Zhang *et al. One Health Advances* (2025) 3:2
https://doi.org/10.1186/s44280-024-00068-6

One Health Advances

REVIEW

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Swine zoonotic viruses: transmission and novel diagnostic technology

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Abstract

Emerging and re-emerging zoonotic viruses pose enormous challenges to public health worldwide. As an important livestock animal, pigs play a vital role in the evolution and spread of many zoonotic viruses. Hence, with the development of globalization and large-scale intensive farming, close human-pig contact increases the threat of zoonotic virus transmission. In this review, to facilitate disease prevention and control efforts, we summarized the prevalence and transmission characteristics of zoonotic viruses associated with pigs, such as influenza virus, coronavirus, and pseudorabies virus. Additionally, we emphasized novel detection techniques including rapid diagnostic tests, biosensor-based detection technology, high-throughput sequencing, and systematic viral epitope scanning. These techniques are instrumental in enabling cost-effective and convenient rapid detection procedures for broader implementation across diverse regions for effective surveillance of viral epidemics. To enhance virus surveillance capabilities and improve strategies for disease prevention in pigs, the improvement of our understanding of viral transmission modes combined with advancements in diagnostic technology is necessary.

Keywords Swine, Viral Zoonoses, Transmission, Detection technology

Introduction

There are several public health security wicked problems in the context of rapid global development and change [1]. Zoonosis is considered an ongoing wicked problem for global health [2]. The World Health Organization defines zoonosis as an infectious disease that can be transmitted naturally between other vertebrate animals and humans, including those transmitted directly to humans from vertebrate animals and indirectly through intermediate hosts, which can lead to emerging or re-emerging zoonotic diseases [3–5]. Viral pathogens (especially RNA viruses) have always been the main emerging infectious disease threat based on their low mutation correction ability and high nucleotide substitution rate, as well as a high capacity to adapt to different hosts [6–8].

With the development of animal husbandry and intensive farming, livestock carry eight times more zoonotic viruses than wild mammals [9, 10]. It is worth noticing that the latest research suggests that wildlife species traded and consumed as food may also play a vital role in the transmission of zoonotic diseases [11]. Livestock usually act as the bridge of epidemiology or an intermediate host in the transmission chain, promoting the cross-species virus spread from wild animals to humans [12]. Since pigs are important livestock and hog cultivation plays a crucial role in the agricultural economy, in past epidemics and pandemics, pigs have served as an amplification, intermediate, and mixing host in the spread of swine influenza virus, Japanese encephalitis virus (JEV) and Nipah virus (NiV) [13–15]. Some infectious diseases

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of pigs, such as pseudorabies virus (PRV) and porcine deltacoronavirus (PDCoV), have shown the ability to spread from pigs to humans [16, 17]. Here we focus on zoonotic viruses that have either been widely prevalent or have demonstrated potential for interspecies transmission in recent years (Fig. 1). We selected ten common viruses that are currently widespread and pose significant threats to both livestock farming and public health security. Recent researches have suggested that some of these viruses may have substantial cross-species transmission potential. While there is no direct evidence to confirm their ability to spread across species, they nonetheless warrant close attention.

At present, all known pathogens may only be the "tip of the iceberg" for potential pathogens, so it is necessary to establish a detection system for emerging pathogens based on "One Health" principles [18, 19]. Over the past few decades, diagnostic techniques have developed rapidly, leading to a greatly increased understanding of zoonotic viruses [20]. Traditional nucleic acid amplification techniques and serological antibody detection methods can provide accurate diagnoses at different stages of virus infection in various host types. The development of rapid diagnostic tests greatly reduces the technical and equipment requirements for detection and has practical value in areas with poor infrastructure or a lack of corresponding technical conditions [21]. Detection technology based on biosensors offers excellent detection performance and easy of operation, but maintaining detection stability in complex environments and across various sample types remains a challenge [22]. High-throughput next-generation sequencing (NGS) technology is revolutionary, focusing on the entire exposure history of an individual's viral pathogens or virome, rather than aiming at a few specific pathogens through traditional detection methods [23–25].

In this review, we summarize ten zoonotic viruses associated with pigs, including their prevalence and transmission characteristics. Next, we summarize existing novel diagnostic technologies with the aim of providing valuable insights for controlling and preventing epidemics caused by these viruses.

