Masteroppgave

NTNU
Norges teknisk-naturvitenskapelige universitet
Fakultet for naturvitenskap
Institutt for bioteknologi og matvitenskap

Eirik Degré Lorentsen

Characterization of two *Janthinobacterium* isolates originating from salmon fry

Violacein operon sequences and growth conditions for violacein production

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Veileder: Ingrid Bakke
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Unfortunately due to the Covid-19 pandemic, I had to make some changes to this project, and make it more theoretical. This was due to restrictions from the government and resulted in less time in the laboratory to finish my experiments and more focus on phylogenetic analysis.

Abstract

The strains worked with in this project (MM5 and 3.116) was isolated from salmon fry skin and classified as *Janthinobacterium* (*Betaproteobacteria, Oxalobacteraceae*). During previous work with these strains in the Analysis and Control of Microbial Systems (ACMS) group at the Norwegian University for science and technology (NTNU), they showed the ability to produce slime and purple colonies, assumed to be EPS and violacein. *J. Lividum* is associated with both human and amphibian skin, and is believed to be a part of the amphibians defense against skin fungal infections. The antifungal properties of *J. Lividum* is associated with violacein, which also has shown among other things antibacterial, antioxidizing, antiviral, and antitumoral properties. The bacterial species have shown capnophilic properties, giving the ability to live in the heightened CO_2 concentrations occurring on amphibian skin. These properties make the bacteria an interesting probiotic candidate in aquaculture, for example as a mean of combating the water mold *Saprolegnia*, which is a problem in the freshwater life stages of salmon.

The main goals of this project was to identify growth conditions for violacein production for MM5 and 3.116, and to study the evolution of the violacein operon by phylogenetic analysis. The growth properties of the strains were studied by the generation of growth curves, antibiograms, and microscopy. The generational time of MM5 and 3.116 was calculated to be 1.50 and 0.88 hours respectively. A test of antibiotic susceptibility showed both strains to be resistant towards Kanamycin (50 μg/ml), polymixin (100μg/ml), Neomycin (20 μg/ml), and Ampicillin (20 μg/ml). MM5 showed purple colonies, indicating violacein production on several media. Incubation temperature (28°C) and reduced agar concentration (1%) seemed to promote violacein production. The 3.116 strain showed no sign of violacein production on any media. None of the strains showed any sign of antagonistic properties against bacteria, however, this could be due to lack of violacein production on the agar media applied. The violacein operon has been observed for *Proteobacteria* families representing the classes *delta-, gamma-* and *betaproteobacteria*. Most of the violacein operon of MM5 was successfully sequenced. PCR amplification failed for 3.116s' operon, indicating a lack of violacein operon, degenerated, or rearranged operon. Violacein gene sequences were downloaded and used in phylogenetic analyses. The 16s rRNA gene was used as a reference representing the vertical evolution of the strains included in the analysis. The phylogenetic analysis indicated that horizontal gene transfer of the violacein operon has occurred during the evolution of the *proteobacteria*.

Sammendrag

Bakteriestammene som det ble jobbet med i dette prosjektet (MM5 og 3.116) var isolert fra skinnet til lakseyngel og ble klassifisert som *Janthinobacterium* (*Betaproteobacteria, Oxalobacteraceae*). Under tidligere arbeid i Analyse og kontroll av mikrobielle samfunn (ACMS) gruppen ved Norges teknisk-naturvitenskapelige universitet (NTNU) med disse stammene har det blitt observert produksjon av slim og lilla kolonier antatt til å være EPS og violacein. *J. Lividum* assosieres med både menneske- og amfibiehud, og er antatt å være en del av amfibienes forsvar mot soppinfeksjoner i huden. De antifungale egenskapene til *J. Lividum* er assosiert med det lilla fargestoffet violacein, som i tillegg har vist blant annet antibakterielle, antioksiderende, antivirale og antitumorale egenskaper. Bakterietypen har vist kapnofile egenskaper, noe som gir evnen til å leve på de forhøyede CO_2 konsentrasjonene som finnes på amfibiehud. Disse nevnte egenskapene gjør bakterien til en interessant kandidat som probiotika i oppdrettsnæringen, for eksempel som en metode for å bekjempe eggsporesoppen *Saprolegnia*, som kan være et problem i ferskvannstadiene av laksens livssyklus.

Hovedmålene med dette prosjektet var å identifisere vekstforhold som promoterer violacein produksjon i MM5 og 3.116, og å studere evolusjonen av violacein operonet ved fylogenetiske analyser. Veksten til stammene ble studert ved å lage vekstkurver, antibiogramer og mikroskopering. Generasjonstiden til MM5 og 3.116 ble beregnet til å være henholdsvis 1.5 og 0.88 timer. En test av mottakelighet for antibiotika, viste resistens mot kanamycin (50 μg/ml), polymixin (100μg/ml), neomycin (20 μg/ml), og ampicillin (20 μg/ml) for begge stammene. MM5 viste lilla kolonier, som indikerer violacein produksjon på flere mediumer. Inkubasjonstemperatur (28 °C) og redusert agarkonsentrasjon (1%) så ut til å promotere violacein produksjon. 3.116 stammen viste ingen tegn til violacein produksjon.. Stammene viste ingen tegn til antagonistiske egenskaper mot bakterier, men dette kan skyldes manglende produksjon av violacein på disse agarplate mediumene. Violacein operonet har blitt observert hos *proteobakterier*, som representerer *delta, beta* og *gammaproteobakterier*. Mesteparten av violaceinoperonet til MM5 ble sekvensert. PCR-amplifiseringen feilet for 3.116 sitt operon, noe som tyder på manglende operon, degenerert sekvens eller annerledes organisert operon. Violacein sekvenser ble lastet ned og brukt i fylogenetiske analyser. 16s rRNA genet ble brukt som en referanse for vertikal evolusjon for stammene inkludert i analysene. De fylogenetiske analysene ga indikasjoner for at horisontal genoverføring har forekommet under evolusjonen av *proteobakteriene*.

3.116 - *Janthinobacterium* strain worked with

ACMS - Analysis and Control of Microbial Systems

BHI - Brain heart infusion

BLAST - Basic Local Alignment Search Tool

CMB - Cooked meat broth

DNA - Deoxyribonucleic acid

EM - Erlenmeyer

EPS - Exopolysaccharides

HGT - Horizontal gene transfer

J. Lividum - *Janthinobacterium Lividum*

LB/LA - Luria-Bertani (Agar)

ML - Maximum Likelihood

MM5 - *Janthinobacterium* strain worked with

NB/NA - Nutrient broth/agar

NCBI - The National Center for Biotechnology Information

NJ - Neighbor-Joining

NTNU - Norwegian university for science and technology

OD - Optical Density

ON - Overnight

PCR - Polymerase chain reaction

rDNA - Ribosomal Deoxyribonucleic acid

RDP - Ribosomal database project

RNA - Ribonucleic acid

rRNA - Ribosomal ribonucleic acid

S_ab - Seqmatch score

TM - Primer melting temperature

TSB/TSA- Tryptic soy broth/agar

v1 - Variable region 1

v3 - Variable region 3

VioA/B/C/D/E - Violacein gene A/B/C/D/E

Contents

1 Introduction

1.1 Background for the project

This master thesis is a continuation of a previous project done on ”Violacein production in a *Janthinobacterium lividum* strain isolated from salmon fry”. The bacteria worked with during this project didn't produce any violacein regardless of the conditions or media composition used. By sequencing the v1-v3 region of the 16s ribosomal ribonucleic acid (rRNA) gene of the bacteria it was concluded to be an *Arthrobacter* strain, and not a *Janthinobacterium* strain [1]. This master thesis and project was written in cooperation with the Analysis and Control of Microbial Systems (ACMS) group at the Institute for biotechnology at Norwegian university for science and technology (NTNU). The bacterial strains used in this project, referenced to as 3.116 and MM5, was isolated from salmon fry skin during previous work in the ACMS group. By sequencing the v1-v3 region of the 16s ribosomal Deoxyribonucleic acid (rDNA) these strains were classified as *Janthinobacterium*. During previous work in the ACMS group with these bacteria strains, the production of slime and a purple pigment was observed. This was assumed to be violacein and exopolysaccharides (EPS) (Professor Ingrid Bakke, NTNU, 2019 [pers.comm.]). A previous master project done in the ACMS group found the strain to be able to colonize the skin of newly hatched salmon fry[2]. Beyond this neither violacein production or growth characteristics are studied for these strains. One of the aims of this master project is similar to the major aim of the previous project, namely to identify growth conditions for violacein production in these strains, 3.116 and MM5.

1.2 Atlantic salmon (*Salmo Salar*)

The Atlantic salmon (*Salmo Salar*) is a species of fish belonging to the Salmonidae family, which is distributed throughout the northern parts of the Atlantic ocean on the European and American side [3, 4]. The Atlantic salmon migrates from the rivers where it spawns to the oceans. This means that these fish species are anadromous [3]. In the oceans, the fish feeds on pelagic species, such as herring and sprat, for up to four years before returning to their river of origin for spawning. The Atlantic salmon cease feeding before returning to the rivers. Typically the salmon are 8-13kg when it starts migrating towards the river for spawning [4]. The Atlantic salmon usually spawns during the period from October to November. The roe is buried 20-40 cm down in the gravel [3]. Following the spawning, most of the fish die, but some return to

the sea for further feeding. After approximately 500 degree days the eggs hatch. This hatching usually occurs during the late winter to early spring [3, 4]. The newly hatched fry hides in the gravel feeding of the yolk sac until it is consumed. This period usually lasts for 300 degree days [4]. During the spring, after the yolk sac is consumed, the fry rises from the gravel, establishes territories in the river, and begins feeding on insects and small fish [3, 4]. The juvenile fish keeps feeding in freshwater for 2-5 years before they undergo smoltification, which is a process that adapts the fish for living in saltwater [4]. The smoltification process consists of multiple changes in biochemistry, behavior, morphology, and physiology. These changes lead to seawater adapted fish with better-adapted color, osmoregulation, oxygen transport, buoyance, shape, and schooling behavior [5]. During the spring to early summer, the smolt migrates towards the ocean where it reaches for deep water for feeding and maturing [4].

The aquaculture industry is one of the major industries in Norway, and is responsible for a considerable share of Norway's export income, with around 5.5%. In addition, aquaculture is an important source of seafood. In Norway, the fish farming industry is mainly based around Atlantic salmon and rainbow trout (*Oncorhynchus mykiss*), but other species like cod, halibut, and lumpsuckers are farmed in Norway, where the amount of cod and halibut is less than two per thousandth[6]. The aquaculture industry is distributed along the whole coast of Norway [6]. The life cycle of Atlantic salmon in fish farms is similar to the life cycle of fish in nature and consists of a freshwater phase and a seawater phase [3]. The fish used for breeding are selected from the seaside production stocks and moved to freshwater two months before stripping. These fish are called broodstock [4]. Next, roe from the female fish are stripped and milt from the male fish are collected. The roe and milt are then mixed, which fertilizes the roe [4, 6]. Similar to the wild salmon, the fertilized eggs start eyeing after 250 degree days and then hatches after a further 250 degree days. The newly hatched fry will then feed of the yolk sac for around 300 degree days before feeding starts. The feeding is usually carried out in flow-through systems or recirculating systems throughout the parr and smolt stages. To induce the smoltification fish can either be maintained at ambient temperature and light regimes, or the light and temperature can be manipulated to provoke early smoltification [4]. The smoltified salmon, which is between 40-120g, are then transferred to sea cages for feeding and growing [4, 6]. The seawater stage usually lasts for two years, until the salmon weighs above 2kg before the fish are harvested [4].

The main challenges in aquaculture in Norway is the fish health and the impact on the surroundings of the cage. Around 15% of the farmed salmon dies or disappears during the seawater stages, where mortality is the major component. The use of antibiotics used to be a major concern in aquaculture in Norway, but has been reduced with 99% from 1987 to 2013. However, in developing countries, the use of antibiotics is still widely distributed. This can lead to antibiotic-resistant microorganisms [6]. A major cause of death for Atlantic salmon in Norway is the delousing treatment to clean the fish from salmon louse (*Lepeophtheirus salmonis*). Salmon louse and viral infections are the most challenging diseases for Atlantic salmon in Norway. Bacterial and eukaryotic infections are also challenging, for example, the bacteria *Yersina Ruckeri*, the eukaryotic amoeba *Paramoeba perurans* and the water mold *Saprolegnia* in freshwater stages, causing enteric redmouth disease, amoebic gill disease and saprolegniosis respectively[7]. The salmon louse is a parasitic copepod living on the skin of fish in the Salmonidae family and is the biggest problem in Norwegian aquaculture. This parasite occurs on fish in marine environments in the northern hemisphere. The life cycle of the lice consists of eight stages, where they first infect the Salmonidae fish in the third stage. These later stages cause harm towards the host because of the lice feeding on the skin, mucous, and blood of the fish. The damages to the fish depend on the life stage of the lice, but heavily infected individuals can suffer from emaciation and large wounds. These wounds can lead to secondary infections from bacteria or fungi [8, 9]. The main treatments against lice infections have traditionally been the usage of medicaments, however, this has led to a widespread resistance towards these substances [9]. Nowadays preventive treatment in combination with continuous treatment. The continuous treatment is carried out by adding cleaner fish to the sea cages [8, 9]. In Norway, the quantity of adult female lice in 2018 was reported to be the lowest since 2013 [9].

Saprolegnia is a water mold causing infections to fish skin during freshwater stages. Spores from Saprolegnia is common in Norwegian water sources running into hatcheries. The water mold may establish and reproduce in biofilm in tubes and tanks, giving the salmon a constant exposure to the spores. The water mold infects weakened individuals and dead roe, where it later spreads to the healthier surrounding roe grains. Infections on fish usually start at areas without shell, the infections then spread with hyphal growth in epidermis, dermis, and hypodermis. This infection leads to a cottony coating on the skin of the fish. Infections can in

some cases give high mortality, both in farmed and wild salmon [7]. Saprolegniosis is usually diagnosed and treated on-site, therefore, few cases are reported to the Norwegian veterinary institute. However, in 2019 there where a few inquires about outbreaks resulting in high mortality on eggs or fry. A survey carried out by the Norwegian veterinary institute suggests a bigger concern for saprolegniosis than the number of diagnoses would indicate [10]. Saprolegniosis ha in Norway been prevented and controlled by using the organic compound malachite green until the year 2000. However, due to the carcinogenic properties of this substance, the use has been banned. Today, Formalin is used to prevent outbreaks due to the low cost. However, the use of formalin in aquaculture is disputed and is currently up for review in the EU. Therefore, limitations or a ban could be introduced on the usage of formalin as a treatment against parasites and water molds. As a consequence of this, a focus point is to find alternative treatments and to reduce the risk of serious outbreaks. Examples of precautions are to reduce the stress factors such as transporting of fish, vaccinating, and sorting as much as possible, and to ensure proper hygiene measurements have been implemented [11]. A *Pseudomonas fluorescens* strain isolated from catfish has shown the ability to inhibit the growth of *Saprolegnia* in vitro [12]. Due to the ability of *J. Lividum* to colonize the skin of salmon fry [2], and the previously reported antifungal properties of the bacteria [13] it's a possible candidate to use as a probiotic to prevent infections by *Saprolegnia*.

1.3 Probiotics

The usage of probiotics for humans have mostly been as a treatment for various diarrhea conditions and vaginal infections. In addition, usage as a treatment for other medical conditions such as allergy, respiratory infections, and lactose intolerance are studied [14]. The use of probiotics is studied in livestock as well, with results showing for example increased growth[15] and increased milk production [16]. Probiotics are the addition of living microorganisms to a host in an adequate amount to give a beneficial health effect on the host organism[14, 17]. The added microorganism are either non-pathogenic bacteria or *Saccharomyces*, which are considered friendly germs with a benefit towards the immune system [17]. Under normal circumstances, the various part of the body has a normal flora of bacteria. This balance can be disturbed, and unwanted bacteria can take over. In probiotic treatment, the addition of wanted bacteria can be used to reintroduce the normal flora. In addition, probiotics have been used to reduce the risk of problems with the stomach and intestine as a consequence of antibiotic use [14]. However,

critics point at the fact that most microorganisms would not survive oral intake due to the acidity of the stomach [17].

A type of probiotics used in the aquaculture industry is called Bactocell®, which is a strain of the bacterial species *Pediococcus acidilactici* used as an additive to fish feed to improve fish health [18]. A study done on Bactocell® showed that salmon fed with the probiotic had milder inflammatory response towards an inflammatory challenge, and the showed quicker recovery when compared to a control group [19]. The food with added Bactocell® is used as the standard food in freshwater stages for both salmon and trout. (Torunn Forberg, Biomar, 2020[pers.comm.]). Additionally, probiotics could be used in aquaculture to improve water quality. The usage of probiotics could result in a reduction of antibiotic usage and an improvement in appetite and/or growth for farmed species in aquaculture [20]. Improvement of water quality is not directly an addition of microorganisms to a host and therefore not included under the traditional definition of probiotics. However, nowadays there seems to be no accepted definition of aquaculture-probiotics, and the proposed definitions include microbial improvement of the host organism or environment [21, 22] The initial usage of probiotics was to enhance the growth and health of the animals, however, the use of probiotics to reduce stress and improve reproduction has also been studied [23]. Various types of probiotics have been studied such as gram-negative and gram-positive bacteria, bacteriophages, yeast, and unicellular algae [20]. The modes of action for a probiotic organism is competition for adhesion sites, energy, and chemicals, production compounds with inhibitory properties, as a source for both macro- and micronutrients, improvement of the immune response of the host, interaction with phytoplankton, an improvement in the general water quality, and as an enzymatic augmentation to digestion [24]. The general mechanism of action for probiotics is through the improvement of the resistance towards colonization and/or inhibition of pathogens. By manipulating the composition of the ingested microorganism, the microbiota in the gastrointestinal tract can be modified. This could result in a reduced number of opportunistic pathogens [25]. The microorganism used as a probiotic should be both antagonistic towards the pathogen, and able to colonize the host. Studies suggest that the place of origin from the fish makes a difference towards effect, as bacteria isolated from skin mucus showed a more pronounced antagonism towards the skin pathogen *Vibrio anguillarum* for turbot and dab [26]. Addition of *Saccharomyces cerevisiae* as a probiotic to the feed of catfish has been shown to improve both growth performance

and resistance towards diseases [27]. A study was done on juvenile sea bass *Dicentrarchus labrax* feed with lactic acid bacteria showed significantly reduced stress measured in cortisol and increased growth for fish feed with lactic acid bacteria for 59 days [28]. The effect of a culture of *Carnobacterium* isolated from the digestive tract of Atlantic salmon used as probiotic has been investigated. To check for antagonism the culture was cross-streaked against several fish pathogens [29]. The results showed antagonism towards several fish pathogens, such as *Aeromonas salmonicida*, *Vibrio anguillarum*, and *Vibrio ordalii*. After feeding the Atlantic salmon with probiotics for 14 days, the fish showed improved survivability towards *Aeromonas salmonicida*, *Vibrio ordalii*, and *Yersinia ruckeri*, but not towards *Vibrio anguillarum* [29].

1.4 *Janthinobacterium Lividum*

J. Lividum is a rod-shaped and motile bacterium species, which is gram-negative. The bacterium is found to be between 0.8 to 1 μm wide and 2.5 to 3 μm long[30]. This bacterium species is aerobic and commonly isolated from soil samples and water samples[31]. In addition, *J. Lividum* has been isolated from more extreme environments, such as Antarctica[32], and Himalaya[33]. The bacterial species have been reported to grow at temperatures between 4°C and 37°C, and with varying optimal temperatures depending on the place of origin [30, 34, 32]. A metabolite produced by *J. Lividum* called violacein has shown antibacterial[35], antifungal[13], antiprotozoal[36], antiviral[37], antitumoral[38] and antioxidizing[39] properties. During microbiota analysis of the human skin, *J. Lividum* was found to be one of the major components [40]. The fact that *J. Lividum* is a major constituent of human skin, and because of the antifungal properties of the species, the bacterium species has been suggested as a probiotic against tinea pedis, which is a widespread fungal infection for human feet[41]. Studies conducted on various amphibian species have shown *J. Lividum* to be a part of the skin microbiota and to be associated with these amphibian species defenses against fungal infections [13, 42]. A study done on dead amphibians of various species following mass mortality events showed evidence of infections by a chytridiomycete fungus called *batrachochytrium dendrobatidis*[43]. These mass mortality events took place in the rain forests of Australia and Central America, demonstrating chytridiomycosis to be a widespread problem[43]. To combat this skin fungus studies have been performed on red-backed salamanders (*Plethodon cinereus*) and mountain yellow-legged frog (*Rana muscosa*). These studies showed a decreased mortality for organisms with *J. Lividum* in their skin mucosa [13, 42, 44]. The results from these studies suggest

that bioaugmentation with *J. Lividum* could be used to prevent skin fungal infections and increase the survival of colonies in captivity or survival assurance institutions[44]. *J. Lividum* has in some studies shown optimal growth in carbon dioxide concentrations above 1%, with an optimum of 5%. These capnophilic properties give this species an advantage when colonizing amphibian skin, where CO_2 concentrations are heightened due to their ability to respire through their skin [45, 46]. Studies of the genome of a *J. Lividum* strain showed the ability to produce enzymes that allow for carbon fixation, which in combination with the glyoxylate cycle can increase the performance of the glucogenesis, this could explain these capnophilic features [46].

The *J. Lividum* strains used in this project, which is referred to as MM5 and 3.116, was during a previous project, isolated from salmon fry skin and characterized as *J. Lividum* based on 16s rRNA gene sequences. These strains were able to grow on mucin media and showed no sign of pathogenicity [2]. In addition, during experiments in the ACMS group the *J. Lividum* showed significantly better colonization of salmon egg sac fry skin when compared to *Bacillus sp., Pedobacter sp., Arthrobacter sp.* and *Psychrobacter cibarius* (unpublished results, personal communication, Ingrid Bakke). The antifungal and capnophilic properties of *J. Lividum* makes it an interesting candidate for dealing with problems with fungal infections in aquaculture. As the water mold, Saprolegnia can be a problem during freshwater stages [11]. These antifungal properties of *J. Lividum* could potentially be effective against Saprolegnia, and the bacteria may, therefore, be an interesting alternative treatment as a probiotic.

