Sulfate-Reducing Bacteria

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Contributor: Ivan Kushkevych

Sulfate-reducing bacteria (SRB) are a group of anaerobic microorganisms that can be present in the environment and gastrointestinal tract as a part of the intestinal microbiome and can be involved in inflammatory bowel diseases (IBDs), including ulcerative colitis in the human and animals.

bacteriophage therapy | combatting corrosion | sulfate-reducing bacteria

1. Introduction

Bacteriophages (phages) have come into increasing prominence since there are viruses of bacteria [1][2]. Phages as antibacterial agents can be used to treat environments, both clinically or veterinary. The treatment can be described as phage-mediated bacterial biocontrol [3][4], phage therapy, or bacterial therapy [5][6]. The application of antibiotics to environments or the use of antibiotics normally employed as treatments of human infections for other means, such as in animal husbandry, has been discouraged [7][8]. Thereby, it has become important to find alternatives to antibiotics to control undesirable bacteria [9][10][11][12][13].

Sulfate-reducing bacteria (SRB) are a group of anaerobic microorganisms that can be present in the environment and gastrointestinal tract as a part of the intestinal microbiome and can be involved in inflammatory bowel diseases (IBDs), including ulcerative colitis in the human and animals [14][15][16][17][18][19]. They play an important role in this environmental sulfur cycle, especially in the dissimilatory sulfate reduction process. Sulfur belongs to group 16 of the periodic element system, and it makes up to 0.04% of the Earth's crust [20]. Though ≈100-fold less abundant than oxygen, sulfur nevertheless plays an important role in biology. Most prominently, sulfur is found as a component of two of the naturally occurring amino acids. These two, methionine and cysteine, are both essential to the functioning of all living organisms and play unique roles in both molecular genetics and protein structure, serving as start codons and disulfide bridges, respectively. Sulfur is found as well as an abiotic component of environments. For example, it contributes to the formation of the minerals pyrite (FeS_2) and gypsum ($CaSO_4 \cdot 2H_2O$). Biogeochemically, sulfur can take on multiple forms involved in chemical and biological oxidation and reduction, since its oxidation numbers range from −2 in the fully reduced state to +6 in the fully oxidized state [21]. Thus, sulfur in different forms can readily serve as electron donors (biologically, these are sources of energetic elections) and electron receptors, thus serving in this latter case as electron sinks, including as analogous to the role of oxygen as a final electron acceptor [22].

SRB are widely distributed in anoxic environments where they utilize sulfate as a terminal electron acceptor, reducing them to sulfides [23][24][25][26][27]. They inhabit terrestrial and aquatic ecosystems, and they are part of the

microbiota of animals and humans [28][29][30][31][32]. As decomposed organic substances serve as the electron donor, SRB thereby represent chemoheterotrophic, anaerobically respiring bacteria. The metabolite that results from this anaerobic respiration is known as hydrogen sulfide (H_2S), and it is chemically analogous to water as the metabolic byproduct of aerobic respiration (water (H_2O)). Unlike water, which represents hydrogen's most commonly fully oxidized state, H_2S can still be oxidized by sulfur bacteria, serving in this case as an energy-carrying electron donor. H_2S also can be released into the atmosphere as hydrogen sulfide gas [22].

H_2S production and release in the course of anaerobic respiration of SRB causes a wide range of issues. For example, SRB found in marine sediments are the cause of sulfur presence in petroleum, generating so-called "sour" crude oil vs. the preferred "sweet" crude oil. SRB-released H_2S is associated as well with the corrosion of steel components of machines used during oil extraction, transport, and processing [33]. In addition, SRB are part of the human and animal intestinal microbiome. *Desulfomonas pigra*, now called *Desulfovibrio piger*, was first isolated in 1976 as the part of the intestinal microbiome [34]. Notably, the sulfide resulting from the presence of these bacteria damages oral mucosa and intestinal cells, with SRB thereby potentially giving rise to bleeding diarrhea, weight loss, periodontitis, or even ulcerative colitis [35][36][37][38][39][40][41][42].