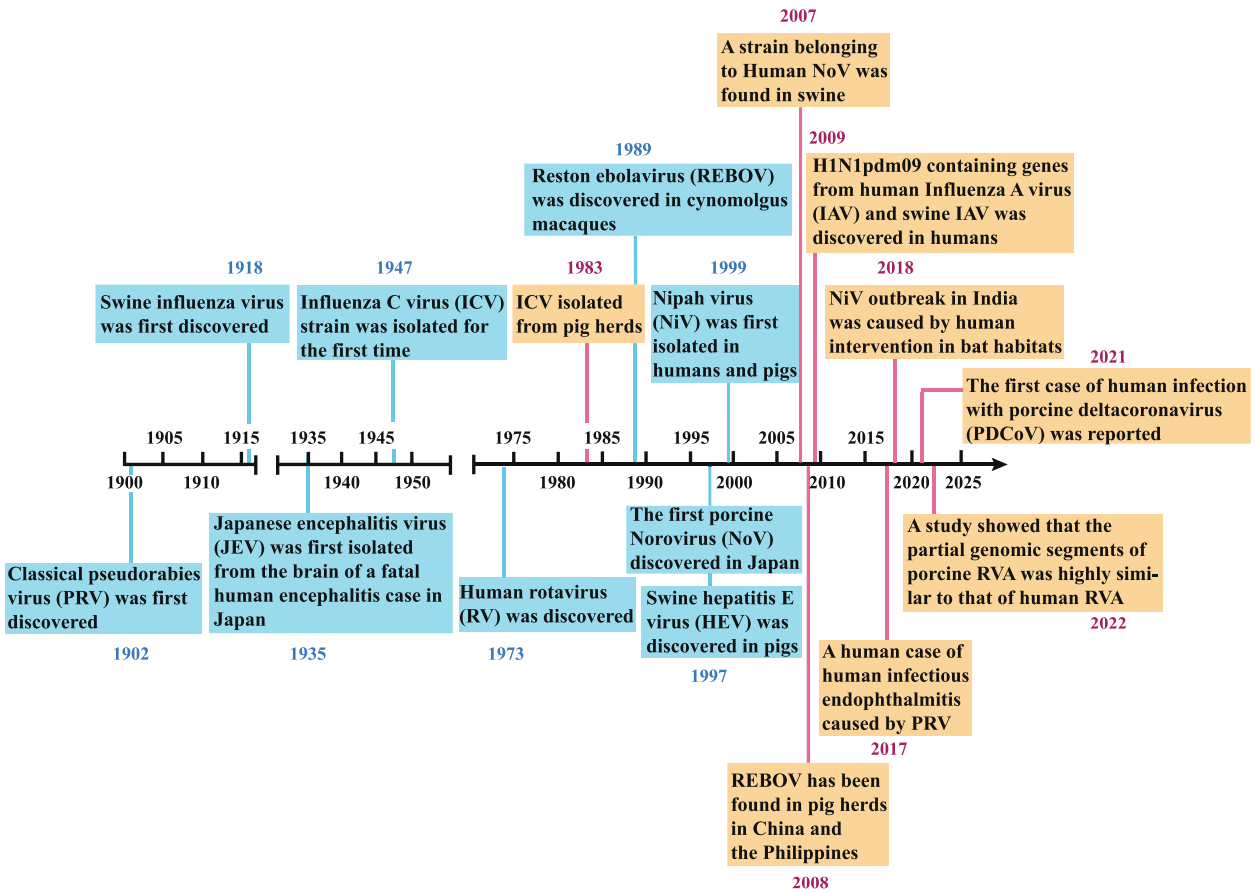

Fig. 1 The discovery timeline and significant epidemic events of ten porcine zoonotic viruses

Transmission of swine viral zoonoses

Based on epidemiological evidence, the transmission directions of ten zoonotic viruses were determined to raise awareness of the threat to humans and pigs (Fig. 2). Swine play the role of intermediate and amplification hosts in the transmission of the following viruses from wild or vector animals to humans: NiV, JEV, and Reston ebolavirus (REBOV). Norovirus (NoV) is transmitted unidirectionally from humans to pigs. Viruses that can infect both humans and swine and induce virus shedding can theoretically spread between the two species, and the following viruses are thought to demonstrate bidirectional transmission according to this principle: hepatitis E virus (HEV), rotavirus A (RVA), influenza A virus (IAV), and influenza C virus (ICV). Pigs serve as the natural hosts for PRV and PDCoV, which have also been detected in humans as these viruses undergo mutations and their transmission range expands.

Influenza A virus

IAV is an important respiratory pathogen that can transmit bidirectionally between humans and swine [26]. The frequent transmission, adaptation, and evolution of different genotypes between different hosts leads to extensive genetic diversity, which constitutes a grave threat to swine and human health [27–29]. H1N1, H1N2, and H3N2 are the main genotypes that are prevalent in swine worldwide, but there is still extensive diversity in the hemagglutinin and neuraminidase genes of IAV [26, 30].

Swine influenza virus was first discovered during the pandemic from 1918 to 1919, when human and swine influenza outbreaks occurred concurrently, suggesting that these pandemics were caused by the same pathogen [31]. Since influenza virus H1N1 was first isolated from pigs in 1931 [32], although there are various prevalent subtypes of IAV appeared over the decades, the subtype H1N1 still exists in the swine population. There were sporadic reports of human swine flu pathology before 2009. A review summarized 50 events of zoonotic swine influenza virus infection from 1958 to 2005, most of which involved direct contact with swine [33]. A number of research studies have demonstrated serological evidence of swine influenza virus in people who have had occupational contact with pigs, such as swine breeders, veterinarians or abattoir workers [34, 35]. This result suggests frequent interspecies transmission and subclinical infections of influenza virus in swine are mixed hosts [36]. In 2009, a variant H1N1pdm09 virus, containing genes from both human influenza and swine influenza viruses was discovered in humans and rapidly spread worldwide [37, 38]. In 2012, it was reported that humans were infected with a variant H3N2 virus in the US. The H3N2 virus obtained the matrix (M) gene from the H1N1pdm09 virus [39]. H1N2 was generated from the reassortment of H1N1 and H3N2 [40]. The sustainable spread and evolution of swine influenza virus in human populations suggest the need to maintain monitoring programs for potential emerging influenza viruses.

