The *Enterobacter* sp. YSU plasmid, pOR1, has many properties of IncHI2 Plasmids

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Bobbi Hope Schragal

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Bobbi Hope Schragal

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Signature:

Bobbi Hope Schragal, Student Date

Approvals:

Dr. Jonathan J. Caguiat, Thesis Advisor Date

Dr. David K. Asch, Committee Member Date

Dr. Xiangjia Min, Committee Member Date

Dr. Salvatore A. Sanders, Dean of Graduate Studies Date

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B. Schragal

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Abstract

Enterobacter sp. YSU was isolated from East Fork Poplar Creek, a heavy metal contaminated stream in Oak Ridge, Tennessee. This strain is resistant to arsenic, mercury, tellurite, zinc, cadmium, silver, copper and selenite. The genome of this strain was recently sequenced. The Basic Local Alignment Search Tool (BLAST) revealed that most of the contigs were related to chromosomal DNA sequences. However, sixteen contigs matched to plasmid sequences, which ranged from 1,000 base pairs to over 90,000 base pairs and may belong to a plasmid, pOR1, that is almost 300 kb in size. Further analysis showed that pOR1 may contain an IncHI2 replication origin, mobilization genes and operons for mercury-, tellurite- and arsenite-resistance. To verify these hypotheses, *Enterobacter* sp. YSU was conjugated with *E. coli* to produce *E. coli* transconjugants that were resistant to mercury, tellurite and arsenite. These results suggest that the contigs that contain these resistances, contig 23, 24 and 25 are found in pOR1 because they transfer from *Enterobacter* sp. YSU to *E. coli* together. Lastly, based off PCR results, three contigs were predicted to be next to each other; 26&33, 23&15, and 25&37. Future work will include running more PCR reactions to link all the contigs together and to obtain a complete plasmid sequence. In addition, the metal resistance genes will be cloned and tested for resistances.

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Chapter I: Introduction

1. Oak Ridge Y-12 Plant

The Y-12 Plant in Oak Ridge, Tennessee contaminated East Fork Poplar Creek (Polar Creek) and the surrounding area with heavy metals. During WWII it processed uranium to make nuclear bombs, while during the Cold War it processed lithium to make hydrogen bombs. Three nearby S-3 ponds stored waste from the plant. Because they were constructed without inner linings, metal waste seeped into the ground and water. Tons of mercury used to process lithium was also spilled into Poplar Creek (Adams, 2000). *Enterobacter* sp. YSU and *Stenotrophomonas matlophilia* Oak Ridge strain 02 (*S. maltophilia* 02) were isolated from this heavy-metal contaminated site (Holmes, 2009).

2. *Enterobacter* sp. YSU

The metal-resistances of *S. maltophilia* 02 and *Enterobacter* sp. YSU were examined in comparison to the control, *Escherichia coli* (*E. coli*) strain HB101, to understand the levels of resistance between bacteria that were and were not from metal-contaminated environments. This evaluation provided a baseline that could be used to further understand levels of resistance of other bacterial isolates from Poplar Creek. *S. maltophilia* 02 is generally more metal resistant than *Enterobacter* sp. YSU. *S. maltophilia* 02 is resistant to Hg(II), Cd(II), Zn(II), Cu(II), Au(III), Cr(VI), As(III), and Se(IV). In comparison to *E. coli* strain HB101, *Enterobacter* sp. YSU was resistant to Hg(II), Cd(II), Zn(II), Au(III), Ag(I), As(III), and Se(IV) (Holmes, 2009). Novel metal resistance and the detection of gene transfer within a bacterial population may also be

possible with the findings from this study.

3. Sequencing of *Enterobacter* sp. YSU

When the genomic sequencing of *Enterobacter* sp. YSU was performed, 40 contigs were obtained. BLAST analysis suggested that many of them contained plasmid sequences (Table 2). The sequencing technique that was used was not designed for plasmids but it showed that the bacterium, *Enterobacter* sp. YSU, probably contains a plasmid that may be as large as 300 kb in size.

BLAST Basic Local Alignment Search Tool

Basic Local Alignment Search Tool (BLAST) is an algorithm that researchers use for sequence alignment analysis (Altschul, 1990). BLAST was used to identify putative metal-resistance genes in the plasmid. To identify a nucleotide or protein sequence, you input the DNA sequence into the Basic Local Alignment Search Tool (BLAST) and it calculates the statistical significance (McGinnis, 2004; Mount, 2007).

Properties of IncHI2 plasmids

According to Whelan (1997), plasmid R478 is a 272 kb, self-transmissible plasmid of the incompatibility subgroup of IncHI2. IncHI2 mediates resistance to kanamycin, chloramphenicol, and ampicillin (Whelan, 1997).

The main defining characteristic of plasmids from the IncHI2 group is their ability to transfer by conjugation at temperatures below 30°C. This allows the spread of multi-

resistance under environmental conditions (Rodriguez-Lemoine et al., 1975; Maher & Colleran, 1987).

Replication Origin of IncHI2 plasmids

According to Page (2001), there are two iteron-controlled auto replicative regions present in IncHI2 plasmids, RepHI2A and RepHI1A$_{(R478)}$. RepHI2A is found in the plasmids of the IncHI2 subgroup and contain a very large number of iteron sequences. These sequences are located downstream of the replication initiator gene. It was previously reported that the IncHI1 subgroup plasmid R27's RepHI1A replicon is similar to the nucleotide sequence of the replication initiator gene and of the iterons found in RepHI1A$_{(R478)}$. The incompatibility between R478 and the plasmids of the IncHI1 subgroup is based upon the presence of RepHI1A$_{(R478)}$ on R478 (Page, 2001).

Mercury Resistance Operon in IncHI2 plasmids

Mer operon genes encode resistance to inorganic mercury and are found in bacteria that confer resistance to mercury. There are many mercury resistance genes that are found in chromosomes, plasmids, integrons and transposons including *merR*, *merT*, *merP*, *merC*, *merA*, *merB*, *merD*, *merE*, *merG* and *merF* (Essa, 2012).

The *mer*R gene regulates the expression of the other genes (Chang, 2015), is always bound to the *mer* operator, and is transcribed in the opposite direction of *merTPCAD.* When Hg^{2+} is absent, MerR represses the expression of *merTPCADE* and in the presence of Hg^{2+}, it activates the expression of the genes. Hg^{2+} is transported into the

cell by MerTPC (Park, 1992). Hg^{2+} is reduced by MerA into harmless elemental mercury (Sotero-Martins, 2008 and Chang, 2015). The *merB* gene, sometimes located between *merA* and *merD,* codes for organomercurial lyase that cleaves the carbon mercury (C-Hg) bond from methylmercury and phenylmercury to yield Hg^{2+}, which is detoxified by *mer*A (Griffin, 1987). The genes, *merE* and *merF,* encode proteins involved in mercury transport (Sone, 2013). When Hg^{2+} is removed from the cell's environment, MerD restores the operon to the repressed state (Summers, 2004). The MerG protein makes the cell membrane impervious to phenylmercury.

