), and incubated in MaxQ 8000 shaking incubator (Thermo Fisher Scientific, Waltham, MA, USA) at 37°C for 2 days to screen for chromium-tolerant bacteria. After tenfold gradient dilution, the agar plate was used to isolate pure cultures. The single purified species were separated by agar plate scribing more than five times until the colony morphology and shape were identical. A total of 1.64 g/L acetate was used as the carbon source. The culture growth was conducted at 30 ± 1°C. Polymerase chain reaction (PCR) analysis was then conducted using the universal primers 27F (5'-AGA GTT TGA TCA TGG CTC AG-3') and 1492R (5'-TAC GAC TTA ACC CCA ATC GC-3'), which were complementary to the conserved regions of the bacterial 16S rRNA gene [3]. The universal primers were designed and synthesized by Sangon Biotech, Shanghai, China. The PCR amplification was performed in a total volume of 25 µL reaction mixture containing 1 µL of DNA template, 12.5 µL of Taq PCR Master Mix (Sangon Biotech, Shanghai, China), 1 µL of each primer, and 9.5 µL of distill water. The PCR reaction was carried out in MyCycler Thermal Cycler (Bio-Rad, Hercules, CA, USA) with 94°C for 5 min followed by 30 cycles of 94°C for 30 s, 55°C for 45 s, 72°C for 90 s, and a final extension at 72°C for 10 min. The PCR products were then stored at -4°C before sending out to Sangon Biotech, Shanghai, China for sequencing. The DNA sequences were compared with available sequences in the GenBank database of the National Center for Biotechnology Information (NCBI) (https://www.ncbi.nlm.nih.gov/) *via* Basic Local Alignment Search Tool (Blastn) software. The sequences with the highest hits on the 16S rRNA gene were extracted to preliminarily identify the species of bacteria.

Determination of the Cr(VI) reduction capacity of *Klebsiella* spp. Shm-1

Identified *Klebsiella* spp. Shm-1 was inoculated in LB media supplemented with Cr(VI) at 30°C for 96 h, while blank LB media supplemented with Cr(VI) was used as the control. The cultural media were collected and the diphenylcarbonic dihydrazine spectrophotometric method was used to determine the residual amount of Cr(VI) in the medium [3]. The absorbances at 540 nm were determined using Multiskan SkyHigh spectrophotometer (Thermo Fisher Scientific, Waltham, MA, USA). A linear relationship (R^2 = 0.9999) was explored between the Cr(VI) concentrations of 0, 0.4, 0.8, 1.2, 1.6, and 20 µg/mL and solution absorbances.

Whole-genome sequencing and analysis

Bacterial genomic DNA from pure cultures was extracted using Quick-DNA Miniprep Plus Kit (Zymo Research, Irvine, CA, USA) according to the manufacturer's instructions, followed by agarose gel electrophoresis to assess the purity and integrity of the DNA, and quantification using Qubit 4.0 Fluorometer (Thermo Fisher Scientific, Waltham, MA, USA). The sequencing library was then constructed by Novogene Bioinformatics Technology Co., Ltd. (Beijing, China). The whole genome of *Klebsiella* spp. Shm-1 was sequenced through the Nanopore PromethION platform and Illumina NovaSeq PE150 at the Novogene Bioinformatics Technology Co., Ltd. (Beijing, China). GeneMarkS (http://topaz.gatech.edu/GeneMark/) (version 4.17) was used to predict the coding genes of the sequenced genome, Five databases including Gene Ontology (GO), Kyoto Encyclopedia of Genes and Genomes (KEGG), Clusters of Orthologous Groups (COG),

Nonredundant Protein Database (NR), and Transporter Classification Database (TCDB) were employed to predict gene functions. A whole-genome BLAST search with *E* value less than 1e-5, minimal alignment length percentage greater than 40% was performed against the above databases. Carbohydrate-active enzymes were predicted using the Carbohydrate-Active enZYmes Database.

Results and discussion

Isolation and Cr(VI) reducing capacity determination of *Klebsiella* spp. Shm-1

Klebsiella spp. Shm-1 was isolated from polluted river water. A comparison with sequences in GenBank suggested that *Klebsiella* spp. Shm-1 was related to the *Klebsiella pneumoniae* strain HCD13-4 with a similarity of 100%. The reduction performance of Cr(VI) by *Klebsiella* spp. Shm-1 showed that, when the LB medium was inoculated with *Klebsiella* spp. Shm-1, the Cr(VI) concentration decreased from 0.13 ± 0.0068 mM to 0.023 ± 0.011 mM after 96 hours. Moreover, when the LB medium was not inoculated with *Klebsiella* spp. Shm-1, the Cr(VI) concentration essentially did not decrease after 96 hours (Figure 1). These results indicated that *Klebsiella* spp. Shm-1 has the ability to reduce Cr(VI) and were the same as those previously reports [10, 11].