Whether as contaminants of oil processing infrastructure or components of the human intestine microbiome, reducing loads of SRB can be desirable. Bacterial resistance to antibiotics has become increasingly prevalent, leading to less effective outcomes of antibiotic treatments, and there is a need for the antibiotic use reduction. The studies are indicating the antibiotic resistance of *Desulfovibrio desulfuricans* isolated from people with colitis [43].

2. SRB Categorization and Characteristics

Sulfate-reducing bacteria (SRB) include a wide range of otherwise unrelated prokaryotic organisms. They mainly belong to the Bacteria, but also are found among the Archaea. There are 220 known species divided into 60 genera [44][45]. SRB use sulfate as a terminal electron acceptor during the dissimilatory sulfate reduction process. The different organic compounds are used as an electron donor and carbon source by SRB. For example, these organic substances include acetate, ethanol, glucose, lactate, malate, and propionate, depending on the species, which collectively serve as electron donors and which also are oxidized to various distinct end products depending on species [22]. The resulting metabolic pathway—movement of electrons from an organic substance to sulfate ions, giving rise to H_2S—is called dissimilatory sulfate reduction, meaning that the resulting reduced sulfur is not assimilated into these organisms but instead is released as a waste product. Examples of different types of sulfate-reducing prokaryotes and their families according to Brenner et al. (2005) are presented in Table 1 [44].

Table 1. Some types of sulfate-reducing bacteria (SRB) [44].

Species	Phylum	Order	Shape	Gram Staining	Mobility
Desulfovibrio piger	*Proteobacteria*	*Desulfovibrionales*	rods	negative	no

Species	Phylum	Order	Shape	Gram Staining	Mobility
Desulfovibrio desulfuricans	*Proteobacteria*	*Desulfovibrionales*	vibrios	negative	yes
Desulfovibrio vulgaris	*Proteobacteria*	*Desulfovibrionales*	vibrios	negative	yes
Desulfobacter hydrogenophilus	*Proteobacteria*	*Desulfovibrionales*	oval rods	negative	yes
Desulfobulbus propionicus	*Proteobacteria*	*Desulfovibrionales*	elliptical rods	negative	yes
Desulfotomaculum acetoxidans	*Firmicutes*	*Clostridiales*	rods	positive	yes
Caldivirga maquilingensis	*Crenarchaeota*	*Thermoproteales*	rods	–	yes

SRB include microorganisms displaying different shapes, sizes, metabolic pathways, cell wall types, and more [44][46][47][48]. However, a dominating component of SRB taxonomy consists of the members of the Gram-negative bacteria, class *Deltaproteobacteria* of phylum *Proteobacteria*, including the SRB-containing orders *Desulfovibrionales* and *Desulfobacterales*. The division is largely based on 16S rRNA gene sequencing [44]. Members of order *Desulfovibrionales* are motile, anaerobic rods that are mostly mesophilic or thermophilic, and rarely psychrophilic. The order *Desulfobacterales* is more morphologically diverse than the order *Desulfovibrionaceae*, including not only rods but cocci and filamentous bacteria as well. They are mobile, thermally mesophilic, and sometimes psychrophilic. Slightly curved rods of *Desulfobacterales* mainly use lactate as an electron donor that is further oxidized to acetate, and they also require vitamins to grow. This order occurs in anoxygenic aquatic habitats. The *Desulfobacterales* family *Desulfobulbaceae* includes the genus *Desulfobulbus*. These lemon-shaped rods populate water sediments (both freshwater and marine water). They use mainly propionate as an electron donor that oxidizes incompletely to acetate [44][45].