Plasmid-mediated Resistance to Tellurite in IncHI2 plasmids

In the *E. coli* chromosome, there are clusters of replication termination sequences which are referred to as Ter sequences. The function of these sequences is to trap the first arriving replication fork in the terminus region in order to prevent over replication. The *terZ*, *A*, *B*, and *C* genes of pKFW4A resulted in the loss of the filamentation phenotype. The TerZ resistance protein seems to contribute to the tellurium resistance mechanism. It is also involved in phage inhibition (Phi) and colicin resistance (PacB). TerA and TerB's functions are not yet known but they are known to be tellurium resistant proteins. TerC is involved in the resistance to tellurium and may be involved in efflux of tellurium ions (Whelan, 1997).

Function of Tellurite Resistance Proteins

Walter and Taylor (1992) showed that *E. coli* takes up tellurite by a phosphate transport system and reduces uptake to provide a low level of resistance. There are two types of tellurite resistances: IncHIII and IncP. Bacteria with the plasmid, pDT1558, carry the IncP tellurite resistant genes. Bacteria with the RP4, or pDT1364 carry the IncHIII tellurite resistant genes. Due to the *E. coli* bacteria carrying either RP4 or pDT1558, the toxicity was only reduced by one half. On the other hand, bacteria containing pDT1364 repeatedly reduced the toxicity levels of the tellurite broth by 128-fold. These results suggest that the IncHIII tellurite resistant determinant on pDT1364 encodes a tellurite detoxification system, whereas the IncP tellurite resistant determinant on pDT1558 may encode a different mechanism of resistance such as efflux or decreased uptake (Walter, 1992).

It is still not understood why gram-negative bacteria developed two different mechanisms of tellurite resistance (Walter, 1992). It is possible that tellurite resistance has a selective advantage to bacteria growing either in the environment or the human body. For the maintenance and spread of antibiotic resistances in bacteria, it is important to understand the placement of tellurite resistant determinants on plasmids. By understanding the placement, it may lead to understanding the maintenance and spread of the antibiotic resistances in bacteria. Tellurite resistant determinants may also have resistance to other metals that are not known of yet. It has been found that tellurite resistance has been linked with other phenotypes. These may also include resistance to bacteriophages and colicins.

Arsenite Resistance in IncHI2 plasmids

According to Whelan (1997), plasmid R478 is a 272 kb, self-transmissible plasmid of the incompatibility subgroup IncH12. IncH12 mediates resistance to kanamycin, chloramphenicol, tetracycline, mercuric chloride, potassium tellurite (Te^r), arsenic compounds along with some resistance to bacteriophages (Phi) and to pore-forming colicins (PacB) (Whelan, 1997).

There are many genes found in arsenic resistance operons that can be arranged in different combinations (Ben, 2018). *Staphylococcus aureus* pI258 was found to be the first plasmid to confer resistance to antibiotics, arsenate, arsenite and other heavy metals (Novick and Roth, 1968). The second plasmid found to contain an arsenic resistance factor was a transmissible plasmid identified in *E. coli*, R773 (Hedges and Baumberg, 1973). According to Ben (2018), the *ars*R gene encodes ArsR, a trans-acting transcriptional repressor protein that allows transcription of the operon. The ArsA protein is an ATPase that interacts with ArsB to form an arsenite efflux pump energized by ATP hydrolysis. The ArsA ATPase may associate with different membrane proteins to form primary arsenite transporters (Castillo and Saier, 2010). ArsC proteins from plasmids pI258 and R773 are arsenate reductase enzymes (Ben, 2018). Prior to extrusion of the latter oxyanion, pI258 and R773 can reduce arsenate to arsenite (Ben, 2018). The ArsC enzymes from the R773 plasmid uses glutathione and glutaredoxin as electron sources (Ben, 2018). The ArsC enzymes from the pI258 plasmid uses thioredoxin as an electron source (Ben, 2018). ArsD binds arsenite and transfers it to the ArsA ATPase prior to the oxyanion extrusion by the ArsB pump (Ben, 2018).

Silver Resistance in IncHI2 plasmids

According to Fang, L., Li, X., Li, L. *et al.* (2016), IncH12 plasmids have many metal tolerance genes. These metals consist of mercury, tellurite, arsenic, and silver. The plasmids from this study that carried silver resistances were found in *Escherichia coli* isolates under one of the most common incompatibility groups IncHI2. According to Kremer (2012), they discovered an IncHI2 plasmid in *Enterobacter cloacae* that encoded a silver resistance determinant. The *sil* operons in this plasmid contain genes for the proteins, SilE, SilR, SilS, SilA, SilB, SilC and SilP. There were three clones that presented homology to plasmic genes but had unknown functions. One clone presented homology to the *silS* gene. In the resistance operons regulatory system, *silS* encodes a membrane sensor functioning. SilS senses the presence of silver and phosphorylates SilR. SilR activates the expression of the other silver resistance genes. SilE is a metal-binding protein, SilCBA and SilP are Ag(I) efflux pumps, (Kremer 2012). With further research, they found that the silver resistance determinant was highly conserved in *E. cloacae* and mediated resistance to up to 600 μM silver nitrate (Kremer, 2012).

Antibiotic Resistance Genes on IncHI2 Plasmids

IncHI2 was the major plasmid lineage that contributed to the spread of antibiotic resistance in *Salmonella. Q*uinolone resistance (PMQR)(*qnrA* and *aac(6')-Ib-cr*) genes and β-lactamase genes (bla_{OXA-1} and bla_{TEM-1}) were shown to be correlated with the molecular mechanism of transferable plasmid-mediated antibiotic resistance of IncH12 plasmids (Chen, 2016).

Chapter II: Objectives and Hypothesis

Objectives

There are about 300 kb of contig sequences that appear to be related to different IncHI2 plasmids. These are the following objectives:

1. To use BLAST to identify potential genes for replication, conjugation, transposition and metal/antibiotic resistances related to IncHI2 plasmids.
2. To transfer the large plasmid, pOR1, to *E. coli* by conjugation.
3. To test the *E. coli* transconjugants for mercury-, arsenite- and tellurite-resistances
4. To use Mauve software and BLAST analysis to predict the order and orientation of the contigs. This will allow us to use PCR, cloning and sequencing to confirm these predictions.

Hypothesis

I expect to find that the *Enterobacter sp.* YSU plasmid will have many of the properties of the IncHI2 plasmids. If the genes of an IncH12 plasmid are present, then it should be possible to transfer metal-resistance phenotypes from *Enterobacter* sp. YSU to *E. coli*.

Since the plasmid contigs contain DANN sequences homologous to mobilization, mercury-resistance, arsenite-resistance and tellurite-resistance operons, I expect that the plasmid will transfer itself to *E. coli* to produce transconjugants that will be resistant to these metals (Zhai, 2016).

Chapter III: Methods

Bacterial Strains

Enterobacter sp. YSU was isolated from East Fork Poplar Creek in Oak Ridge, TN. *E. coli* strain NEBα (*fhuA2 Δ(argF-lacZ)U169 phoA glnV44 Φ80 Δ(lacZ)M15 gyrA96 recA1 relA1 endA1 thi-1 hsdR17)* x pACYC177 and was used to test for conjugation.

