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Rhabdoviruses as Vectors for Vaccines and Therapeutics

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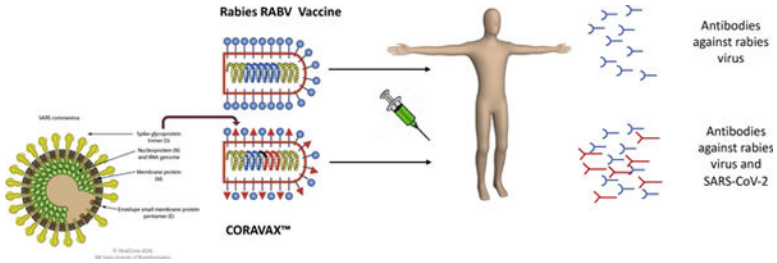
Abstract

Appropriate choice of vaccine vector is crucial for effective vaccine development. Rhabdoviral vectors, such as rabies virus and vesicular stomatitis virus, have been used in a variety of vaccine strategies. These viruses have small, easily manipulated genomes that can stably express foreign glycoproteins due to a well-established reverse genetics system for virus recovery. Both viruses have well-described safety profiles and have been demonstrated to be effective vaccine vectors. This review will describe how these Rhabdoviruses can be manipulated for use as vectors, their various applications as vaccines or therapeutics, and the advantages and disadvantages of their use.

Graphical Abstract



Keywords

rabies virus; vesicular stomatitis virus; vaccine

Introduction

The *Rhabdoviridae* family are bullet-shaped, negative-sense single-stranded RNA (ssRNA) viruses. They have a single segment genome that encodes five proteins: the nucleoprotein

Conflict of interest

M.J.S. is an inventor on different Patents and Provisional Patent Application related to rhabdoviral vectors and vaccine. All remaining authors declare no competing interests.

(N), phosphoprotein (P), matrix protein (M), glycoprotein (G), and RNA dependent RNA polymerase (L) [1]. Two well-studied rhabdoviruses are rabies virus (RABV), from genus *Lyssavirus*, and vesicular stomatitis virus (VSV) from genus *Vesiculovirus*. While both viruses are neurotropic zoonoses, and have similar length genomes (~11–12kb) [1], they differ in their biology.

RABV infects a variety of mammals and is typically maintained in nature through mesocarnivores (e.g., dogs, coyotes, foxes, raccoons, skunks) and bats [2]. In addition to causing disease in animals, RABV also causes severe encephalitis in humans that, if untreated, is almost always fatal [3]. Prompt treatment with the rabies vaccine before the onset of symptoms avoids the disease in almost all individuals exposed to RABV [4]. The first record of rabies disease dates back to the 4th century BC [5], and while significant advances have been made to eradicate the virus, it is still prevalent in many parts of the world [2].

VSV is an arbovirus with a limited host range compared to RABV, only causing disease in cattle, horses, and swine [1,6]. Unlike RABV, which replicates slowly and does not kill the host cell [1], VSV replicates rapidly to high titers and is a lytic virus, an effect caused by the M protein, which blocks host messenger RNA (mRNA) export [7]. VSV has been shown to induce a strong interferon response [8], in contrast to RABV which evades the innate immune response [9].

Research on rhabdoviruses has benefited significantly from the development of reverse genetics systems to recover them from cDNA [10,11]. Briefly, a cDNA plasmid encoding the entire rhabdoviral anti-genome is transfected into cells along with individual plasmids encoding the N, P, and L proteins (Figure 1, 1). A T7 promoter controls the expression of the different viral genes from each plasmid. Initially, a recombinant vaccinia virus expressing a T7 RNA polymerase was utilized to express the viral genes via the T7-promotor. Currently, most investigators use plasmids expressing the T7 polymerase, under control of a cytomegalovirus (CMV) promoter, that is included in the transfection. In both cases, the T7 polymerase produces mRNAs of the individual viral proteins and a positive-sense full-length anti-genome (2). Once translated from their mRNAs, the N protein encapsulates the anti-genome and the polymerase complex composed of P and L proteins and transcribes a full-length viral genome (3). The viral genome then serves as a template for the transcription of the mRNAs as well as full-length anti-genomes (4). Viral particles can assemble after translation of these mRNAs and reverse transcription of the full-length anti-genomes (5). Figure 1 illustrates this process for RABV.

The so-called reverse genetics system allows for manipulation of rhabdoviral genes and determination of their functions and host interactions [7,12]. It was first shown for RABV that foreign genes can be introduced into the genome and expressed utilizing short transcription start and stop signals [13] (Figure 2), and then similar findings were made for VSV [14]. A large number of foreign proteins have since been expressed from these recombinant viruses. For example, both viruses can express and incorporate the cellular receptors CD4 and CCR5 into their viral particles, allowing them to specifically target HIV-1 infected cells [15,16]. RABV and VSV can also carry foreign glycoproteins in their

viral envelope that can act as a functional substitute for the rhabdoviral glycoproteins or be expressed simultaneously. Two examples are the currently U.S. Food and Drug Administration (FDA)-approved VSV-based Ebola virus vaccine [17] and a RABV expressing the Lassa Fever Virus glycoprotein complex [18].