1.5 Violacein

Violacein is a metabolite produced by various bacterial strains, for example *Chromobacterium violaceum (C. Violaceum)*[47], *Duganella* sp.[48], *Collimonas* sp.[49], *Pseudoalteromonas*, *microbulbifer*[50], *Iodobacter*[51], and *J. Lividum*[52]. These bacteria do all belong to the proteobacteria phylum, and the class, order, and family of the mentioned bacteria are shown in Table 1. Violacein is a purple pigment that is insoluble in water [35, 38]. Violacein produced by *C. Violaceum* is most studied, as the production of the purple pigment was first discovered in this species [47]. The synthesis of violacein is regulated by a five gene operon, consisting of VioA, VioB, VioC, VioD, and VioE [53]. The expression of this operon is regulated by a quoring sensing mechanism, which increases expression with increasing concentrations of signaling molecules called N-acyl homoserine lactones[54]. Studies on *J. Lividum* has shown

that violacein production is regulated by janthinobacterial autoinducer, which is synthesized by an autoinducer synthetase (JqsA) [31]. The purple pigment is a secondary metabolite formed by a condensation reaction between two tryptophan molecules [55, 56]. The maximum absorbance of violacein is reported to be at 585nm [54]. This secondary metabolite accounts for *J. Lividums* antiviral[37], antiprotozoal[36], antibacterial[35], antifungal[13], antitumoral[38] and antioxidizing[39] properties. A study [57] has shown that violacein targets the cytoplasmic membrane in bacteria leading to rips and holes in the membrane and that this leads to leakage of ATP from the cell. The purple pigment binds to liposomes made with bacterial phospholipids and disturbs their structure and their permeability[57]. Violacein seems to be most active against gram-positive bacteria[57]. Studies of inhibition of viral replication have shown a weak inhibition of the following virus types; herpes simplex virus type 1 (Strain KOS and ATCC/VR-733), poliovirus type 2, and simian rotavirus SA11 [37]. Studies on the effect of violacein on the protozoa *Plasmodium falciparum* showed that the pigment killed the protozoa and protected infected mice from death[36]. Violacein has shown strong antioxidizing potential, this is suggested to play an important role in the violacein producing bacterias defense against oxidative stress[39]. In vitro studies of leukemia and lymphoma cells has shown that violacein is effective against these cells, these results indicate promising potential as a therapeutic agent against tumors[58]. These properties make the purple pigment an attractive target for research. The mentioned properties and others make violacein an interesting substance to use as a commercial product. Due to the biodegradability of violacein, and the production method used, it is considered as an environmentally-friendly alternative to synthetic dyes. Because of this, the application of the bacterially produced dye is suggested in the textile, toy, and food industries[59, 60]. The antimicrobial and antioxidizing properties of violacein allow for utilizing the pigment as a dye in cleansing or medicinal clothing, bags, or other packaging uses[60]. In addition, violacein is suggested as an ingredient in cosmetics [61], sunscreen[62] and insecticide[63].

Table 1: The class, order and family for various violacein producing proteobacterias according to The National Center for Biotechnology Information (NCBI)-Taxonomy classifications [64, 65]

Genus	Class	Order	Family
Chromobacterium	Betaproteobacteria	Neisseriales	Chromobacteriaceae [66]
Iodobacte	Betaproteobacteria	Neisseriales	Chromobacteriaceae[66]
Duganella	Betaproteobacteria	Burkholderiales	Oxalobacteraceae [67]
Collimonas	Betaproteobacteria	Burkholderiales	Oxalobacteraceae [68]
Janthinobacterium	Betaproteobacteria	Burkholderiales	Oxalobacteraceae [67]
Massilia	Betaproteobacteria	Burkholderiales	Oxalobacteraceae [67]
Pseudoalteromonas	Gammaproteobacteria	Alteromonadales	Pseudoalteromonadaceae [69]
Microbulbifer	Gammaproteobacteria	Cellvibrionales	Microbulbiferaceae [70]
Myxococcus	Deltaproteobacteria	Myxococcales	Myxococcaceae [71]

Production of violacein has been reported to be dependent on various culturing conditions. pH has been shown to affect the production, where a neutral pH of 7.0 was reported to yield a 3.8 fold higher violacein production compared with pH 6.0 or 8.0 for a *J. Lividum* strain [60]. A pH of 6.7 was reported to be optimum for a *Duganella* strain [48]. A lower pH of 5.0 gave inhibition of the violacein production, while a higher pH of 9.0 was hostile towards the *J. Lividum* strain [60]. The optimal temperature for violacein production varies depending on the strain and its place of origin. A *J. Lividum* strain isolated from antarctic snow gave the best violacein yield at 22°C [72], while other strains produced the most violacein at 25°C [73, 60]. A *J. Lividum* strain isolated from low-temperature sewage showed violacein production at a temperature between 10°C and 37°C [73]. A study done on a *J. Lividum* strain isolated from cold, non-permafrost soil in Alaska showed no violacein production when temperatures rise above 20°C [74]. The carbon source has also been shown to affect the violacein production in *C. Violaceum*. While violacein production has been shown on glucose, an increased concentration of glucose resulted in a decrease in violacein production [75]. The addition of glycerol to nutrient broth medium to a concentration of 1% has been shown to increase the violacein production in a *J. Lividum* strain[60]. An increased violacein production has also been observed after the addition of concentrations of ampicillin in the range of 0.1-0.4 μg/ml [60].

1.6 The violacein operon

An operon is a unit consisting of genes with related properties and regulatory sequences [76]. The operon is a mechanism for the co-regulation of biochemical processes in cells, where genes coding for products that participate in related processes are transcribed together. Many mRNAs in prokaryotic organisms are polycistronic, which means that multiple genes are transcribed together [77]. The regulatory sequences of the operon are called operator and promoter [76]. The promoter act as a binding site for the polymerase initiating transcription. The promoter sequence varies between different operons, which affects the binding affinity of the polymerase. This affects the frequency of transcription. To down-regulate the transcription activity of the operon proteins called repressors can bind to the operator site, this action blocks the movement of the polymerase and stops the transcription. Binding of a signal molecule to the repressor causes dissociation, and the transcription can proceed. This is called negative regulation. Positive regulation is when the binding of a molecule called an activator to the regulatory sequences enhance the polymerase activity. Prokaryotic operons usually consist of two to six genes, but can occasionally consist of more than 20 genes[77]. The lac operon of *E. Coli* was the first described operon. The genes of this operon give the bacteria the ability to break down lactose to glucose and galactose and utilize them as a source of energy. This operon consists of three genes, and regulatory sequences[76].

The violacein operon is the regulatory sequence responsible for regulating the production of the pigment violacein. The violacein operon consists of five genes, VIOA-E, responsible for catalyzing steps in the production of violacein [53]. The expression of the violacein operon is regulated by a quorum sensing mechanism, which is a system for intracellular communication regulating gene expression based on population density. This communication system is based on a variety of extracellular signaling molecules called autoinducers. These autoinducers are a variety of N-acyl homoserine lactones [78]. For *J. Lividum* these autoinducers are called janthinobacterial autoinducer, and are synthesized by an autoinducer synthetase [31]. The violacein operon is proposed to be a better candidate to distinguish between violacein producing organism at species level compared to the 16s rRNA gene because of it's length (about 7kb) and a higher degree of variability [79].

1.7 Aims

The first major aim of this master thesis is to identify growth conditions for violacein production *Janthinobacterium* strains, 3.116 and MM5, isolated from salmon fry skin. The second major aim of this master thesis is to do a phylogenetic analysis of the evolution of the violacein operon. Other objectives are:

- To describe the growth of the MM5 and 3.116 strain on general media.
- Examine potential antagonistic effects of MM5 and 3.116 on other bacteria.
- Isolate and sequence the violacein operon of MM5 and 3.116.

2 Material and Methods

2.1 Characterization of the growth of MM5 and 3.116

Growth characteristics, including generational time, violacein production on different media and conditions, antagonistic properties, and susceptibility to antibiotics was examined.

2.1.1 Generation of the growth curve for MM5 and 3.116

To find the growth rate of MM5 and 3.116 on a general rich medium a growth curve was made by measuring the optical density (OD) of a growing batch culture. For both strains, an overnight culture was prepared in 13 milliliters (ml) tubes containing 3ml of Luria-Bertani (LB) medium. Four Erlenmeyer (EM) flasks (250ml) were sterilized and filled with 50 ml LB-medium. Two EM flasks were inoculated with 1 V/v% overnight culture of MM5, and two flasks were inoculated with 3.116. The flasks were incubated at 22 °C and 120 rpm. OD_{600} was measured after inoculation, and every hour for 15 hours using (LB-Medium as blank). Then measurements were done at 26, 27, 30, 31, 52, and 53 hours. The results from the OD measurements were used to make growth curves. For calculation of the generational time of MM5 and 3.116, OD data from the exponential phase was used (Eq. 1 and Eq. 2).

$$\mu = \frac{lnOD_2 - lnOD_1}{t_2 - t_1} \tag{1}$$

$$\text{Generation Time} = \frac{ln2}{\mu} \tag{2}$$

2.1.2 Cultivation conditions and media

To examine which cultivation conditions were promoting violacein production, different media and conditions were utilized. The agar media used were Luria-Bertani agar (LA), brain heart infusion (BHI), Cooked meat broth (CMB), R2A (with various glycerol concentrations), EPS-sucrose medium, and NA (with and without glycerol). In addition, different agar concentrations (1.5% and 1% agar) was used. Recipes for the media are shown in Appendix A. Additionally, LB medium was used as a liquid medium. The temperatures and light conditions used for incubation are specified with the results. A single colony from an LA plate was used as inoculum.

2.1.3 Cross-streaking of MM5 and 3.116 with other bacterial strains

To examine the potential antagonistic properties of the *Janthinobacterium* strains, MM5 and 3.116, cross-streaking on agar-plates was performed. For 3.116, three different agar plate media were used (BHI, NA, and R2A 2% Glycerol, see Appendix A). For MM5, two (different) agar plate media were used (R2A 2% Glycerol and LB, see Appendix A). The *Janthinobacterium* isolates, MM5 and 3.116, were streaked on their own agar plates in a straight line. This procedure was repeated for the different plates used for the two strains. The agar plates were incubated at 20°C for three days, to get considerable growth of the *Janthinobacterium* strains. Then strains representing the genera *Arthrobacter, Pedobacter, and Psychrobacter*, isolated from salmon fry skin, were streaked out perpendicular to the outgrown *Janthinobacterium* streak, as shown in figure 1. Then the agar plates were incubated at 20°C for three days (until considerable growth was observed for each strain) [80]. The plates were visually inspected for growth inhibition of the growth of the *Arthrobacter, Pedobacter, and Psychrobacter* isolates.

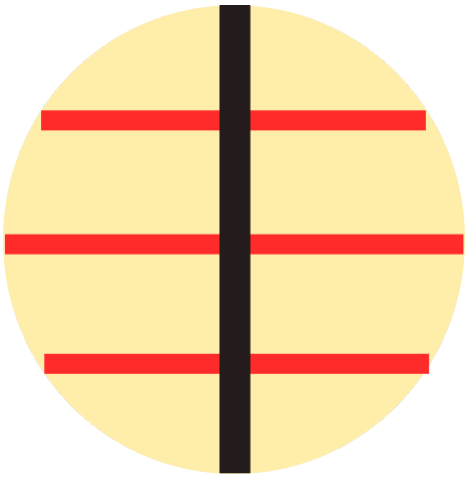


Figure 1: Schematic presentation of cross-streaking of bacterial isolates on agar plates. The black line represents the strain with the potential antagonistic properties (in this case *Janthinobacterium*), and the red lines represents three other strains that were cross-streaked[80]

2.1.4 Examination of antibiotics' susceptibility using an antibiogram approach

The susceptibility of the *Janthinobacterium* strains, MM5 and 3.116, for various antibiotics, was examined using and antibiogram approach. The antibiotics used in the antibiograms were Ampicillin, Chloramphenicol, Kanamycin, Neomycin, and Polymixine. MM5 and 3.116 were grown in 13 ml growth tubes with 3ml LB medium at 28°C overnight. Of the overnight cultures, 100 μl were streaked out on five LB-plates by using a Drigalski spatula. The five antibiotic types were diluted to three different concentrations (Table 2). Three Whatman filter paper

disks were dispersed on each LB-plate. Dependent on the size of the Whatman filter paper disk, 50 μ (on large disks) or 25 μ (on small disks), of antibiotics was applied to each filter paper disk. The plates were incubated at 20°C for two days, before visual inspection, and the potential inhibition was determined

Table 2: The concentrations used for antibiotics used in the antibiograms.

Antibiotica	Concentrations in μg/ml		
Ampicillin	100	50	25
Kanamycine	50	25	12.5
Chloramphenicol	25	12.5	6.5
Polymixine	100	50	25
Neomycine	50	25	12.5

2.1.5 Microscopy

To observe the strains (and their potential tendency to grow in aggregates) observation with a Carl Zeiss Axio Imager.Z2 microscope was performed with overnight cultures of MM5 and 3.116.

2.2 Isolation and amplification of DNA

2.2.1 Isolation of DNA

DNA of 3.116 and MM5 was isolated to use as a template in PCR-reactions. Overnight cultures grown in 13 ml growth tubes with 3ml LB medium was centrifuged at 13000rpm for one minute in a tabletop centrifuge to harvest the cells. The supernatant was removed, and the precipitate was used for further DNA isolation. Isolation was performed using DNeasy® PowerSoil® kit(Qiagen) according to the protocol showed in Appendix B. To determine the amount and purity of the product of the isolated DNA, the isolate was analyzed using the NanoDrop™ One (Thermo Scientific).

2.2.2 PCR of the violacein operon and 16s rRNA gene

To amplify the violacein operon and the 16s rRNA gene, for the MM5 and 3.116 genes, PCR was conducted. The previously isolated DNA of MM5 and 3.116 was used as a template. The DNA extracts were diluted to 1:10 with PCR-grade water to final concentrations of approximately 9.3 ng/μL for MM5 and 4.0 ng/μL for 3.116. The template was added to a 24 μL

master mix made according to table 3. The primer combinations used are shown in table 4. To find the most effective PCR-cycling conditions various elongation times and an annealing temperature gradient between 53-63 °C was tested. The optimal elongation time seemed to be 20 seconds, while the optimal temperature was found to be 63°C for MM5 templates and 53°C for 3.116 templates. The PCR was carried out in a T100^{TM} Thermal Cycler (BioRad). The cycling conditions used were as follows: Initial denaturation at 98 °C for one minute, followed by 38 cycles of 98 °C for 15 seconds, annealing with previously stated temperatures depending on the template for 20 seconds, followed by elongation at 72 °C for 20 seconds. After the 38 cycles, a final elongation at 72 °C for five minutes followed. Finally, the temperature was reduced to 4 °C for one minute and hold at 10 °C until the samples were collected.

Table 3: The components needed to make 24 μL of mastermix for PCR-reaction.

Component	**Supplier**	**Amount x1 (µL)**
PCR-grade water		16,6
5x Phusion buffer HF (7,5 mM MgCl2	Phusion Kit Illumina	5,0
Rev primer (10mM)	Sigma-Aldrich	0,75
Fwd Primer (10mM)	Sigma-Aldrich	0,75
dNTP (10mM each)	VWR	0,5
$MgCl_2$ (50mM)		0,25
Phusion Hot Start DNA polymerase	Phusion Kit Illumina	0,15
Total		24

Table 4: The combinations of primers, their target gene, and their expected length, used in PCR reactions

Primer pair	**Target gene**	**Expected product length (Kb)**
VIOA-1.F+VIOB-2896.R	Vio-A + first half of Vio-B	2.9
VIOB-2840.F+VIOC-5617.R	Last half of Vio-B + Vio C	2.8
VIOD-5622.F+VIOE-7335.R	Vio-D + Vio E	1.7
VIOA-1.F+VIOA-1207.R	Vio-A	1.2
VIOB-2840.F+VIOB-4322.R	Last half of Vio-B	1.5
VIOC-4336.F+VIOC-5617.R	Vio-C	1.3
VIOE-6752.F+VIOE-7335.R	Vio-E	0.5
EUB8F+1492R	16s rRNA	1.5
Eub8F+518R	V1-V3 region of 16s rRNA	0.5

2.2.3 Gel electrophoresis

To examine the size, amount, and quality of the PCR product, analysis by using agarose gel electrophorese was conducted. Agarose solution (1%) was prepared by dissolving agarose in a TEA-buffer (1%) by boiling in a microwave oven. Of the Agarose solution, 50ml was poured

into an EM-flask and stained by adding 2.5μL of GelRed®(Biotium). To make the gel, the gel solution was poured into a gel chamber containing a gel comb. The solution solidified (to a gel) after around 20 minutes. PCR product (4μL) mixed with 1μL 6x Loading dye (Thermo Scientific) was applied to the gel wells. GeneRuler ™ 1 kb Plus DNA Ladder (Thermo Scientific) was used as a reference to indicate size. The gel electrophoresis was performed at 100-115v for around 1 hour. Then the gel was visualized by using a G:Box HR Geldoc (Syngene).

2.2.4 Purification of PCR-product and Sanger sequencing

Before the sequencing, the PCR-product was purified to remove salts, primers, and nucleotides. The purification was done using the QIAquick® PCR Purification Kit (Qiagen) by following the protocol, as shown in Appendix C. The purified PCR product (5μL) were mixed with 5μL PCR primer (table 5) and sent to Eurofins Genomics for Sanger sequencing. The DNA sequences were sequenced by Eurofins Genomics and returned as sequences with associated chromatograms to verify the quality of the given sequence

Table 5: The PCR-primer sequences (Sigma-Aldrich) used to amplify the gene regions of the violacein operon and the 16s rRNA gene.

Primer	Sequence (5'-3')	Target Gene
VioA-1.F	ATG AGC ACG TAT TCT GAC ATT TGC	VIOA
VioA-1207.R	TGA TCA GGC TGC CTT CCA TCC	VIOA
VioB-1311.F	ATG AGC CTA CTT GAC TTC CCC CG	VIOB
VioB-2840.F	CTA CGC CTT CCT CTA CCG GC	VIOB
VioB-2896.R	ATG AAG GGA TAC ACG AGC TCG	VIOB
VioB-4322.R	TGA CAT CTT TCC CCG AGA TAA ATC GG	VIOB
VioC-4336.F	ATG CAT AAA ATC ATT ATC GTC GGC G	VIOC
VioC-5617.R	CCC TTC CAA GTT TGT ACC AAA CG	VIOC
VioD-5622.F	TTA ATG AAN ATT CTC GTC ATC GGC G	VIOD
VioD-7071.R	GAA CGG NGT CAC CTC ATC GG	VIOD
VioE-6752.F	CCA TGC CGA CAC ACG TCN C	VIOE
VioE-7335.R	TCA GGT GTT GCA AGA CGT AAA GAC G	VIOE
Eub8F	AGA GTT TGA TCM TGG CTC AG -	16s rRNA
805R	ATT ACC GCG GCT GCT GG	16s rRNA
1492R	TAC GGY TAC CTT GTT ACG ACT T	16s rRNA

2.2.5 Isolation of PCR products from agarose gels

For PCR products with unspecified products in addition to the expected product, the part of the gel containing the desired band was cut out. Firstly, to separate the wanted PCR products from the unspecified products, agarose gel electrophoresis was conducted using 20 μL PCR product

mixed with 5 μL 6x Loading dye (Thermo Scientific). After the electrophoresis, the gel was put under UV light by using a G:Box HR GelDoc (Syngene). The bands with the desired length were cut out from the gel using a scalpel. The DNA was extracted from the gel by following the QIAquick® Gel Extraction Kit and QIAquick® PCR Gel Cleanup Kit protocol showed in Appendix D. The extracted DNA was purified using the method described in subsection 2.2.4.

2.3 DNA sequence analyses

2.3.1 Editing, assembly, and aligning of DNA sequences

The sequences returned from Eurofins Genomics was quality checked, edited, and assembled by using the Clone Manager 9 (Sci Ed Software). Chromatograms were used to review the quality of the sequences, and to correct eventual uncertain nucleotide positions. Regions of low quality (especially at the start and end of the sequences) were removed before sequences belonging to the same gene were aligned and assembled together using the tool Global-Ref in the software Clone Manager 9 program package.