Growth Medium

Genomic Grade ™ Culture Media LB (Lennox) Broth (20 g/L) composed of 10 g/l tryptone, 5 g/l yeast extract and 5 g/l sodium chloride was obtained and prepared according to the manufacturers instructions from Growcells.com (Irvine, CA. USA), a subsidiary of Molecular Biologicals International Inc. When needed, LB broth was supplied with 1.6% (w/v) bacteriological agar (Amresco, Solon, OH), 50 µg/ml kanamycin (Amresco Solon, OH) and 100 µg/ml ampicillin.

M-9 minimal medium was prepared by adding 0.8 g of bacteriological agar into 39 ml of deionized water and then autoclaved. Once finished in the autoclave, the following was added: 10 ml of 5X M-9 salts (239 mM disodium phosphate, 110 mM monopotassium phosphate, 43 mM sodium chloride, and 93 mM ammonium chloride), 0.5 ml of 0.2% glucose, 5 µl of 0.5% thiamine, 0.05 ml of 1 M $MgSO_4$.

SOC medium was composed of 2% tryptone, 0.5% yeast extract, 10 mM sodium chloride (NaCl), 2.5 mM potassium chloride (KCl), 10 mM magnesium chloride ($MgCl_2$), 20 mM magnesium sulfate ($MgSO_4$) and 20 mM glucose. The mixture was added together, and filter sterilized through a 0.2 µm filter and stored at room temperature.

Genomic Preparation

The Promega Wizard® Genomic DNA Purification Kit protocol (Madison, WI) was used in order to prepare and purify the genomic DNA. From an overnight culture, 1 ml was pipetted, centrifuged for 2 minutes at 14,000 × g, and the supernatant was poured off while the excess was pipetted out. The cells were lysed by adding 600 µl Nuclei Lysis solution and gently mixed by pipetting. The mixture was then incubated at 80°C for 5 minutes and cooled to room temperature. 3 µl of 4 mg/ml Rnase solution was added, mixed by inversion, incubated at 37°C for 15 minutes and cooled to room temperature. 200 µl of Protein Precipitation solution was mixed in by vortexing at high speed for 20 seconds, incubated on ice for 5 minutes and centrifuged at 14,000 × g for 3 minutes. The DNA was precipitated by transferring the supernatant to a clean 1.5 ml tube containing 600 µl room temperature isopropanol, thoroughly mixed by inversion, centrifuged for 2 minutes at 14,000 × g and then carefully pouring off the supernatant. In order to wash the DNA pellet, 600 µl of room temperature 70% ethanol was added and the tube was gently inverted several times. Then, the DNA pellet was centrifuged for 2 minutes at 14,000 × g. The ethanol was poured off, and the pellet was air dried for 10-15 minutes. The DNA pellet was rehydrated by adding 100 µl of DNA Rehydration Solution at 65°C for 1 hour. Periodically, the solution was mixed by gently flicking the tube. The DNA was stored overnight at 2-8 ^{o}C.

*Eco*RI Digestions

DNA was digested by mixing 2 µl of New England BioLabs (Ipswich, MA) 10X Cutsmart Buffer, 5 µl nuclease-free water, 12 µl DNA sample, and 1 µl of *Eco*R I. Digestions were incubated at 37°C for one hour.

Agarose Gel Electrophoresis

A 1% agarose gel was prepared by adding 1.4 g of BioExcell® Agarose LE (Worldwide Medical Products, Bristol, PA) into 140 ml of 1× TBE (Amresco, Solon, OH) which contained 0.089 M Borate and 0.002 M EDTA. To prevent overflow while microwaving, the solution was swirled to mix approximately every 30 seconds until the clear solution was formed. The solution was poured into a graduated cylinder and thoroughly mixed with 14 µl of Gel Green Nucleic Acid Stain (Embi Tech, San Diego, CA) using a stirring bar. The gel was poured into trays and the comb was inserted to form the wells. The gel was placed and run in a RunOne™ Electrophoresis system (San Diego, CA) and submerged in 1X TBE Buffer (Amresco, Solon, OH). The gels were loaded by mixing 3 µl of Amresco Agarose Gel Loading Dye and 5 µl of each digested and undigested sample. 10 µl of 1 kb DNA Ladder was loaded into the gel well to compare the sizes of the bands. The gel was run at 100 volts. Once the gel was finished running, it was analyzed using an Embi Tech PrepOne™ Sapphire (San Diego, CA) to take a picture.

Polymerase Chain Reaction (PCR)

GoTaq PCR

Primers were used on the samples in order to perform the PCR reaction. The primers were dissolved in TE buffer to 100 µM and further diluted to 4 µM in nuclease free water for the PCR reactions. The PCR reaction mix was made using 2X GoTaq DNA Polymerase Master Mix (Promega, Madison, WI). For a 20 µl reaction, the mix contained 10 µl GoTaq, 4 µl nuclease-free water, 2.5 µl of 4 µM forward and reverse primers, and 1 µl of DNA template. The samples were run in a thermocycler using the following program: 95°C for 2 minutes, 95°C for 1 minute, 55°C for 1 minute for 34 cycles, 72°C for 5 minutes, and 72° for 10 minutes. Samples were then stored at –20°C.

Table 1: Primers used for sequencing and PCR amplification

Primers	Sequence	Purpose
pOR1_25_F	5'- TCA GCA TTG CGT TGC CAT TC -3'	PCR amplification, sequencing
pOR1_25_R	5'- CTG GGC TTT TCG TTT GCC TG -3'	PCR amplification, sequencing
pOR1_30_F	5'- TCA GAT CAC GCA TCT TCC CG -3'	PCR amplification, sequencing
pOR1_33_F	5'- GTC CAG TTC AGG AGC CTC AC -3'	PCR amplification, sequencing, cloning
pOR1_33_R	5'- CTG ACC GGC GAT TAC CTC TG -3'	PCR amplification, sequencing
pOR1_37_F	5'- GCA TAA AGT GAG CAG CAG CC -3'	PCR amplification, sequencing
pOR1_37_R	5'- ACT GAA GGA TGC TGT TAC GGA -3'	PCR amplification, sequencing
pOR1_23_R	5'- GAA CAT GCC TGC TTT GGT GT -3'	PCR amplification, sequencing, cloning
pOR1_15_F	5'- GTC GCT AGT CGC TTG TTT GC -3'	PCR amplification, sequencing, cloning
pOR1_26_R	5'- GGG TCG TCT CAG AAA ACG GA -3'	PCR amplification, sequencing, cloning
pYSU_33_R	5'- TGG GAG CAC ATC AAC CTG AC -3'	PCR amplification, sequencing, cloning
pYSU_15_F	5'- AGT CCA GCC AGC CTC ATA GA -3'	PCR amplification, sequencing, cloning
pYSU_25_R	5'- CGA ACA AAG TCA CGC ACT CC -3'	PCR amplification, sequencing, cloning
pYSU_30_F	5'- TTA TGG GCA GAC ACC AAC CC -3'	PCR amplification, sequencing, cloning
pYSU_23-15-33-26_F	5'- AGC ATT CCA GTA AAT GCC TTC C -3'	PCR amplification, sequencing
pYSU_23-15-33-26_R	5'- CCG TAG CGG GTT GTG TTT TC -3'	PCR amplification, sequencing
pYSU_24-38-30-25_F	5'- CAC CGT CTT CTT TTG CAC CG -3'	PCR amplification, sequencing
pYSU_24-38-30-25_R	5'- GTT GCA ATA TCT GTC GCC GC -3'	PCR amplification, sequencing