Because rhabdoviral genomes can be easily manipulated and can integrate foreign proteins in the viral envelope, they are excellent candidates for vaccine vectors. Examples of their use as vaccine vectors and further discussion of their advantages and disadvantages are discussed in the sections below.

Rabies Virus

The RABV vaccine has had a long history of successful use [19], however, no recombinant RABV-vectored vaccines have been developed for humans. This section will describe the history of the RABV vaccine, the qualities that support its use as a vaccine vector, and experimental vaccines that have been developed with this vector.

Human Rabies Vaccine—The first human rabies vaccine was discovered by Louis Pasteur in the 19th century and consisted of dried spinal cord from rabbits injected with RABV [20]. It protected some individuals from rabies, but it had many limitations ranging from incomplete viral inactivation to severe allergic reactions. Since then, a variety of other strategies have been tested, including other nerve tissue vaccines, such as the Semple and suckling mouse brain vaccines and avian embryo vaccines [19]. Once cell culture methods were developed, production was easier and more efficient, eventually leading to the development of four rabies vaccines that are currently World Health Organization (WHO) pre-qualified: Rabipur (purified chick embryo cell [PCEC] vaccine); Verorab (purified Vero cell rabies vaccine [PVRV]); RABIVAX-S (PVRV); and VaxiRab-N (PCEC) [21]. These vaccines are produced by infecting either chick embryo cells or Vero cells with the Flury LEP or Pitman-Moore strains of RABV, followed by virus purification and beta-propiolactone (BPL) inactivation [22–25]. All four vaccines efficiently induce rabies neutralizing antibody titers at a level considered protective, and are comparable to the previous gold standard rabies vaccine, the human diploid cell vaccine (HDCV) [4,19,26–28]. Additionally, vaccine safety has been demonstrated through use in essentially all patient populations with very few adverse effects (Reviewed for Rabipur in [29]).

Currently, human rabies vaccines are used world-wide in both pre- and post-exposure settings. Typically, rabies pre-exposure prophylaxis consists of 3 vaccine doses and is only recommended for those regularly exposed to the virus, such as laboratory workers and veterinarians [4]. Post-exposure prophylaxis (PEP) consists of 4–5 vaccine doses, and for the previously unvaccinated is typically accompanied with rabies immunoglobulin (RIG) treatment to promote immediate neutralization of the virus while the adaptive immune response to the vaccine develops [4,19,30]. When applied before symptom onset and following the proper dosing schedule, the rabies vaccine can prevent rabies disease in almost all cases [4,19,30]. Unfortunately, RABV is still prevalent in many parts of the world due to a lack of PEP accessibility [31].

Wildlife Rabies Vaccine—Rabies is maintained in nature through a variety of mammalian hosts, including bats, foxes, racoons and dogs [2]. Dogs are the major source of human rabies infections world-wide and are the major target for efforts attempting to end human disease caused by the virus [32–34]. In various studies, vaccination of at least 70% of the dog population in an endemic area effectively prevented rabies transmission [35–37]. The WHO has guidelines for carrying out campaigns to vaccinate dogs against rabies [38], which are based on similar efforts that were effective in North America, Europe, and some Latin American countries [39,40].

Dog and wildlife vaccination efforts may employ a combination of vaccine strategies, including live-attenuated, recombinant, and inactivated vaccines [4]. Typically, domestic animals are given injections of inactivated vaccines in a veterinary setting, as these vaccines pose little risk to the animal or humans in contact with it [4]. Given the difficulty and potential dangers in capturing and administering vaccine injections to wildlife, wildlife vaccination campaigns typically employ live-attenuated or recombinant oral vaccines in the form of bait [38,41,42]. The standard live-attenuated viruses used for wildlife vaccines are derived from either the Street Alabama Dufferin (SAD) strain or its derivative strain, Evelyn-Rokitnicki-Abelseth (ERA), and frequently contain an attenuating mutation at amino acid 333 in the glycoprotein [43,44]. The attenuated SAD strain is also used as a vaccine vector for other pathogens, as will be discussed in the next section.

RABV as a Vaccine Vector—Wide-spread use of modern rabies vaccines has highlighted their safety profile, ease of large-scale production, safe administration, and efficacy. Additionally, RABV shares endemic regions with several pathogens, thus increasing the potential impact of a bivalent vaccine in affected areas.

To use RABV as a vaccine vector the foreign gene of interest is typically inserted into the rabies genome and the native rabies glycoprotein (G) is either retained or removed. The rabies vectors used typically contain attenuating mutations, like the 333 amino acid mutation in RABV-G [12], or have a gene deleted to render them replication deficient (Figure 3). These attenuations ensure the viruses are safe to work with, produce, and administer [45,46]. Examples of these kinds of RABV-based vaccines include live recombinant vaccines against human immunodeficiency virus (HIV) [45] and Lagos Bat Virus [47], and a replication-deficient vaccine against lymphocytic choriomeningitis virus [48]. Live-attenuated vaccines are advantageous for the strong immune responses they induce, whereas replication-deficient viruses are safe for use in immunocompromised people because they cannot spread.