Influenza C virus

ICV is another respiratory pathogen from influenza virus family and it can cause lower respiratory tract infection, especially in children under 2 years old [41, 42]. Although human is the natural host of ICV, this virus has been isolated from naturally infected swine [43, 44]. ICV is known to coexist alongside IAV and influenza B virus (IBV), and it can also lead to localized epidemics [45]. The swine ICV strains were closely related to the human ICV strains, suggesting that interspecies transmission events have occurred. When swine are exposed to ICV, they typically exhibit mild respiratory symptoms and have the capability to transmit the virus to other susceptible

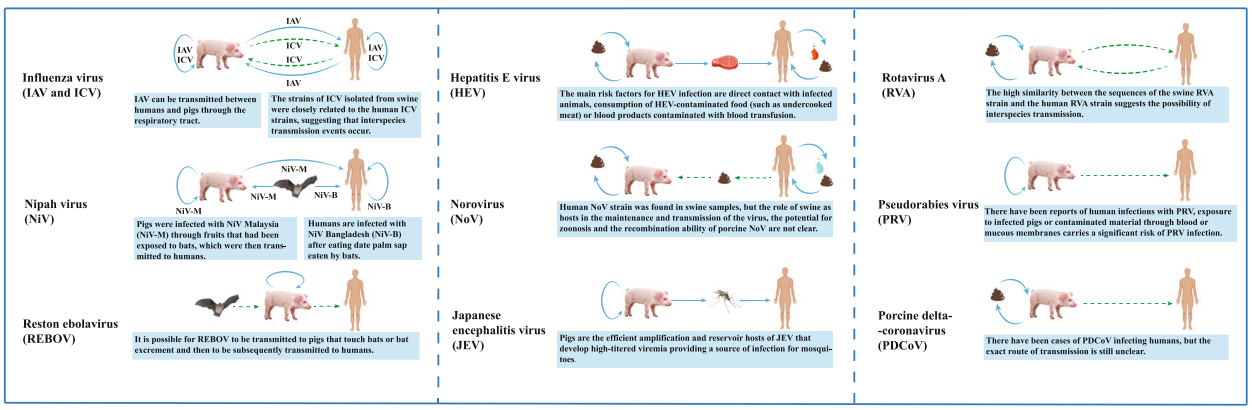

Fig. 2 The transmission directions of ten swine viral zoonoses described in this review. The dashed arrow represents a speculative transmission route

swine through direct contact [43]. Influenza C viruses are similar to influenza A viruses in that they have different subtypes, and there is the possibility of reassortment between different subtypes. Virus phenotypes that pose a threat to public health may emerge. Reassortment between strains isolated from pigs and human ICV strains in swine is possible due to their ability to spread among swine. Swine may also serve as mixers of ICV reassortment, similar to their role in the spread of IAV [46].

Nipah virus

NiV belongs to the *Henipavirus* genus, *Paramyxoviridae* family [47]. In 1999, NiV was first isolated in Malaysia in humans and pigs, and it was confirmed that swine played the role of intermediate host during the simultaneous outbreak [48]. The *Pteropus* fruit bat is regarded as a natural reservoir host, and swine are considered to be the intermediate and amplifying host of NiV [49].

NiV has many routes of infection, usually, the virus will spill over and transmit to other animals such as humans and pigs by bats. The outbreak of NiV epidemic happened in Malaysia from 1998 to 1999. Total 265 cases of Nipah encephalitis were recorded, of which 105 (39.6%) deaths were reported. Additionally, many infected individuals were adults who were associated with hog farms. The measurement aims to control the NiV outbreak including pig culling, prohibition of pig transportation and virus surveillance [50, 51]. The NiV Malaysia (NiV-M) outbreak is related to the encroachment of *Pteropus* fruit bat habitats due to deforestation for hog farms [52]. Strains isolated from local bats, pigs and humans were detected to contain more than 99% nucleotide homology, indicating that limited viral adaptation is necessary for transmission between hosts [48, 53, 54]. NiV-M nucleic acid was detected in 30% of throat swabs from infected animals, so it is speculated that the threat of infected humans to pigs is low [55]. After 2010, India had a large outbreak of NiV, most of these patients were adults who had no direct contact with pigs or other animals, and the virus spread mainly among humans. In 2018, when the most recent NiV epidemic happened in India was caused by human intervention in bat habitats [50, 56]. Since 2001 the NiV had outbroke, sporadic cases of infection have been reported almost every year in Bangladesh, resulting in 261 confirmed cases and 199 deaths by 2015 [57, 58]. It is worth noticing that NiV-M ultimately causes 40% human mortality through the bat-pig-human transmission path, while NiV Bangladesh is spread from bats to humans through contaminated date palm sap, resulting in more than 70% mortality [59–61]. It is speculated that nucleotide changes in the virus in the intermediate host lead to viral attenuation [5].

Reston ebolavirus

REBOV is an RNA virus which belongs to the *Filoviridae* family, and viruses from this family are associated with acute fatal hemorrhagic fever in primates, including humans [62]. In 1989, REBOV was discovered in cynomolgus macaques transported from the Philippines to the US for research purposes [63]. REBOV infection can cause death in nonhuman primates, but infection in human does not lead to obvious clinical symptoms [64, 65].

In addition to primates, bats and swine are also considered hosts of REBOV. Molecular and serological studies have shown that REBOV infection exists in a variety of bats in Philippines [66]. Since 2008, REBOV has been found in pig herds in China and Philippines [62, 67]. Full-genome sequencing of REBOV strains from the lungs and lymph nodes of pigs collected from three hog farms suggested that there was no discernible grouping with strains isolated from macaques. Phylogenetic studies suggest that REBOV has been spread in pigs at almost the same time as it has spread in non-human primates [62]. The result of experimental REBOV infection in pigs shows severe lymphatic and respiratory abnormalities of pigs. REBOV is excreted from nasopharyngeal secretions and transmits viruses to neighboring pigs [68]. This suggests that infected animals increasing risk of transmission to farm workers, veterinarians and slaughterhouse workers. The role of pig in the transmission cycle of REBOV remains to be determined, but it is possible for REBOV to transmit to pigs in contact with bats or bat faeces and then to be subsequently transmitted to humans.