PCR Cloning Ligations using StrataClone Kit

To clone the PCR product, StrataClone PCR Cloning Kit (Agilent Technologies, Inc. Santa Clara, CA) was used. The ligation mixture was prepared by gently mixing with repeated pipetting 3 µl of StrataClone™ cloning buffer, 2 µl of PCR product (5-50 ng) and 1 µl of StrataClone Vector Mix amp/kan. The cloning reaction mixture was incubated at room temperature for 5 minutes and placed in ice.

StrataClone Transformation

A tube of StrataClone SoloPack competent cells was thawed out in ice. 1 µl of cloning reaction mixture was added to the tube and gently mixed, and then incubated on ice for 20 minutes. During the incubation period, LB medium was pre-warmed to 42°C in a hot water bath. The transformation mixture was heat-shocked at 42°C for 45 seconds and returned to ice for another 2 minutes. 250 µl of the pre-warmed, 42°C LB medium was added to the transformation mixture and the competent cells recovered for at least an hour at 37°C in the shaker. The transformation mix was plated on an LB agar plate containing 100 µg/ml ampicillin (Amresco, Solon, OH) and 40 µg/ml X-gal (Amresco).

Plasmid Preparation

Plasmid DNA was purified according to Promega Wizard® Plus SV Minipreps DNA Purification System (Madison, WI). 5 ml of overnight bacterial culture was pelleted by centrifugation for 5 minutes at 10,000 × g at 4°C, and the supernatant was poured off and blotted to discard excess media. 250 µl of Cell Resuspension Solution was added to resuspend the pellet by pipetting. 250 µl of Cell Lysis Solution was added and mixed by

inverting the tube 4 times followed by incubating for approximately 5 minutes at room temperature for the cell suspension to clear. 10 µl of Alkaline Protease Solution was added and mixed by inverting 4 times and incubated for 5 minutes at room temperature. 350 µl of Neutralization Solution was added and immediately mixed by inverting the tube 4 times. The samples were then centrifuged at 14,000 × g for 10 minutes at room temperature. A spin column was inserted into a 1.5 ml collection tube and the cleared lysate was transferred into a spin column by decanting. The supernatant was centrifuged at 14,000 × g for 1 minute at room temperature. The flow through was discarded and the spin column was reinserted into the collection tube. 750 µl of previously diluted Column Wash Solution was added into the spin column and centrifuged at 14,000 × g for 1 minute at room temperature. The spin column was removed, the flowthrough was discarded, and the spin column was reinserted into the collection tube. The wash procedure was repeated with 250 µl of Column Wash Solution and centrifuged for another 2 minutes at 14,000 × g at room temperature. The flowthrough was discarded and centrifuged for another 1 minute at 14,000 × g at room temperature. The spin column was inserted into a new sterile 1.5 ml microcentrifuge tube. The plasmid DNA was eluted by adding 100 µl of nuclease free water and centrifuging for 1 minute at 14,000 × g at room temperature. The spin column was discarded, and the purified plasmid DNA was stored at -20°C.

Plasmid Conjugation

Overnight plates were made with 50 µg/ml kanamycin and 50 µM $HgCl_2$, then another with 50 µg/ml kanamycin and 2.5 µM Na_2TeO_3, and lastly 50 µg/ml kanamycin

and 5 mM $NaAsO_2$. LB plates, lacking antibiotic and metal, were divided in three sections. The first section was spread with *Enterobacter* sp. YSU. The second section was spread with *E.coli* strain NEBα (PACYC177). In the third section, both *Enterobacter* sp. YSU and NEBα (PACYC177) were mixed together. These were then incubated overnight at 30°C. Bacteria from each section was then streaked out onto the kanamycin/mercury and kanamycin/tellurite plates, which were incubated overnight at 30°C.

Replica Plating

Enterobacter sp. YSU, *E. coli* strain NEBα (PACYC177) and the mix of the two bacterial strains (transconjugants) were replica plating on different metal concentrations of sodium arsenite (2 mM, 4 mM, 6 mM, 8 mM and 10 mM), mercuric chloride (20 µM, 40 µM, 60 µM, 80 µM, 100 µM), and sodium tellurite (1 µM, 2 µM, 4 µM, 6 µM, 8 µM, 10 µM). This technique was used to determine the minimal inhibitory concentrations (MICs) for the transconjugates.

BLAST Basic Local Alignment Search Tool

Basic Local Alignment Search Tool (BLAST) was used to identify putative metal-resistance genes in the plasmid. In order to identify a nucleotide or protein sequence, the DNA sequence was input into the Basic Local Alignment Search Tool (BLAST) and the statistical significance was calculated (McGinnis, 2004; Mount, 2007).

Chapter IV: Results

1. Plasmids in *Enterobacter* sp. YSU

Previous agarose gel electrophoresis analysis showed that *Enterobacter* sp. YSU contains at least 2 small plasmids about 2 kb and 4 kb in size. Genomic sequencing of *Enterobacter* sp. YSU identified a potentially much larger plasmid, named pOR1, which may be at least 300 kb in size. This plasmid has never been observed in agarose gels of *Enterobacter* sp. YSU genomic or plasmid preparations.

2. Putative plasmid contigs from *Enterobacter* sp. YSU

Genomic sequencing of *Enterobacter* sp. YSU resulted in 40 contigs, and 14 of them appeared to be from plasmids (Table 2). Contig 13 contains putative genes for silver resistance and plasmid transfer while contig 15 contains a tellurite-resistance operon. Contig 17 contains a putative replication origin for IncHI2 plasmids. Contig 23 does not have any distinguishing features. Contig 24 appears to contain a mercury-resistance operon. Contig 25 appears to contain an arsenic-resistance operon. Contig 26 contains a HNH endonuclease. Contig 29, 33 and 37 contains an IS family transposase. Contig 30 contains a tgtA5 cluster protein 2. Contig 35 appears to be from a 4 kb plasmid that was mostly sequenced by undergraduates. Contig 36 seems to be the 2 kb plasmid. Contig 38 contains a transposase InsH for insertion sequence element IS5.