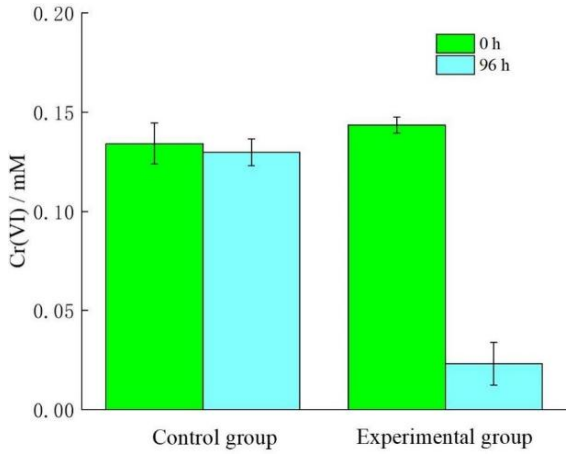

Figure 1. Cr(VI) reduction capacity of *Klebsiella* spp. Shm-1.

Whole-genome sequencing of *Klebsiella* spp. Shm-1

The full length of *Klebsiella* spp. Shm-1 genome was 5,430,044 bp with the GC content of 57.62% and 5,187 coding genes. According to the NR analysis, 4,466 genes of *Klebsiella* spp. Shm-1 belonged to the genus *Klebsiella*, accounting for 86.10% of all genes (Figure 2). The results confirmed that *Klebsiella* spp. Shm-1 belonged to the genus *Klebsiella*. The whole-genome map of the *Klebsiella* spp. Shm-1 gene was then drawn in Figure 3. The whole-genome DNA sequence of *Klebsiella* spp. Shm-1 was submitted to NCBI with the BioSample accession number of SAMN42391532.

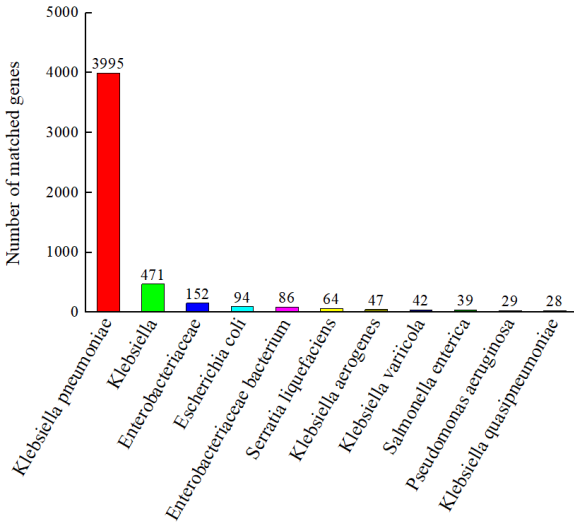

Figure 2. NR database annotation of *Klebsiella* spp. Shm-1.

Cr(VI) reduction mechanism of *Klebsiella* spp. Shm-1

The currently known genes that may be involved in extracellular and intracellular Cr(VI) reduction and transfer were analyzed. The results showed that CrO_4^{2-} could enter biological cells through phosphate transport channels because it could form stable binding bonds with inorganic phosphate transport proteins through chemical compatibility [13]. Moreover, CrO_4^{2-}, MoO_4^{2-}, and SO_4^{2-} have similar structures, and CrO_4^{2-} competes with MoO_4^{2-} and SO_4^{2-} for transporting carriers to enter cells [14]. The genes *cysA* (Shm-