Inactivated RABV-based vaccines benefit from not requiring supplementation for production, unlike replication-deficient vaccines, and are safer to administer than live virus. For an inactivated vaccine to be effective, the foreign protein must incorporate into the membrane of the RABV virion. For many viral glycoproteins, no modifications are necessary to achieve this, as is the case for the Ebola virus (EBOV) [49] and Lassa fever virus glycoproteins [18]. Other proteins require modifications for successful virion incorporation. For example, Rift Valley Fever virus buds from the Golgi complex and its glycoproteins do not localize to the plasma membrane. Thus, this glycoprotein requires replacement of its transmembrane domain and cytoplasmic tail with that of RABV-G for

incorporation into RABV virions [50]. Such modifications can also be applied to non-viral proteins, as was done for anthrax protective antigen (PA) [51]. Specifically, to allow the protein to integrate into RABV particles, a chimeric PA domain 4 protein was engineered to contain a signal sequence and the proximal 51 amino acids of the RABV-G ectodomain along with the RABV-G transmembrane domain and cytoplasmic tail. Table 1 lists experimental RABV-vectored vaccine strategies.

In response to the current Severe Acute Respiratory Syndrome Coronavirus 2 (SARS-CoV-2) outbreak, one group has developed an inactivated recombinant rabies-based vaccine against SARS-CoV-2 [52]. The vaccine, CORAVAX™ uses the S1 domain of the SARS-CoV-2 spike protein that, as described above for the anthrax PA, was engineered to contain a RABV ectodomain, transmembrane domain and cytoplasmic tail for incorporation into RABV virions [52]. CORAVAX™ was shown to induce neutralizing antibodies in mice as both a live and inactivated vaccine [52]. This strategy is illustrated in the graphical abstract. Additional studies will be needed to determine whether this vaccine is protective against SARS-CoV-2 challenge and effective in humans.

Limitations—While there are many advantages to using RABV as a vaccine vector, there are some special considerations for their use. In particular, even though live RABV vaccine vectors are extremely safe, their use will be difficult because all risks must be eliminated before they can be applied in healthy populations. Additionally, RABV-G is highly immunogenic [53], and while this is ideal for rabies vaccines, the immune response to RABV-G could potentially interfere with the response to the foreign protein. In the case of foreign viral glycoproteins, this issue of RABV-G immunodominance can be avoided by removing RABV-G from the genome [18]. However, this would likely not be possible with other kinds of proteins, since glycoproteins are necessary for propagation of the virus.

Vesicular Stomatitis Virus

Since the establishment of the reverse genetics system, VSV has been used to develop biologic assays to study many different pathogens. Recently, the first recombinant VSV-based vaccine was approved for use in humans by the FDA [17], paving the way for future therapeutics using this platform. This section will discuss the numerous uses of VSV as a vector to study and treat various diseases.

VSV as a Tool—VSV vectors have a variety of applications. A common use is as a vector for the production of pseudoviruses, where foreign glycoproteins are incorporated into VSV virions either through genetic manipulation or infection of cells expressing a foreign glycoprotein with VSV lacking its native glycoprotein gene [54]. These pseudoviruses have been employed in virus neutralization assays [18,55], surrogate challenge viruses [18], and studies of foreign glycoprotein mediation of attachment and entry [56–58]. Since VSV is a biosafety level 2 (BSL-2) pathogen, VSV pseudoviruses are used in this way for studying BSL-4 restricted viruses.

The glycoprotein of VSV (VSV-G), has also been incorporated onto other viruses because of its stability and broad tissue and host tropism [59,60]. Specifically, VSV-G has been used to produce stable retro- and lentiviruses with better transduction efficacy for various

applications, including gene therapies [61,62]. Another use of VSV-G is the preparation of virosomes (essentially VSV-G coated vesicles) for delivery of several therapeutic agents, such as antibodies and DNA, directly into cells [63,64]. These strategies employ VSV-G to deliver genome editing machinery and specific genes directly to cells therapeutically, most notably as anti-cancer treatments [65–67].

While the above-mentioned applications of VSV are widely used, the more well-known therapeutic uses of VSV are as a vaccine vector and anti-cancer oncolytic virus, both of which will be discussed in detail in the sections below.

VSV as a Vaccine Vector—In addition to the ability of VSV to stably express foreign genes [14], the virus is also advantageous as a vaccine vector because it does not typically cause disease in humans and can be produced efficiently due to its fast replication and high titers in tissue culture. Most vaccine strategies employ VSV as a replication competent vector and either insert a foreign gene into the VSV genome with the addition of vector attenuating mutations, or replace the native VSV-G with a foreign glycoprotein. This vector has been used to develop an assortment of experimental vaccines, including those against pulmonary tuberculosis [68], HIV [69], and most successfully, EBOV [70]. A more comprehensive list of VSV-vectored vaccine candidates can be found in Table 2.