Hepatitis E virus

HEV belongs to the *Orthohepevirus* genus, *Orthohepevirinae* subfamily, and *Hepeviridae* family [69]. In 1997, HEV was first isolated from domestic pigs in the midwestern US [70]. To date, HEV has been detected in pig herds in almost all around the world [71–74].

Until now, eight major genotypes of HEV (HEV-1 to HEV-8) have been discovered and reported. HEV-1 and HEV-2 are prevalent in developing regions such as Asia, Africa and the Middle East [75]. In these highly endemic regions, HEV-1 and HEV-2 are mainly transmitted through fecal–oral routes, and drinking water contaminated by human feces is considered to be the main cause [76–78]. HEV-3 and HEV-4 are pathogenic to humans, and Suidae species are possible reservoirs of HEV-3 and HEV-4 [79]. In developed countries (the US, Britain and France, etc.), HEV-3 and HEV-4 are the main genotypes of HEV. In economically developed regions of Asia, the characteristic disease pattern involves the transmission of HEV-3 and HEV-4 through animals [80]. In the past few decades, China has changed from a pattern with

frequent outbreaks of HEV-1 to a low epidemic model of sporadic HEV-4 infection. This trend may be the result of upgrades to sanitary conditions [81, 82]. Hepatitis E caused by HEV-4 infection is now the most common among middle-aged men in China. The main risk factors for HEV-3 and HEV-4 infection are consumption of HEV-contaminated food (such as undercooked meat), direct contact with infected animals, or transfusion of contaminated blood products [82]. In Europe, eating contaminated food is the primary mode of transmission of zoonotic HEV infection. Pork products, with or without liver, are generally regarded as the origin of numerous human foodborne HEV cases and small-scale outbreaks. Pigs are acknowledged as the primary reservoir of the zoonotic HEV-3, which is the genotype that most commonly found in human cases throughout the EU [83]. The ability of HEV to spread from pigs to humans and the experimental infection of human HEV in pigs has been proven [84, 85].

Norovirus

NoV is an RNA virus belonging to the family *Caliciviridae* [86]. Human-associated norovirus (HuNoV) is a common cause of acute gastroenteritis [87].

In 1997, the first porcine NoV discovered in Japan was classified as GII-11 [88]. At present, NoVs are divided into 10 genogroups and 48 genotypes [89]. The current consensus is that the GII-11, GII-18, and GII-19 genotypes infect only pigs, and the genotypes of the GI, GII, GIV, GVIII, and GIX are commonly appear in humans [87, 90]. NoV shows high genetic diversity and has a wide range of hosts, but the GII strains infect humans and swine exclusively [86]. In 2007, a strain belonging to the GII-4 genotype of HuNoV was found in Canadian swine samples, which drew more attention to pigs' role as virus reservoir [87]. Under experimental conditions, HuNoV has been observed to replicate in gnotobiotic pigs, and it has been proven that recombinant HuNoV-like particles can bind to the intestinal epithelium of pigs, suggesting that the transmission of NoV can be bidirectional [91, 92]. Until now, the pathogenic mechanism and transmission mechanism of NoV in swine, the role of swine as hosts in virus maintenance and transmission, the potential for zoonosis and the recombination ability of porcine NoV are still not clear. Continuous virus surveillance and research are necessary.

Japanese encephalitis virus

JEV is a zoonotic virus mainly transmitted by *Culex* mosquitoes, with ardeid wading birds as reservoirs and swine as important maintenance and amplification hosts [93]. Encephalitis caused by JEV infection has a high mortality rate and leads to persistent sequelae in survivors [94]. JEV is currently geographically distributed in most parts of the Western Pacific and Southeast Asia. Because of the intensive pig production in Southeast Asia and East Asia, swine play a significant part in the transmission cycle [95, 96]. Pigs infected by JEV usually remain asymptomatic or experience mild symptoms, which makes it difficult to notice the spread or outbreak in swine [97, 98]. Recent studies have confirmed that contact with infected animals directly by oral and nasal routes can lead to vector-free transmission of JEV in pig herds [99]. Vaccination for pig herds can reduce the risk of infection in pigs and subsequent transmission of the virus to humans. Human cases of Japanese encephalitis often originate from spillover events during pig epizootics. Pigs not only develop viremia, which enables sustained transmission, but also exhibit signs of neurotropic and reproductive disease [100]. JEV is a persistent public health threat, and the lack of effective vector control methods, the geographic expansion of mosquitoes, and climate change may all facilitate the spread of JEV, indicating the need to remain vigilant against the virus [93].

Rotavirus A

RVA is a common diarrhea pathogen that mainly causes acute gastroenteritis and diarrhea in children and piglets [101]. Currently, more and more evidence suggests the zoonotic potential of RVA [102]. The emerging G9 and G12 subtypes of human rotavirus may originate from swine through genetic recombination, based on similar VP7-specific areas of G9 and G12 which are frequently found in piglets [103, 104]. A recent study on the sequence analysis of the Indian porcine RVA gene revealed that the partial genomic segments (VP7, VP4, and NSP4 genes) were highly similar to that of human rotavirus strains, suggesting that interspecies transmission may have occurred [105]. The fact that strain KCH148 originates from pigs implies the possibility of zoonotic transmission, particularly in developing countries in Africa where humans are in close contact with livestock, including swine. This close proximity increases the risk of human-pig transmission [106]. A high degree of similarity to porcine strains may suggest direct zoonotic transmission, whereas lower similarity could indicate strains of unknown origin or indirect transmission through other human sources [107]. Hence, ongoing surveillance of RVA) following the principles of "One Health" is crucial. This surveillance can provide valuable data for evaluating the effectiveness of currently available vaccines and their ability to protect against diverse strains of RVA [108].