Table 2: Contigs found in *Enterobacter* sp. YSU

CONTIG	NUMBER OF BASES (LENGTH)	FEATURES
>YY1706231_YSU-9-10-18_contig_13	91,625	ATP-dependent helicase May contain silver-resistance Largest contig
>YY1706231_YSU-9-10-18_contig_15	62,019	Hypothetical protein May contain tellurite-resistance Large Paired with contig 23 Paired with contig 33 Sequence 15 and 33 to see similarity to Enterobacter sp. YSU
>YY1706231_YSU-9-10-18_contig_17	54,839	Hypothetical protein Contains putative replication origin for IncHI2 plasmids Large
>YY1706231_YSU-9-10-18_contig_23	23,234	Hypothetical protein Large Paired with contig 15 Paired with contig 15, 33, 26
>YY1706231_YSU-9-10-18_contig_24	18,041	Hypothetical protein May contain a mercury-resistance operon Large Paired with contig 38, 30, 25
>YY1706231_YSU-9-10-18_contig_25	13,383	Hypothetical protein May contain an arsenic-resistance operon Large Paired with contig 30 Paired with contig 24, 38, 30 Sequence 25 and 30 to see similarity to *Enterobacter* sp. YSU
>YY1706231_YSU-9-10-18_contig_26	13,197	HNH endonuclease Large Paired with contig 33 Clone 26 and 33
>YY1706231_YSU-9-10-18_contig_29	9,076	IS1 family transposase Medium sized
>YY1706231_YSU-9-10-18_contig_30	7,827	May contain a tgtA5 cluster protein 2 Medium sized Paired with contig 25 Paired with contig 24, 38, 25 Sequence 25 and 30 to see similarity to *Enterobacter* sp. YSU
>YY1706231_YSU-9-10-18_contig_33	6,333	IS110-like element IS4321 family transposase Medium sized Paired with contig 26 Paired with contig 15 Sequence 15 and 33 to see similarity to *Enterobacter* sp. YSU
>YY1706231_YSU-9-10-18_contig_35	3,979	Nuclease Matched to a 4 kb plasmid that was sequenced by Aaron Sweeney, Travis Denmeade and Robert DeVita. Small
>YY1706231_YSU-9-10-18_contig_36	1,854	Mobilization protein Seems to be a 2 kb plasmid Small
>YY1706231_YSU-9-10-18_contig_37	1,443	IS3-like element ISKpn8 family transposase Small
>YY1706231_YSU-9-10-18_contig_38	1,204	May contain a transposase InsH for insertion sequence element IS5 Small Paired with contig 24, 30, 25

3. Plasmid, pOR1, appears to be an IncHI2 plasmid

A BLAST alignment using a gene for a putative Rep HI2A protein (U62006.1) from *Serratia marcescens* IncHI2 plasmid R478 (Page, 2001) against a segment of contig 17 identified a similar sequence (Appendix 1, sequence 1) in this contig. Translation of this sequence and comparison by protein BLAST showed that it was similar to a replication initiator protein RepHI2 (Figure 1). This result confirms that pOR1 contains an *incHI2* replication origin.

MULTISPECIES: IncHI-type plasmid replication initiator protein RepHI2 [Enterobacterales]

Sequence ID: WP_000159528.1 Length: 362 Number of Matches: 1

See 50 more title(s) See all Identical Proteins(IPG)

Range 1: 1 to 362 GenPept Graphics ▼ Next Match ▲ Previous Match

Score	Expect	Method	Identities	Positives	Gaps
744 bits(1920)	0.0	Compositional matrix adjust.	362/362(100%)	362/362(100%)	0/362(0%)

```
Query  1    MTKEKDTEQQDLVTRAFSVREKESGKDIILRPNSNRTVQSIALMRLGLFVPSPKSVGRQN  60
            MTKEKDTEQQDLVTRAFSVREKESGKDIILRPNSNRTVQSIALMRLGLFVPSPKSVGRQN
Sbjct  1    MTKEKDTEQQDLVTRAFSVREKESGKDIILRPNSNRTVQSIALMRLGLFVPSPKSVGRQN  60

Query  61   REYKTVGFDATKELQTLSLMESEGFTNISIVGERLDMSVDFKTWMGIIRTYANHPINNDT  120
            REYKTVGFDATKELQTLSLMESEGFTNISIVGERLDMSVDFKTWMGIIRTYANHPINNDT
Sbjct  61   REYKTVGFDATKELQTLSLMESEGFTNISIVGERLDMSVDFKTWMGIIRTYANHPINNDT  120

Query  121  ISLKFTEFLKLCTPENYRSSTASRKRIDASLRRLASVTLSFTSNNSSKVYTTHLVQSALL  180
            ISLKFTEFLKLCTPENYRSSTASRKRIDASLRRLASVTLSFTSNNSSKVYTTHLVQSALL
Sbjct  121  ISLKFTEFLKLCTPENYRSSTASRKRIDASLRRLASVTLSFTSNNSSKVYTTHLVQSALL  180

Query  181  DPESDQVVLQVDPKIFELYQYDHKVLMQLKAIKELAKKESAQALYTFIESLPPNPIPISL  240
            DPESDQVVLQVDPKIFELYQYDHKVLMQLKAIKELAKKESAQALYTFIESLPPNPIPISL
Sbjct  181  DPESDQVVLQVDPKIFELYQYDHKVLMQLKAIKELAKKESAQALYTFIESLPPNPIPISL  240

Query  241  TRLKNRLNLKTRANSQNATVRKALEELASIGYLQYTEIKKDGKVYFQIHKRDPDLNLNNT  300
            TRLKNRLNLKTRANSQNATVRKALEELASIGYLQYTEIKKDGKVYFQIHKRDPDLNLNNT
Sbjct  241  TRLKNRLNLKTRANSQNATVRKALEELASIGYLQYTEIKKDGKVYFQIHKRDPDLNLNNT  300

Query  301  QPPLEVVEDEEENSGSSVLEGELCPPADPIDGDDVLTVHDLTAEELRYIRSLRSQKKNSN  360
            QPPLEVVEDEEENSGSSVLEGELCPPADPIDGDDVLTVHDLTAEELRYIRSLRSQKKNSN
Sbjct  301  QPPLEVVEDEEENSGSSVLEGELCPPADPIDGDDVLTVHDLTAEELRYIRSLRSQKKNSN  360

Query  361  AS  362
            AS
Sbjct  361  AS  362
```

Figure 1. Protein BLAST Result for the putative RepHI2 protein encoded by contig 17.

4. ***Enterobacter* sp. YSU plasmid Resistance to Mercury**

A sequence for an *Enterobacter* sp. YSU mercury-resistance operon is located on contig 25. The mercury resistance genes, *merRTPCADE*, found in pOR1 (Baya, 2021) are similar to the ones found in IncHI2 plasmids (Figure 2).

Figure 2. Mercury resistance operon from the *Enterobacter* sp. YSU plasmid, pOR1.

5. ***Enterobacter* sp. YSU plasmid Resistances to Tellurite**

A sequence for an *Enterobacter* sp. YSU tellurite-resistance operon is located on contig 15 and shown below (Figure 3). This tellurite resistance operon is an IncHIII due to it consisting of *terZF* which is common in these plasmids and encodes a tellurite detoxification system. The *ter* genes are located on a prophage-like element of the chromosome (Nguyen, 2021). IncHI2 plasmids along with *Enterobacter sp.* YSU have been shown to be composed of *terZABCDF* and are involved in tellurite resistance in relatively large concentrations (Whelan, 1995). As seen in pOR1, unlike in IncHI2 plasmids, there are two *terD* genes which suggests that there may have been a duplication. IncHI2 plasmids also contain *terE* which is not seen in pOR1 (Fang 2016).