In a recent example of a successful VSV-based vaccine, the replication-competent VSV-ZEBOV replaces the native VSV-G with the glycoprotein (GP) of EBOV (Zaire strain) [71–74]. VSV-ZEBOV mediates protection mainly through production of anti-EBOV-GP antibodies [75] and provides cross-protection against heterologous strains of *Ebolavirus* [76–78]. In various clinical trials evaluating the immunogenicity and safety of VSV-ZEBOV in humans [79–84], the vaccine was linked to some mild to moderate side-effects, but was otherwise shown to be safe and to induce an EBOV-GP specific immune response in humans, resulting in its approval by the U.S. FDA [17].

VSV has also been used to develop vaccines against SARS-CoV-2. Specifically, there have been two groups that have developed a recombinant VSV expressing a modified SARS-CoV-2 spike protein [85,86]. Both vaccine strategies elicited anti-SARS-CoV-2 antibodies and showed protection in either human angiotensin-converting enzyme-2 (ACE2) expressing mice [85], or hamsters challenged with SARS-CoV-2 [86]. Future studies will be needed to see whether these vaccines are safe and effective in humans.

VSV as an Oncolytic Virus—Another characteristic of VSV that has been exploited for therapeutic use is the virus's ability to specifically kill cancer cells. VSV-G acts as a fusogenic membrane protein, which, when expressed in cells, causes syncytia formation and eventually cell death [87]. Many cancer cells down-regulate expression of various molecules in the interferon system, making them susceptible to VSV infection, as the virus is very sensitive to interferon and preferentially replicates in interferon deficient cells [88]. Additionally, due to VSV-G's broad tissue tropism [1] and ability to express foreign genes [14] it can naturally infect a wide range of cells and be further targeted for specific cancer cell receptors or genes.

Numerous approaches have been taken to use VSV as an anti-cancer therapy (reviewed in [89]). Two recombinant VSV examples will be discussed here. In one, VSV-G was replaced with the Sindibis Virus glycoprotein modified to targeted the Her2/neu receptor, which is commonly overexpressed on breast cancer cells [90]. This virus, called rrVSV, protected mice in a Her2/neu receptor-dependent manner and, upon rechallenge with tumor cells lacking the Her2/neu receptor, some mice previously treated with rrVSV were protected from tumor regrowth, showing that they gained immunity against the tumor cells themselves. Another strategy used VSV-G in Moloney murine leukemia virus (MoMLV) either with or without the Gibbon ape leukemia virus (GALV) *env* gene [91]. These recombinant viruses both induced syncytia formation and cell death in various cell lines *in vitro*, highlighting their potential use as an anti-cancer therapy.

Limitations—As discussed above, VSV is typically used as a replication competent virus since it does not typically cause disease in humans. However, there is a concern for immunocompromised individuals and pregnant women who are more susceptible to infection from even attenuated live viruses. While some studies have tested the safety of these vectors in immunocompromised populations, such as VSV-ZEBOV trials in patients with HIV [83], there are many different immunocompromising conditions and more wide-spread testing should be conducted. Another concern when using replication competent VSV vectors is that much of the world is not endemic to VSV, and introducing live virus to these areas could have consequences for wildlife there, given that VSV causes disease in cattle, horses, and swine [1,6]. To address these concerns, testing needs to be done to ensure that these vectors will not undergo mutations resulting in restoration of virus pathogenesis. Using inactivated VSV-based vaccines, a strategy shown to induce immunogenicity in mice, could potentially overcome both of these issues [92,93].

Conclusions

As demonstrated throughout this review, RABV and VSV are attractive candidates for vaccine vectors. RABV and VSV are both well-studied and have well-established reverse genetics recovery systems [10,11] that can be used in combination with genome manipulation. This allows for foreign gene expression and incorporation into Rhabdovirus virions [13,14]. Both vectors have been successful vaccine vectors, as illustrated through the current use of the rabies vaccine world-wide [21] and FDA approval of VSV-ZEBOV [17]. Additionally, both vectors have excellent safety profiles for manufacturing and administration. Thus, in spite of the necessity of live virus handling during their production and other limitations, these viruses have a wide range of applications. Future studies are needed to see whether some of these limitations can be addressed. Overall, RABV and VSV are suitable vectors for the development of vaccines and other therapeutics.