Pseudorabies virus

PRV is the causative agent for Aujeszky's disease which belongs to the *Varicellovirus* genus, *Alphaherpesvirinae* subfamily, *Herpesviridae* family [109]. The natural host of PRV is swine. Infection with PRV can lead to neurological disease in piglets, while reproductive disorders can occur in sows [110]. Previous studies have shown that there are frequent recombination events in PRV genomes, which may lead to cross-species transmission [111].

PRV is highly contagious, and it can cause a massive infection in body secretions and excreta in pig sheds. PRV primarily spreads through direct contact but can also be transmitted through water, air and contaminated fomites. The outbreaks of PRV in pig herds are challenging to control and cause great economic losses to the hog industry [112]. In areas where classical swine fever has been successfully eradicated, pseudorabies is regarded as the most economically important viral disease for the hog industry. There were many reports of human infections with PRV in recent years, and the number of cases has been increasing since 2017 [113]. Differential diagnosis should include PRV encephalitis if symptoms associated with central nervous system (CNS) infection are acute or rapidly progressing, especially in patients with recent exposure to pigs [114–116]. Current researches suggest that PRV infection can cause human illnesses such as encephalitis and endophthalmitis with high fever persisting. Exposure to infected pigs or contaminated material through blood or mucous membranes carries a significant risk of PRV infection. This suggests that practitioners should exercise strict self-protection when handling PRV-infected sick and dead pigs.

Porcine deltacoronavirus

PDCoV is a newly identified member of the *Deltacoronavirus* genus, *Coronaviridae* family [117]. Fecal–oral route is the primary route of PDCoV transmission, either through direct contact or contact with contaminated environments. Infected pigs may exhibit severe diarrhea symptoms, and the virus poses an economic and production threat to the swine industry. Currently, protocols that can effectively prevent and control PDCoV are still in research process, and implementing proper biosecurity measures is crucial in reducing its transmission [118]. The increasing spread of PDCoV in pig population of China represents a more pronounced threat to the well-being of animals and humans. PDCoV infection has been reported in 26 provinces across China since it was first discovered in Hong Kong in 2012 [119]. The results of phylogeographic exploration show that there are frequent long-distance dispersal events of PDCoV in China, which may involve in human-mediated transmission [120].

Phylogenetic studies have shown that cross-species transmission occurs frequently during the evolution of coronaviruses (CoVs) and shaped the diversity of CoVs [121]. From an epidemiological perspective, the global distribution of PDCoV in pigs and its potential for multiple host infections are striking [122, 123]. The first human PDCoV case reported in 2021 [124]. Due to the unexpected complexity and difficulty of tracing the movement of swine and their pathogens on a global scale, the risk of PDCoV infecting humans has significantly increased. Therefore, there is a need to improve the detection of PDCoV.

Novel diagnostic technologies

Globalization and large-scale intensive livestock farming have increased the risk of emerging and re-emerging zoonotic pandemics [125, 126]. The preliminary discovery of the threat of emerging infectious diseases must begin at the level of community health services, so it is important to establish an effective virus detection network system from local community breeding enterprises or health departments to national public health laboratories. The innovation and development of pathogen detection technology is an important link in the establishment of zoonotic comprehensive surveillance system. In addition to traditional laboratory detection techniques such as serological antibody detection and nucleic acid amplification, some new technologies have provided new ideas for pathogen detection as well, such as high-throughput NGS and biosensors. Biosensors are analytical devices that target biological materials or their derived material, typically achieved by integrating biorecognition elements and signal transducers [127]. Biosensors are based on optics, electrochemistry, and electrochemiluminescence, which have been widely studied due to their excellent detection performance, portability, and low operating threshold [128]. NGS provides comprehensive genomic information, detecting a wide range of viruses, including unknown and mutant strains, but it is expensive, time-consuming, and necessitates expertise in data analysis and interpretation [129–132]. Each detection technology has its advantages, limitations and application scenarios (Fig. 3). To select an appropriate virus detection technique, factors such as virus characteristics, detection requirements, available resources, and time constraints need to be considered.

Lateral flow assays

Lateral flow assays (LFAs) play an important role in the field of point-of-care tests (POCTs), which are commonly employed in the detection of infectious disease pathogens, biomarkers and environmental monitoring [133] (Fig. 4a). LFAs have the advantages of low cost and quick

	Lateral Flow Assays	Vertical Flow Assays	Optical/Electrochemical/ Electrochemiluminescence Biosensors	High-Throughput Sequencing	Systematic Viral Epitope Scanning
Advantages	1. Low cost 2. Quick response time for detection 3. Low requirements for testing equipment and environment	1. Low cost 2. Quick response time for detection 3. Low requirements for testing equipment and environment 4. Multiple detectability	1. High sensitivity and specificity of detection 2. Quick response time for detection	1. Conduct a comprehensive analysis of the genetic information of all pathogens in the sample 2. Unknown pathogens and mutant strains can be discovered	1. Comprehensive analysis of host antiviral antibodies
Limitations	1. Limited number of pathogens detected 2. Low detection sensitivity 3. Unable to detect unknown pathogens	1. Low detection sensitivity 2. Unable to detect unknown pathogens	1. Requirements for detection devices 2. Unable to detect unknown pathogens 3. High cost	1. High requirements for sample processing, sequencing and analysis equipment 2. High cost	1. High requirements for sample processing, sequencing and analysis equipment 2. High cost
Applications	Point-of-care tests (POCTs)	POCTs	1. POCTs 2. Laboratory detection requiring high sensitivity	1. Diagnosis and traceability of unknown and rare pathogens 2. Bioinformatics analysis of all pathogen genetic information in samples	Exploring the viral range of immune responses in a large number of individuals at the epitope level