2.3.2 16s rRNA gene-based classification of MM5 and 3.116

The 16s rRNA gene sequence results were analyzed using the SeqMatch tool and the Classifier tool made by the Ribosomal database project (RDP). The Classifier and SeqMatch tool search the database for similar 16s rRNA sequences. The classifier gives the result on the family level, with percent confidence in the classification. The SeqMatch tool gives the results on the genus level, with a SeqMatch score (S_ab) to verify the quality of the match. The SeqMatch score (S_ab) is calculated by comparing the number of unique 7-base oligomers shared between the query sequence and the sequence given by RDP, divided by the lowest number of shared oligomers in one of the two sequences [81]

2.3.3 Screening for violacein operon

Violacein production is regulated by an operon consisting of five genes, VioA, VioB, VioC, VioD, and VioE[53]. To confirm that MM5 and 3.116 possess this gene, a study on violacein operons in *Janthinobacterium* was conducted. The violacein operon of related strains given from the 16s rRNA analysis was searched for using the NCBI nucleotide database [82]. In addition, a nucleotide Basic Local Alignment Search Tool (BLAST) was done with the resulting

operons, where some of the best results were selected for further use [83, 84]. Using the SnapGene® software (SnapGene software (from Insightful Science; available at snapgene.com), a Multiple Sequence Alignment was performed of the violacein operons. The resulting consensus sequence was used to check for conserved regions and to annotate primers consisting of 20-25 base pairs, with a primer melting temperature (TM) of 58-60 °C. A schematic representation of the violacein operon with annotated primers and primer location are shown in fig. 2

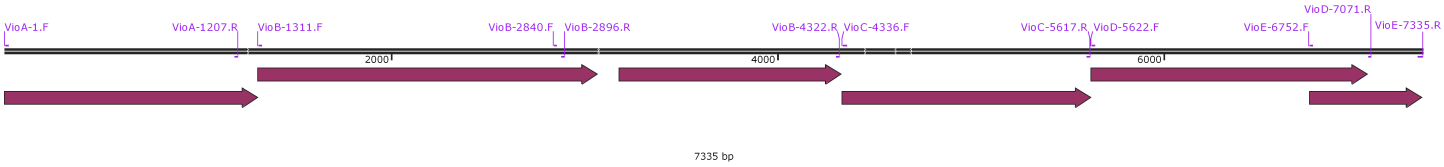


Figure 2: A schematic representation of the violacein operon of *Janthinobacterium* with annotated genes and primers. The primers are named after the gene, transcription direction and the base number the primer starts at. The figure is made with the SnapGene® software (SnapGene software (from Insightful Science; available at snapgene.com)

2.3.4 Identification and retrieval of DNA sequences for bacterial violacein operons from the NCBI database

The sequences used to make the primers for the violacein operon in section 2.3.3 was reused. In addition, the NCBI database was used to search for gene-sequences of bacteria known to produce violacein. Their violacein operons and 16s rRNA sequences were saved [82]. The accession numbers and taxonomic information for the relevant sequences are given in table 6. The UGENE software (unigene software) was used to identify and extract sequences representing the violacein operon and the 16s rRNA gene [85].

Table 6: The strains used for analysis of violacein operon and 16s rRNA gene with accession numbers and classification on species level.

Strain	Species	NCBI accession number
257-1	*Chromobacterium sp.*	CP043473
XC0014	*Chromobacterium Vaccinii*	CP022344.1
ATCC12472	*Chromobacterium Violaceum*	AE016825.1
ATCC 31532	*Chromobacterium Violaceum*	LC000628
cv1192	*Chromobacterium Violaceum*	CP024028
—-	*Chromobacterium Violaceum*	AF172851
—-	*Chromobacterium Violaceum*	AB032799
MPS11E8	*Collimonas sp.*	FJ965838
B2	*Duganella sp.*	GQ266676
ZLP-XI	*Duganella sp.*	KJ131413
BHSEK	*Janthinobacterium Agaricidamnosum*	CP033019
BP01	*Janthinobacterium Lividum*	EF063591
DSM1522	*Janthinobacterium Lividum*	DQ074977
NBRC12613	*Janthinobacterium Lividum*	LC000630
LM6	*Janthinobacterium sp.*	CP019510
B2	*Massilia Violaceinigra*	CP024608
DSM14675	*Myxococcus stipitatus*	CP004025
520P1	*Pseudoalteromonas sp.*	AB573101
S40542	*Pseudoalteromonas Luteoviolacea*	CP015413

2.3.5 Alignment of sequences and construction of phylogenetic trees

The violacein operon and the 16s rRNA gene sequences of MM5 and the sequences retrieved from the NCBI database were aligned by using the software MEGA X (Molecular Evolutionary Genetics Analysis across computing platforms), the multiple alignment function, and the default settings[86]. Using the aligned sequences, Maximum likelihood (ML) and Neighbor-joining (NJ) phylogenetic trees were constructed using the bootstrap method with 500 replications and the Tamura-Nei model for DNA sequence evolution. The Tamura-Nei model is a mathematical model for DNA sequence evolution that takes unequal nucleotide frequencies, excess transitions, and variation of substitution range between various sites into account [87]. Neighbor-joining is a method for constructing phylogenetic trees based on pairs of operational taxonomic units (neighbors), these neighbors are put together in a way that minimizes the branch length at each stage of the clustering by using evolutionary distance data [88]. NJ is a less computationally intractable method then ML phylogenetic trees, which is considered a computer heavy method [89]. ML computes the probability of different topologies, and the topology with the highest probability (likelihood) is chosen as the ML phylogenetic tree [90].

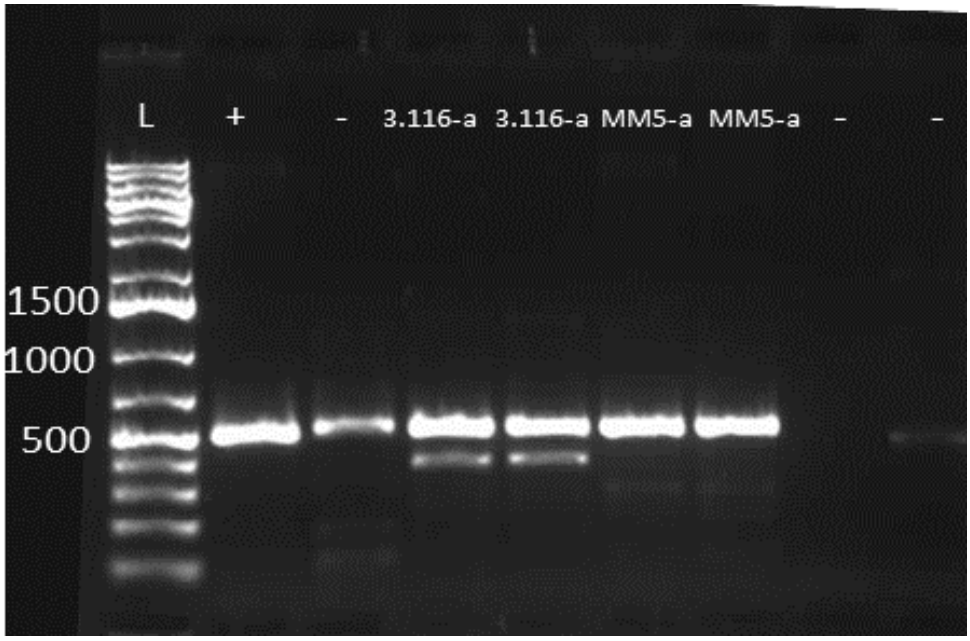
Bootstrapping is a statistical method used among other things in phylogenetic analysis. A higher bootstrap value indicates higher confidence in the result. A bootstrap value of more than 95 is usually considered to represent a correct node [91]. The *Myxococcus* strain was selected as a root in the trees due to being more distantly related to the *betaproteobacteria* and *gammaproteobacteria* [92].

3 Results

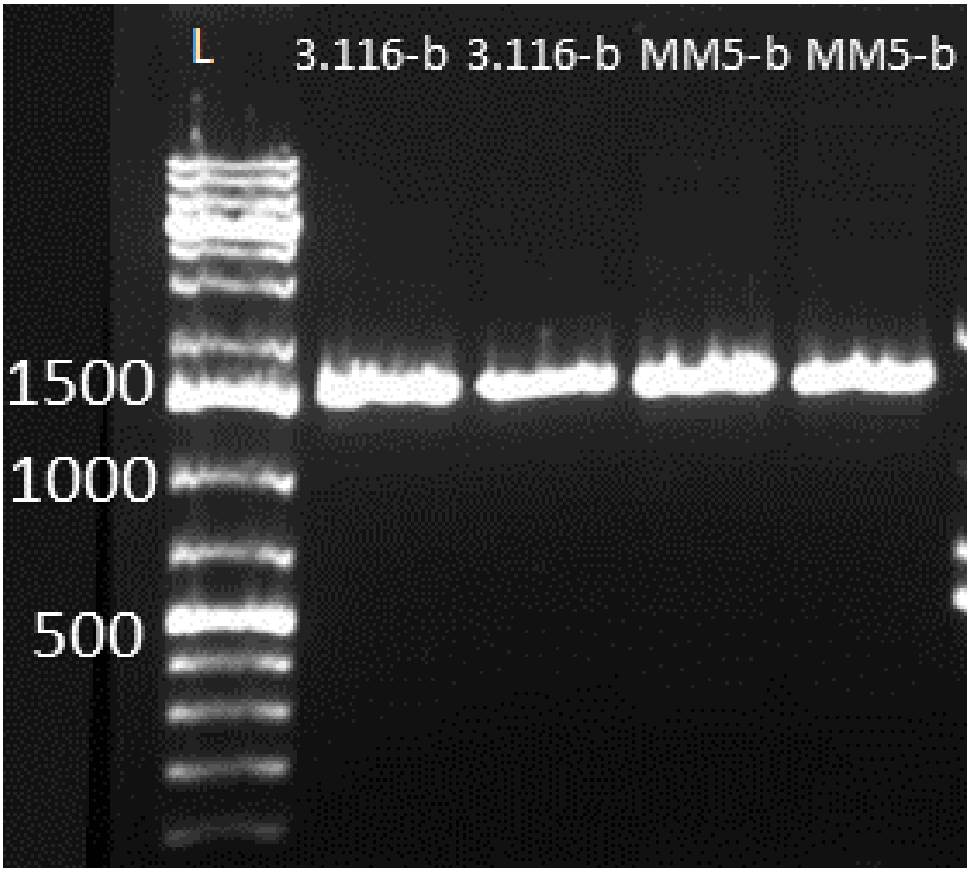
3.1 16s rRNA gene sequences for the *Janthinobacterium* strains 3.116 and MM5

To classify the two strains isolated from salmon fry, amplification of the 16s rRNA gene was performed by using combinations of the primers EUB8F, 1492R, and 518R. The 16s rRNA gene was further determined by using the EUB8F, 1492R, and 805R primers in Sanger sequencing. Agarose gel electrophoresis was conducted to examine the size and amount of PCR product. This resulted in strong bands at the expected size of about 500bp for both MM5 and 3.116 when using EUB8F and 518R as a primer, and around 1500bp when using EUB8F and 1492R as primers. However, the PCR product of 3.116 using EUB8F and 518R included a weaker band. The PCR product was purified and sent to Sanger sequencing. Along with the base sequences the result included a chromatogram indicating a high-quality result for large parts of the sequence. The 16s rRNA sequences of MM5 and 3.116 can be seen in Appendix E.

By the use of the Ribosomal database project (RDP) tool called Classifier the two strains, MM5 and 3.116 were identified to be of the *Janthinobacterium* genus with 100% confidence [81]. By using the RDP SeqMatch tool the closest matching type strain was determined. For MM5 the 16s rRNA gene sequence is closest related to *Janthinobacterium lividum* with an s_ab score of 0.981. For 3.116 the 16s rRNA sequence is closest related to *Janthinobacterium lividum* with a S_ab score of 0.975 and *Janthinobacterium sp. 68* with a S_ab score of 1. The 16s rRNA gene sequences of MM5 and 3.116 was aligned with the 16s rRNA sequence of the *J. Lividum* type strain by using the clone manager 9 software to compare the strains. This resulted in 99% match for both strain, and 6 non-matching bases for MM5 and 8 non-matching bases for 3.116. The alignment can be seen in Appendix F.



(a)



(b)

Figure 3: Pictures of electrophorese gels with amplified 16s rRNA gene of the two *Janthinobacterium* strains, MM5 and 3.116. Gel a) contains PCR product amplified with EUB8F and 518R as primers. While gel b) contains PCR product using EUB8F and 1492R as primers.

3.2 Characterization of growth for the *Janthinobacterium* strains

3.2.1 Growth-curve for the MM5 and 3.116 strains cultivation in liquid LB medium

Using the nutritional rich LB medium, growth curves of the two strains, MM5 and 3.116, characterized as *Janthinobacterium*) was made. OD_{600} of two replicate cultures of each strain was measured during 53 hours (Fig4). For 3.116, exponential growth took place approximately between eight and fourteen hours. While for MM5 the exponential phase was found to take place approximately between three and ten hours. For 3.116 the generation time was calculated to be 0.88 hours, while the generational time for MM5 was calculated to be 1.50 hours.

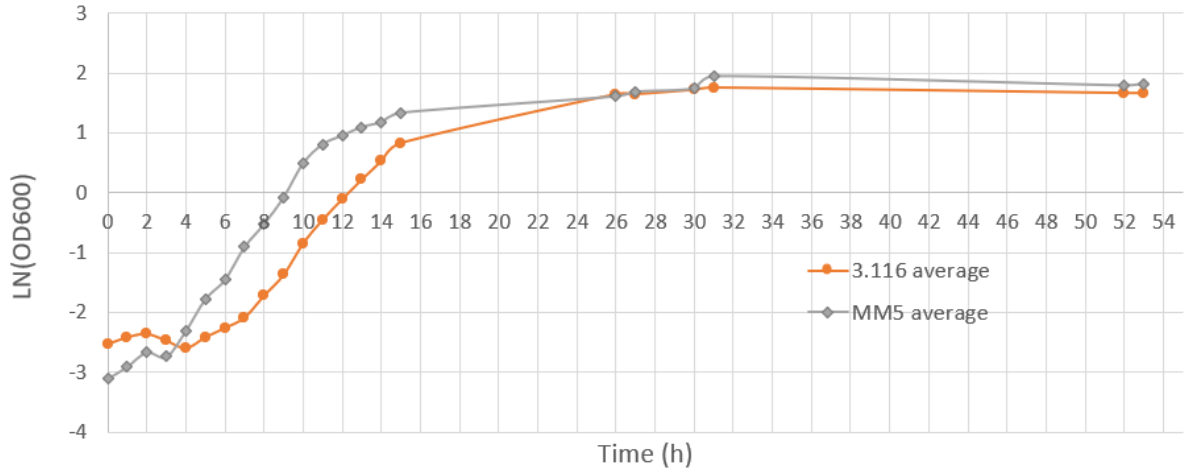


Figure 4: Growth curves for the averages of the MM5 strain and the 3.116 strain in LB medium. OD_{600} was measured once every hour for the first 15 hours, thereafter with larger time intervals. The curves are generated by averaging two samples of each strain, and by using the natural logarithm of the absorbance values.

3.2.2 Microscopy

Microscopy was used to visually observe the two strains used in this project. Since biofilm-producing strains have a tendency of growing in aggregates, microscopy was performed the examine whether the *Janthinobacterium* strains MM5 and 3.116 grow planktonic or in aggregates in liquid cultures. The microscopy showed that both *Janthinobacterium* strains grew in aggregates, this can be seen from Fig. 5.

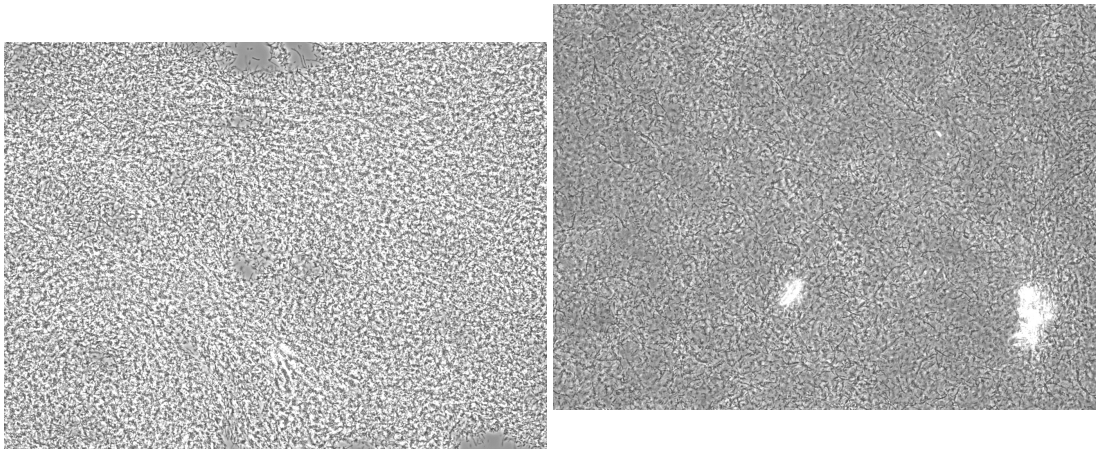


Figure 5: Photographs of MM5 and 3.116 through a Carl Zeiss Axio Imager.Z2 microscope at 20x magnification. The pictures are showing sections of the culture growing in biofilm.

3.2.3 Identifying antibiotic susceptibility of MM5 and 3.116 by using antibiograms

Resistance towards antibiotics can be used to make selective media for bacterial strains. To examine the susceptibility of MM5 and 3.116 towards selected antibiotic types, an antibiogram test was conducted. MM5 showed resistance towards all tested concentrations of kanamycin (50 μg/ml) and polymixin (100μg/ml), while it showed susceptibility to ampicillin and chloramphenicol with inhibition increasing with concentration. In addition, neomycin seemed to cause some inhibition of growth at the highest concentration. The other strain, 3.116, showed the same tendencies as MM5. A summary of the inhibition and resistance results are shown in table 7. The resulting antibiogram agar plates can be seen in Appendix G. An example of an antibiogram agar plate is shown in Fig. 6 displaying the results from the antibiogram for 3.116 tested with chloramphenicol. The example antibiogram is showing inhibition zones around the filter papers, with increasing size with increasing concentration.

Table 7: Showing results from antibiogram with antibiotic type and concentrations in μg/ml. Resistance is marked with -, and inhibition is marked with a +. Multiple + signs indicate more inhibition.

	Concentration in μg/ml	MM5	3.116
Kanamycin	50	-	-
	25	-	-
	12,5	-	-
Ampicillin	100	+++	++
	25	++	+
	20	-	-
Chloramphenicol	25	+++	+++
	12,5	++	++
	6,5	++	+
Neomycin	50	+	+
	25	-	-
	12,5	-	-
Polymixin	100	-	-
	50	-	-
	25	-	-

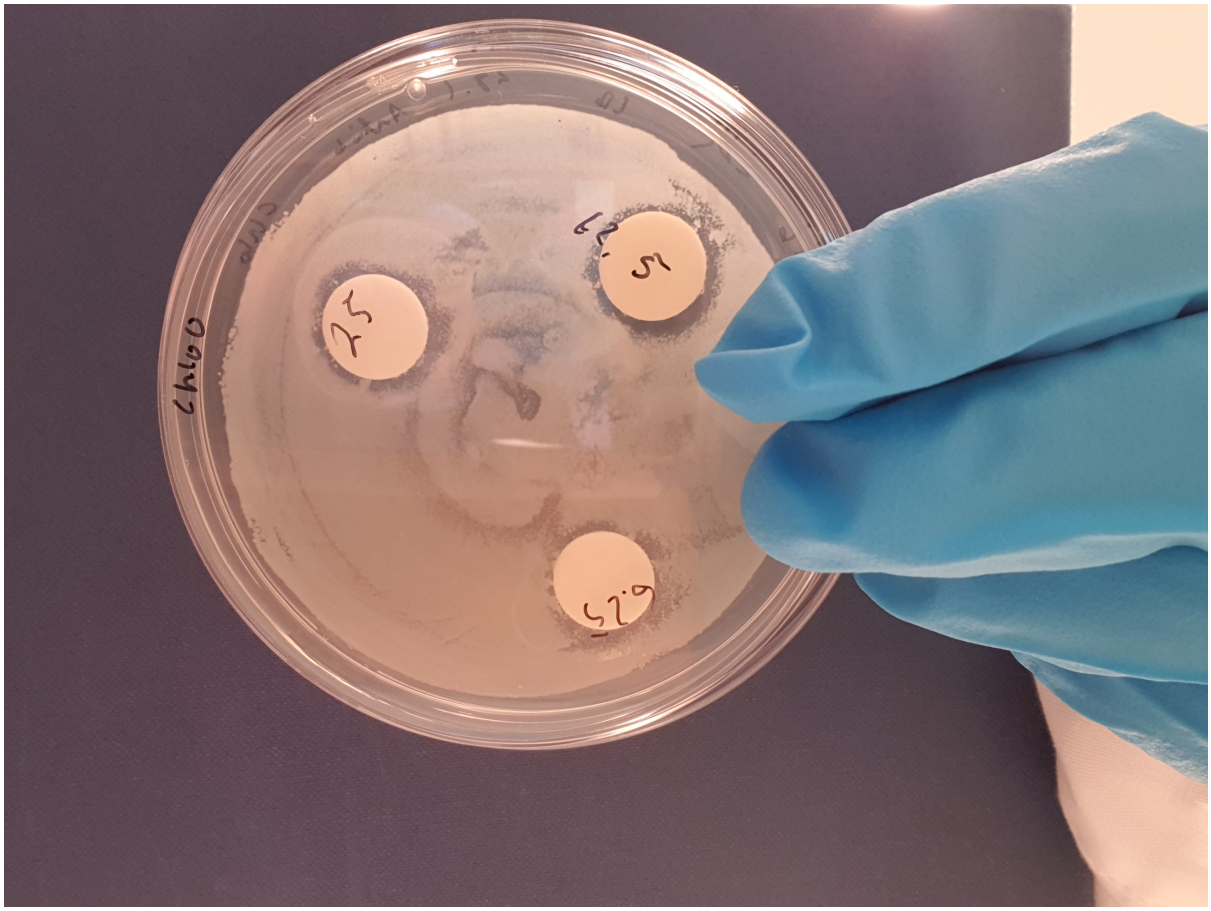


Figure 6: Antibiogram for strain 3.116 using three different concentrations of chloramphenicol (25, 12.5, and 6,5 μg/ml). The antibiogram shows increasing inhibition with increasing concentration.