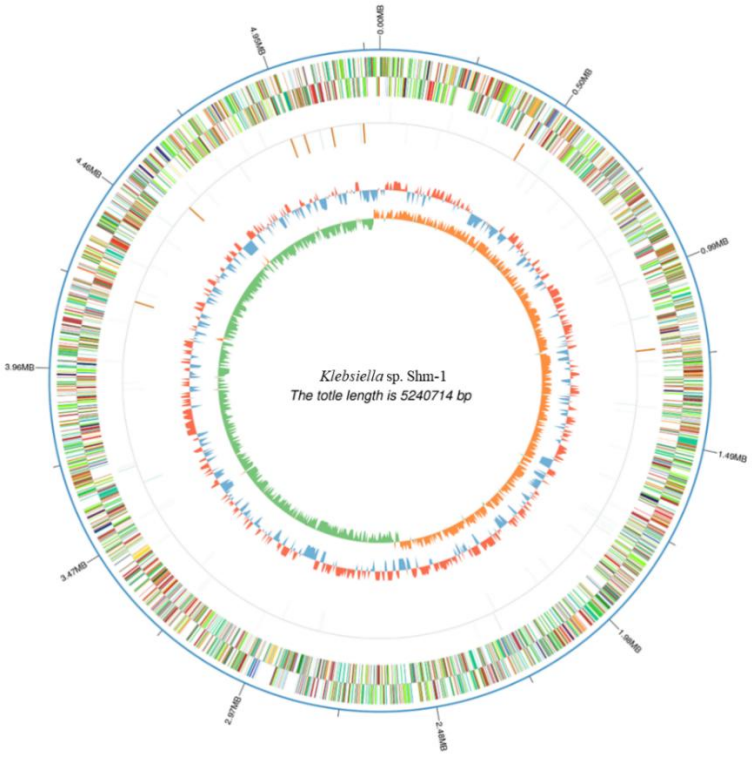

Figure 3. Whole-genome map of *Klebsiella* spp. Shm-1.

Table 1. Genes involved in Cr(VI) reduction in *Klebsiella* spp. Shm-1.

Gene Id	Gene name	Gene production
Shm-1_GM002278	*chrA*	chromate transporter
Shm-1_GM005172, Shm-1_GM005173, Shm-1_GM005171, Shm-1_GM005170, Shm-1_GM005174	*pstABCS*, *phoU*	phosphate transport system protein
Shm-1_GM000302, Shm-1_GM001521, Shm-1_GM001522, Shm-1_GM001523	*cysAPUW*	sulfate transport system protein
Shm-1_GM002197, Shm-1_GM003653, Shm-1_GM003652, Shm-1_GM003656, Shm-1_GM003657	*modABCEF*	molybdate transport system protein
Shm-1_GM005180	*chrR*	chromate reductase
Shm-1_GM002247, Shm-1_GM002248, Shm-1_GM002249, Shm-1_GM002250	*ccmEFGH*	cytochrome c-type biogenesis protein
Shm-1_GM004046, Shm-1_GM004047, Shm-1_GM004048, Shm-1_GM004049	*cyoABCD*	cytochrome o ubiquinol oxidase
Shm-1_GM003679, Shm-1_GM003678, Shm-1_GM003677	*cydABX*	cytochrome bd-I ubiquinol oxidase
Shm-1_GM005163, Shm-1_GM005159, Shm-1_GM005166, Shm-1_GM005165, Shm-1_GM005160, Shm-1_GM005161, Shm-1_GM005164, Shm-1_GM005162	*atpABCDEFGH*	F-type H^+-transporting ATPase
Shm-1_GM000697	*yrbG*	cation:H^+ antiporter
Shm-1_GM000936	*galP*	galactose:H^+ symporter
Shm-1_GM001055	*araE*	arabinose:H^+ symporter
Shm-1_GM002042	*citA*	citrate/tricarballylate:H^+ symporter
Shm-1_GM002504	*ydjE*	putative metabolite:H^+ symporter
Shm-1_GM004425, Shm-1_GM002008	*nhaAB*	Na^+:H^+ antiporter

1_GM000302), *cysP* (Shm-1_GM001521), *cysU* (Shm-1_GM001522), and *cysW* (Shm-1_GM001523) encoded sulfate transport system proteins were detected in *Klebsiella* spp. Shm-1. The genes *pstA* (Shm-1_GM005172), *pstB* (Shm-1_GM005173), *pstC* (Shm-1_GM005171), *pstS* (Shm-1_GM005170), and *phoU* (Shm-1_GM005174) encoded phosphate transport system proteins were also detected in *Klebsiella* spp. Shm-1. In addition, *Klebsiella* spp. Shm-1 had