Fig. 3 Advantages, limitations, and application scenarios of each detection technology

response time for rapid detection and diagnosis in areas with limited resources, but LFAs are usually a qualitative diagnostic test, and the intrinsic single antigen–antibody design of conventional LFAs limits its use for single pathogen detection [134]. Therefore, under the premise of maintaining the advantages of LFAs, there is a demand for LFAs technology with higher sensitivity, simultaneous detection of multiple pathogens and quantitative analysis.

For conventional LFAs detection, the user will get a conclusion based on visual assessment of the staining, that is, controlled compounds in the sample reach the threshold concentration. At present, there are detection tools with quantification of the analyte content in the test sample to quantify the LFAs test results [135]. For quantitative LFAs based on optical signal analysis, portable digital cameras are regarded as convenient tools to obtain high-resolution images. In this kind of detector, light sources with specific spectral characteristics are used to ensure high contrast between the specific staining area and the background [136]. This parameter increases with increasing dye intensity, and different color channels also provide opportunities for multiple detection. Hou's team developed a dual-modality imaging system based on smartphones, which can quantitatively measure the color or fluorescent tag of the test strip. The device can work with white light and ultraviolet light depending on the type of label used (color or fluorescence) [137].

Magnetic or superparamagnetic nanoparticles can also be used as analytical labels for immunochromatographic detection, and the magnetic powder is not affected by the colored components in the sample, which prevents the background coloring problem in the optical immunochromatographic system [138]. The effectiveness of magnetic detection in immunochromatography has been proven by a number of biomarker targets, but it has not been widely used in pathogen detection. Wang's team built an LFAs method that detects *Bacillus anthracis* by depositing superparamagnetic nanoparticles [139].

Vertical flow assays

The fundamental principle of vertical flow assays (VFAs) is similar to that of LFAs, relying on the immobilization of capture antibodies on reagent pads for analysis (Fig. 4b). In LFAs detection, the detection signal strength of the analyte may be reduced when the sample flows parallel to the paper surface, and the signal intensity is affected by interference at the detection line position [140]. VFAs detection equipment typically includes a membrane with some immunoreaction spots, where a specific antigen, captured antibody, and markers interact to produce a red dot that can be observed with the smartphone reader or naked eye [141]. Compared with LFAs, VFAs have the advantages of higher detection efficiency, multiple detectability, and reduced false-negative rates [134]. Clarke's team established a detection method for hepatitis C biomarkers by coupling surface-enhanced Raman spectroscopy (SERS) with VFAs. The limit of antibody concentration was as low as 53.1 μg/mL, which can be detected by the naked eye by using SERS signals [142]. MedMira Inc. has developed multiple VFAs-based detection platforms to detect pathogen antigen–antibody interactions. For example, MedMira recently developed a triple detection method for human immunodeficiency virus (HIV), hepatitis B virus, and hepatitis C virus.

Optical biosensors

Surface plasmon resonance (SPR) is a widely used optical technology used to develop virus detection methods by monitoring the refractive index (RI) changes in the sensing layer after the binding of target molecules [143] (Fig. 4c). The principle is that the electromagnetic (EM) resonance of the collective oscillation of free electrons