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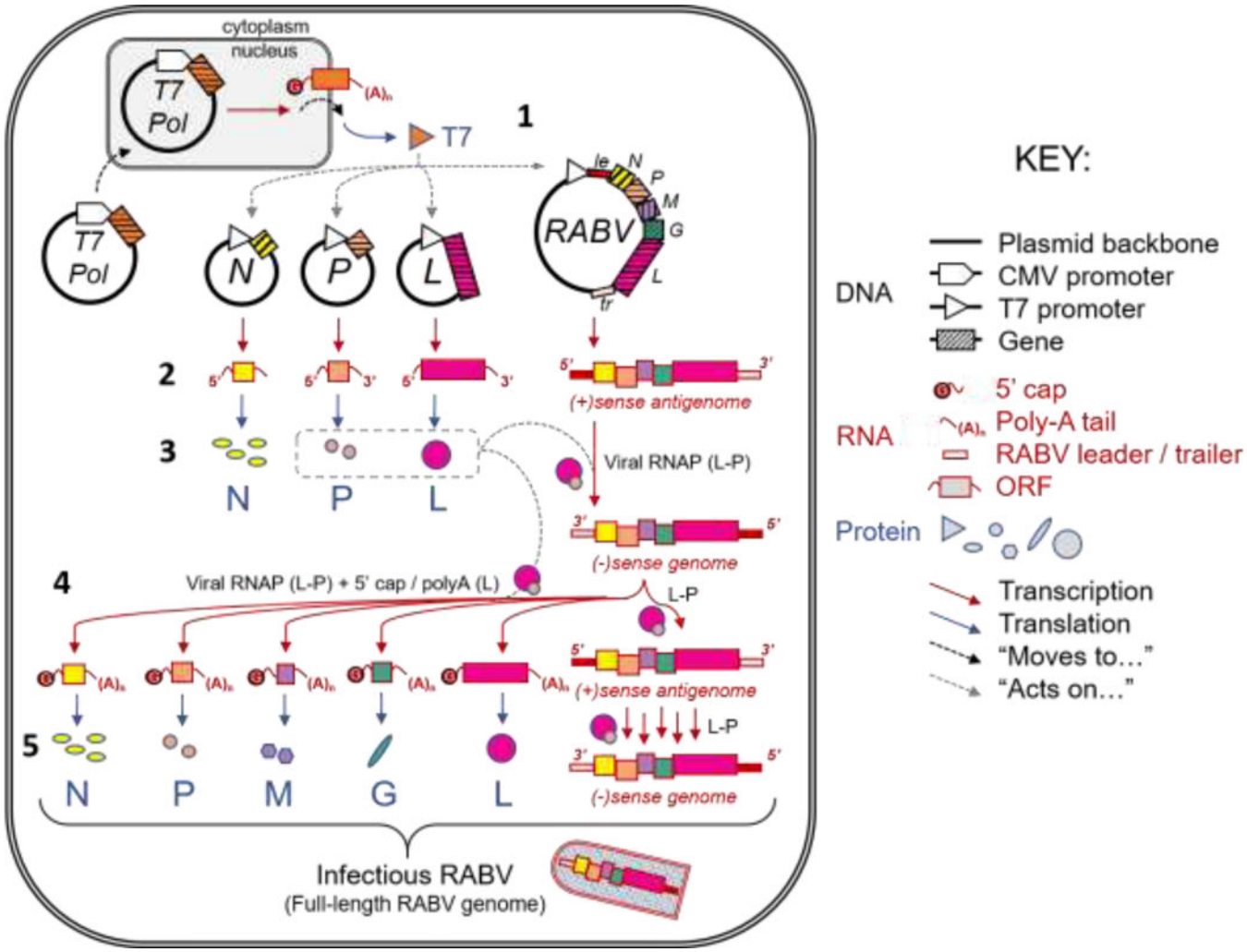

Figure 1. Rhabdoviral reverse genetics virus recovery system.

Diagram of virus recovery through cDNA reverse genetics system, exemplified by RABV. Abbreviations are defined as follows: Nucleoprotein (N), Phosphoprotein (P), Matrix Protein (M), Glycoprotein (G), RNA-dependent RNA polymerase (L), Cytomegalovirus (CMV), Open Reading Frame (ORF), T7 Polymerase (T7 Pol), RNA Polymerase (RNAP), Leader (le), Trailer (tr). Figure adapted from Davis, B.M. (unpublished).