The *Desulfovibrionaceae* family consists of the following genus: *Bilophila*, *Desulfobaculum*, *Desulfocurvibacter*, *Desulfocurvus*, *Desulfohalovibrio*, *Desulfolutivibrio*, and *Desulfovibrio*. *Desulfohalobiaceae*, a family within the order *Desulfovibrionales*, embraces the genera *Desulfohalobium*, *Desulfonatronospira*, *Desulfonatronovibrio*, *Desulfothermus*, *Desulfonauticus*, *Desulfovermiculus*, and *Desulfohalophilus* [44][48]. The Desulfovibrionaceae family consists of mesophilic organisms that oxidize organic substances to acetate, most of which have a vibrio shape and one polar flagellar. An important representative is the genus *Desulfovibrio*, since this genus is the most often found in the environment (it encompasses the majority of species, and they are the most often found within the human and animal intestinal microbiota, especially among patients with developed intestinal bowel diseases) [44][49]. *Desulfovibrio piger*, which in contrast to *D. desulfuricans* consists of non-motile straight rods, represents the most abundant SRB in the human gastrointestinal tract [34]. This species in particular has been found to be present at significantly higher levels in patients suffering from chronic bowel inflammation [50][51]. By contrast, *Desulfovibrio ferrophilus* occurs in the marine environments that are oxygen free, where it forms crusts on the iron surfaces, resulting in corrosion. Both species are using iron as an electron donor [52]. *Desulfopila* corrodens requires an

organic substrate to grow, such as acetate [53]. The family *Desulfohalobiaceae* also includes the genus *Desulfomonas*, an irregular, immobile rod found in human stool [32][54].

2.2. Other SRB-Containing Taxa

Sulfate-reducing bacteria are also found in other bacterial taxa. The genus *Desulfotomaculum* belongs to phylum *Firmicutes*, class *Clostridia*, order *Clostridiales*, and the family *Peptococcaceae*. These are spore-forming Gram-positive bacteria presenting morphologically as straight or curved rods. Their spores are oval, terminal, and subterminal. In terms of temperature sensitivity, both mesophilic and thermophilic species are included. For example, they occur in soil or deep sea sediments [55]. Among the SRB also is genus *Thermodesulfovibrio*, which belongs to the bacterial phylum *Nitrospirae*. These strict anaerobes have entirely been isolated from hot springs and hydrothermal vents [56]. In the domain Archaea, sulfate-reducing representatives (some authors use the term SRM—sulfate-reducing microorganisms) are found among the *Crenarchaeota*, which is a phylum historically associated with sulfur-based metabolisms [21].

3. SRB Impact on Environments and Humans

SRB are found in a wide variety of water and soil habitats where the environment is oxygenated and sulfates are available. They occur in freshwater, marine or brackish waters, in wetlands, hot springs, oil wells, and in sewers. Up to fifty percent of the mineralization of organic matter in the continental shelf is due to dissimilatory sulfate reduction. The resulting sulfite metabolite is oxidized by sulfur-oxidizing bacteria in the same environment [57]. The impact of SRB on the environment can be overseen through the fact that *Desulfovibrio desulfuricans* has been found to be able to methylate mercury (MeHg) [58]. The release of MeHg in marine environments occurs under anaerobic (or low oxygen) conditions, and the methylation of Hg(II) in freshwater systems is mainly done by sulfate-reducing bacteria or iron-reducing bacteria [59].

3.1. Sewer System Negative Impacts of SRB Action

Sewer systems are by nature nutrient-rich and are therefore home to a wide range of microorganisms, including SRB that grow either in sediment or biofilm at the bottom of the pipes. Problems are caused by their H_2S production. It diffuses from the lower layers of the biofilm up to the oxic conditions, where it is oxidized biologically (for example by bacteria of the family *Thiomonas* and *Thiobacillus*) or instead abiotically [60]. Abiotic oxidation of sulfide represents the oxidation where physico-chemical processes are included, meaning that the reduced iron and/or manganese oxidation leads to the improvement of the kinetics of sulfide oxidation with the formation of oxidized metals [60].