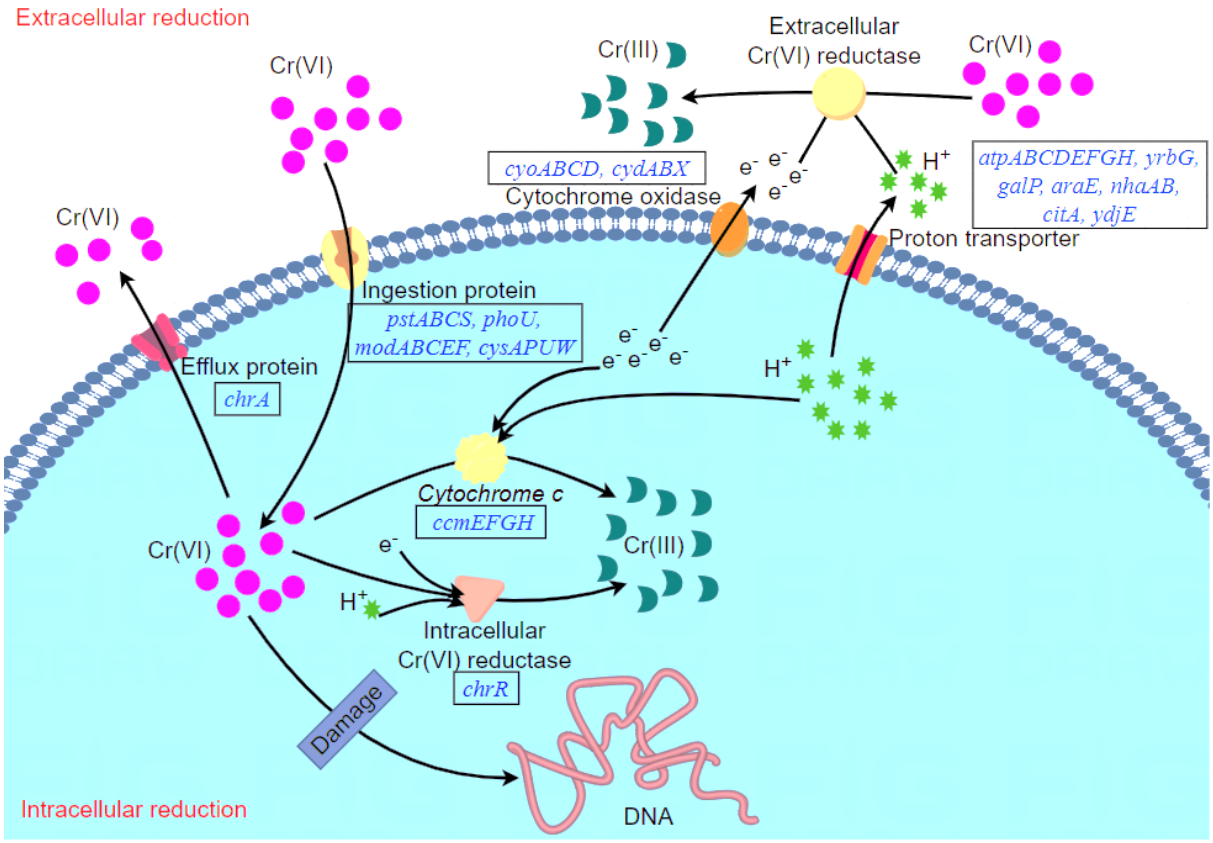

Figure 4. Schematic diagram of the Cr(VI) reduction mechanism of *Klebsiella* spp. Shm-1. The blue font represented the gene encoding the relevant protein.

genes such as *modA* (Shm-1_GM002197), *modB* (Shm-1_GM003653), *modC* (Shm-1_GM003652), *modE* (Shm-1_GM003656), and *modF* (Shm-1_GM003657), which encoded molybdate transport system proteins (Table 1). These genes might play important roles in the intake of Cr(VI) by *Klebsiella* spp. Shm-1. When Cr(VI) enters a cell, it can cause DNA damage [15], and the active expulsion of Cr(VI) is one of the important methods by which microorganisms resist chromium toxicity [16]. The gene *chrA* (Shm-1_GM002278) of *Klebsiella* spp. Shm-1 encoded a chromate transporter, which was an efflux transporter that could expel hexavalent chromium from the cell [17]. In addition, the extracellular reduction and intracellular reduction of Cr(VI) constitute another important way for microorganisms to resist chromium toxicity [18]. For intracellular Cr(VI) reduction, a series of soluble reductase-mediated enzymatic reductions are important pathways for microbial intracellular resistance to Cr(VI) [19]. The gene *chrR* (Shm-1_GM005180) of *Klebsiella* spp. Shm-1 encoded an intracellular chromate reductase, while the genes *ccmE* (Shm-1_GM002247), *ccmF* (Shm-1_GM002248), *ccmG* (Shm-1_GM002249), and *ccmH* (Shm-1_GM002250) of *Klebsiella* spp. Shm-1 encoded cytochrome C-type biogenesis proteins (Table 1). Chromate reductase and cytochrome C can transfer electrons to Cr(VI) and reduce it to Cr(III) [20, 21]. Therefore, the genes *chrR*, *ccmE*, *ccmF*, *ccmG*, and *ccmH* might be the key regulatory genes for intracellular Cr(VI) reduction. For extracellular Cr(VI) reduction, microorganisms can secrete protons through the cell membrane surface to facilitate the reduction of Cr(VI) to Cr(III) in the extracellular environment [22]. The H^+ produced in the cell is transferred to the outside of the cell through channels such as the proton pump on the cell