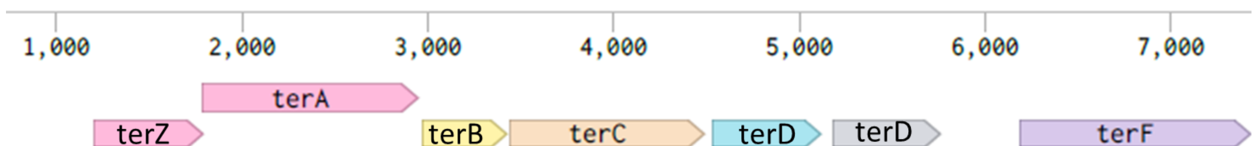

Figure 3. Tellurite resistance operon from the *Enterobacter* sp. YSU plasmid.

6. ***Enterobacter* sp. YSU plasmid Resistance to Arsenite**

A sequence for an *Enterobacter* sp. YSU arsenic-resistance operon is found on contig 25 (Figure 4). They provide an increase resistance to arsenate and arsenite and are present in almost all IncHI2 plasmids (Falgenhauer et al., 2017). IncHI2 plasmids and pOR1 both contain *arsCBRH* resistance genes. Unlike IncHI2 plasmids, this strain contains a second arsenic resistance on its chromosome which could be why it has an arsenite MIC of ~12 mM.

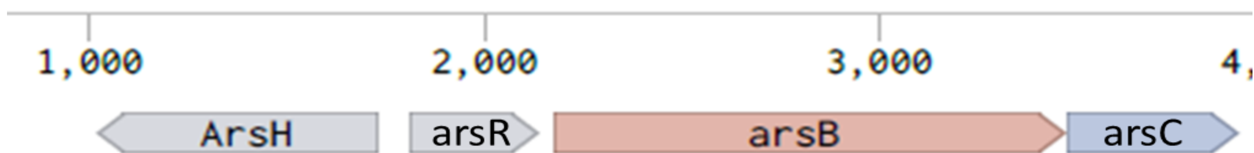

Figure 4. Arsenic resistance operon from the *Enterobacter* sp. YSU plasmid.

7. **Potential *Enterobacter* sp. YSU silver-operon**

A sequence for an *Enterobacter* sp. YSU silver-resistance operon is found on contig 13 (Figure 5). The silver resistance genes found in both IncHI2 plasmids and pOR1 consist of *silESRCBAP* (Kremer, 2012).

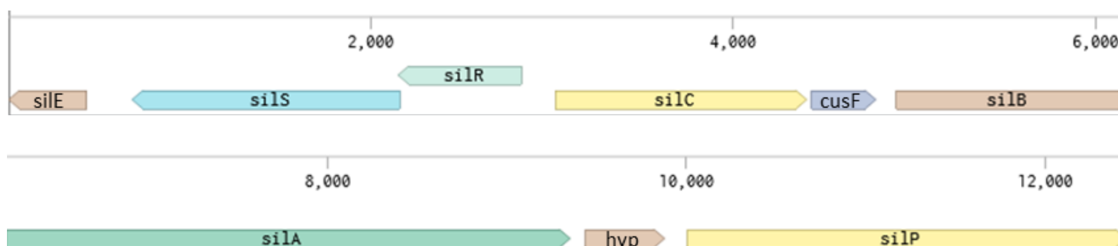

Figure 5. Silver resistance operon from the *Enterobacter* sp. YSU plasmid.

8. Plasmid Conjugation

If the mercury-, tellurite-, arsenic- and silver-resistance operons are located on the same plasmid, it should be possible to transfer pOR1 to *E. coli*, rendering it resistant to these metals (Table 3). *Enterobacter* sp. YSU and *E. coli* strain NEBα (PACYC177) were blobbed onto an LB plate in separate sections then mixed together in a third section. As expected, they all grew. Then, the three sections were streaked onto kanamycin/mercury and kanamycin/tellurite LB agar plates. *Enterobacter* sp. YSU, did not grow on any of these plates because it lacks a gene for kanamycin-resistance. *E. coli* strain NEBα (PACYC177), which contains the antibiotic kanamycin-resistance gene, did not grow on any of the plates because it lacks metal-resistance genes. Bacteria from the mixture grew on these plates because the plasmid transferred to NEBα (PACYC177) making it resistant to both kanamycin and each metal. Thus, it appears that mercury- and tellurite resistance are linked on the same plasmid.

Table 3: Plasmid conjugation of pOR1 to *E. coli*

Strains	LB Medium	Kanamycin/mercury LB agar	Kanamycin/tellurite LB agar
Enterobacter sp. YSU	+	-	-
E. coli strain NEBα (PACYC177)	+	-	-
Mix of *Enterobacter* sp. YSU and *E. coli* strain NEBα (PACYC177)	+	+	+

9. Replica Plating

Enterobacter sp. YSU, *E. coli* strain NEBα (PACYC177) and the transconjugants were replica plating on different metal concentrations of arsenite (2 mM, 4 mM, 6 mM, 8 mM and 10 mM), mercury (20 µM, 40 µM, 60 µM, 80 µM, 100 µM), and tellurite (1 µM, 2 µM, 4 µM, 6 µM, 8 µM, 10 µM). *Enterobacter* sp. YSU grew on the M-9 plate, but the NEBα, *E. coli* strain does not. Failure of the transconjugants to grow on M-9 plates proves the successful transfer of the YSU plasmid into *E. coli.* As shown below in Tables 4, 5, and 6, the positive control YSU grew on all metal concentrations as expected while the negative control, *E. coli,* did not grow on any of the metal concentrations. All the transconjugants grew on the different metal concentrations of arsenite (2 mM, 4 mM, 6 mM, 8 mM and 10 mM), mercury (20 µM, 40 µM, 60 µM, 80 µM, 100 µM), and tellurite (1 µM, 2 µM, 4 µM, 6 µM, 8 µM, 10 µM). Since the transconjugants grew in the presence of all three metals, this suggests that the operons are linked on one big plasmid.