The resulting sulfates (based on the SO_4^{2-} ion) and sulfuric acid (H_2SO_4) react with concrete, which is a material frequently used for the construction of sewers. One of the common components of concrete is gypsum ($CaSO_4$), which comes into contact with sulfates corrodes to ettringite ($Ca_6Al_2(SO_4)_3(OH)_{12}{\cdot}26H_2O$) [61]. Ettringite expands and causes cracks and loss of concrete coherence. Due to the production of sulfuric acid, pH also decreases,

resulting in biofilms formed by acidophilic microorganisms, which further increases the surface acidity. H2S and acetate produced by SRB are lowering pH on the metal surface. This process could lead to a higher corrosion rate [62]. Additionally, sulfane threatens the health and life of sewer workers [63][64].

Constantly, new strains of SRB are found, such as *Desulfovibrio vulgaris* strain Hildenborough (isolated from sediment of a heavy metal impacted lake). Bacteriophages related to specific SRB are also usually revealed with new strains [65][66].

Already in 1973, scientists from the University of Kansas observed phage-infecting *Desulfovibrio vulgaris*. Bacterial cells were stressed by both UV radiation and mitomycin C. At first glance, no lysis was observed after antibiotic addition, but the size of individual cells increased and appeared more pleomorphic. Therefore, the suspension was centrifuged several times, and then, the pellet was examined under an electron microscope. The observers were not sure whether they were phage, but they mention that “particle morphology is typical of phage belonging to Bradley Group A” [67]. The differences among bacteriophages of different *Desulfovibrio vulgaris* strains can be overviewed through the differences between *D. vulgaris* NCIMB 8303 and *D. desulfuricans* ATCC 13541. These strains showed different restriction enzyme cleavage patterns and different protein profiles [65][66][67].

Rapp and Wall (1987) found phage capable of gene transduction in *Desulfovibrio desulfuricans*. It was observed that the virus is capable of transferring rifampicin and nalidixic acid resistance between strains [68]. A lytic bacteriophage was isolated in 1988 in Japan. Scientists separated phage from muddy sediment samples collected at low tide and tested it on a laboratory strain of *Desulfovibrio salexigens*. Based on electron microscope observations, they reported that these viruses have a regular icosahedral head and a long non-contractile flagellum. They were morphologically similar to coliphage λ, which is a member of the family *Styloviridae*. The nucleic acid has been characterized as dsDNA [69][70].

In the early 1990s, further attempts were made in Kansas to induce lysogenic phages in *Desulfovibrio vulgaris*, which is a strain of Hildenborough and *Desulfovibrio desulfuricans*. This was successful, based on restriction analysis and DNA hybridization, and it was found that the viruses of the two organisms did not share DNA homology and thus probably did not share a common ancestor. Further research has focused on comparing strains of *D. vulgaris* Hildeborough, which has been described in earlier studies, and strain DePue, which was isolated from sediment of a heavy metal contaminated lake. The sequence similarity of the 16S rRNA gene was over 99%; however, the DePue strain had a significantly reduced genome compared to the previous one. Its genome lacked most of the genes that were annotated as phages or phage-related in strain Hildeborough. Strain DePue were also susceptible to prophages induced in the Hildeborough strain. This correlates with the finding that DNA does not contain prophages related to those induced. The analysis indicated that prophages have a strong influence on the overall genome of individuals of this species; perhaps, they may also provide a selective advantage in certain environments [71][72].