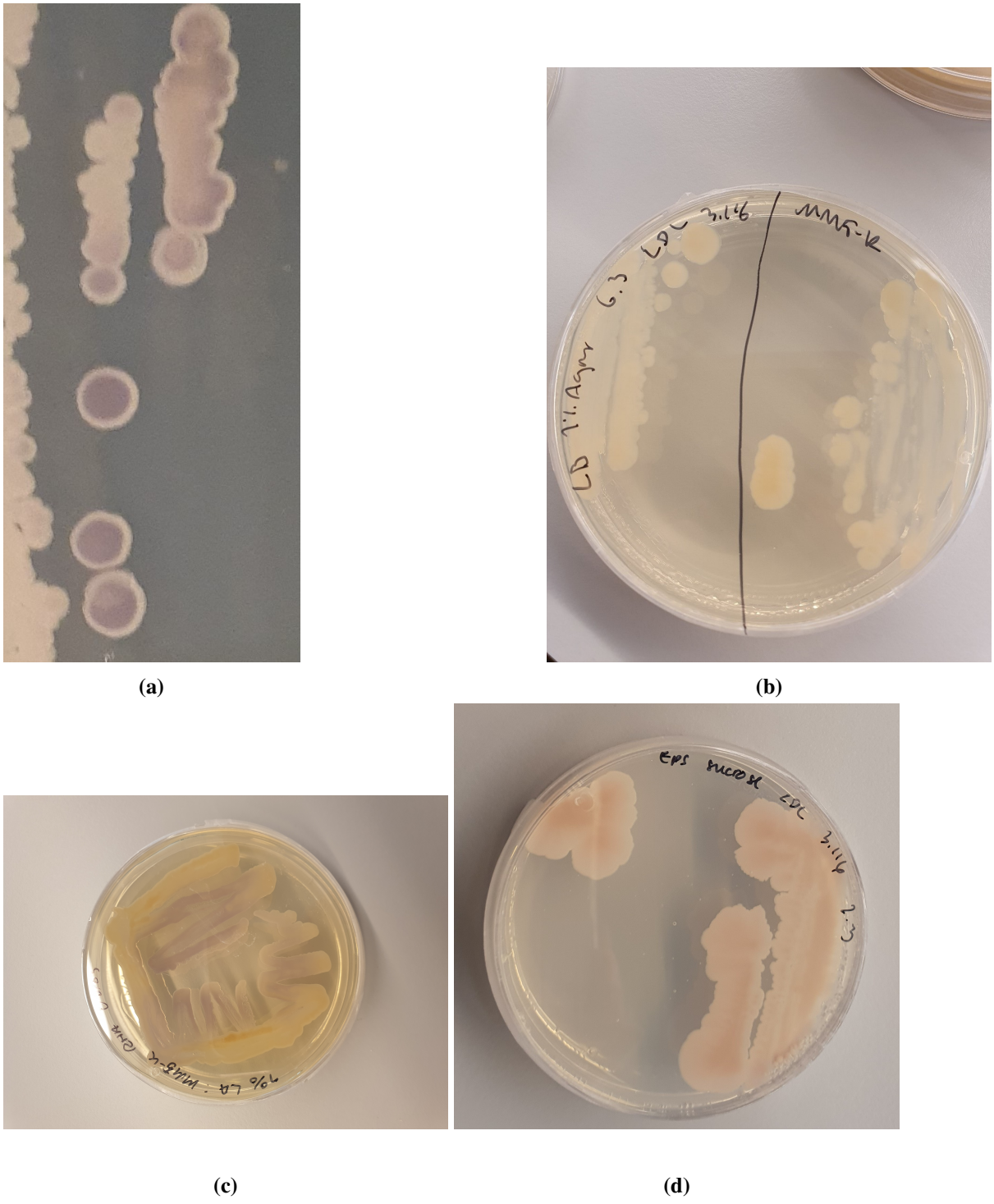
3.3 Various media and conditions tested for violacein production by MM5 and 3.116

Janthinobacterium is a known producer of the compound violacein, which can be observed as purple color when grown in a liquid medium and on agar plate medium. The strain MM5 has previously been observed to grow in purple colonies when growing on the agar plate medium. An examination of which agar plate medium and temperatures that were promoting violacein production was conducted. After growth in 28 °C for four days, MM5 was growing in purple colonies on LA 1% agar (with and without glycerol) plates, EPS-sucrose (with 1% and 1.5% agar), and R2A 1% agar (table 8). The plates containing EPS-sucrose medium gave the strongest purple color, while the other two plates only gave a slight purple tint, None of the other plates showed any indication of violacein growth after 14 days, neither for MM5 or 3.116. After 14 days the purple hue was observed to disappear, and only the plates previously observed with the strongest purple color were still purple. None of the plates cultivated at 18 °C

gave any indication of purple color. Both strains had a tendency to grow in slimy colonies, but MM5 was observed to be slimier and more sticky. Fig. 7 Shows examples of cultures growing on various agar plates. Some of the colonies of MM5 growing on the LA agar plate medium with a reduced amount of agar (1%) showed a clear purple color as shown in Fig 7c this plate was incubated on the lab bench at room temperature. The plates growing on the lab-bench would have been exposed to light. When 3.116 was grown on EPS-Sucrose media the colonies showed pink color, as shown in Fig. 7d. The remaining plates with purple growth can be seen in Appendix H.

Table 8: Showing results for growth of MM5 and 3.116 on different agar plate mediums at 18 °C and 28 °C. The plates were incubated in darkness. Growth indicates just ordinary growth, while purple indicates purple colored colonies. + and - indicates the strength of the colour.

Agar plate medium	MM5 18°C	MM5 28°C	3.116 18°C	3.116 28°C
LA 1% agar	Growth	Growth	Growth	Growth
LA 1% agar + glycerol	Growth	Purple -	Growth	Growth
LA 1.5% agar + glycerol	Growth	Growth	Growth	Growth
Mucin 1% agar	Growth	Growth	Growth	Growth
Mucin 1.5% agar	Growth	Growth	Growth	Growth
R2A 1.5% agar	Growth	Growth	Growth	Growth
R2A 1% agar	Growth	Purple -	Growth	Growth
EPS-sucrose 1% agar	Growth	Purple +	Growth	Growth
EPS-sucrose 1.5% agar	Growth	Purple +	Growth	Growth



(a) **(b)**

(c) **(d)**

Figure 7: Agar plates showing growth on LA medium with 1% agar and EPS-sucrose medium for MM5 and 3.116. a) Close up of purple colonies with MM5 growing on an agar-plate with EPS-sucros medium and 1.5% agar incubated at 28°C. b) MM5 and 3.116 growing on an agar-plate with LA medium and 1% agar incubated in an incubator at 20 °C without light. c) MM5 growing on an agar-plate with LA medium and 1% agar incubated in room temperature showing purple growth. d) 3.116 growing on agar-plate with EPS-sucrose medium showing pink growth.

3.4 Examination of potential antagonistic properties and violacein production using cross-streaking

To examine the potential antagonistic properties of 3.116 and MM5 towards three other bacterial isolates, a cross-streaking approach on agar plates was used. The three strains used, representing the genera *Arthrobacter, Pedobacter, and Psychrobacter* are all previously isolated from salmon fry in the ACMS group. In addition, the cross-streaking was performed to examine whether or not it could provoke violacein production by MM5 or 3.116. The plates were incubated at room temperature on various types of agar plate medium. None of the cross-streaked plates indicated any antagonistic effect of the MM5 or 3.116 strain towards *Arthrobacter, Pedobacter, and Psychrobacter*. No indication of violacein production was observed. An example of cross-streaking is shown in Fig. 8, the growth on this plate shows no sign of inhibition of any of the three tested strains. The remaining agar plates with cross-streaking are shown in Appendix I.

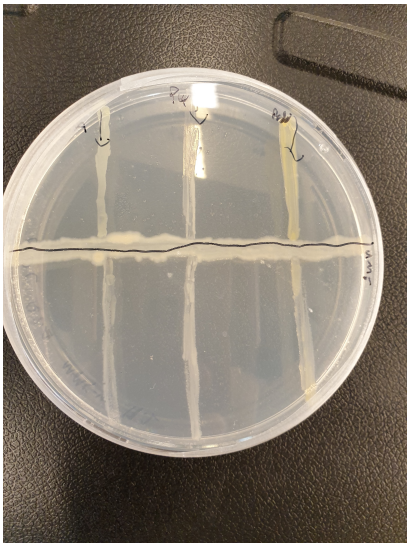


Figure 8: Agar plate showing cross-streaking of *Arthrobacter, Pedobacter, and Psychrobacter* strains, previously isolated from salmon fry, against MM5 to examine potential antagonistic effects of MM5. The agar plate with cross-streaking shows no indication of growth inhibition.

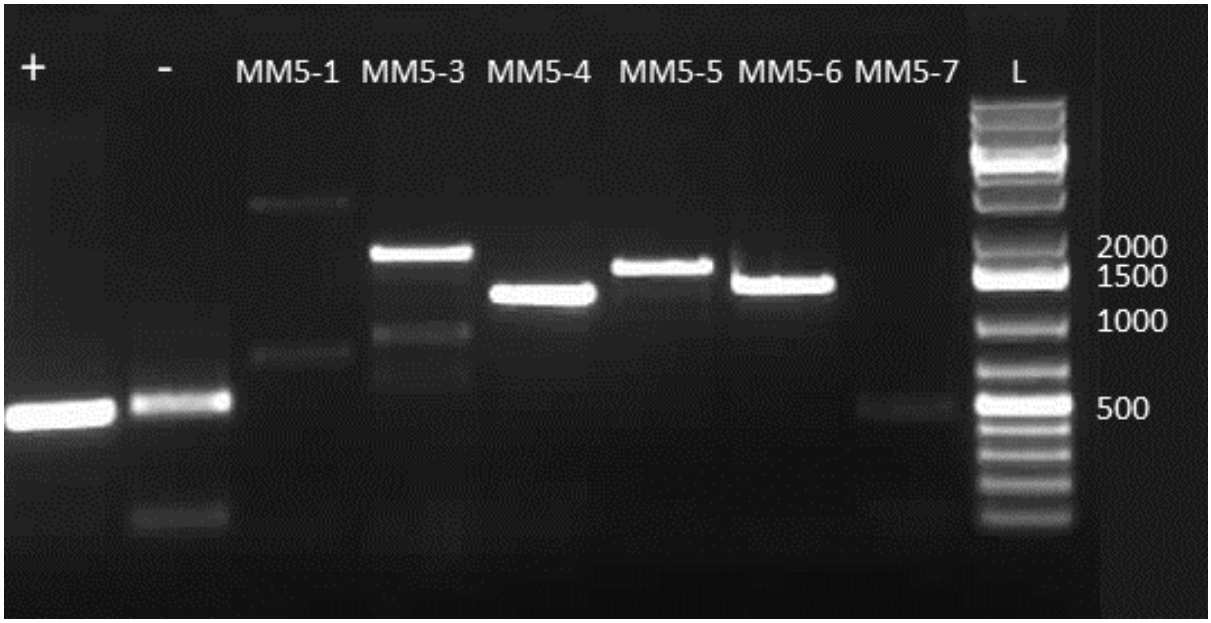
3.5 Sequence analysis of the violacein operon of MM5 and 3.116

Growth of the two *Janthiobacterium* strains, MM5 and 3.116 on different medium gave purple colonies for MM5 indicating violacein production. The aim of this part was to examine the presence of the violacein operon and to compare the violacein operons with known violacein producers.

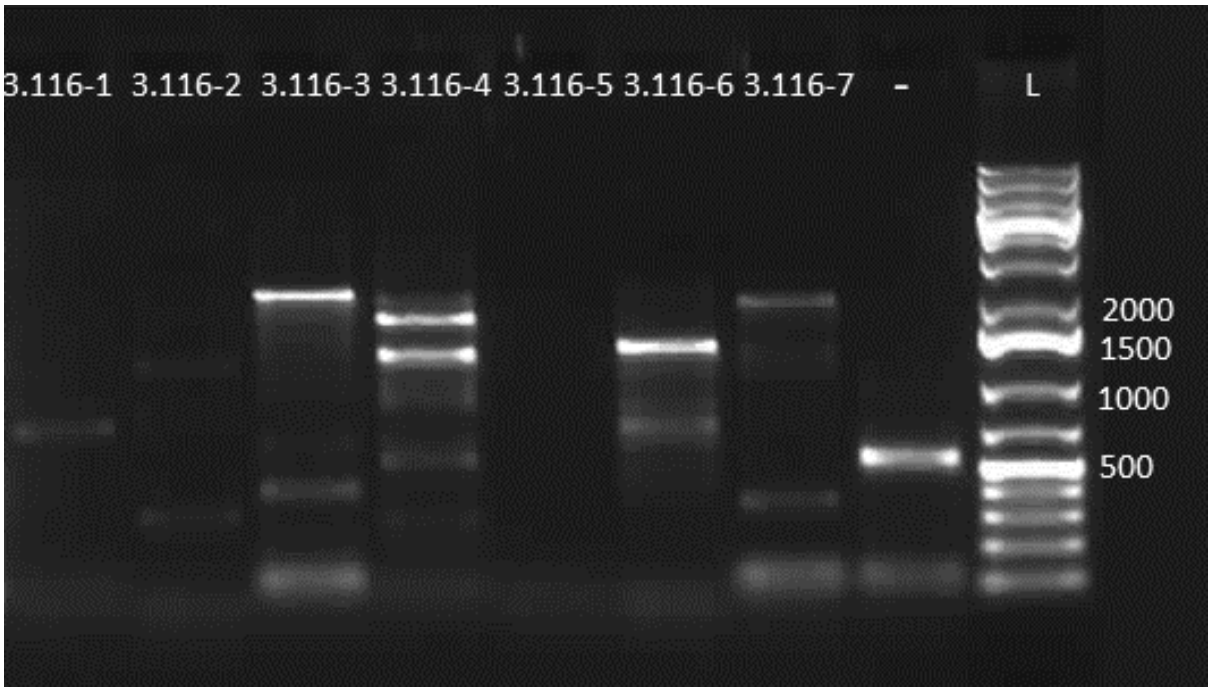
3.5.1 Amplification of the violacein operon of the MM5 and 3.116 strains

To obtain the DNA sequences for the MM5 and 3.116 violacein operon, the relevant sequence regions were first amplified in PCR reactions. To design PCR primers, conserved regions of the violacein operon were identified by sequence analysis of violacein operon sequences from various Janthinobacterium strains. Using the NCBI blast function [83, 84] and the NCBI nucleotide database [82], violacein operon sequences of strains closely related to MM5 and 3.116 was retrieved. These sequences were used to produce a consensus sequence by using the SnapGene® software (SnapGene software (from Insightful Science; available at snapgene.com), which was used to design PCR primers for amplifying the violacein operon in several PCR products. The resulting PCR primer sequences are shown in table 5, and a schematic presentation of the violacein operon and primer location is shown in Fig. 2.

By using the designed primers (table 5) seven fragments of the violacein operon was amplified by several PCR reactions. The seven fragments was using the following primers 1. VIOA1F+VIOB2896R with an expected length of 2,9kbp, 2. VIOB2840F+VIOC5617R with an expected length of 2,8kbp, 3. VIOD5622F+VIOE7335R with an expected length of 1,7kbp, 4. VIOA1F+VIOA1207R with an expected length of 1,2kbp, 5. VIOB2840F+VIOB4322R with an expected length of 1,5Kbp, 6 VIOC4336F+VIOC5617R with an expected length of 1,3kbp and 7. VIOE6752F+VIOE7335R with an expected length of 0,5kbp. To examine the size and quality of the PCR product and the an agarose gel electrophoresis was conducted. For MM5 all PCR products was of the expected size and of good quality (9a). While for 3.116 all the PCR reactions resulted in multiple products where some was of the expected size. Since none of the PCR products of 3.116 gave single bands when examined on the agarose gel (9b), bands at anticipated length were cut out, purified, and sent to sequencing. For MM5 the Sanger-sequencing was succesfull and gave sequences of good quality covering most parts of the violacein operon, except for approximately 150bp before the start of the VIOB2840F primer(Appendix E). For 3.116, on the contrary the quality of the sequences was low and could not be used for further analysis.



(a)



(b)

Figure 9: Agarose gels for PCR amplification of violacein operon. The numbers represent the following primer combinations with the following expected base pair lengths. 1: VIOA1F+VIOB2896R 2,9kbp, 2: VIOB2840F+VIOC5617R 2,8kbp, 3: VIOD5622F+VIOE7335R 1,7kbp, 4: VIOA1F+VIOA1207R 1,2kbp, 5: VIOB2840F+VIOB4322R 1,5Kbp, 6: VIOC4336F+VIOC5617R 1,3kbp and 7: VIOE6752F+VIOE7335R 0,5kbp. Gel a) contains PCR prodcuts of the violacein operon of MM5, while gel b) contains PCR products of the violacein operon of 3.116.

3.5.2 Phylogenetic analysis of the violacein operon and 16S rRNA gene sequences

To compare the violacein operon sequence of MM5 and 16s rRNA gene sequence of MM5 and 3.116 phylogenetic analysis and Multiple Sequence Alignment were conducted. The aim was to do a phylogenetic analysis of the evolution of the violacein operon. Several bacterial families is known to produce contain violacein producing genuses, such as *Chromobacterium*[47], *Duganella* [48], *Collimonas* [49], *Pseudoalteromonas*, and *J. Lividum*[52]. The strains used for these analyses are shown in table 6. The class, order, and family for these bacterias are shown in table 1. The analysis of the 16s rRNA gene is used as a marker representing vertical evolution. A schematic presentation of the alignment is shown in Fig. 10, with 70% consensus selected. 70% consensus is a threshold dictating how much similarity is needed to indicate similarity. Based on the % of matching bases (table 9) and the violacein operon of the *Janthinobacterium* species seems to be well conserved. The same tendency can be observed for the other strains of the *Oxalobacteraceae* family. The *Chromobacterium* seems to have slightly fewer matching bases and conserved regions. The *Janthinobacterium* strain MM5 has a lower % of matching bases when compared to the other *Janthinobacterium* strains. The two *Pesudoalteromonas* strains had few conserved regions compared to the other strains. In addition, the end of the *Myxoccocus* sequence seemed to be different from the other sequences. The full alignment can be seen in Appendix J.

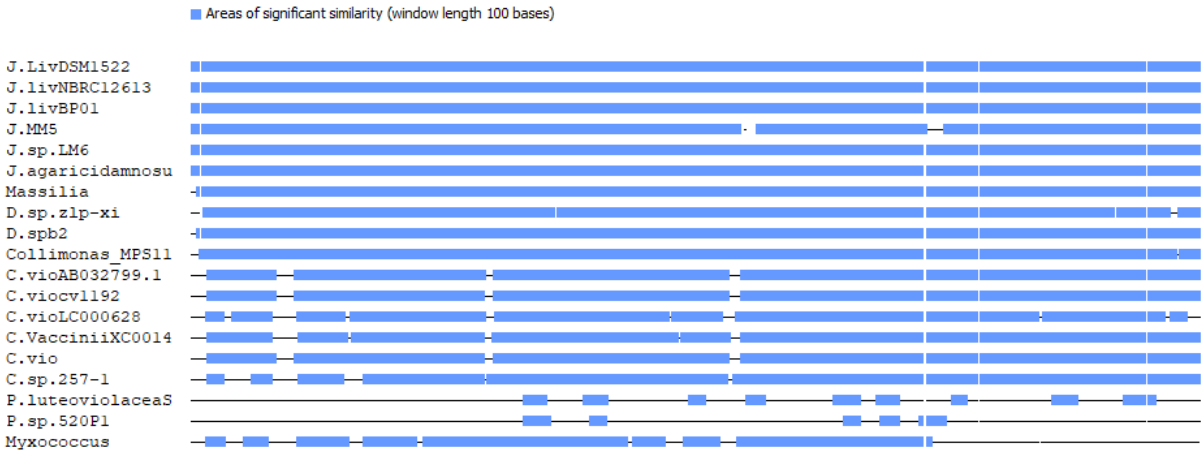


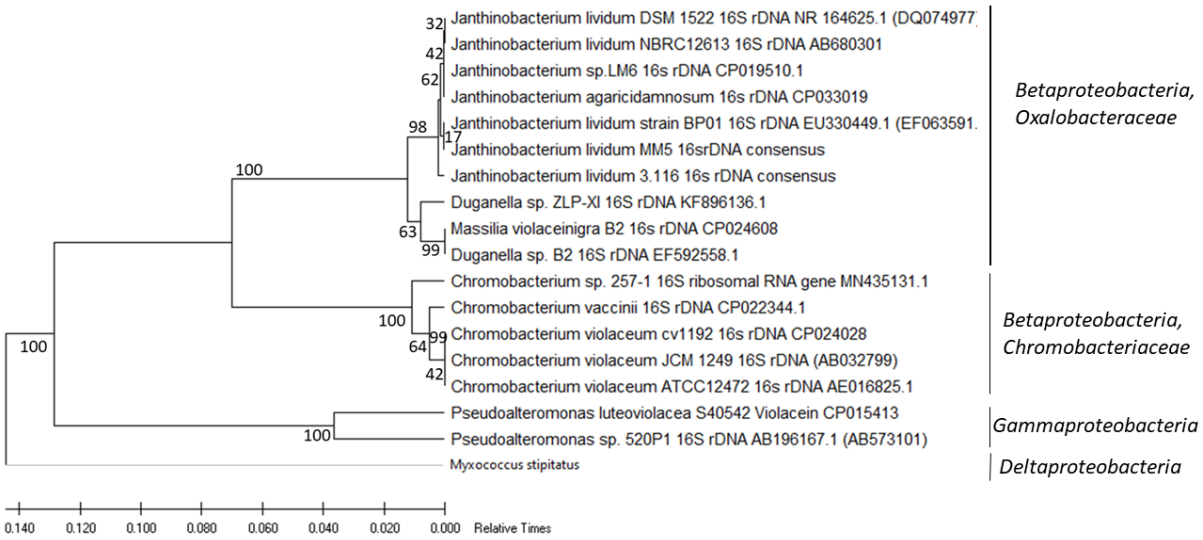
Figure 10: Alignment of the various violacein operon using the clone manager 9 software and 70% consensus. Lines without blue represent dissimilarity, while blue represents areas with significant similarity. The gaps for MM5 is missing parts of the sequence

Table 9: Showing results for the multiple alignment of violacein operons.