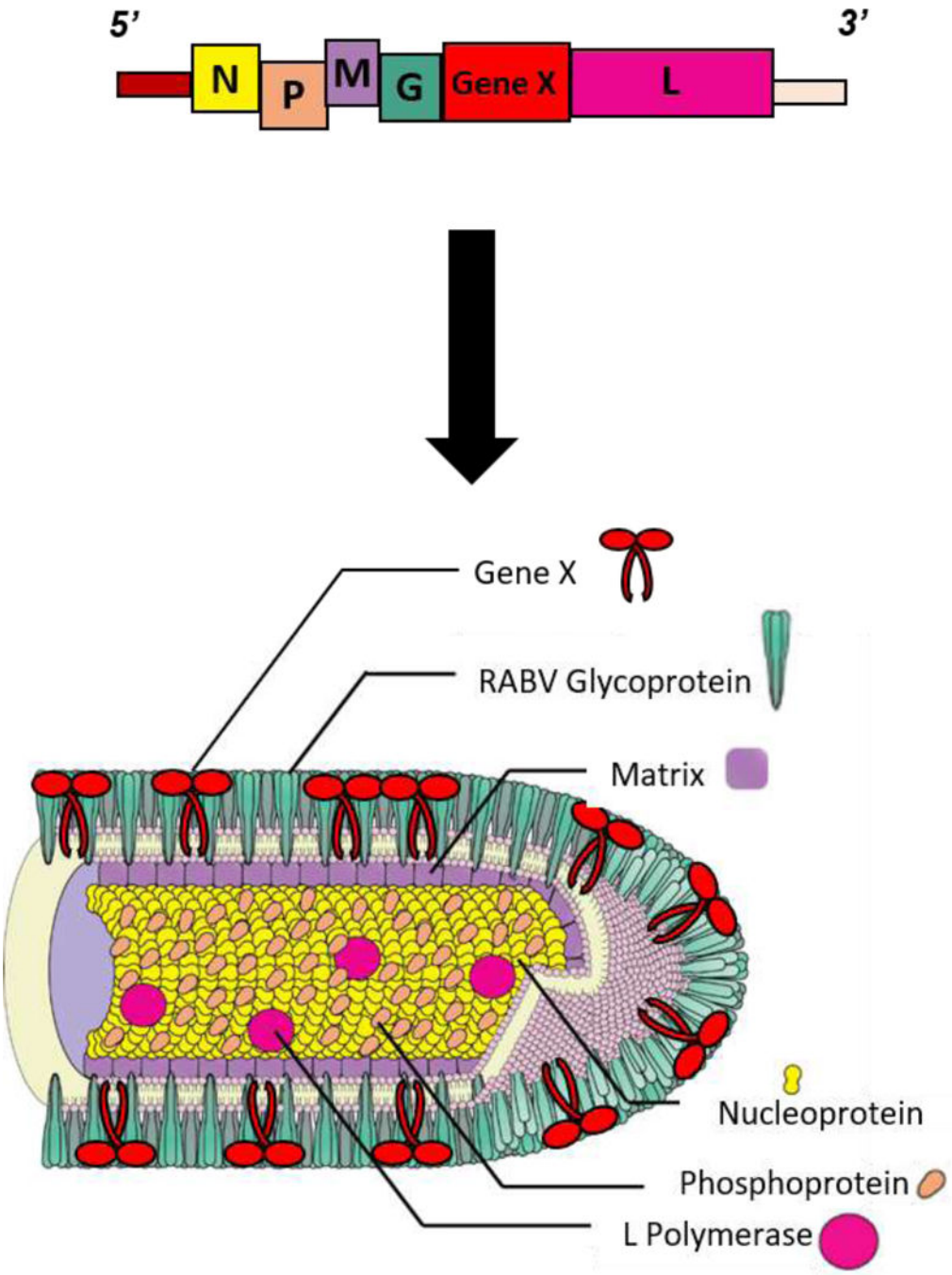

Figure 2. Incorporation of foreign protein into Rhabdovirus.

Diagram of how genetic engineering leads to foreign protein incorporation into rhabdovirus virions, exemplified by RABV. Abbreviations are defined as follows: Nucleoprotein (N), Phosphoprotein (P), Matrix Protein (M), Glycoprotein (G), RNA-dependent RNA polymerase (L). Figure adapted from Davis, B.M. *et al.* 2015 [184].