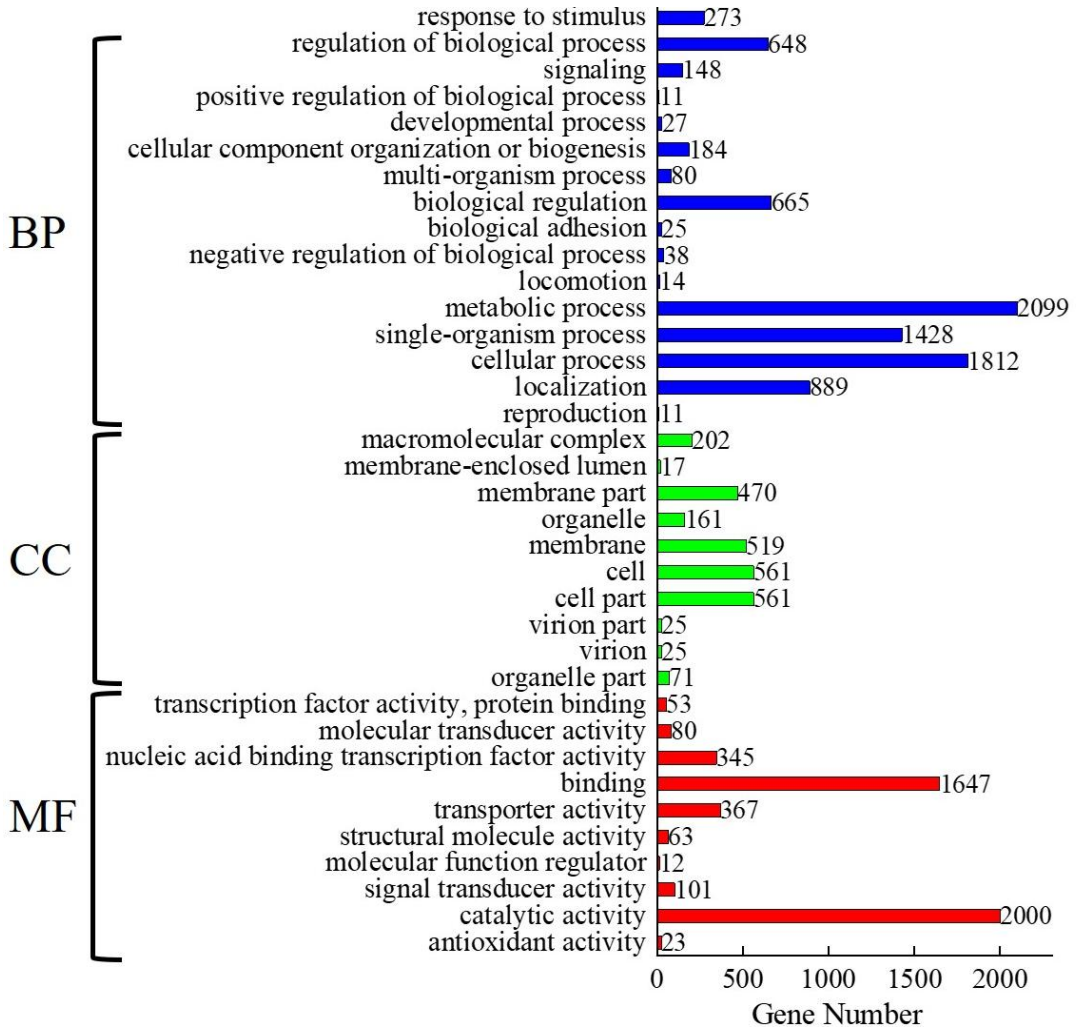

Figure 5. GO functional classification of *Klebsiella* spp. Shm-1 genes. BP: biological processes. CC: cellular components. MF: molecular functions.