Species	**NCBI accession number**	**%Matching bases**
Janthinobacterium MM5		80
Janthinobacterium Agaricidamnosum	CP033019	85
Janthinobacterium Lividum	EF063591	85
Janthinobacterium Lividum	DQ074977	85
Janthinobacterium Lividum	LC000630	85
Janthinobacterium sp.	CP019510	84
Duganella sp.	GQ266676	83
Duganella sp.	KJ131413	79
Collimonas sp.	FJ965838	81
Chromobacterium sp.	CP043473	74
Chromobacterium Vaccinii	CP022344.1	74
Chromobacterium Violaceum	AE016825.1	75
Chromobacterium Violaceum	LC000628	72
Chromobacterium Violaceum	CP024028	75
Chromobacterium Violaceum	AB032799	75
Massilia Violaceinigra	CP024608	81
Myxococcus stipitatus	CP004025	61
Pseudoalteromonas sp.	AB573101	51
Pseudoalteromonas Luteoviolacea	CP015413	53

Based on the Multiple Sequence Alignment, phylogenetic trees were made by using NJ and ML analysis. Generally, the bootstrap values seem to be higher for the phylogenetic trees based on the violacein operons, indicating a higher degree of certainty. The relative times on the 16s rRNA time trees are generally lower than the relative times for the violacein operon. Both the ML and NJ tree for violacein indicates that the *pseudoalteromonas* are more closely related to *Chromobacterium*, than the 16s rRNA tree (Fig.11b and 11d). This may indicate horizontal gene transfer (HGT), therefore an unrooted tree for the violacein operon was made (Fig. 11e). The 16s rRNA trees are assumed to show the evolutionary relationship between these bacterial strains. For the ”time trees” the *Myxococcus stipitatus* are selected as outgroup, this strain is selected because it belongs to the *Deltaproteobacteria* which is more distantly related than the *gammaproteobacteria* and *betaproteobacteria* [92]. The resulting trees can be seen in Fig. 11. Fig. 11b-11d are time trees, with relative times representing the relative divergence times.

In these trees, branch length indicates how related the sequences are, where a shorter branch length indicates closer related. The low bootstrap values in multiple trees indicate a higher degree of uncertainty.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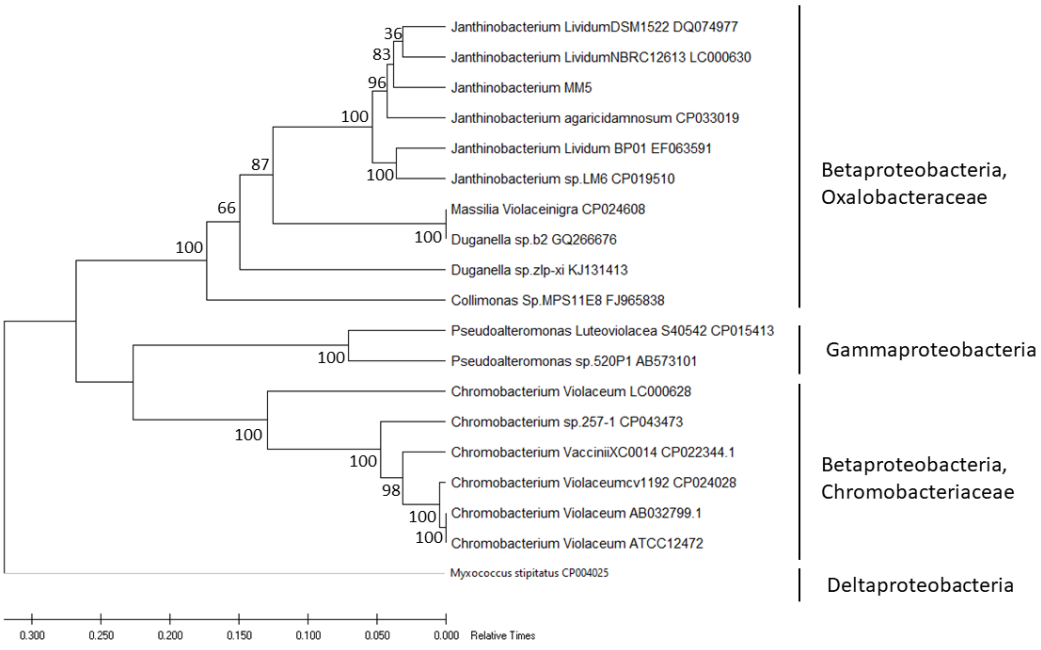
Janthinobacterium lividum NBRC12613 16S rDNA AB680301
Janthinobacterium sp.LM6 16s rDNA CP019510.1
Janthinobacterium agaricidamnosum 16s rDNA CP033019
Janthinobacterium lividum strain BP01 16S rDNA EU330449.1 (EF063591.
Janthinobacterium lividum MM5 16srDNA consensus
Janthinobacterium lividum 3.116 16s rDNA consensus
Duganella sp. ZLP-XI 16S rDNA KF896136.1
Massilia violaceinigra B2 16s rDNA CP024608
Duganella sp. B2 16S rDNA EF592558.1
Chromobacterium sp. 257-1 16S ribosomal RNA gene MN435131.1
Chromobacterium vaccinii 16S rDNA CP022344.1
Chromobacterium violaceum cv1192 16s rDNA CP024028
Chromobacterium violaceum JCM 1249 16S rDNA (AB032799)
Chromobacterium violaceum ATCC12472 16s rDNA AE016825.1
Pseudoalteromonas luteoviolacea S40542 Violacein CP015413
Pseudoalteromonas sp. 520P1 16S rDNA AB196167.1 (AB573101)
Myxococcus stipitatus
Betaproteobacteria, Oxalobacteraceae
Betaproteobacteria, Chromobacteriaceae
Gammaproteobacteria
Deltaproteobacteria
0.140 0.120 0.100 0.080 0.060 0.040 0.020 0.000 Relative Times

(a)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Janthinobacterium MM5
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Duganella sp.b2 GQ266676
Duganella sp.zlp-xi KJ131413
Collimonas Sp.MPS11E8 FJ965838
Pseudoalteromonas Luteoviolacea S40542 CP015413
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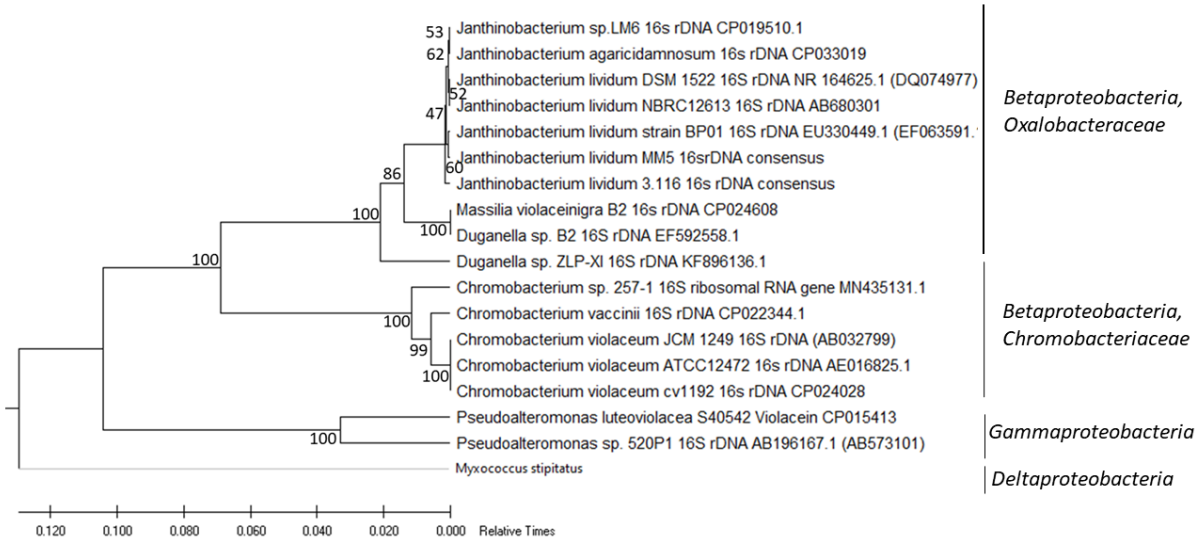
Chromobacterium Violaceum LC000628
Chromobacterium sp.257-1 CP043473
Chromobacterium VacciniiXC0014 CP022344.1
Chromobacterium Violaceumcv1192 CP024028
Chromobacterium Violaceum AB032799.1
Chromobacterium Violaceum ATCC12472
Myxococcus stipitatus CP004025
Betaproteobacteria, Oxalobacteraceae
Gammaproteobacteria
Betaproteobacteria, Chromobacteriaceae
Deltaproteobacteria
0.300 0.250 0.200 0.150 0.100 0.050 0.000 Relative Times

(b)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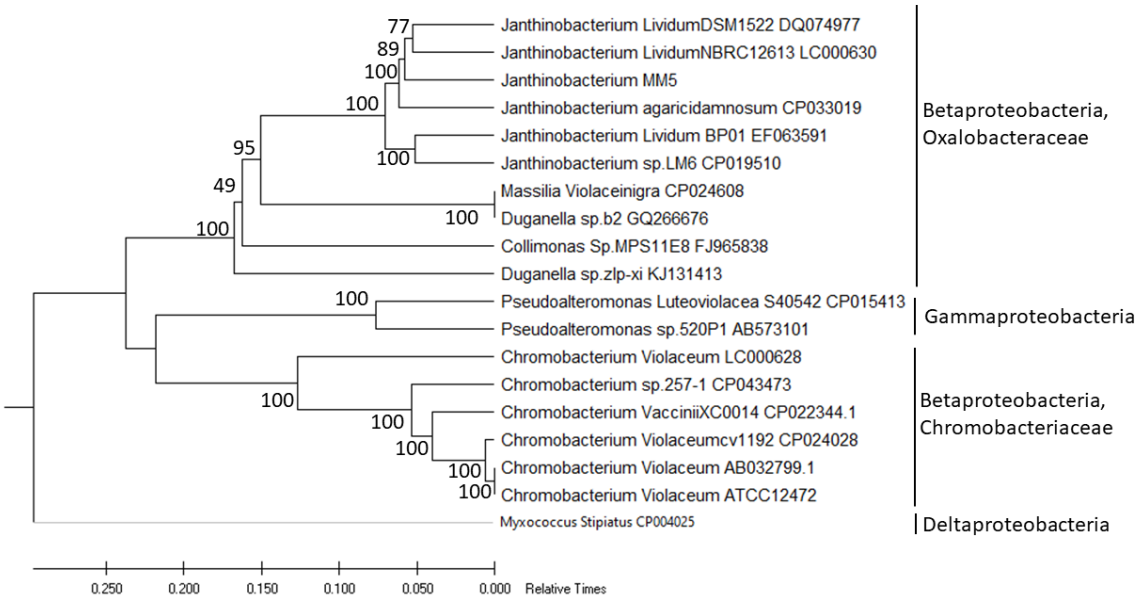
Pseudoalteromonas luteoviolacea S40542 Violacein CP015413
Pseudoalteromonas sp. 520P1 16S rDNA AB196167.1 (AB573101)
Myxococcus stipitatus
0.120 0.100 0.080 0.060 0.040 0.020 0.000 Relative Times
Betaproteobacteria, Oxalobacteraceae
Betaproteobacteria, Chromobacteriaceae
Gammaproteobacteria
Deltaproteobacteria

(c)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Janthinobacterium LividumNBRC12613 LC000630
Janthinobacterium MM5
Janthinobacterium agaricidamnosum CP033019
Janthinobacterium Lividum BP01 EF063591
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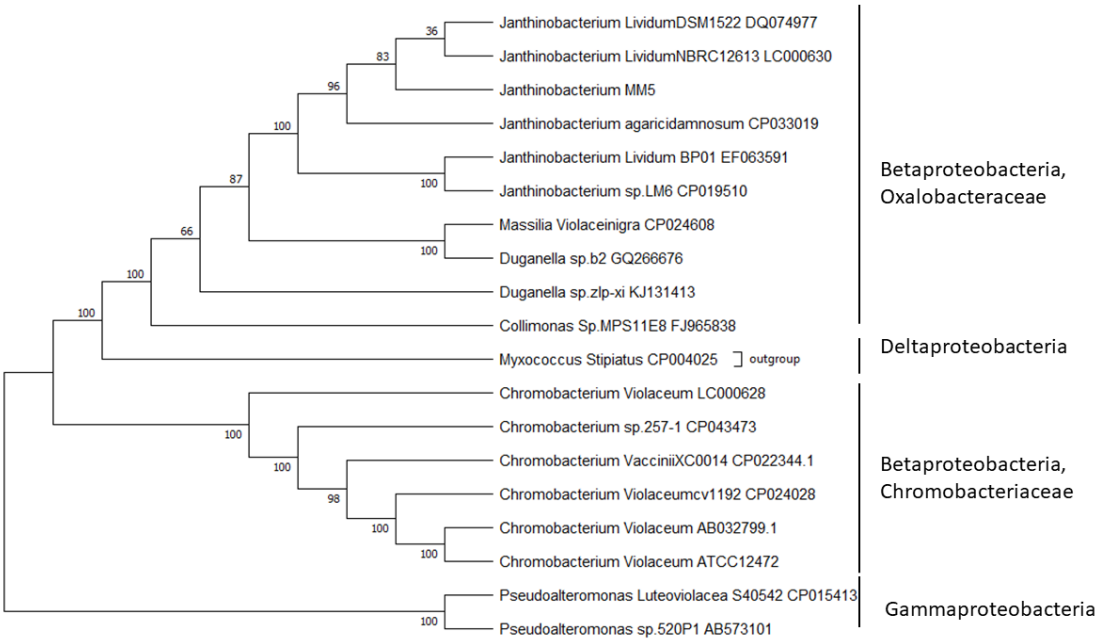
Chromobacterium VacciniiXC0014 CP022344.1
Chromobacterium Violaceumcv1192 CP024028
Chromobacterium Violaceum AB032799.1
Chromobacterium Violaceum ATCC12472
Myxococcus Stipiatus CP004025
0.250 0.200 0.150 0.100 0.050 0.000 Relative Times
Betaproteobacteria, Oxalobacteraceae
Gammaproteobacteria
Betaproteobacteria, Chromobacteriaceae
Deltaproteobacteria

(d)



(e)

Figure 11: Phylogenetic trees for the violacein operons and 16s rRNA sequences of the analyzed strains. Both maximum likelihood and neighbor-joining phylogenetic trees were constructed using the bootstrap method with 500 replications and the Tamura-Nei model. a) Maximum likelihood time tree 16s rRNA genes of the analyzed sequences, where relative times represent relative divergence times, and the node values represent bootstrap values. b) The maximum likelihood time tree for the violacein operons of the analyzed sequences, where relative times represent relative divergence times, and the node values represent bootstrap values. c) Neighbor-joining time tree for 16s rRNA genes of the analyzed sequences, where relative times represent relative divergence times, and the node values represent bootstrap values. d) Neighbor-joining time tree the violacein operons of the analyzed sequences, where relative times represent relative divergence times, and the node values represent bootstrap values. e) Maximum likelihood time tree for the violacein operons of the analyzed sequences, where the node values represent bootstrap values.

4 Discussion

4.1 16s rRNA sequencing for taxonomy assignment

To characterize the two bacterial strains, MM5 and 3.116, studied in this project, sequencing of the entire 16s rRNA gene was conducted. The 16s rRNA gene consists of 9 regions (V1-V9) and is used as a marker gene for bacterial diversity, taxonomy and phylogeny due to its presence in all bacteria and the fact that its function is conserved over time, implying that random changes in the sequence are an accurate measurement of evolution [93]. The 16s rRNA gene is seldom exposed to HGT, even though it occasionally happens [94]. For the PCR reaction amplifying the entire 16s rRNA gene (EUB8F and 1492R as primers), was of the expected size of approximately 1500 base pairs. The sequencing resulted in sequences with high quality, except for the first several basepairs, where the quality was more questionable. By using the RDP tool called Classifier both MM5 and 3.116 were classified as *Janthinobacterium* on a genus level with a 100% confidence[81]. The RDP SeqMatch tool was used to find the DNA sequence with the highest similarity to the query sequence. This resulted in both MM5 and 3.116 being most similar to *J. Lividum* sequences with an s_ab scores of 0.995 and 0.975 respectively indicating relatedness. This indicates a high degree of shared 7-mers, and therefore a high degree of similarity towards *J. Lividum*. However, whether or not both strains belong to the species *J. Lividum* is not certain.

4.2 Comparing MM5 and 3.116

The discrepancy in the results 16s rRNA sequencing results for the two *Janthinobacterium* strains indicates that they are different strains isolated from salmon fry. This suspicion is further strengthened when aligning the 16s rRNA genes of MM5 and 3.116 with the 16s rRNA gene sequence for the type strain for *J. Lividum* as a reference. Based on the alignment of the 16s rRNA gene sequence, the MM5 and 3.116 had a similar amount of non-matching bases between them (6) as between the type strain sequence (6 and 8 respectively). The two strains showed different properties when growing on agar-plate medium, as MM5 was slimier then 3.116 and grew in purple colonies on the EPS-sucrose medium. 3.116 on the other hand grew in pink colonies on the EPS-sucrose medium. While 3.116 had a shorter generational time (0.88 hours) than MM5 (1.5 hours), MM5 had a shorter lag phase This difference further strengthens the suspicion that these two strains are different. This impression is further substantiated by the

fact that the amplification of the violacein operon failed for 3.116, while it was successful for MM5. At last, based on the phylogenetic analysis of the 16s rRNA gene, where the two strains are on different nodes, MM5 and 3.116 seems to be two different *Janthinoabacterium* strains isolated from salmon fry. *Janthinobacterium* strains are previously found on human[40] and amphibian skin [13, 42], and now two strains have also been found on salmon skin.

4.3 Characterization of growth for a *J. Lividum* strain

When bacteria grow in a batch culture, the growth is usually divided into four distinct phases. The first phase is the lag phase, which is a period with little growth where the bacteria prepares for exponential growth[95]. The exponential phase is a period with rapid growth and a surplus of nutrients. This phase continues until the culture runs out of nutrients or oxygen, or a build-up of toxic compounds and enters the stationary phase, where cell division decreases or stops completely. The final phase is called the death phase and is when the population declines. This is usually caused by multiple factors, many cells die and lyse, but some enter dormancy and might remain viable but not growing [96]. By using the data from OD_{600} measurements of bacterial growth in LB-medium in the exponential phase of 3.116 and MM5, the generational times were calculated to be 0.88 hours and 1.5 hours respectively. This huge difference is quite surprising due to the fact that the 16s rRNA sequence of the two strains is very similar indicating a close evolutionary relationship. In addition, the lag phase of MM5 was found to be shorter when compared to 3.116. A previous master project done in the ACMS group calculated the generational time of *J. Lividum* isolated from salmon fry to be 2.3 hours. However, This growth curve was made in Tryptic soy broth (TSB) medium [2]. The difference in medium might explain some of these differences.

The antibiograms were performed to examine the susceptibility of MM5 and 3.116 to five types of antibiotics. Both MM5 and 3.116 was inhibited by all tested concentrations of ampicillin (100 μg/ml) and chloramphenicol (25 μg/ml). In addition, the highest concentration of neomycin (50 μg/ml) seems to cause slight inhibition of growth for both strains. 3.116 and MM5 were resistant towards all tested concentrations of polymixin (100 μg/ml) and kanamycin (50μg/ml). Previous studies with *J. Lividum* and ampicillin showed an increased production of violacein for concentrations up to 200 μg/ml [52, 60]. This result is not replicated in these experiments as no indication of violacein production was observed, and the growth was inhib-

ited by ampicillin. The highest concentration of ampicillin tested was 100 μg/ml, which still resulted in an inhibition zone around the filter paper, and no sign of purple color. A study was done on an opportunistic pathogenic strain of *J. Lividum* isolated from rainbow trout in Korea showed resistance to Chloramphenicol and kanamycin, however, no tested concentrations were specified [97]. As mentioned MM5 and 3.116 were resistant towards kanamycin, which corresponds with these results. However, MM5 and 3.116 were not resistant towards chloramphenicol which contradicts the result from the study on *J. Lividum* isolated from rainbow trout (as seen in Appendix G). These results indicate that susceptibility towards antibiotics varies between *Janthinobacterium* strains.

The *J. Lividum* is known to produce biofilm[52]. Biofilm is a structural consortium of bacteria attached to each other and usually a surface. As biofilm-producing strains tend to grow in aggregates[98], microscopy was conducted to visually observe the two *Janthinobacterium* strains MM5 and 3.116. The observations indicated a tendency for both strains to grow in aggregates in liquid culture. These results indicate that multiple methods for quantifying cell density, such as colony-forming units and flow cytometry would be inaccurate. This correlates with previous studies on a *J. Lividum* strain producing exopolysaccharides and with a tendency to grow in biofilm [52].