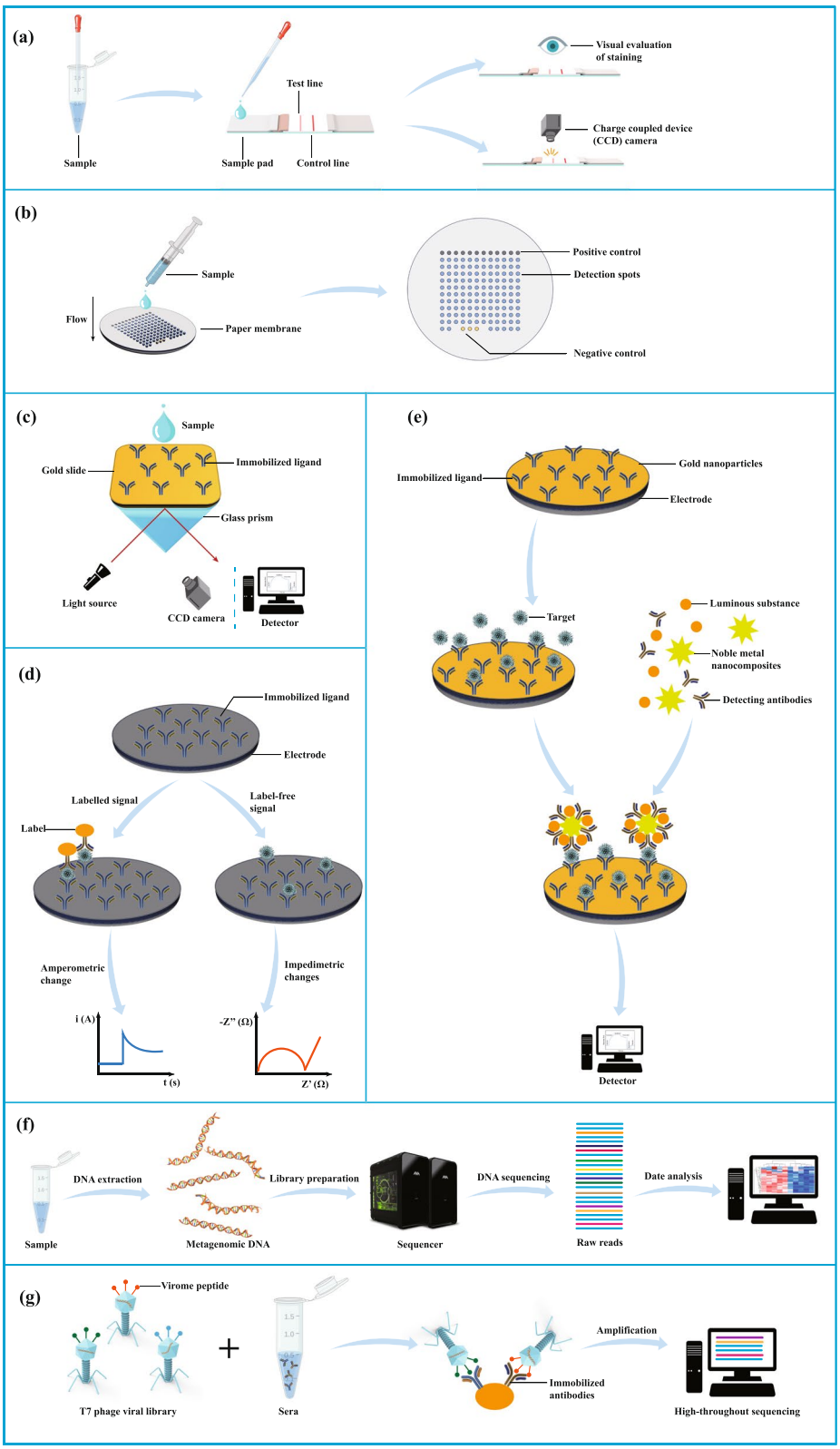

Fig. 4 The schematic diagram of the detection technologies introduced in this review. **a** Lateral flow assays. **b** Vertical flow assays. **c** Optical biosensor based on surface plasmon resonance. **d** Electrochemical biosensors. **e** Electrochemiluminescence biosensors. **f** Next-generation sequencing technology. **g** Systematic viral epitope scanning

related to the plasmonic metal dielectric semi-infinite interface generates a coupled propagation surface EM field. The high sensitivity of this electromagnetic field to changes in the dielectric layer RI can be used to design SPR-based sensors [144]. Wong's team developed a phase-intensity SPR biosensor for detecting avian influenza H5N1 antibody, which does not require time-consuming phase extraction and interference fringe analysis, and its detection limit can reach 193.3 ng/mL [145].

Surface-enhanced fluorescence (SEF) is a phenomenon in which plasma nanomaterials enhance the fluorescence intensity of fluorophores. When the fluorescent group is close to the metal nanostructure, the electrons of the fluorophore are coupled with the local plasma electric field, which subjects the fluorophore to an enhanced electric field and consequently enhances the fluorescence intensity [146]. When the distance between the surface of the plasma and the fluorophore is 1-10 nm, the non-radiative localized field of the plasmon dipole can excite the fluorophore, which is called Förster resonant energy transfer [147]. Hu's team prepared a novel multifunctional nanosphere (RNs@Au) containing hundreds of RN quantum dots and dozens of Au nanoparticles (NPs) as reporters, combined with SEF and LFAs to establish a method for detecting Ebola virus glycoproteins [148].

SERS technology uses the localized EM field of plasmonic metallic nanostructures to enhance the Raman scattering cross section of Raman-active materials close to plasmonic NPs, thus affecting the Raman signal of the materials [149]. Tripathi's team deposited silver NPs on a glass coverslip as a substrate for the sensing platform and established a JEV antigen detection method based on a SERS biosensor, with the limit of detection reaching 7.6 ng/mL [150].

Electrochemical biosensor

The electrochemical biosensor is distinguished by an electrode energy exchanger. Current common electrochemical technologies include chronoamperometry, square wave voltammetry, differential pulse voltammetry (DPV), cyclic voltammetry and electrochemical impedance spectroscopy [151] (Fig. 4d). Diba's team developed an electrochemical biosensor for detecting avian influenza H5N1 virus. The H5N1-specific DNA aptamer was covalently immobilized on a screen-printed carbon electrode deposited by gold NPs, the H5N1 protein was then adsorbed, and finally, the monoclonal antibody labeled with alkaline phosphatase (ALP) was adsorbed to form a sandwich complex. The electrocatalytic reaction of surface-bound ALP with 4-amino phenyl phosphate causes the current to increase with increasing H5N1 protein concentration. DPV is used for detecting current changes, with a detection limit of 100 fM [152]. Nidzworski's team developed an electrochemical biosensor for the M1 protein of influenza virus. The boron-doped diamond (BDD) electrode was treated with 4-aminobenzoic acid to form a self-assembled monolayer (SAM), and then the anti-M1 antibodies were immobilized on the SAM. When the influenza virus M1 protein was captured on the BDD electrode, the virus was detected according to the change in impedance spectroscopy, and the limit of detection reached 1 fg/mL [153].