membrane [22]. The genes *atpA* (Shm-1_GM005163), *atpB* (Shm-1_GM005159), *atpC* (Shm-1_GM005166), *atpD* (Shm-1_GM005165), *atpE* (Shm-1_GM005160), *atpF* (Shm-1_GM005161), *atpG* (Shm-1_GM005164), and *atpH* (Shm-1_GM005162) of *Klebsiella* spp. Shm-1 encoded F-type H^+-transporting ATPases. The genes *yrbG* (Shm-1_GM000697), *galP* (Shm-1_GM000936), *araE* (Shm-1_GM001055), *nhaAB* (Shm-1_GM004425, Shm-1_GM002008), *citA* (Shm-1_GM002042), and *ydjE* (Shm-1_GM002504) encoded cation:H^+ antiporters, galactose:H^+ symporters, arabinose:H^+ symporters, Na^+:H^+ antiporters, citrate/tricarballylate:H^+ symporters, and putative metabolite:H^+ symporters, respectively (Table 1). These genes might be involved in intracellular and extracellular proton transport, providing the necessary conditions for extracellular Cr(VI) reduction. In addition, electrons are important participants in the microbial reduction of Cr(VI) [23]. The genes *cyoA* (Shm-1_GM004046), *cyoB* (Shm-1_GM004047), *cyoC* (Shm-1_GM004048), and *cyoD* (Shm-1_GM004049) of *Klebsiella* spp. Shm-1 encoded cytochrome or ubiquinol oxidase, while the genes *cydA* (Shm-1_GM003679), *cydB* (Shm-1_GM003678), and *cydX* (Shm-1_GM003677) encoded cytochrome bd-I ubiquinol oxidase (Table 1). These genes might play important roles in the extracellular export of electrons. Based on these results, a possible Cr(VI) reduction

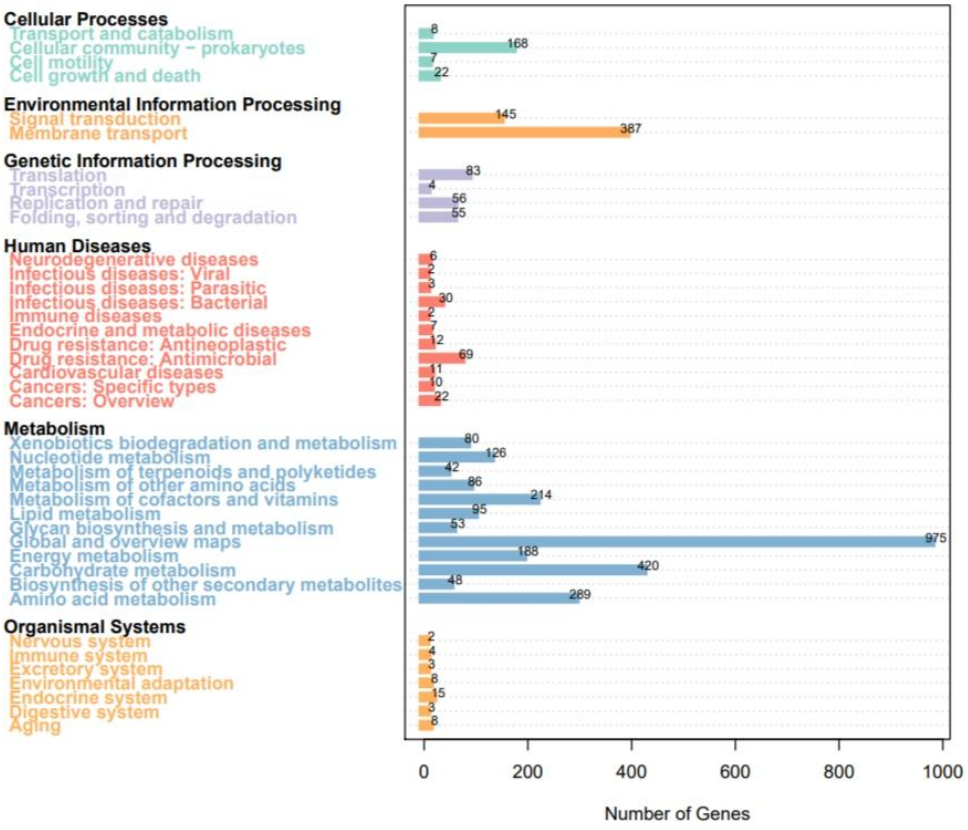

Figure 6. KEGG metabolic pathway annotation of *Klebsiella* spp. Shm-1 genes.

mechanism diagram of *Klebsiella* spp. Shm-1 was constructed (Figure 4).