4.4 Growth on various media

Both MM5 and 3.116 showed the ability to grow on every tested agar plate medium, and at temperatures between 18°C and 28°C. The *Janthinobacterium* strain 3.116 showed no sign of purple colonies when grown on any medium or temperature. However, when growing on the EPS-sucrose medium the strain had a tendency to grow in pink-colored colonies. A strain of *J. Lividum* isolated from glacier water in Himalaya, which could not produce violacein, has in a previous study been reported to grow in pink colonies. The inability to produce violacein was determined based on the sequencing of the whole genome [33]. As no purple colonies were observed, and the failure of sequencing a violacein operon from 3.116, the strain might lack the ability to produce the purple pigment. The other strain, MM5 grew in purple colonies on EPS-sucrose (both 1% agar and 1.5% agar), LA 1% agar, LA with glycerol, and 1% agar, and R2A with 1% agar. The agar concentration seemed to affect the production of purple pigment, as multiple of the mediums only showed purple colonies on plates with lower agar concentra-

tion. It is possible that the lowered amount of agar made the plate medium more similar to the skin mucous of the salmon. In previous studies, glycerol has been shown to increase the production of violacein [60]. While multiple agar plates with medium containing glycerol gave purple colonies, the amount of pigment seemed to be higher on mediums without glycerol. However, as the addition of glycerol to an EPS-sucrose agar plate, which gave the strongest pigmentation, was not tested, the effect of glycerol is uncertain. In addition, MM5 seemed to produce violacein mainly when grown on room temperature and at 28 °C. Temperature has previously been reported to be an important factor for violacein production, as some *J. Lividum* strains could only produce the pigment at temperatures below 20 °C [74], and other strains had an optimal temperature for violacein production at 25 °C[73, 60]. As the higher temperature would promote more rapid growth of MM5, the strain would reach the stationary phase quicker. This could result in increased stress on the bacteria, and therefore the production of the secondary metabolite violacein. As young salmon fry usually is kept at temperatures below 10 °C [4], the *Janthinobacterium* inhabiting the fry could be adapted to these kinds of temperature. This can support the theory about increased stress on the MM5 and 3.116 strains with increasing temperatures. The increased growth rate would also give an increased cell density, which could promote violacein production as the production is regulated by quorum sensing mechanisms [35]. If the growth density was the only factor promoting the production of purple pigments, one could expect to observe this on the colonies at a lower temperature after some time. However, no indication of purple was observed at 20°C after fourteen days.

4.5 Antagonistic properties of MM5 and 3.116

To examine the potential antagonistic properties of the two *Janthinobacterium* strains MM5 and 3.116 the cross-streaking approach was used. Three strains previously isolated from salmon fry, representing the genera *Arthrobacter, Pedobacter*, and *Psychrobacter* was used. The cultures growing on the agar plates showed no sign of inhibition from MM5 nor 3.116. These results might indicate that neither MM5 or 3.116 has any antagonistic properties towards these strains. However, as the antimicrobial properties of *J. Lividum* is believed to be connected to violacein[35], and no production of purple color was observed, indicating a lack of violacein production, this result was not unexpected. Expression of the violacein operon is regulated by quorum sensing mechanisms, which increase production based on cell population density [54]. Considering these quorum sensing mechanisms violacein production could have been

promoted by the more densely growing bacteria as a result of the cross-streaking, however, this was not observed. *J Lividum* has been shown to inhibit growth of the fungi *batrachochytrium dendrobatidis* om amphibians [13, 42, 44]. As the bacterial species *Pseudomonas fluorescens* previously have shown the ability to inhibit the growth of the water mold *Saprolegnia* [12], *Janthinobacterium* could have the same effect. However, whether or not these strains inhibit *Saprolegnia* was not examined.

4.6 Phylogenetic analysis for the violacein operon and 16S rRNA gene sequences

Amplification and sequencing of the violacein operon of MM5 and 3.116 were attempted. The sequences were thereafter used in phylogenetic analysis with equivalent sequences of other violacein producing bacteria. By using the results from the 16s rRNA gene taxonomy assignment, strains related to MM5 and 3.116 was found. Sequences for the violacein operon of these strains were used to design PCR primers to amplify the violacein operon. Most of the primer-pairs seemed to work for MM5, and most of the violacein operon was successfully sequenced. For 3.116, none of the primers gave specific PCR products, as most of the PCR reactions resulted in multiple products. Therefore, PCR products of the expected lengths were cut out from a gel and sequenced. Unfortunately, the resulting sequences were of low quality and could not be used for further analysis. This might be because the sequencing reaction consisted of too little free DNA after isolation from the gel, or that the primers didn't correspond with the violacein operon sequences of 3.116. The lack of success in the sequencing of the violacein operon of 3.116 could indicate that the operon either is missing, have a significant different sequence (for example due to degeneration), or is arranged differently. As seen from the alignment and phylogenetic analysis of the violacein operon, the genes seem to be quite conserved for the *Oxalobacteraceae*. This suggests that the operon of 3.116 either are degenerated or missing. A *J. Lividum* strain has previously been reported to lack the violacein operon, and therefore could not produce violacein. This strain grew in light pink colonies when grown on antarctic bacterial medium [33]. While purple colonies were observed on multiple agar plate mediums for MM5, none was observed for 3.116. When 3.116 was cultivated on the EPS-sucrose medium, the colonies grew pink. These results combined with the lack of success when attempting to sequence the violacein operon could strengthen the suspicion that 3.116 lacks the genes to produce violacein.

To compare the evolution of the violacein operon to the 16s rRNA gene, phylogenetic trees were created. Rooted and unrooted Neighbor-Joining and Maximum likelihood trees were constructed for both the violacein operon and the 16s rRNA gene. The trees based on 16s rRNA sequences are anticipated to represent the vertical evolution [99]. Therefore, eventual differences between the violacein operon tree and the 16s rRNA tree could indicate HTG. The violacein operon has been sequenced for multiple species of *Proteobacteria*, where some represent *betaproteobacteria, gammapreoteobacteria* and *deltaproteobacteria* [47, 50]. *Myxococcus* was selected as outgroup for rooting due to being more distantly related to the *betaproteobacteria* and *gammaproteobacteria* [92]. One difference between the "time trees" (with scaled branches) for violacein and 16s rRNA is that the branch lengths are longer. This applies to both the ML and the NJ trees. Based on the branch lengths, the 16s rRNA trees (fig. 11a and 11c) indicates less divergence in the *Oxalobacteracea* family, then for the violacein operon trees. The same tendency can be seen for the *Chromobacterium*. This observation applies to both the NJ and the ML trees. This suggests a more rapid sequence evolution in the violacein operon. Additionally, more variability is found in the violacein operon then the 16s rRNA gene[79], which would contribute to the branch length. The bootstrap values were generally high for both violacein operon and 16s rRNA trees, except for the most related sequences, This implies that its impossible to resolve the relationships between closely related species with these gene sequences. When comparing the 16s rRNA gene trees to the violacein operon trees, the *Chromobacterium* (*Betaproteobacteria*) sequences are more closely related with the *Pseudoalteromonas* sequences than the rest of the *Betaproteobactera* in the violacein operon trees. This could indicate HGT, which is the transmission of DNA between different genomes [100]. If HGT of the violacein operon has occurred, it would be uncertain whether or not the *Myxococcus* strain would represent the most ancient violacein operon. Consequently, an unrooted ML tree was made for the violacein operon. The unrooted tree matches the rooted trees and indicates that the *Pseudoalteromonas* sequences are closest related to *Chromobacterium* sequences. Also, the strain representing *Myxococcus* seems to be more closely related to the *Oxalobacteracea* than the *Chromobacterium*, which is strange due to the fact that both the *Oxalobacteracea* and the *Chromobacterium* belongs to the *Betaproteobacteria* class. The *Myxococcus* belongs to another class and would, therefore, be expected to be more distantly related. These results indicates a different source of the violacein operon in the two families (*Ox-*

alobacteracea and *Chromobacteriaceae*) belonging to the *Betaproteobacteria*. HGT between the *Collimonas, Janthinobacterium* and *duganella* species has previously been hypothesized to occur [49]. Additionally, HGT of genes responsible for the production antimicrobial secondary metabolites from the bacteria naturally producing these to other bacteria has been reported to occur [101, 102]. These studies support the likeliness of HGT occurring during the evolution of the violacein operon in the *Proteobacteria*.

4.7 Future work

A further study of the violacein production in a *Janthinobacterium* isolated from salmon fry should be conducted to clarify and further examine findings in this master project. A goal of the further work could be to isolate the purple pigment from a liquid culture of the *Janthinobacterium* strain to conclude whether or not the purple pigment in fact are violacein. To do this, conditions for violacein production in liquid cultures should be studied. This was not covered by this thesis, but both strains were cultivated in liquid LB medium and no indication of violacein was observed. If one could get predictable violacein production in liquid culture, a study on production during the growth of *Janthinobacterium* could be done in various liquid media. As the EPS-sucrose medium showed the most promising results regarding the production of purple colonies, a liquid media using the same components should be tested at 28 °C. Due to limited access to the laboratory as a result of the Covid-19 pandemic, a test of antagonistic properties with media and conditions known to produce purple pigment was not conducted. Therefore a test for antagonistic properties of a violacein producing *Janthinobacterium* should be tested, both with regards to bacteria, but also the water mold *Saprolegnia*. In this study of antagonistic properties, a medium known to promote purple colonies should be applied at 28 °C. As the bacterial species *Pseudomonas fluorescens* previously have shown the ability to inhibit the growth of *Saprolegnia* [12], *Janthinobacterium* could have the same effect. Further on, experiments regarding the use of *Janthinobacterium* as a probiotic to prevent outbreaks of *Saprolegnia* could be studied. The capnophilic properties of *Janthinobacterium* contribute to the possibility of utilizing the strain as a probiotic. In addition, a new project should compare the ability of the two strains to colonize salmon fry. Also, to verify whether or not the 3.116 strain, have violacein genes, a new sequencing attempt should be conducted, either by amplification of shorter gene fragments or by sequencing of the whole genome.

5 Conclusion

By sequencing the 16s rRNA gene of MM5 and 3.116, both strains were classified as *Janthinobacterium* and closely related to the *J. Lividum* type strain. Further, sequence analysis showed the 16s rRNA gene sequence of MM5 and 3.116 to be different in some nucleotide positions, indicating that this could be two different *Janthinobacterium* strains.

To study the growth of the *Janthinobacterium* strains MM5 and 3.116, growth curves based on OD_{600} were generated. The generational time of MM5 and 3.116 was calculated to be 1.50 and 0.88 hours respectively. Based on microscope observations, MM5 and 3.116 seemed to grow in aggregates when cultivated in liquid media. A test of the antibiotic susceptibility was performed and showed resistance towards Kanamycin (50 μg/ml), polymixin (100 μg/ml), Neomycin (20 μg/ml), and Ampicillin (20 μg/ml) for both strains.

To promote violacein production, growth on different media and conditions was tested. 3.116 showed no sign of purple colonies but grew pink on the EPS-sucrose medium, however, this is most likely not an indication of violacein production. The growth of MM5 several media resulted in purple colonies, indicating violacein production. Reduced agar concentration (from 1.5% to 1%) and sucrose seemed to promote purple colonies. While some of the plates incubated at 28°C gave purple colonies, none of the plates incubated at 18°C gave any indication of violacein production, suggesting that the violacein production of MM5 is dependent on temperature. No antagonistic behavior was observed during the cross-streaking experiment for MM5 nor 3.116, but this could be due to lack of violacein production on these plates.

Most of the violacein operon of MM5 was amplified, however, for 3.116 amplification of the violacein operon failed indicating a lack of a functional operon. Based on the phylogenetic analysis, MM5s' violacein operon showed the highest similarity towards the operons of strains belonging to the *betaproteobacteria* class, and especially those belonging to the *Oxalobacteraceae* family represented by *Duganella, Janthinobacterium, Collimonas* and *Massila*. The violacein operon of the *Chromobacteriaceae (Betaproteobacteri)* strains seemed to be closer related to the *Pseudoalteromonas* strains-, than the *Oxalobacteraceae* indicating that the violacein operon has been exposed to HGT during the evolution of the *Proteobacteria*. This indicates a different source of the violacein operon in the two *Betaproteobacteria* families.

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A Appendix - Growth media

Table 10: Recipies for growth mediums used in this project. Different variants where made for some of the mediums.

Luria-Bertani (LB)	
Yeast extract	5g
Tryptone	10g
NaCl	5g
Agar[1]	15g
Glycerol[2]	2%
Brain heart infusion (BHI)	
BHI Broth	18,5g
Agar	15g
Cooked meat broth (CMB)	
CMB	57g
Agar	15g
R2	
Casein yeast Pepton	0,5g
Bacteriological tryptone	0,5g
Yeast extract	0,5g
Soluble starch	0,5g
KH_2PO_4	0,3g
NaPyruvate	0,3g
$MgSO_4 \cdot 7\,H_2O$	0,024g
Agar[1]	15g
Glycerol [2]	1%, 2%, 5%
Nutrient Broth	
Nutrient Broth	8,0g
Agar	15g
Glycerol[2]	1%
EPS-Sucrose-Medium	
Sucrose	30,00g
Casein yeast peptone	5,00g
$MgSO_4 \cdot 7\,H_2O$	1,33g
KH_2PO_4 (83,5g/l)	20,0ml/l
$CaCl_2 \cdot 2\,H_2O$ (50g/l)	1,00 ml/l
Vitamin solution[3]	2,00 ml/l
Trace elements solution[3]	1,00 ml/l

[1]To make liquid media agar was omited. 10 g/l Agar was also used

[2]Glycerol was added in different amounts to different mediums

[3]Vitamin solution and trace element solution was premade.

B Appendix - DNeasy® PowerSoil® Kit (Qiagen) protocol

Protocol: Experienced User

Important points before starting

- Perform all centrifugation steps at room temperature (15–25°C).
- If Solution C1 has precipitated, heat at 60°C until precipitate dissolves.
- 2 ml Collection Tubes are provided.

Procedure

1. Add 0.25 g of soil sample to the PowerBead Tube provided. Gently vortex to mix.
2. Add 60 µl of Solution C1 and invert several times or vortex briefly.
   Note: Solution C1 may be added to the PowerBead tube before adding soil sample
3. Secure PowerBead Tubes horizontally using a Vortex Adapter for 24 (1.5–2.0 ml) tubes (cat. no. 13000-V1-24).
4. Vortex at maximum speed for 10 min.
   Note: If using the 24-place Vortex Adapter for more than 12 preps, increase the vortex time by 5–10 min.
5. Centrifuge tubes at 10,000 x *g* for 30 s.
6. Transfer the supernatant to a clean 2 ml Collection Tube.
   Note: Expect between 400–500 µl of supernatant. Supernatant may still contain some soil particles.
7. Add 250 µl of Solution C2 and vortex for 5 s. Incubate at 2–8°C for 5 min.
   Note: You can skip the 5 min incubation. However, if you have already validated the DNeasy PowerSoil extractions with this incubation we recommend you retain the step.
8. Centrifuge the tubes for 1 min at 10,000 x *g*.
9. Avoiding the pellet, transfer up to 600 µl of supernatant to a clean 2 ml Collection Tube.
10. Add 200 µl of Solution C3 and vortex briefly. Incubate at 2–8°C for 5 min.

Note: You can skip the 5 min incubation. However, if you have already validated the PowerSoil extractions with this incubation we recommend you retain the step.

11. Centrifuge the tubes for 1 min at 10,000 x *g*.
12. Avoiding the pellet, transfer up to 750 µl of supernatant to a clean 2 ml Collection Tube.
13. Shake to mix Solution C4 and add 1200 µl to the supernatant. Vortex for 5 s.
14. Load 675 µl onto an MB Spin Column and centrifuge at 10,000 x *g* for 1 min. Discard flow-through.
15. Repeat step 14 twice, until all of the sample has been processed.
16. Add 500 µl of Solution C5. Centrifuge for 30 s at 10,000 x *g*.
17. Discard the flow-through. Centrifuge again for 1 min at 10,000 x *g*.
18. Carefully place the MB Spin Column into a clean 2 ml Collection Tube. Avoid splashing any Solution C5 onto the column.
19. Add 100 µl of Solution C6 to the center of the white filter membrane. Alternatively, you can use sterile DNA-free PCR-grade water for this step (cat. no. 17000-10).
20. Centrifuge at room temperature for 30 s at 10,000 x *g*. Discard the MB Spin Column. The DNA is now ready for downstream applications.
    Note: We recommend storing DNA frozen (–20°C to –80°C) as Solution C6 does not contain EDTA. To concentrate DNA, see the Troubleshooting Guide.

C Appendix - QIAquick ® PCR Purification Kit (Qiagen)

QIAquick PCR Purification Kit Protocol

using a microcentrifuge

This protocol is designed to purify single- or double-stranded DNA fragments from PCR and other enzymatic reactions (see page 8). For cleanup of other enzymatic reactions, follow the protocol as described for PCR samples or use the MinElute Reaction Cleanup Kit. Fragments ranging from 100 bp to 10 kb are purified from primers, nucleotides, polymerases, and salts using QIAquick spin columns in a microcentrifuge.

Important points before starting

- Add ethanol (96–100%) to Buffer PE before use (see bottle label for volume).
- All centrifugation steps are carried out at 17,900 x *g* (13,000 rpm) in a conventional tabletop microcentrifuge at room temperature.
- Add 1:250 volume pH indicator I to Buffer PB (i.e., add 120 µl pH indicator I to 30 ml Buffer PB or add 600 µl pH indicator I to 150 ml Buffer PB). The yellow color of Buffer PB with pH indicator I indicates a pH of ≤7.5.
- Add pH indicator I to entire buffer contents. Do not add pH indicator I to buffer aliquots.
- If the purified PCR product is to be used in sensitive microarray applications, it may be beneficial to use Buffer PB without the addition of pH indicator I.

Procedure

1. **Add 5 volumes of Buffer PB to 1 volume of the PCR sample and mix. It is not necessary to remove mineral oil or kerosene.**

   For example, add 500 µl of Buffer PB to 100 µl PCR sample (not including oil).
2. **If pH indicator I has beein added to Buffer PB, check that the color of the mixture is yellow.**

   If the color of the mixture is orange or violet, add 10 µl of 3 M sodium acetate, pH 5.0, and mix. The color of the mixture will turn to yellow.
3. **Place a QIAquick spin column in a provided 2 ml collection tube.**
4. **To bind DNA, apply the sample to the QIAquick column and centrifuge for 30–60 s.**
5. **Discard flow-through. Place the QIAquick column back into the same tube.**

   Collection tubes are re-used to reduce plastic waste.
6. **To wash, add 0.75 ml Buffer PE to the QIAquick column and centrifuge for 30–60 s.**
7. **Discard flow-through and place the QIAquick column back in the same tube. Centrifuge the column for an additional 1 min.**

   IMPORTANT: Residual ethanol from Buffer PE will not be completely removed unless the flow-through is discarded before this additional centrifugation.

8. **Place QIAquick column in a clean 1.5 ml microcentrifuge tube.**
9. **To elute DNA, add 50 µl Buffer EB (10 mM Tris·Cl, pH 8.5) or water (pH 7.0–8.5) to the center of the QIAquick membrane and centrifuge the column for 1 min. Alternatively, for increased DNA concentration, add 30 µl elution buffer to the center of the QIAquick membrane, let the column stand for 1 min, and then centrifuge.**

   IMPORTANT: Ensure that the elution buffer is dispensed directly onto the QIAquick membrane for complete elution of bound DNA. The average eluate volume is 48 µl from 50 µl elution buffer volume, and 28 µl from 30 µl elution buffer.

   Elution efficiency is dependent on pH. The maximum elution efficiency is achieved between pH 7.0 and 8.5. When using water, make sure that the pH value is within this range, and store DNA at –20°C as DNA may degrade in the absence of a buffering agent. The purified DNA can also be eluted in TE buffer (10 mM Tris·Cl, 1 mM EDTA, pH 8.0), but the EDTA may inhibit subsequent enzymatic reactions.
10. **If the purified DNA is to be analyzed on a gel, add 1 volume of Loading Dye to 5 volumes of purified DNA. Mix the solution by pipetting up and down before loading the gel.**

    Loading dye contains 3 marker dyes (bromophenol blue, xylene cyanol, and orange G) that facilitate estimation of DNA migration distance and optimization of agarose gel run time. Refer to Table 2 (page 15) to identify the dyes according to migration distance and agarose gel percentage and type.

D Appendix - QIAquick® Gel Extraction Kit and QIAquick® PCR Gel Cleanup Kit protocol

July 2018

Quick-Start Protocol

QIAquick® Gel Extraction Kit
QIAquick® PCR & Gel Cleanup Kit

The QIAquick Gel Extraction Kit and the QIAquick PCR & Gel Cleanup Kit (cat. nos. 28704, 28706, 28506 and 28115) can be stored at room temperature (15–25°C) for up to 12 months.

Further information

- *QIAquick Spin Handbook*: **www.qiagen.com/HB-1196**
- Safety Data Sheets: **www.qiagen.com/safety**
- Technical assistance: **support.qiagen.com**

Notes before starting

- This protocol is for the purification of up to 10 µg DNA (70 bp to 10 kb).
- The yellow color of Buffer QG indicates a pH ≤7.5. DNA adsorption to the membrane is only efficient at pH ≤7.5.
- Add ethanol (96–100%) to Buffer PE before use (see bottle label for volume).
- Isopropanol (100%) and a heating block or water bath at 50°C are required.
- All centrifugation steps are carried out at 17,900 *x g* (13,000 rpm) in a conventional table-top microcentrifuge.

1. Excise the DNA fragment from the agarose gel with a clean, sharp scalpel.
2. Weigh the gel slice in a colorless tube. Add 3 volumes Buffer QG to 1 volume gel (100 mg gel ~100 µl). The maximum amount of gel per spin column is 400 mg. For >2% agarose gels, add 6 volumes Buffer QG.
3. Incubate at 50°C for 10 min (or until the gel slice has completely dissolved). Vortex the tube every 2–3 min to help dissolve gel. After the gel slice has dissolved completely, check that the color of the mixture is yellow (similar to Buffer QG without dissolved agarose). If the color of the mixture is orange or violet, add 10 µl 3 M sodium acetate, pH 5.0, and mix. The mixture turns yellow.
4. Add 1 gel volume isopropanol to the sample and mix.
5. Place a QIAquick spin column in a provided 2 ml collection tube or into a vacuum manifold. To bind DNA, apply the sample to the QIAquick column and centrifuge for 1 min or apply vacuum to the manifold until all the samples have passed through the column. Discard flow-through and place the QIAquick column back into the same tube. For sample volumes >800 µl, load and spin/apply vacuum again.
6. If DNA will subsequently be used for sequencing, in vitro transcription, or microinjection, add 500 µl Buffer QG to the QIAquick column and centrifuge for 1 min or apply vacuum. Discard flow-through and place the QIAquick column back into the same tube.
7. To wash, add 750 µl Buffer PE to QIAquick column and centrifuge for 1 min or apply vacuum. Discard flow-through and place the QIAquick column back into the same tube.
   Note: If the DNA will be used for salt-sensitive applications (e.g., sequencing, blunt-ended ligation), let the column stand 2–5 min after addition of Buffer PE.
   Centrifuge the QIAquick column in the provided 2 ml collection tube for 1 min to remove residual wash buffer.
8. Place QIAquick column into a clean 1.5 ml microcentrifuge tube.
9. To elute DNA, add 50 µl Buffer EB (10 mM Tris·Cl, pH 8.5) or water to the center of the QIAquick membrane and centrifuge the column for 1 min. For increased DNA concentration, add 30 µl Buffer EB to the center of the QIAquick membrane, let the

column stand for 1 min, and then centrifuge for 1 min. After the addition of Buffer EB to the QIAquick membrane, increasing the incubation time to up to 4 min can increase the yield of purified DNA.