Table 4: MIC Results of Arsenite

Strains	**2 mM**	**4 mM**	**6 mM**	**8 mM**	**10 mM**
YSU	+	+	+	+	+
E. coli Recipient	-	-	-	-	-
Transconjugant E. coli with PACYC177 (Hg)	+	+	+	+	+
Transconjugant E. coli with PACYC177 (Te)	+	+	+	+	+

Table 5: MIC Results of Mercury

Strains	20 µM	40 µM	60 µM	80 µM	100 µM
YSU	+	+	+	+	+
E. coli Recipient	-	-	-	-	-
Transconjugant E. coli with PACYC177 (Hg)	+	+	+	+	+
Transconjugant E. coli with PACYC177 (Te)	+	+	+	+	+

Table 6: MIC Results of Tellurite

Strains	1 µM	2 µM	4 µM	6 µM	8 µM	10 µM
YSU	+	+	+	+	+	+
E. coli Recipient	-	-	-	-	-	-
Transconjugant E. coli with PACYC177 (Hg)	+	+	+	+	+	+
Transconjugant E. coli with PACYC177 (Te)	+	+	+	+	+	+

10. Cloning and Sequencing PCR Products

To determine if some of the contigs are linked, PCR was used. Approximated, 500 bp segments of the 3' and 5' ends of each contig were analyzed by BLAST to identify segments of reference sequences that were homologous to each end of two contigs. Then, the Contig Editor program from GeneStudio was used to align the two contigs with the reference sequence. If the sequences aligned, PCR primers for the ends of each contig were designed (Table 2). Predicted sizes of the PCR products were determined from the contig alignments.

The primers pOR1_25_F and pOR1_37_R were used in PCR reactions using different annealing temperatures to see if contigs 25 and 37 were linked (Fig 6). Likewise, the primers pOR1_37_F and pOR1_33_R were used in PCR reactions to see if contigs 33 and 37 were linked. Also, the primers pOR1_30_F and pOR1_25_R were used in PCR reactions using different annealing temperatures to see if contigs 25 and 30 were linked. The agarose gel of the PCR reactions suggested that contigs 25 and 37 were linked because they all produced a predicted 700 bp band (Figure 6, Lanes 5, 8, 11 and 14). Contigs 33 and 37 are probably not linked because PCR reaction for these contigs did not produce any bands (Figure 6, Lanes 3, 6, 9 and 12). It is not clear if contigs 25 and 30 are linked because non-specific PCR amplification produced multiple bands (Figure 6, Lanes 4, 7, 10, 13 and 16).

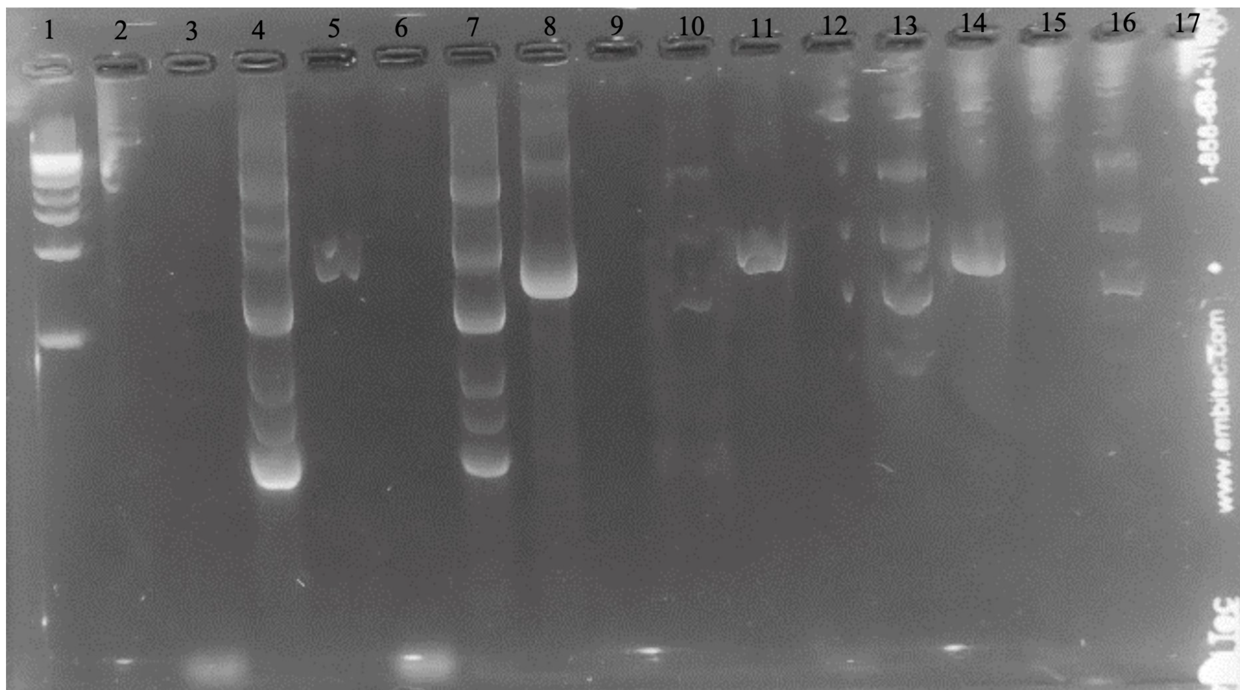

Figure 6. Agarose gel of PCR using GoTaq, forward and reverse primers of the contigs. Lane 1- 1kb Ladder, lane 2- contigs 25&37 at 50.8 °C, lane 3- contigs 37&33 at 50.8 °C, lane 4- contigs 25&30 at 50.8 °C, lane 5- contigs 25&37 at 56.1 °C, lane 6- contigs 37&33 at 56.1 °C, lane 7 contained the control- contigs 25&30 at 56.1 °C, lane 8- contigs 25&37 at 56.1 °C, lane 9- contigs 37&33 at 56.1 °C, lane 10- contigs 25&30 at 56.1 °C, lane 11- contigs 25&37 at 61.1 °C, lane 12- contigs 37&33 at 61.1 °C, lane 13- contigs 25&30 at 61.1 °C, lane 14- contigs 25&37 at 64.5 °C, lane 15- contigs 37&33 at 64.5 °C, and lane 16- contigs 25&30 at 64.5 °C.