Research into SRB-targeting bacteriophages may have practical implications in suppressing and controlling their population. The cell can prevent the virus from being infected in the first step of the phage process by preventing

the phage adsorption to the cell. The structure of the receptor to which the bacteriophage binds may be mutated, or the receptor may be masked by other proteins, but the phage may adapt to this change [73]. Bacteria can secrete into the extracellular space a polysaccharide matrix that forms a physical barrier between the bacteriophage and the microbe. However, some phages are able to enzymatically cleave this barrier or use the matrix itself as a recognition site [74]. Sometimes, bacteria produce competitive receptor inhibitors. These substances naturally occur in the vicinity of bacteria and can specifically bind to receptors that then are unusable for phages [75]. Mostly, bacteria and archaea contain a restriction modification system that prevents the cell from foreign DNA. Restriction enzymes in the cytoplasm recognize and degrade unmethylated DNA. In some cases, nucleic acid is methylated by methylase, causing a loss of sensitivity of bacteriophage DNA to restriction enzymes [76][77].

3.2. The Relationship between Iron Corrosion and SRB Presence

Another material that corrodes as a result of SRB action is metallic iron (Fe^0), including as a component of steel. Iron corrosion in the presence of SRB is accelerated [53]. Corrosive SRB prefer the direct consumption of electrons derived from iron than from H_2 [78][79]. According to this theory, the iron in contact with water loses positive ions and thereby is polarized. In an anoxic environment, the released electrons then combine with protons dissociated from water to form H_2. This remains in equilibrium on the metal surface. However, this equilibrium is perturbed by SRB utilizing H_2, resulting in a driving of the reaction instead toward further metal oxidation. Other possible corrosion mechanisms have been proposed. More than a decade ago, a study suggested that bacterial strains that use iron as a direct electron donor without a hydrogen intermediate can also be involved in corrosion [80][81]. These strains include species later called *Desulfovibrio ferrophilus* and *Desulfopila corrodens*. Electrons are also gained through the formed crust of iron sulfate (FeS) and ferrous carbonate ($FeCO_3$), and they form a conductive mixture. Since SRB damage worldwide pipelines and result in hundreds of millions of dollars lost annually, bacteriophage treatment of SRB can reduce these costs significantly. It is well known that corrosion control is a big economic issue [82].

3.3. Oil and Gas Industry

SRB can be found both below and above the ground, and their presence raises several problems in terms of oil extraction and processing. For example, their presence within oil extraction and processing equipment raises several problems due to the aforementioned corrosion of metals. This results in damage to numerous equipment components, thereby increasing costs. In addition, metabolites such as H_2S are dangerous for workers associated with this sector. By burning oil, the sulfur it contains—another consequence of SRB action, which in this case occurs predominantly below the ground—also gets into the atmosphere, resulting in the acidification of rain by the oxidation of H_2S to sulfuric acid [78].

As noted in the Introduction, in the mining industry, oil is classified according to its sulfur content into “sweet” (sweet crudes), common, and “sour” (sour crudes). Sweet crudes, so named owing literally to its sweet taste, can contain by convention a maximum of 0.5% sulfur, and this is both the highest quality and the most valued of crude oils. By contrast, ordinary crude oil contains 0.5–1.5% sulfur, and crude oils containing even higher percentages of

sulfur are considered to be sour. Sulfur content not only can lead to the formation of H_2S, it also has to be removed from oil prior to burning, and doing so is costly. Oil “acidification” is often associated with the tertiary phase of oil extraction, that is, when oil from wells no longer reaches the surface without additional pressurization. That additional pressurization is accomplished via what is known as the irrigation method, and this involves the pumping of sea water into wells to increase volumes and therefore pressure levels. A mixture of water, oil, and natural gas is formed by this process, which is subsequently fractionated on the surface, and the released water again forced into the deposit. In this way, the extraction of residue oil is achieved, which would not be otherwise achievable due to pressure loss. However, by introducing sea water, a certain amount of sulfate and SRB enters into the well. Then, this can significantly increase the content of sulfide due to SRB metabolic activity [83].