10. If purified DNA is to be analyzed on a gel, add 1 volume of Loading Dye to 5 volumes of purified DNA. Mix the solution by pipetting up and down before loading the gel.

Revision History

Revision no.	Description of change
R3 07/2018	Updated document title and introductory paragraph with additional applicable product QIAquick PCR & Gel Cleanup Kit. Also added additional product's related cat. nos.

Scan QR code for handbook.

For up-to-date licensing information and product-specific disclaimers, see the respective QIAGEN kit handbook or user manual.

E Appendix - DNA sequences

DNA sequence of 16s rRNA gene of 3.116

GCTCAGATTGAACGCTGGCGGCATGCCTTACACATGCAAGTCGAACGGCAGCACGGAGCTTGCTCTGGTGGC
GAGTGGCGAACGGGTGAGTAATATATCGGAACGTACCCTAGAGTGGGGGATAACGTAGCGAAAGTTACGCTA
ATACCGCATACGATCTAAGGATGAAAGTGGGGGATCGCAAGACCTCATGCTCGTGGAGCGGCCGATATCTGA
TTAGCTAGTTGGTAGGGTAAAAGCCTACCAAGGCATCGATCAGTAGCTGGTCTGAGAGGACGACCAGCCACA
CTGGAACTGAGACACGGTCCAGACTCCTACGGGAGGCAGCAGTGGGGAATTTTGGACAATGGGCGAAAGCCT
GATCCAGCAATGCCGCGTGAGTGAAGAAGGCCTTCGGGTTGTAAAGCTCTTTTGTCAGGGAAGAAACGGTGA
GAGCTAATATCTCTTGCTAATGACGGTACCTGAAGAATAAGCACCGGCTAACTACGTGCCAGCAGCCGCGGT
AATACGTAGGGTGCAAGCGTTAATCGGAATTACTGGGCGTAAAGCGTGCGCAGGCGGTTTTGTAAGTCTGAT
GTGAAATCCCCGGGCTCAACCTGGGAATTGCATTGGAGACTGCAAGGCTAGAATCTGGCAGAGGGGGGTAGA
ATTCCACGTGTAGCAGTGAAATGCGTAGATATGTGGAGGAACACCGATGGCGAAGGCAGCCCCCTGGGTCAA
GATTGACGCTCATGCACGAAAGCGTGGGGAGCAAACAGGATTAGATACCCTGGTAGTCCACGCCCTAAACGA
TGTCTACTAGTTGTCGGGTCTTAATTGACTTGGTAACGCAGCTAACGCGTGAAGTAGACCGCCTGGGGGAGT
ACGGTCGCAAGATTAAAACTCAAAGGAATTGACGGGGACCCGCACAAGCGGTGGATGATGTGGATTAATTCG
ATGCAACGCGAAAAACCTTACCTACCCTTGACATGGCTGGAATCCTTGAGAGATCGAGGAGTGCTCGAAAGA
GAACCAGTACACAGGTGCTGCATGGCTGTCGTCAGCTCGTGTCGTGAGATGTTGGGTTAAGTCCCGCAACGA
GCGCAACCCTTGTCATTAGTTGCTACGAAAGGGCACTCTAATGAGACTGCCGGTGACAAACCGGAGGAAGGT
GGGGATGACGTCAAGTCCTCATGGCCCTTATGGGTAGGGCTTCACACGTCATACAATGGTACATACAGAGCG
CCGCCAACCCGCGAGGGGGAGCTAATCGCAGAAAGTGTATCGTAGTCCGGATTGTAGTCTGCAACTCGACTG
CATGAAGTTGGAATCGCTAGTAATCGCGGATCAGCATGTCGCGGTGAATACGTTCCCGGGTCTTGTACACAC
CGCCCGTCACACCATGGGAGCGGGTTTACCAGAAGTAGGTAGCTTAACCGTAAGGAGGGCGC

DNA sequence of 16s rRNA gene of MM5

CTCAGATTGAACGCTGGCGGCATGCCTTACACATGCAAGTCGAACGGCAGCACGGAGCTTGCTCTGGTGGCG
AGTGGCGAACGGGTGAGTAATATATCGGAACGTACCCTGGAGTGGGGGATAACGTAGCGAAAGTTACGCTAA
TACCGCATACGATCTAAGGATGAAAGTGGGGGATCGCAAGACCTCATGCTCGTGGAGCGGCCGATATCTGAT
TAGCTAGTTGGTAGGGTAAAAGCCTACCAAGGCATCGATCAGTAGCTGGTCTGAGAGGACGACCAGCCACAC
TGGAACTGAGACACGGTCCAGACTCCTACGGGAGGCAGCAGTGGGGAATTTTGGACAATGGGCGAAAGCCTG
ATCCAGCAATGCCGCGTGAGTGAAGAAGGCCTTCGGGTTGTAAAGCTCTTTTGTCAGGGAAGAAACGGTGAG
AGCTAATATCTCTTGCTAATGACGGTACCTGAAGAATAAGCACCGGCTAACTACGTGCCAGCAGCCGCGGTA
ATACGTAGGGTGCAAGCGTTAATCGGAATTACTGGGCGTAAAGCGTGCGCAGGCGGTTTTGTAAGTCTGATG

TGAAATCCCCGGGCTCAACCTGGGAATTGCATTGGAGACTGCAAGGCTAGAATCTGGCAGAGGGGGGTAGAA
TTCCACGTGTAGCAGTGAAATGCGTAGATATGTGGAGGAACACCGATGGCGAAGGCAGCCCCCTGGGTCAAG
ATTGACGCTCATGCACGAAAGCGTGGGGAGCAAACAGGATTAGATACCCTGGTAGTCCACGCCCTAAACGAT
GTCTACTAGTTGTCGGGTCTTAATTGACTTGGTAACGCAGCTAACGCGTGAAGTAGACCGCCTGGGGAGTAC
GGTCGCAAGATTAAAACTCAAAGGAATTGACGGGGACCCGCACAAGCGGTGGATGATGTGGATTAATTCGAT
GCAACGCGAAAAACCTTACCTACCCTTGACATGGCTGGAATCCTCGAGAGATTGAGGAGTGCTCGAAAGAGA
ACCAGTACACAGGTGCTGCATGGCTGTCGTCAGCTCGTGTCSTGAGATGTTGGGTTAAGTCCCGCAACGAGC
GCAACCCTTGTCATTAGTTGCTACGAAAGGGCACTCTAATGAGACTGCCGGTGACAAACCGGAGGAAGGTGG
GGATGACGTCAAGTCCTCATGGCCCTTATGGGTAGGGCTTCACACGTCATACAATGGTACATACAGAGCGCC
GCCAACCCGCGAGGGGGAGCTAATCGCAGAAAGTGTATCGTAGTCCGGATTGTAGTCTGCAACTCGACTGCA
TGAAGTTGGAATCGCTAGTAATCGCGGATCAGCATGTCGCGGTGAATACGTTCCCGGGTCTTGTACACACCG
CCCGTCACACCATGGGAGCGGGTTTACCAGAAGTAGGTAGCTTAACCGCAAGGAGGGCGC

DNA sequence of Violacein operon of MM5, where n is filled in as missing bases

TGGGGCGGCATCGGCGGCCTGACCTGCGCCAACCACCTGATCCATCCCGCCGGCAACAGGAAGCTGCGCATC
CGCGTATTCGACCTCAATCCCGCTGTCGGCGGCCGCATCCAGTCGCACAAAATAGATGGCGAGGAAATCGCC
GAACTCGGCGCCGCCCGCTACTCGCCGCAACTGCATCCACATTTCCAGCAACTGATGCAGGGCAGCGGCCTG
CCGCATGCGGTCTACCCGTTCACCGAGGTGGTTTCCCACGATAGCGTGCTGGCAGAGCTGAAGGCCACGCTG
GACGAGCTGAACCCGATGCTGAAAGCCCATCCGAACCACTCTTTCCTCGAGTTCGTCAGCCATTACCTGGGC
GCCGACAAGGCGACCCACATTCATCAAGGCCACCGGCTATGACGCCTTGCTGCTGCCGATGGTGTCGGCTGC
CATGGCCTACGACATCATCAAGAAGCACCCGGAAACGCAGCACTTTACGGAAAACGCCGCCAACCAGTGGCG
CTATGCCACCGACGGCTATCACGAGCTGCTGTGCCGCTTGCAGCACCAGGCACAGGCCGCCGGCGTCGAATT
CCAGCTCGAACATTGTCTGCTGTCCGTGAAAAAATCGGGCGCCGACCACGTGCTCGCCTTCAGCCACCTGGG
CGACACGCAGATGCACCGGACACGCCACCTGGTGATGGCCATCCCGCCGTCCGCCATGCCGCGCCTGAACCT
GGATTTCCCGCACGCCTGGAGTCCGTTCCAGTATGACTCGCTGCCCCTGTTCAAGGGCTTCCTCACCTTCGA
CACGGCTTGGTGGGACGGGCTGGGGCTGACCGACAAGGTGCTGATGGCGGCAAACCCGCTGCGCAAGATCTA
CTTCAAGGGGGATAAATACGTGCTGTTCTATACCGACAGCAAAAGCGCCACCTACTGGCGCGACAGCCTGGA
ACTCGGCGAAGACGTGTACCTGGGAACGTGTCCGCAGCCACCTGGAAGAAGTCCTGCCCCTCGATGGCCGGC
CGCTGCCGCGCATCAAGGCGCACTTCCACAAGTTCTGGSCGCATGGCGTCCRARTTTTGCGTGGAGCCGGAA
GCCGAGCACCCGGCCGTGCTGCTGCACCGGGACGGCATCATCTCCTGTTCGGnnnnnnnnnnnnnnnnnnn
nnnnnnnnnnnnnnnnnnnnnnnnnnnnnnnnnnnnnnnnnnnnnnnnnnnnnnnnnnnnnnnnnnnnnnnn
nnnnnnnnCGCATCGCCTGGTGGCCGAAGACAGTCCCTACATCTCCTTTTCCGCCGCCGGCCAGGGTTTTAT
TGCCACCGTTGAAGAAAGCGCCGCCCTCAAGGCCCGCGCCAGGGCCATCCGCGACGAGCTCGTGTATCSCTT

SMTAMCCGCTTCAATGCCGAAGGCAAGCCCGATCCGGACGGCATCTTCAGCCAGGCGGCAGGCTACAATTTT

GGCGGCAATAATCATTTCTCGTGGGAGAACGCGCGGATCACGGGCGTCCAGCTTGGCGCTGGCGAGGTCGAC

ACGCAGGATGCACTGGTGGGCGCCAGGCTGGGCCTGTGGGGCCACTACAACGAATACCTGCGCACCACGTTC

AACCGCGCCAGGTGGATCGACAACAACCCCGCCGCGCCCGACACCACGCTGATCTACGCCGGCCAGTTCACC

TTGAGCGACAAGCTGGCCACGCCCAACACGCCCACCTTGTTCACGGCCGACATCGCGCAGGCGCACTCGGTG

CGCTGGCTCGGCAGCGGCCATATCATGGAACGCAGCGGGCATTTCCTGGACGAGGAATTCGGCCGCGCCAGG

CTGTTSCAGTTYTCGGTGGCCAAGCAGGACMCGCATKTCCTGTTCAATGMGGACCTGCCGYTGCCGGSCAGC

ATGCAGRCCTTGCGGCACGCCCTGKCYGACGACGACGTGCTGGGCCTGACGGTGCAGTATGCCTTGTTCAAT

ATGTCGACGCCGCTCAAACCGGACTCGCCCGTGTTCTACGACCTGGCCGGCAGCATCGGCCTGTGGCGGCGC

GGCGAGCTGGCCACCTATCCGGCCGGCCGCCTGCTGCAGCCGCGCCAGCAGAGCCTGSGGCCGRTGCTGGTG

CAAGTGCACGCGGACCGGGTCGCGTTCAWCATGMCGACCGYCGWTGCCTTCACCACGCGCGGCGAGGGCGCC

GTTTCGGAACAGCATCCCACGCATGCACTGGGCGGCAAGCAGGCGCTCGGCGACCTGCTGCTGCACGACGGC

ACCGGCACCTTGCTGGCGCGCATACCCGAGCAGCTGTACCGCGACCACTGGCGCCATCACGGCGTTTTCGAC

GTGCCGCGGCAGCACGCTGGCGACGCTACCGGTTCGCTGAGCCTGGGCAGCGCGCAAGCGCAGTGGGAAGAA

GCGGACTGGGTGCTGCAATCGGACAGCAACCAGTTGTACCTGGAAGCGCCGAACCGCAACAAGCATGAGCAA

TTTCCGCAGACCATCACCGTGCAAAGCCGCTACCGCGGCGCGCTGGCGGCGCCGCCTCCCCTGTCGGCGCAG

GCCGAGGACGGCGTGCTGCTGGGCGTGGAACAGCAGCCATCACCGCTGGGGCCTGGCTACACGATGCTGATn

nnnnnnnnnnnnnnnnnnnnnnnnnnnnnnnnnnnnnnnnnnnnnnnnnnnnnnnnnnnnnnnnnnnnnnnnn

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nnnnnnnnnnnnnnnnnnnnnnnnnnnnnnnnnnnnnnnnnnnnnnnnnnnnnnnnnnnnnnnnnnnnnnnnTCGTGTA

TCCCTTCATGTCGGACAGGTCTTCAGCCTGGCGGACCAGTGCAAATGCGAAACGTATTCGCGCCTGATGTGG

CAGATGTGCGATCCGCGCAACCGCGACAAGAGCTACTACATGCCCAGCACCCGCGAACTGTCGCTGCCAAAG

TCGCGCCTGTTCCTCAAATACCTGACCCAGGTCGAGGCGACGGCCGCGGCCAGGGCGGCGGTGCCGGAAGCG

GCCTTGCCGCCTGTCATYGGCAGCAAGGCCGGGCTGATCGAGGAACTGAAAAAGGCCATCGACCTGGAACTG

TCGCTGATGCTGCAATACCTGTACGCCGCGTATTCGATTCCCAACTATGCGCAGGGGGCGGCGCTGGTGCAG

GCCGGCCGCTGGCTGCCTGCCGAGCTGGCGCTGGCCTGCGGCACCGAAGACCGGCGCCGCGACAGCGGTACG

CGCGGCGTGCTGCTGGAAATCGCGCATGAAGAAATGATTCACTATTTATTGGTCAACAATGTGCTGATGGCG

CTGGGCGAAGGGTTTTACAGCGGCACACCGCTGCTGGGCCAGCAGGCGCGCCAGCGTTTTGGCCTGGACACG

GAATTTGCGTTCGAGCCATTTTCCGAACACGTGCTGGCGCGCTTCGTGCGTTTCGAATGGCCCGACTACCTT

CCCACGCCGGGCAAGTCGATTGCCACCTTCTATATCGCAATCCGCCAGGCCCTGGCCGATCTGCCCGGCCTG

TTTGACAGCGGCGGTGGCAAGCGCGGCGGCGAACACCATTTGTTCCTGAAAGAACTGACCAACCGCGCCTAC

CCCGGCTACCAGCTGGAAGTATCCGACCGCGACAGCGCGCTGTTCGCCATCGACTTCGTCACGGAACAGGGC

GAAGGCGTGGCCGTCGATTCGCCGCATTTCGCCGCGTCGCATTTCCAGCGCCTGCGCAGCGTCGCAGGCAAG

TACGCCGCCTGCGGCAAACCGTTCGAGCCGGCGCTGCCGGCGCTGAAGAATCCCGTGCTGGAAGCACGCGCG

GACTGCACCGTGGTGACCGACCGGAAGGCGCGCGCGCTGATGCAGCTGTATCAAGGCTGCTACGAACTGACC

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GGCCGCCATGCGGGGCCGCCCGTGCCCGAGCCGGTCAGCAGCCGGGTCAGCAGCGACTACAGCCAGGGCTGC

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GCCTGGRTAGTCGAGCSRGCGGGCAAGCCGCCATCKGTCTTTTACCTGGAGRCCGGNGGCAACCGCCTGCTG