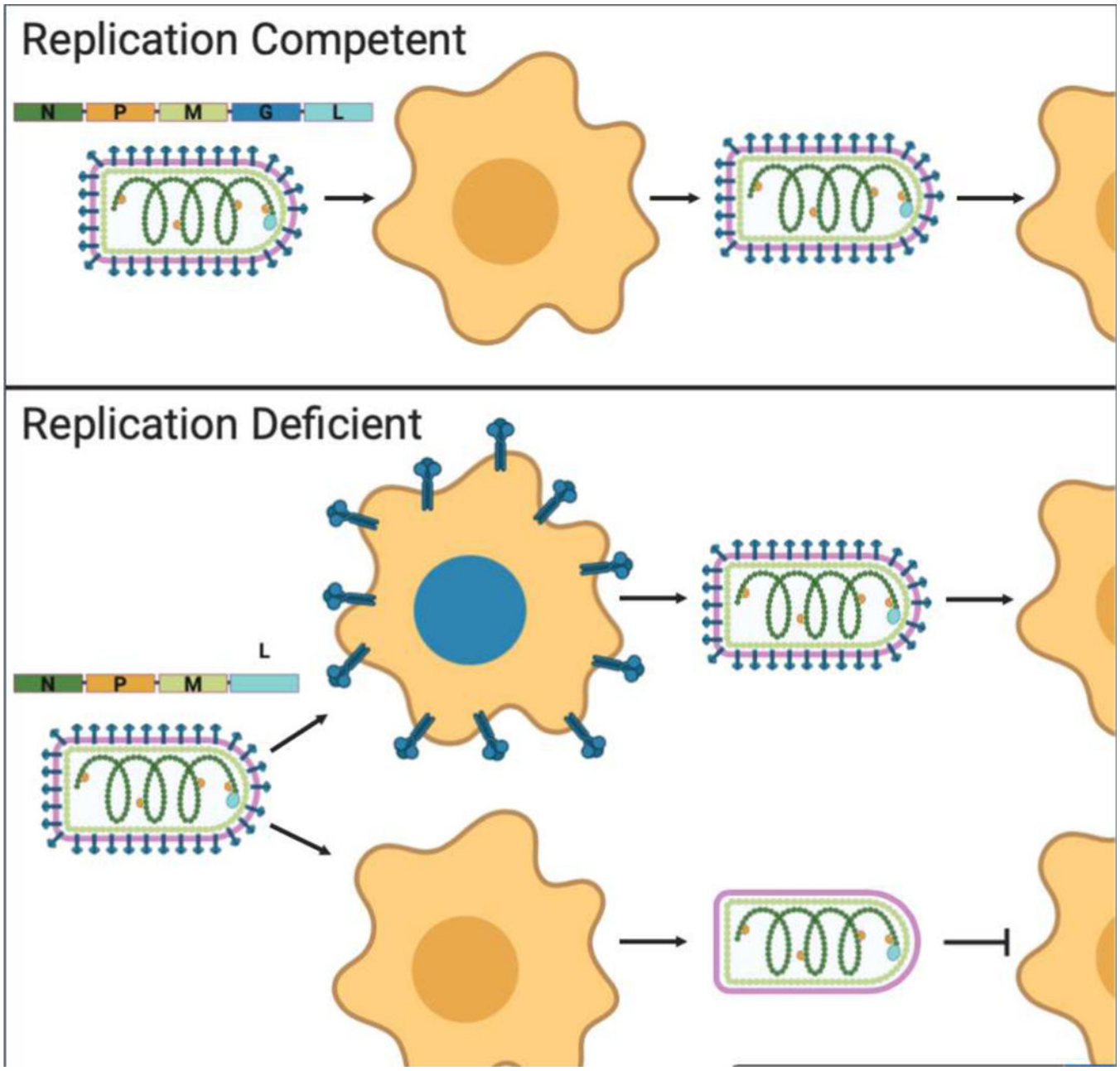

Figure 3. Schematic of replication competent vs. replication deficient rhabdoviruses.

Top panel shows replication competent rhabodovirus that encodes for all five rhabdoviral proteins is able to undergo multiple rounds of infection. Bottom panel shows a replication deficient rhabdovirus whose genome does not encode for a glycoprotein. This virus can only undergo one round of infection unless the missing gene is supplemented, as illustrated by the cell expressing the blue glycoproteins. Abbreviations are defined as follows: Nucleoprotein (N), Phosphoprotein (P), Matrix Protein (M), Glycoprotein (G), RNA-dependent RNA polymerase (L). Created with BioRender.com

Table 1.

RABV-based vaccine candidates.

Vaccines are listed chronologically, by the type of vaccine and the target antigen used.

Vaccine Type	Vaccine Target	Refs.
Live attenuated and inactivated	Severe Acute Respiratory Syndrome Coronavirus 2 S1 Spike Protein	[52]
Inactivated	Rift Valley Fever Virus Glycoprotein	[50]
Inactivated	Marburg Virus Glycoprotein	[94]
Inactivated	Nipah Virus Glycoprotein	[95]
Inactivated	Lassa Fever Virus Glycoprotein	[18]
Replication-deficient	Lymphocytic Choriomeningitis Virus Glycoprotein	[48]
Live attenuated	Lagos Bat Virus Glycoprotein	[47]
Inactivated	Middle East Respiratory Syndrome Coronavirus Spike Protein	[96]
Inactivated	Canine Distemper Virus Glycoproteins	[97]
Live attenuated and inactivated	Canine Parvovirus Virion Protein 2	[98]
Live attenuated and inactivated	Hendra Virus Glycoprotein	[92]
Live attenuated	Canine Distemper Virus Hemagglutinin Protein	[99]
Inactivated	Botulinum Neurotoxins, serotypes /A, /B and /E	[100,101]
Live attenuated and inactivated	Ebola Virus Glycoprotein	[49,102–105]
Live attenuated	Gonadotropin-Releasing Hormone (Immunocontraception)	[106]
Inactivated	Anthrax Protective Antigen	[51]
Live attenuated	Severe Acute Respiratory Syndrome Coronavirus Spike Protein	[107]
Replication-deficient	Simian Immunodeficiency Virus Env Protein	[108]
Live attenuated	Simian Immunodeficiency Virus GagPol Proteins	[109]
Live attenuated	Simian Immunodeficiency Virus Gag Protein	[110]
Live attenuated	Simian-Human Immunodeficiency Virus Env Protein	[110]
Live attenuated	HIV Env Protein	[111,112]
Live attenuated	HIV Chimeric Env Protein (gp120/gp41)	[113]
Live attenuated	HIV Gag-Pol or Gag-Pol and Env Proteins	[114]
Live attenuated and inactivated	Hepatitis C Envelope Proteins	[115]
Live attenuated	HIV Gag Protein	[45,112,116–118]
Inactivated	Rabies, Mokola and European bat lyssavirus 1 glycoproteins	[119]
Replication-deficient	Mokola Virus Glycoprotein	[120]

Table 2.

VSV-based vaccines candidates.

Vaccines are listed chronologically, stating the type of vaccine and the target antigen used.