3.4. Intestinal SRB and Their Association with Diseases

SRB are a natural part of the colonic microbiota of animals and humans [84][85][86][87][88][89]. They are involved in the utilization of H_2 produced in the intestine as a result of the fermentation of sugars. Intestinal SRB use organic compounds as an electron donor [90][91][92][93]. In this respect, they have a competitive relationship with other H_2 metabolizing organisms for the acquisition of electrons, namely methanogenic archaea (for example, *Methanobrevibacter smithii*). The availability of sulfate, which also is a component of food, plays important roles in intestinal SRB growth as well. Endogenous sources of sulfate, such as mucin or chondroitin sulfate, are also present in the intestine but must be treated by the lytic action of other bacteria such as clostridia [94].

The defining metabolic by-product associated with SRB is, of course, H_2S [95][96][97]. At higher concentrations, H_2S has carcinogenic and toxic effects on intestinal cells. It also blocks the binding of oxygen to cytochrome c and inhibits its functionality [98][99]. By binding to heme *a*3 cytochrome, the binding of oxygen is disabled and thereby causes oxidative phosphorylation, interrupting the formation of ATP [99]. H_2S also acts mutagenically on DNA and, by its ability to reduce disulfide bridges, it can also disrupt protein structures [99][100][101][102][103]. SRB are often associated with idiopathic intestinal inflammation, such as ulcerative colitis. In this disease, an increased amount of SRB [101] and an increased concentration of H_2S have been found as compared to healthy patients [102][103]. However, the results are not showing fully unambiguous correlations. On the other side, the high prevalence of intestinal bowel disease among inhabitants, especially in Western countries, emphasizes the importance of studies dealing with SRB occurrences as well as their intestinal environments [84][85][86].

Bacteria are constantly developing new anti-phage defenses, due to which phages go through constant evolution, too. Anti-phage systems are mainly based on protein components that mediate defense. Protein involvement in anti-phage bacterial systems is the most understood bacterial defense against phages. Chemical anti-phage defense systems are widely developed in *Streptomyces* [104]. Another common bacterial anti-phage system is the microbial cell surface modification that does not allow phage attachment. The CRISPR–Cas defense system represents a more advanced anti-phage bacterial strategy, since it is based on phage sequences, capturing and using it to prime a response that inhibits phage growth. The addition of methyl groups to DNA and degrading other DNA without methyl groups is another bacterial tactic against phages. Certainly, there are also other more specific bacterial single cell developed anti-phage systems and strategies [105].

Epithelial cells secrete mucin, which creates a chemical and mechanical barrier against bacteria, while also lubricating the intestines and hydrating them. These glycoproteins contain the rigid MUC2 protein. H_2S degrades the structural integrity of mucous layers by reducing the disulfide bridges that bind mucin units. This causes a decrease in polymer binding, and bacteria can therefore more easily reach the epithelial cells where they can induce an immune response or directly damage the cells [103].

3.5. Research in the Field of SRB Bacteriophages

All of the above negative effects associated with H_2S production lead to considerations of how to suppress SRB metabolic activities [106][107][108][109][110][111][112][113]. Alternatively, it may be possible to combat the nuisance of SRB through the use of bacteriophages [10][66][65][70]. Superinfection (SI) exclusion systems are complexes of proteins in the membrane that prevent viral DNA from penetrating to the cell. These proteins are often encoded by prophage genes and are intended to counteract the body's superinfection, preventing the bacterium from being infected with the same or a similar virus several times, thereby reducing the viability of an already infected bacterium [76].

Viruses in total are the most abundant group of "organisms" in the world with the amount measured microscopically in aquatic systems present, e.g., at 10^7 per milliliter [114], which is somewhat higher in sediments [115]. The total population is estimated to be 10^{31} entities [116]. Given the great abundance of bacteria, most of these viruses are thought to be bacteriophages.

Bacteriophages can be divided in two main groups [117]: tailed and tailless. They can also be distinguished into a number of different infection types [118]: lytic phage, chronic phage, and latent phage. Lysogenic cycles are associated with what are known as temperate phages [67], while phages that are unable to display lysogenic cycles, but instead only lytic cycles, can be described as strictly or obligately lytic. Temperate phages are of interest especially due to their ability to modify bacterial hosts both genetically and phenotypically [68][70][71][72], whereas strictly lytic phages ideally are what is employed for phage-mediated biocontrol and phage therapy. It is thought that most phages are lytic (whether strictly lytic or instead temperate); in nature, both types of phages serve as natural antagonists of bacteria.