CGCATGGTCACNGGCAANGACCCGCAGCACCTNTCGGTACGCGACTTTCCCAACCTGTTTGTCNGCGACATT

CCGGACAGCGTCTTTACGTCTTGCAACA

F Appendix - Type strain alignment of MM5 and 3.116

```
12 May 2020                        Alignment Results

Alignment:   Global DNA alignment against reference molecule
Parameters:  Scoring matrix:  Linear (Mismatch 2, OpenGap 4, ExtGap 1)

   Reference molecule:  J.Lividum(T), Region 1 to 1429
   Number of sequences to align:  3
   Total length of aligned sequences with gaps:  1430 bps
   Settings:  Similarity significance value cutoff:  >= 60%


Summary of Percent Matches:
   Ref:  J.Lividum(T)          1 to   1429   (  1429 bps)     --
     2:  J.MM5                 1 to   1428   (  1428 bps)     99%
     3:  J.3.116               1 to   1429   (  1429 bps)     99%


J.Lividum(T)          1 ctcagattgaacgctggcggcatgccttacacatgcaagtcgaacggcagcacggagctt
J.MM5                 1 ..........................................................
J.3.116               1 ..........................................................

J.Lividum(T)         61 gctctggtggcgagtggcgaacgggtgagtaatatatcggaacgtaccctagagtggggg
J.MM5                61 ..........................................................
J.3.116              61 ..........................................................

J.Lividum(T)        121 ataacgtagcgaaagttacgctaataccgcatacgatctaaggatgaaagtgggggatcg
J.MM5               121 ..........................................................
J.3.116             121 ..........................................................

J.Lividum(T)        181 caagacctcatgctcgtggagcggccgatatctgattagctagttggtagggtaaaagcc
J.MM5               181 ..........................................................
J.3.116             181 ..........................................................

J.Lividum(T)        241 taccaaggcatcgatcagtagctggtctgagaggacgaccagccacactggaactgagac
J.MM5               241 ..........................................................
J.3.116             241 ..........................................................

J.Lividum(T)        301 acggtccagactcctacgggaggcagcagtggggaattttggacaatgggcgaaagcctg
J.MM5               301 ..........................................................
J.3.116             301 ..........................................................

J.Lividum(T)        361 atccagcaatgccgcgtgagtgaagaaggccttcgggttgtaaagctcttttgtcaggga
J.MM5               361 ..........................................................
J.3.116             361 ..........................................................

J.Lividum(T)        421 agaaacggtgagggctaatatctcttgctaatgacggtacctgaagaataagcaccggct
J.MM5               421 ............a.............................................
J.3.116             421 ............a.............................................

J.Lividum(T)        481 aactacgtgccagcagccgcggtaatacgtagggtgcaagcgttaatcggaattactggg
J.MM5               481 ..........................................................
J.3.116             481 ..........................................................

J.Lividum(T)        541 cgtaaagcgtgcgcaggcggttttgtaagtctgatgtgaaatccccgggctcaacctggg
J.MM5               541 ..........................................................
J.3.116             541 ..........................................................

J.Lividum(T)        601 aattgcattggagactgcaaggctagaatctggcagaggggggtagaattccacgtgtag
J.MM5               601 ..........................................................
J.3.116             601 ..........................................................

J.Lividum(T)        661 cagtgaaatgcgtagatatgtggaggaacaccgatggcgaaggcagccccctgggtcaag
J.MM5               661 ..........................................................
J.3.116             661 ..........................................................

J.Lividum(T)        721 attgacgctcatgcacgaaagcgtggggagcaaacaggattagataccctggtagtccac
J.MM5               721 ..........................................................
J.3.116             721 ..........................................................
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```
J.Lividum(T)        781 gccctaaacgatgtctactagttgtcgggtcttaattgacttggtaacgcagctaacgcg
J.MM5               781 ............................................................
J.3.116             781 ............................................................

J.Lividum(T)        841 tgaagtagaccgcctgggg-agtacggtcgcaagattaaaactcaaaggaattgacgggg
J.MM5               841 ..................-.........................................
J.3.116             841 ..................g.........................................

J.Lividum(T)        900 acccgcacaagcggtggatgatgtggattaattcgatgcaacgcgaaaaaccttacctac
J.MM5               900 ............................................................
J.3.116             901 ............................................................

J.Lividum(T)        960 ccttgacatggctggaatccccgagagattggggagtgctcgaaagagaaccagtacaca
J.MM5               960 ..................t.........a.............................
J.3.116             961 ..................tt.......c.a.............................

J.Lividum(T)       1020 ggtgctgcatggctgtcgtcagctcgtgtcgtgagatgttgggttaagtcccgcaacgag
J.MM5              1020 ............................s...............................
J.3.116            1021 ............................................................

J.Lividum(T)       1080 cgcaacccttgtcattagttgctacgaaagggcactctaatgagactgccggtgacaaac
J.MM5              1080 ............................................................
J.3.116            1081 ............................................................

J.Lividum(T)       1140 cggaggaaggtggggatgacgtcaagtcctcatggcccttatgggtagggcttcacacgt
J.MM5              1140 ............................................................
J.3.116            1141 ............................................................

J.Lividum(T)       1200 catacaatggtacatacagagcgccgccaacccgcgagggggagctaatcgcagaaagtg
J.MM5              1200 ............................................................
J.3.116            1201 ............................................................

J.Lividum(T)       1260 tatcgtagtccggattgtagtctgcaactcgactgcatgaagttggaatcgctagtaatc
J.MM5              1260 ............................................................
J.3.116            1261 ............................................................

J.Lividum(T)       1320 gcggatcagcatgtcgcggtgaatacgttcccgggtcttgtacacaccgcccgtcacacc
J.MM5              1320 ............................................................
J.3.116            1321 ............................................................

J.Lividum(T)       1380 atgggagcgggttttaccagaagtaggtagcttaaccgcaaggagggcgc
J.MM5              1380 ............-...........................................
J.3.116            1381 ............-.........................t...........
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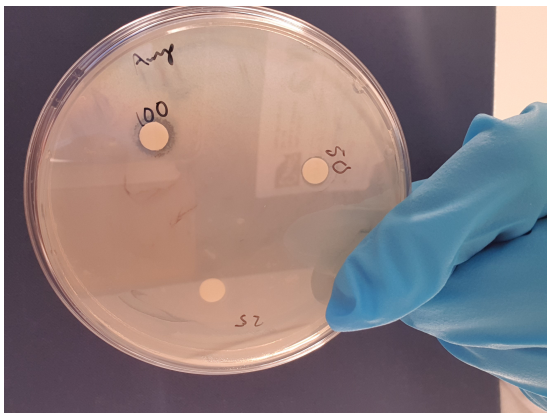
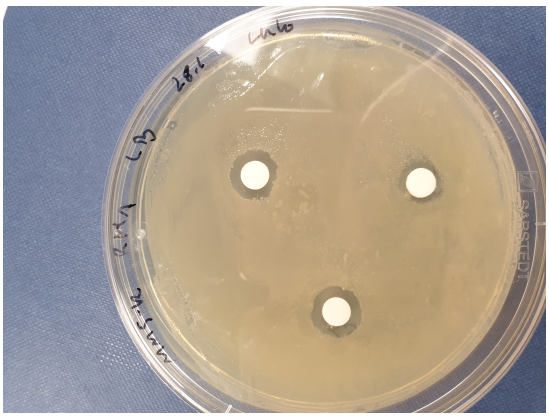
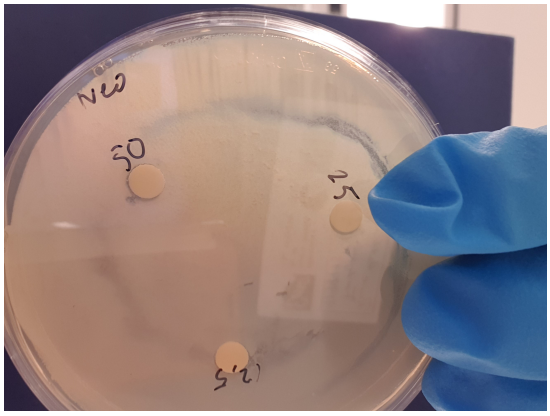
G Appendix - Antibiogram results



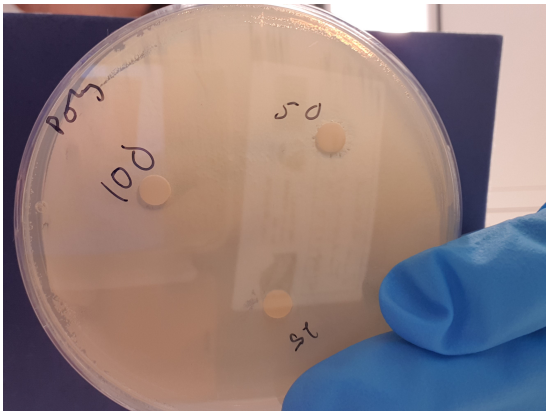
(a) Antibiogram for MM5 with ampicillin



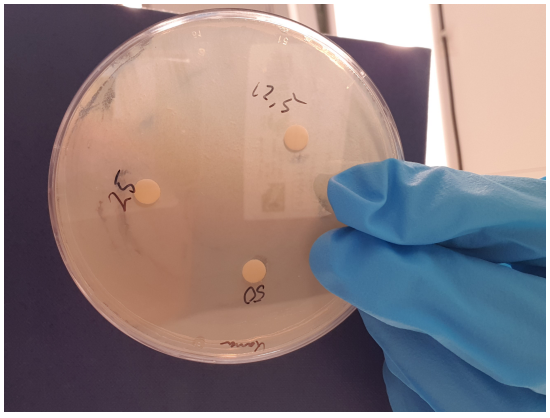
(b) Antibiogram for MM5 with chloramphenicol



(c) Antibiogram for MM5 with neomycin

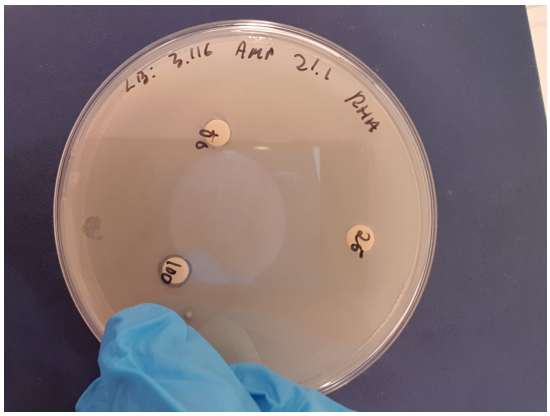


(d) Antibiogram for MM5 with polymixin

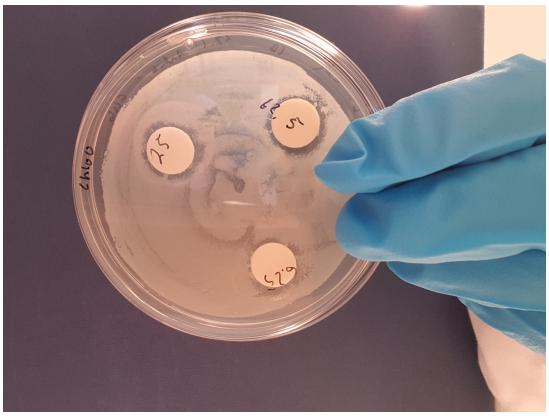


(e) Antibiogram for MM5 with kanamycin

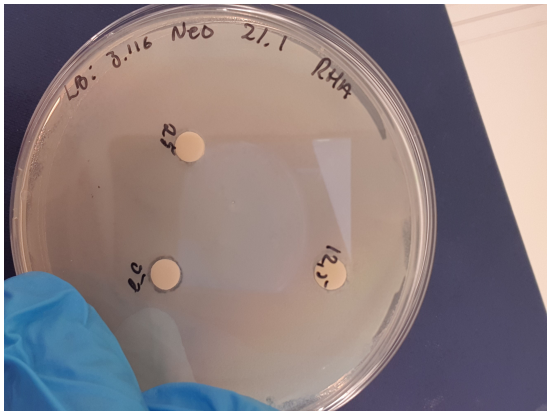
Antibiogram for MM5 tested with ampicillin, polymixin, neomycin, chloramphenicol, and kanamycin. The result shows inhibition for chlorampenicol and ampicillin.



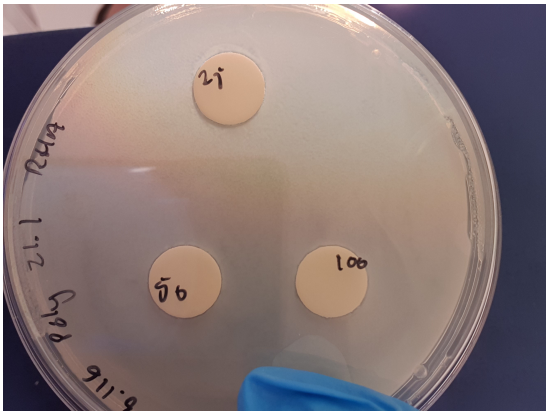
(a) Antibiogram for 3.116 with ampicillin



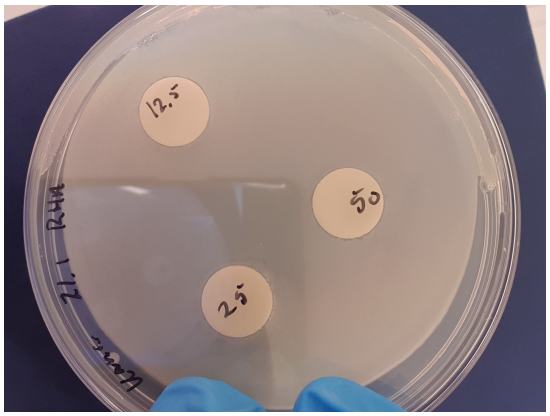
(b) Antibiogram for 3.116 with chloramphenicol



(c) Antibiogram for 3.116 with neomycin



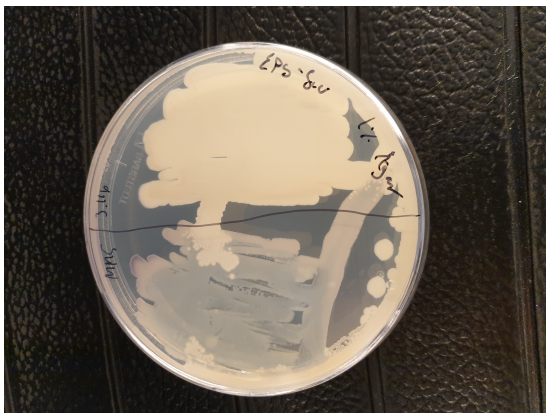
(d) Antibiogram for 3.116 with polymixin



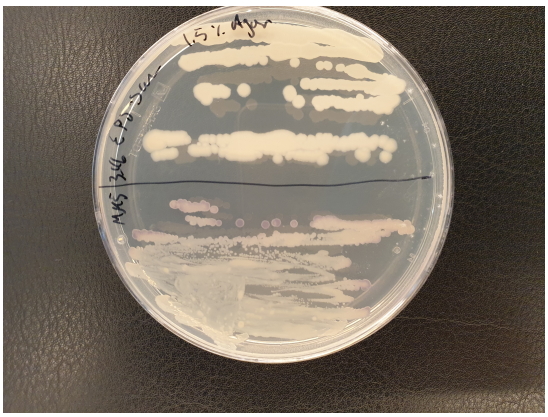
(e) Antibiogram for 3.116 with kanamycin

Antibiogram for 3.116 tested with ampicillin, polymixin, neomycin, chloramphenicol, and kanamycin. The result shows inhibition for chlorampenicol and ampicillin.

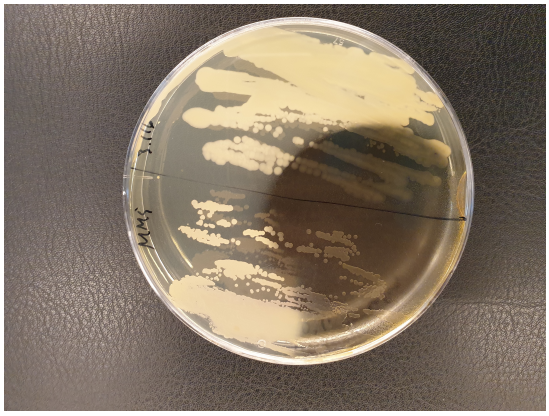
H Appendix - Agar-plates



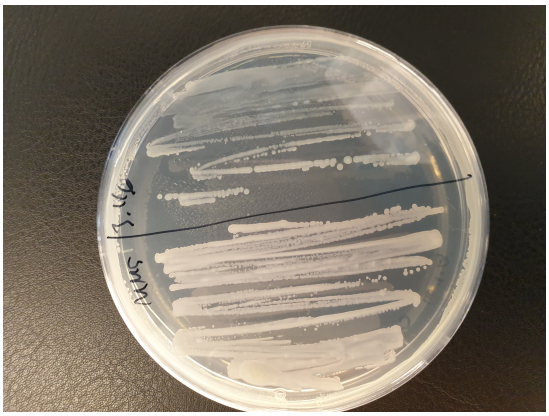
(a) MM5 and 3.116 growing on an agar-plate with EPS-sucrose with 1% agar incubated at 28 °C showing purple colonies for MM5.



(b) MM5 and 3.116 growing on an agar-plate with EPS-sucrose with 1.5% agar incubated at 28 °C showing purple colonies for MM5.

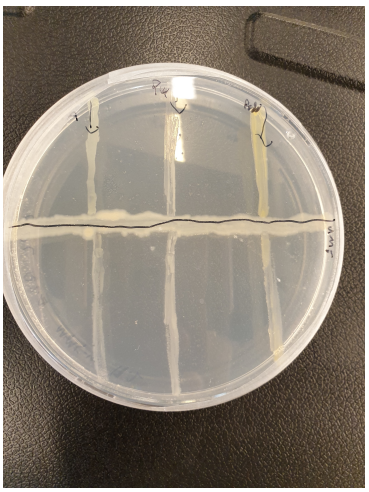


(c) MM5 and 3.116 growing on an agar-plate with LA medium with 1% agar and 2% glycerol incubated at 28 , showing slightly purple colonies for MM5.



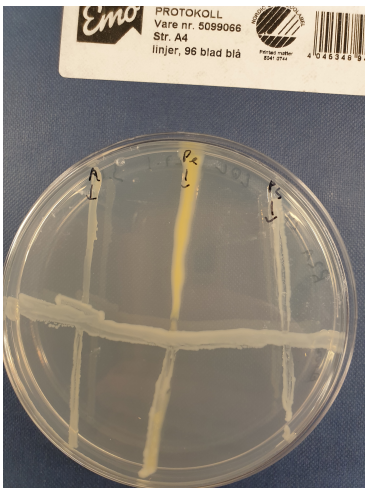
(d) MM5 and 3.116 growing on an agar-plate with R2A medium with 1% agar incubated at 28 °C showing tendencies of purple growth for MM5.

I Appendix - Cross-streaking

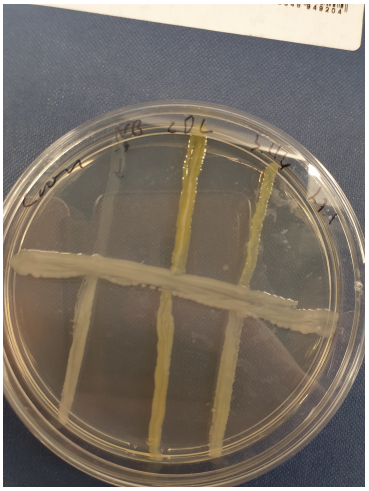


(a) Cross-streaking of MM5 with *Arthrobacter, Pedobacter, and Psychrobacter* on R2A 2% glycerol agar-plates.

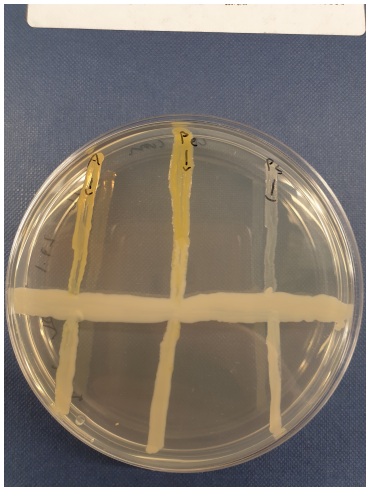
(b) Cross-streaking of MM5 with *Arthrobacter, Pedobacter, and Psychrobacter* on LB agar-plates.



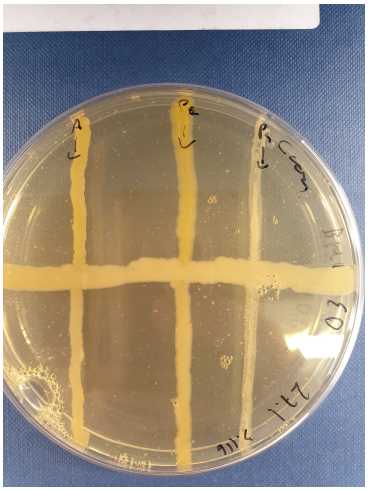
(c) Cross-streaking of 3.116 with *Arthrobacter, Pedobacter, and Psychrobacter* on R2A 2% glycerol agar-plates.



(d) Cross-streaking of 3.116 with *Arthrobacter, Pedobacter, and Psychrobacter* on NA agar-plates.



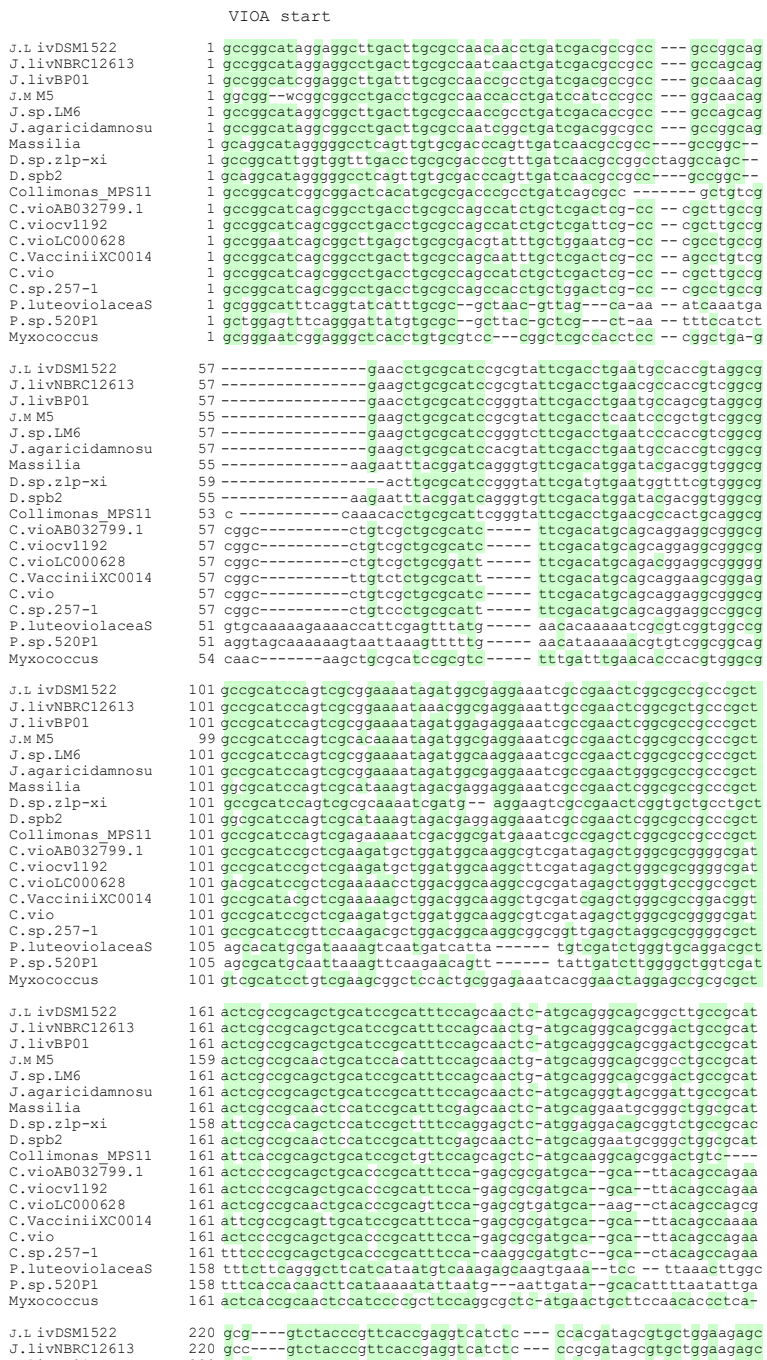
(e) Cross-streaking of 3.116 with with *Arthrobacter, Pedobacter, and Psychrobacter* on LB agar-plates.



(f) Cross-streaking of 3.116 with *Arthrobacter, Pedobacter, and Psychrobacter* on BHI agar-plates.

Cross-streaking of MM5 and 3.116 with *Arthrobacter, Pedobacter, and Psychrobacter* on different agar-plate mediums. None of the pictures indicate any inhibition of growth.

J Appendix - Alignment of violacein operon



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C.sp.257-1           216 gagcgaggtgtacccccttcacccagctgcggtt--- caagaaccatgcccagcaaacgc
P.luteoviolaceaS     213 ctatgaaaaattccctttttacacaactaaagcgcccacaagcat--- tgcataaaagtt
P.sp.520P1           213 acatgaaagttttccttttacacaattaacacgaccacaagaac--- ttcatagtgaat
Myxococcus           219 ---tgaagcctacccattcacccatgccatctt--- ccaggacggcatgaggggcagc

J.L ivDSM1522        272 tgaaggcaacgctggatgagctg-agcccgatgctgaaaatgcatccgaacgactccttc
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Massilia             272 tgaaggcaactctgctgagcctg-agtgcgatgctgaaaaaacatccgaacgattccttc
D.sp.zlp-xi          269 tgaaggatacctgctcagcttgcagcccaatg-tgaaagagcatccagaggaatccttc
D.spb2               272 tgaaggcaactctgctgagcctg-agtgcgatgctgaaaaaacatccgaacgattccttc
Collimonas_MPS11     272 tgaaggcaaccttgctcggcctg-agttccatgctgaaggagcatccggaagattccttc
C.vioAB032799.1      272 tgaagcgggcgatgaacgagttg-tcgcccaggctgaaagagcatggcaaggaatccttt
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VIO C end VIO D start

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```

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Myxococcus           6322 tcc-gtc----------gggtgcg-------tgcccctccgctcccctcagcg -----ct
                     VIO E end

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D.sp.zlp-xi          6333 ctgcgcatggtcac
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C.vio                6336 ctgaggatggtgac
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P.sp.520P1           6356 gtacgtatgataac
Myxococcus           6358 tcgagga-------
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Eirik Degré Lorentsen

Characterisation of two Janthinobacterium isolates originating from salmon fry

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Kunnskap for en bedre verden