GO database annotation

The GO annotation results showed that *Klebsiella* spp. Shm-1 had a total of 3,762 genes with GO annotation functions, which were classified into biological process (BP), molecular function (MF), and cellular component (CC) categories. In BP, gene functions were involved mainly in localization (889 genes), cellular process (1,812 genes), single-organism process (1,428 genes), metabolic process (2,099 genes), biological regulation (665 genes), cellular component organization or biogenesis (184 genes), signaling (148 genes), regulation of biological process (648 genes), and response to stimulus (273 genes). In MF, gene functions were involved mainly in catalytic activity (2,000 genes), signal transducer activity (101 genes), transporter activity (367 genes), binding (1,647 genes), and nucleic acid binding transcription factor activity (345 genes). In CC, gene functions were mainly involved in cell parts (561 genes), membranes (519 genes), organelles (161 genes), membrane parts (470 genes), and macromolecular complexes (202 genes) (Figure 5). Furthermore, the genes that might be involved in Cr(VI) reduction were analyzed. The results showed that these genes were involved mainly in cell transmembrane transport, oxidoreductase activity, membranes, hydrogen ion transmembrane transporter activity, and oxidation–reduction processes. The results also revealed that these genes were important for the resistance of *Klebsiella* spp. Shm-1 to Cr(VI).

KEGG database annotation

KEGG annotated a total of 5,088 genes, which were divided into 6 categories (Figure 6), including cellular processes (195 genes), environmental information processing (532

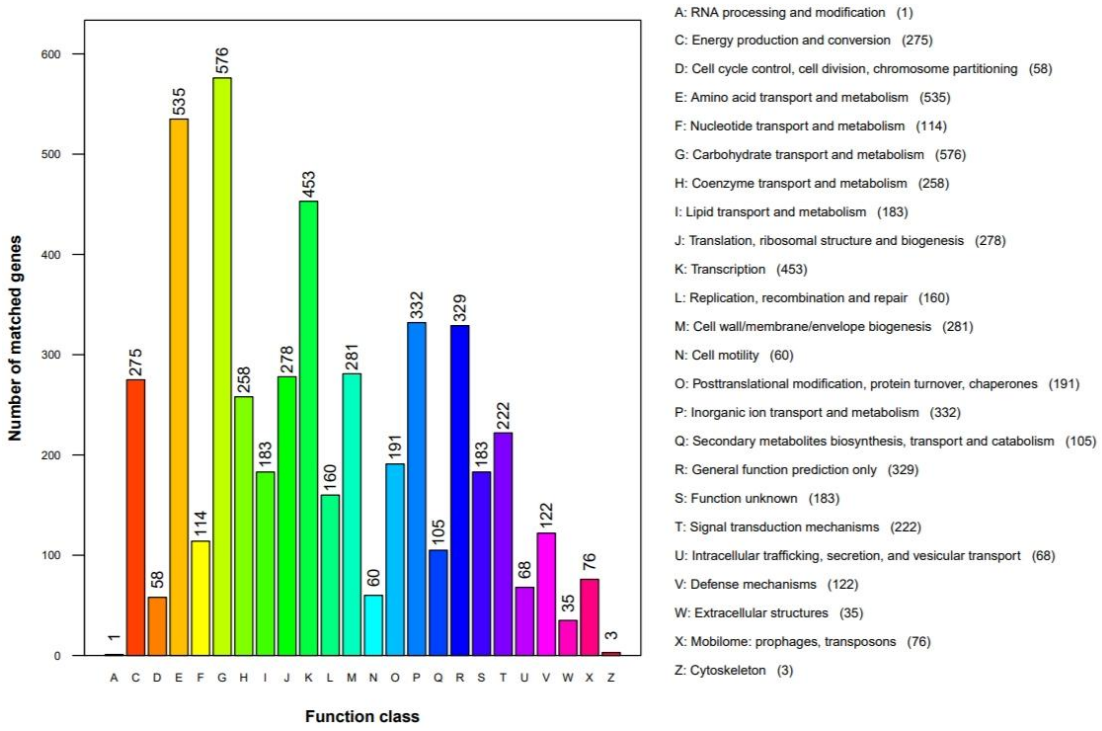

Figure 7. COG functional annotation of *Klebsiella* spp. Shm-1 genes.

genes), genetic information processing (198 genes), human diseases (174 genes), metabolism (2,616 genes), and organismal systems (43 genes). Among these genes, the most annotated genes were associated with the metabolism pathway, followed by the environmental information processing pathway. In metabolism, genes' functions were mainly involved in nucleotide metabolism (126 genes), metabolism of cofactors and vitamins (214 genes), global and overview maps (975 genes), energy metabolism (188 genes), carbohydrate metabolism (420 genes), and amino acid metabolism (269 genes). In environmental information processing, genes were involved mainly in signal transduction (145 genes) and membrane transport (387 genes). Among the cellular process terms, there were 168 genes involved in the cellular community-prokaryotes.