Since H_2S is produced by SRB and it represents the harmful compound in the environment, phages represent an important factor for the elimination of SRB genera. The main sulfide-producing bacteria (SPB) phages belong to families of *Siphoviridae* and *Myoviridae*. Phage activities toward SPB are the most effective at 30 °C and less effective at 20 °C [119]. The lysogenic bacteriophage belonging to *Styloviridae* (*Siphoviridae* is a new name according to the ICTV (International Committee on Taxonomy of Viruses)) lyses salt-requiring SRB, *Desulfovibrio salexigens* [70].

Bacteriophages are responsible for 60–70% of all problems occurring during the fermentation of different food commodities (bacteriophages can delay and inhibit fermentation processes) [120]. Spontaneous fermentation is changed with starter cultures due to more controlled processes. *Lactobacillus plantarum* strains (mainly used in vegetable fermentation) were found to be 25% sensitive to bacteriophages [121]. However, there is a difference in

phage infection rate. Phage infection rate is considered fast if bacterial lysis occurs within 2 h after infection [122]. Bacteriophages found during fermentation processes are usually eliminated after 30 min treatment at 80 °C and 90 °C (they can survive the time and temperature used in standard food pasteurization). It means that they are resistant to the environments during food fermentation, especially because it was found that bacteriophages grow under broad pH values [123]. When phages titer increases over 10^6 PFU/mL, the fermentation is usually inhibited [124].

As outlined in previous sections, a number of taxa include members that are sulfate reducing, and these bacteria can be found within a variety of contexts, where in some of those contexts, they can be problematic, e.g., such as due to negative impacts on infrastructure (e.g., pipes) or health (e.g., the human intestine). As generally, it is thought that all or at least most bacteria types possess at least one associated phage, it should be assumed that most or all SRB also have associated phages. A variety of methods exist toward phage discovery, the most traditional of which is simply isolation as plaques against a given bacterial host [118]. Generally, this isolation is most conveniently and therefore most typically takes place when working with bacteria that are able to readily form lawns on agar surfaces. For bacteria requiring anaerobic environments for growth, phages are still readily isolated and propagated, e.g., as within anaerobic chambers. Generally, many more phages have been isolated, and their role in bacterial infection has been studied. Here, we provide a comprehensive overview of SRB-infecting phages isolated from specific SRB hosts.

Previous studies induced bacteriophages from cultures of *Desulfovibrio vulgaris* NCIMB 8303 and *Desulfovibrio desulfuricans* ATCC 13541 by UV light. The UV effect during 9 to 10 h resulted in the phage maximum yield. Nucleic acids of phages from both cultures (*D. vulgaris* NCIMB 8303 and *D. desulfuricans* ATCC 13541) were cut by restriction endonucleases (specific for double-stranded DNA). DNAs of phages from these two cultures showed different restriction enzyme cleavage patterns. The homology was not noticed between a 25 kb phage DNA of *D. vulgaris* and *D. desulfuricans*. The protein profiles of isolated phages from these two cultures were also analyzed, and it was found that the *D. vulgaris* phage contained two major bands (Mr values of 37,000 and 56,000) and the *D. desulfuricans* phage contained only one major band (Mr 38,000) [125].

Bacteriophage isolated from *D. vulgaris* was defined through establishing a preliminary endonuclease restriction map. The mapping succeeded in linking four BamHI fragments into two DNA segments, though not linking was detected between the two segments. The obtained results from the authors lead to the conclusion that two phages were induced from *D. vulgaris* culture. The results in the study were supported by the size approximation of restriction enzyme fragments, electron micrographs, and density gradients [126].

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