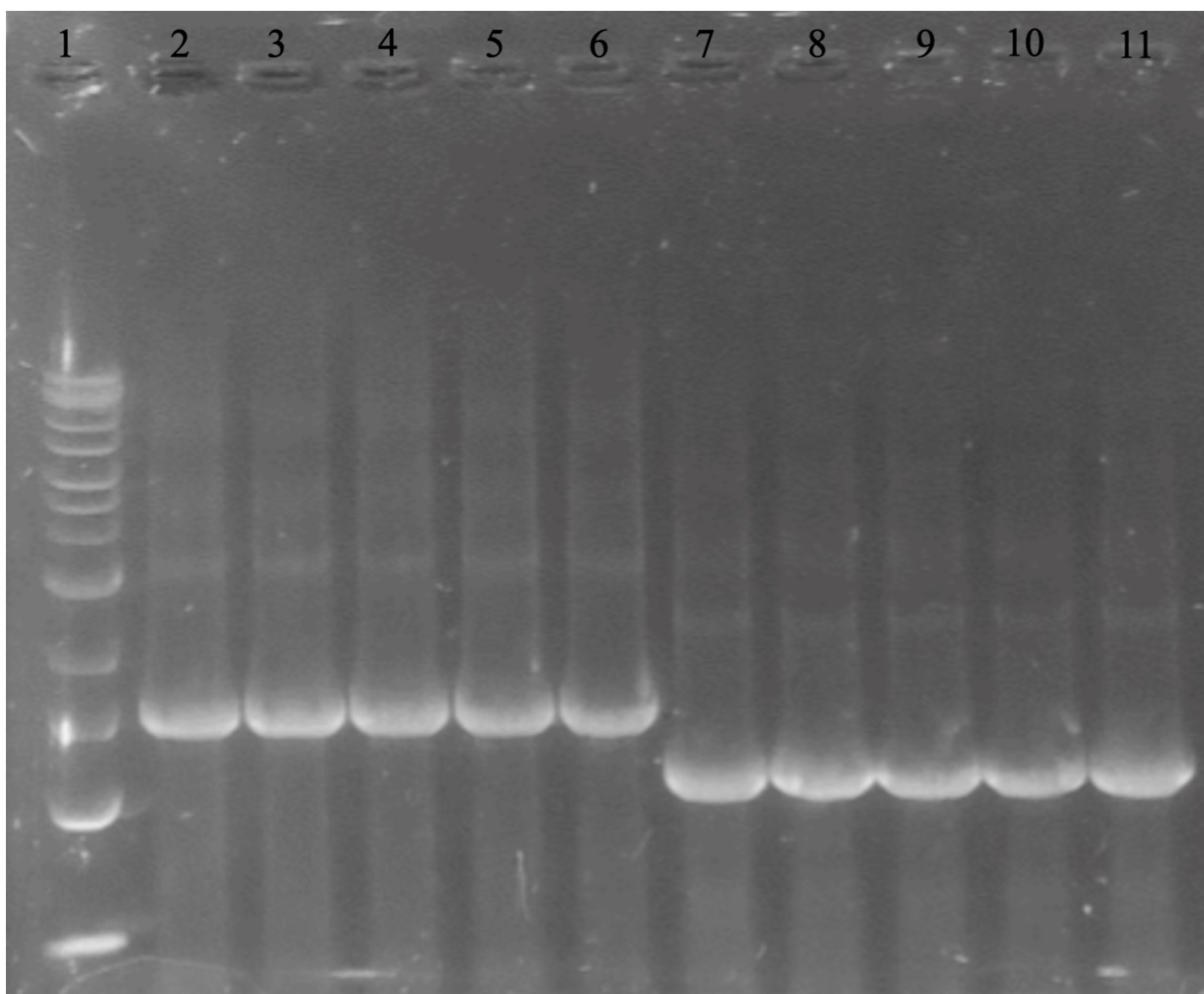

Figure 7. Agarose gel of PCR using GoTaq, forward and reverse primers of the contigs. Lane 1- 1kb Ladder, lane 2- contigs 26&33 at 56.1 °C, lane 3- contigs 26&33 at 50.8 °C, lane 4- contigs 26&33 at 56.1 °C, lane 5- contigs 26&33 at 61.1 °C, lane 6- contigs 26&33 at 64.5 °C, lane 7 contained the control- contigs 23&15 at 56.1 °C, lane 8- contigs 23&15 at 50.8 °C, lane 9- contigs 23&15 at 56.1 °C, lane 10- contigs 23&15 at 61.1 °C, lane 11- contigs 23&15 at 64.5 °C.

The primers pOR1_33_F and pOR1_26_R were used in PCR reactions using different annealing temperatures to see if contigs 26 and 33 were linked (Fig 7). Likewise, the primers pOR1_15_F and pOR1_23_R were used in PCR reactions to see if contigs 23 and 15 were linked. The agarose gel of the PCR reactions suggested that contigs 26 and 33 were linked because they all produced a predicted 1,500 bp band (Figure 7, Lanes 2, 3, 4, 5 and 6). The agarose gel of the PCR reactions also suggested that contigs 23 and 15 were linked because they all produced a predicted 1,000 bp band (Figure 7, Lanes 7, 8, 9, 10 and 11).

Chapter V: Discussion

Among the 14 contigs, contig 13, 15, 24, and 25 contained mercury, arsenite or tellurite-resistance operons while contig 36 contained a DNA sequence homologous to mobilization. The translation and protein BLAST analysis showed that the sequence of contig 17 showed a similar replication initiator protein RepHI2 which confirms that pOR1 contains an *incHI2* replication origin. IncHI2 plasmids along with *Enterobacter sp.* YSU have been shown to be composed of *terZABCDF, arsCBRH,* and *silESRCBAP* resistance genes. Since the plasmid contigs contain DNA sequences homologous to mobilization, mercury, arsenite and tellurite-resistance operons, it has been confirmed that these resistance factors could be transferred from *Enterobacter* sp. YSU to *E. coli*.

Previous research showed that a plasmid pH11, an IncH12 plasmid, conferred multiple antibiotic and heavy metal resistance determinants resulting in the spread of resistance genes. The heavy metals included tellurite, mercury, arsenic and silver which could lead to a stable environment for IncH12 plasmids in bacterial populations (Zhai,

2016). My data supports my hypothesis because by using protein BLAST, the comparison between a gene for a putative Rep HI2A protein (U62006.1) from *Serratia marcescens* IncHI2 plasmid R478 (Page, 2001) against a segment of contig 17 identified a similar sequence. Once translated and compared by protein BLAST, it showed that it was similar to a replication initiator protein RepHI2 (Figure 1). This result confirms that pOR1 contains an *incHI2* replication origin. Lastly, BLAST was used to design primers to use in PCR. This allowed PCR to suggest that contigs 25 and 37, contigs 26 and 33, and contigs 23 and 15 are adjacent. Sequencing the PCR fragments and aligning them with the sequences of the contigs will confirm these results.

Due to the difficulty of purifying the plasmid, there are other methods that could be used. Other methods that could be used are polyethylene glycol (PEG) (Humphreys, G.O. 1975) precipitation or the kado/liu method (Kado, 1981). PEG precipitation can be used to prepare large quantities of plasmid DNA by being incorporated during the standard plasmid isolation process. The kado/liu procedure is the second procedure that could be used. This procedure is normally used for the detection and isolation of various sized plasmids some of which are harbored in the species *Escherichia*. This procedure is similar to PEG but uses alkaline sodium dodecyl sulfate at elevated temperatures in order to denature the DNA. In addition, in-well cell lysis might make it possible to observe pOR1 because it avoids shearing which may occur during other purification methods (Pedraza, R.O. and Ricci, J.C. 2002). The isolation of plasmid DNA could then be used in experiments like DNA cloning, transformation, restriction endonuclease analysis and Southern blotting to obtain a complete map of the pOR1.

Future Work

In order to obtain a complete circular plasmid sequence, more PCR reactions need to be run in order to link all the contigs together. If the plasmid can be purified, a restriction endonuclease map of it could be created. This would be done by digesting it with restrictions endonucleases and cloning different fragments. Restriction endonuclease digestions of digested plasmid DNA would be separated by agarose gel electrophoresis and transferred to nylon membrane by Southern blotting. Then, cloned fragments could be used as probes in Southern blots to determine the order of each fragment in the plasmid. Lastly, the metal resistance genes need to be cloned and tested for resistances.

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Appendix

DNA sequences

>1) Plasmid replication initiator protein RepHI2 gene from contig 17
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