Vaccine Type	Vaccine Target	Refs.
Live attenuated	Severe Acute Respiratory Syndrome Coronavirus 2 Spike Protein	[85,86]
Live attenuated	Andes Virus and Sin Nombre Virus Glycoproteins	[121]
Live attenuated	Crimean-Congo Hemorrhagic Fever Virus Glycoprotein	[122]
Live attenuated	Porcine Epidemic Diarrhea Virus Spike Protein	[123]
Live attenuated	Ebola Virus Glycoprotein and Zika Virus Pre-Membrane and Envelope Proteins or Pre-Membrane and Soluble Envelope Proteins	[124]
Live attenuated	Chikungunya Virus Envelope Polyprotein and Zika Virus Membrane-Envelope Glycoproteins	[125]
Live attenuated	Zika Virus Capsid Protein	[126]
Live attenuated	Middle East Respiratory Syndrome Coronavirus Spike Protein	[127]
Replication deficient	Ebola Virus Glycoprotein	[128]
Live attenuated	Venezuelan Equine Encephalitis Virus E2/E1 Glycoproteins	[129]
Live attenuated	Zika Virus Envelope Protein	[130]
Live attenuated	Enterovirus 71 VP1 Protein	[131]
Live attenuated	Dengue-2 Virus Pre-membrane and Envelope Proteins	[132]
Live attenuated	Porcine Reproductive and Respiratory Syndrome Virus Envelope Proteins GP5, M, GP4, GP3, GP2 and Nucleocapsid Protein	[133]
Live attenuated	Lassa Virus Glycoprotein	[134]
Replication deficient	*Mycobacterium ulcerans* Proteins MUL2232 and MUL3720	[135]
Live attenuated and inactivated	Hendra Virus Glycoprotein	[92]
Live attenuated	Nipah Virus Glycoprotein	[136]
Live attenuated	Bluetongue Virus Serotype 8 VP2 Protein	[137]
Live attenuated	Coxsackievirus B3 VP1 Protein	[138]
Live attenuated	Bundibugyo Ebolavirus Glycoprotein	[78]
Live attenuated	Andes Virus Glycoprotein	[139]
Live attenuated	Simian Retrovirus Type 2 Gag and Env Proteins	[140]
Live attenuated	Human Norovirus VP1 Protein	[141,142]
Live attenuated	Hepatitis B Virus Middle Envelope Surface Protein	[143,144]
Live attenuated	Vaccinia Virus B5R and L1R Proteins	[145]
Live attenuated	Human Immunodeficiency Virus gp160 Protein	[146]
Live attenuated	Influenza Virus Nucleoprotein and Hemagglutinin Protein	[147,148]
Replication deficient	Highly Pathogenic Avian Influenza Virus Hemagglutinin Protein	[149,150]
Live attenuated	West Nile Virus Envelope Glycoprotein	[151]
Replication deficient	Severe Acute Respiratory Syndrome Coronavirus Spike Protein	[152]
Live attenuated	Sudan Ebolavirus Glycoprotein	[153]
Live attenuated	Murine Cytomegalovirus Glycoprotein B	[154]
Live attenuated	*Mycobacterium tuberculosis* Ag85A Protein	[68]

Vaccine Type	Vaccine Target	Refs.
Live attenuated	Human Paillomavirus Type 16 E7 Protein	[155]
Live attenuated	Human Immunodeficiency Virus Gag Protein	[156,157]
Live attenuated	Cottontail Rabbit Papillomavirus E1, E2, E6 and E7 Proteins	[158]
Live attenuated	Cottontail Rabbit Papillomavirus Early Protein E6	[159,160]
Live attenuated	*Yersinia pestis* LcrV protein	[161,162]
Live attenuated	Human Immunodeficiency Virus gp120 Protein	[163]
Live attenuated and replication deficient	Human Immunodeficiency Virus Env Protein	[164]
Live attenuated	Marburg Virus Glycoprotein	[72,73,165]
Live attenuated	Ebola Virus Glycoprotein	[72,73]
Live attenuated	Severe Acute Respiratory Syndrome Coronavirus Spike Protein	[166]
Live attenuated	Human Immunodeficiency Virus gp41 and Porcine Endogenous Retrovirus p15E Proteins	[167]
Live attenuated	Simian Immunodeficiency Virus-Human Immunodeficiency Virus Env, Gag and Pol proteins	[168,169]
Live attenuated	Cottontail Rabbit Papillomavirus L1 Protein	[170,171]
Live attenuated	Hepatitis C Virus Glycoproteins	[172]
Live attenuated and replication deficient	Respiratory Syncytial Virus G and F Proteins	[173,174]
Live attenuated	Bovine Viral Diarrhea Virus E2 Glycoprotein	[175]
Live attenuated	Measles Virus Hemagglutinin Protein	[176,177]
Live attenuated	Human Immunodeficiency Virus Env and Gag Proteins	[69,178,179]
Live attenuated	Influenza HA Protein	[93,180,181]
Live attenuated	Human Immunodeficiency Virus Env Protein	[111,182,183]