COG database annotations

COG is a database used for direct homologous classification of proteins. By comparing the amino acid sequences of sequenced genes with those of the eggNOG database, the functions of these proteins can be predicted, and statistical functional classification can be conducted [24]. A total of 4,355 genes from *Klebsiella* spp. Shm-1 strain were annotated with COG annotation, accounting for 83.96% of the total number of genes (Figure 7). The number of genes with unknown functions was the highest with a total of 1,120 genes, accounting for 16.04% of the annotated genes. The functional classification of COGs related to heavy metal reduction was analyzed, and the results revealed that energy production and conversion, amino acid transport and metabolism, nucleotide transport and metabolism, coenzyme transport and metabolism, and inorganic ion transport and metabolism accounted for 275, 535, 114, 258, and 332 genes, respectively, representing 5.30%, 10.31%, 2.20%, 4.97%, and 6.40% of the total number of annotated genes.

Transporter classification database annotation

Microorganisms can counteract chromium toxicity through the active excretion of Cr(VI) and

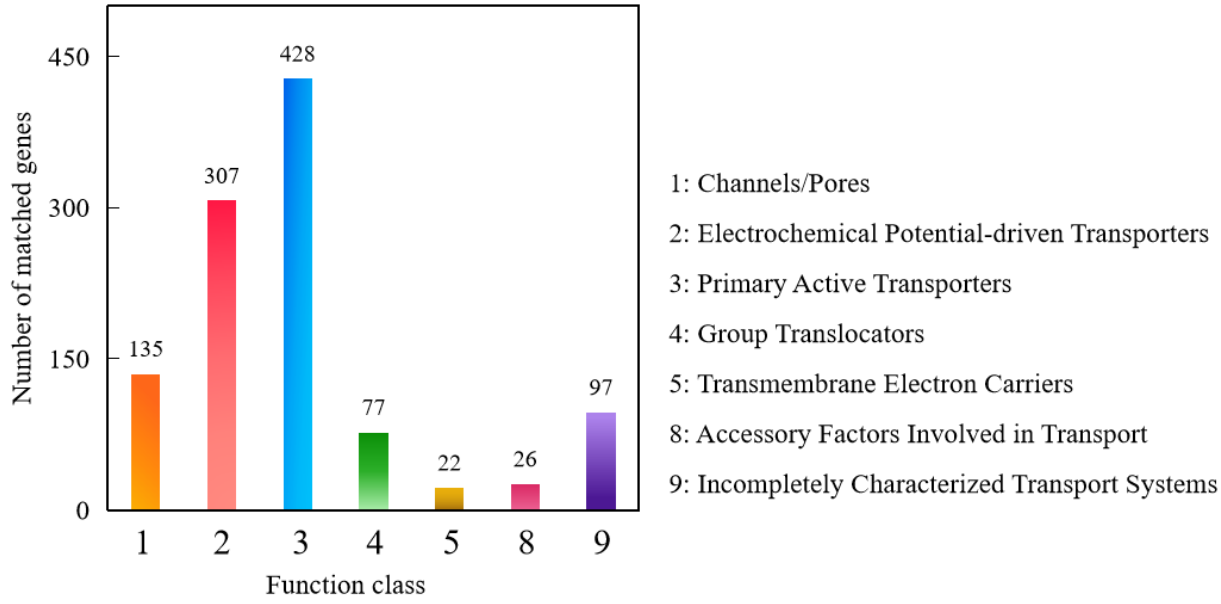

Figure 8. TCDB functional annotation of *Klebsiella* spp. Shm-1 genes.

extracellular reductase with membrane transport proteins playing a pivotal role in this process [25]. The Transporter Classification Database (TCDB) was utilized to analyze the membrane transport protein classification system of *Klebsiella* spp. Shm-1. The results showed that a total of 1,092 genes from the *Klebsiella* spp. Shm-1 strain were annotated with TCDB annotation, accounting for 21.05% of the total number of genes. These functional categories of TCDB annotation included channels/pores (135 genes), electrochemical potential-driven transporters (307 genes), primary active transporters (428 genes), group translocators (77 genes), transmembrane electron carriers (22 genes), accessory factors involved in transport (26 genes), and incompletely characterized transport systems (97 genes) (Figure 8). The results indicated that *Klebsiella* spp. Shm-1 had a high diversity of primary active transporters, electrochemical potential-driven transporters, and channels/pores in TCDB, which provided great potential for Cr(VI) transport and reduction.

Availability of data

The whole genome DNA sequence of *Klebsiella* spp. Shm-1 was submitted to NCBI with the BioSample accession No. SAMN42391532.

Acknowledgements

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