Electrochemiluminescence biosensor

Electrochemiluminescence (ECL) is a technology that emits light from electrochemically excited ECL emitters through effective electron transfer (Fig. 4e). ECL's lack of need for external light sources results in no background noise from spontaneous fluorescence of the sample or scattered light [154, 155]. Hosseini's team developed an ECL-based biosensor to detect SARS-CoV-2. Au-plated glassy carbon electrodes were used as working electrodes, and their surfaces were modified with 3-mercapto propionic acid and 11-mercapto undecanoic acid for the covalent immobilization of antibodies. Luminol was covalently linked to the Au-based nanocomposite, and finally, a specific antibody to SARS-CoV-2 was bound to the material to ensure the high specificity of the sensor. The detection limit of this detection method reached 1.93 ng/mL [156].

High-throughput sequencing

NGS technology is an innovation in the field of genomics that is crucial to improve the understanding and research of pathogen transmission and dynamics at animal-human interfaces [157]. Bioinformatics is an important component of high-throughput sequencing (HTS) applications, which concentrates on methodologies for retrieving, interpreting, and archiving biological information obtained from sequencing [158]. The research of involving metagenomic analysis combined with HTS technology has high requirements for computing power, usually involve in the use of various sequence classification algorithms to process and analyze millions of reads (Fig. 4f). In the preliminary preparation stage, sampling, sample preparation, and enrichment methods seriously affect the HTS results. The viral genome sequences in the samples are translated into sequencing libraries, and clusters are created and sequenced in the HTS system. Metagenomic NGS has been used to detect emerging pathogens and describe viral diversity in environmental, animal and human samples, providing new insights into the transmission and prevention of zoonotic diseases [159].

Systematic viral epitope scanning

Systematic viral epitope scanning (VirScan) is a high-throughput method that combines immunoprecipitation and massively parallel DNA sequencing to comprehensively analyze antiviral antibodies (Fig. 4g). The phage library displays the proteome-wide peptides of whole human viruses. VirScan is a method of exploring the viral range of immune responses in a large number of individuals at the epitope level. It is considered as an important tool for revealing the impact of host–virus interactions on human health and disease and can be extended to emerging viruses in the future [160]. Although several studies have used this technique to analyze the serological characteristics of specific viruses in humans, cost reduction or optimization strategies could further extend this technique to animal viral serology studies.

Conclusions

Modern molecular and antibody detection techniques have made progress in identifying emerging zoonotic viruses. The advantages of LFAs and VFAs are that their devices are usually thermostable, require no electricity, and have low difficulty of operation, and there are more use scenarios in areas where infrastructure and resources are scarce [161]. Biosensors based on optics, electrochemistry and electrochemiluminescence have the advantages of excellent detection performance, portability and easy operation [162]. However, the problems of high development cost and poor stability of sustainable detection equipment need to be further ameliorated. The HTS method has significant advantages in virus surveillance and increasing awareness of infectious diseases. However, the inference of pathogens based on HTS still has limitations [163], the coverage of the pathogen database is notably lower than that of other organisms, leading to uncertainty in identification and inaccurate estimation of pathogen richness [157]. Considering that a wide range of swine-associated viruses carry a zoonotic transmission risk, it is necessary to further develop diagnostic technology with high throughput and sensitivity. Similarly, lowering the cost and reducing the operational technical requirements of the assay will facilitate initial screening to monitor the epidemiology of swine zoonotic virus diseases in remote areas.

We believe there is significant potential for advancement in detection technologies in the future. For LFAs, VFAs, and biosensor-based detection methods, their key advantages lie in ease of use and rapid response times. If these technologies can be further developed to detect multiple pathogens simultaneously, detection efficiency would be substantially enhanced. Moreover, biosensor-based methods still have room for improvement, particularly in terms of stability, which will require innovations in materials science and other interdisciplinary fields. POCT technologies have broad application potential, particularly for pathogen monitoring in resource-limited settings. HTS presents another promising avenue for addressing detection challenges. This technology enables comprehensive genetic analysis of samples. If high-throughput sequencing devices can be miniaturized and made portable, the pathogen genetic database can be expanded, and computational models optimized, thereby improving data analysis speed. This would facilitate the rapid detection of both known and novel pathogens, an essential capability given the growing threat of emerging infectious diseases and the rapid evolution of existing pathogens.

With the ongoing expansion of pig farming and pork trade, increasing contact between humans and pigs has led to the rise of zoonotic viruses that affect both species. Some pathogens, such as influenza viruses, have already spread between humans and pigs, raising public health concerns. Additionally, other coronaviruses, such as Deltacoronavirus, have shown potential for cross-species transmission between pigs and humans. Research and monitoring of zoonotic viruses in the context of human-pig coinfections are of utmost importance. Early detection and identification of the transmission of these pathogens in human and pig populations contribute to the implementation of timely and effective preventive measures, reducing the spread of outbreaks. Strengthening capabilities for health surveillance and clinical diagnosis, along with improving hygiene standards in pig farms and trading facilities, are key measures to mitigate the transmission of zoonotic viruses between humans and pigs. Overall, in keeping with the concept of "One Health", the study of zoonotic viruses in human-pig coinfections is an ever-evolving field that requires continuous efforts to enhance scientific research and cooperation. This is essential to ensure public health safety and protect the health of both humans and pigs.

Authors' contributions

S.S. conceived and designed this review. L.Z. and Z.J. wrote this manuscript. Y.Q. and Y.B. checked the manuscript. All authors have read and approved the manuscript.

Funding

This work was financially supported by the Project of Sanya Yazhou Bay Science and Technology City (SCKJ-JYRC-2022-08).

Data availability

Not applicable.

Declarations

Ethics approval and consent to participate

Not applicable.

Consent for publication
Not applicable.

Competing interests
All authors declare that they have no conflicts of interest.

Received: 10 June 2024 Revised: 24 November 2024 Accepted: 28 November 2024
Published online: 31 January 2025

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