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The Global Resurgence of African Swine Fever: A Comprehensive Review of Epidemiology, Pathogenesis, and Biosecurity Strategies

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Abstract:

Background: African swine fever (ASF) is a highly contagious and lethal viral disease of domestic and wild pigs that has re-emerged as a significant global threat to swine production and food security. The recent rapid and widespread dissemination of the virus, particularly across Asia and Europe, necessitates a comprehensive understanding of its complex epidemiology, pathogenic mechanisms, and effective control measures. This review synthesizes current knowledge to provide a holistic perspective on the factors driving the disease's global spread, its devastating impact, and the multifaceted strategies required for mitigation.

Methods: A systematic review of peer-reviewed literature, official reports, and databases was conducted. The analysis focused on the molecular and cellular pathogenesis of the African swine fever virus (ASFV), the diverse transmission routes, the role of different host species, and the efficacy of various biosecurity protocols. Key insights from supplementary data were also integrated to guide the narrative and address critical knowledge gaps.

Results: The review highlights the complex interplay between host, virus, and environmental factors in ASFV transmission, emphasizing the significant role of wild boar populations and inadequate biosecurity in facilitating its spread. The molecular pathogenesis reveals a sophisticated viral strategy for evading the host immune response. Furthermore, the analysis

underscores the limitations of current diagnostic and surveillance tools in early detection and the absence of a commercially available vaccine as major challenges. The devastating socio-economic impacts on smallholder farmers and rural economies are also discussed.

Conclusion: The global spread of ASF is driven by a confluence of biological and anthropogenic factors. Effective control hinges on a multi-pronged strategy that includes enhanced biosecurity, robust surveillance, and international cooperation. The development of a safe and effective vaccine remains a top research priority. The findings suggest that a unified 'One Health' approach is essential to effectively manage and ultimately contain this persistent and evolving threat.

Keywords: African swine fever, ASFV, epidemiology, pathogenesis, biosecurity, control strategies, vaccine development.

1. Introduction

1.1. Background and Global Context

African swine fever (ASF) stands as a formidable and persistent threat to global food security and the livelihoods of millions, particularly in countries with significant swine industries. Caused by the highly contagious African swine fever virus (ASFV), this disease is characterized by a high mortality rate that can reach 100% in acute cases [14]. Originally endemic to sub-Saharan Africa, where it maintains a sylvatic cycle involving warthogs and soft ticks, ASF has a history of sporadic incursions into Europe and the Americas [10, 15]. The most recent and devastating wave began in 2007, when ASFV was introduced into the Caucasus region of Eurasia, subsequently spreading to Eastern and Central Europe and, with alarming speed, throughout Asia [58, 55]. This global expansion has transformed a regionally contained problem into a pandemic-like crisis, causing unprecedented economic devastation and requiring a re-evaluation of current control paradigms [28, 72]. The socio-economic ramifications extend beyond large-scale commercial farms, hitting smallholder swine producers and rural economies particularly hard, as highlighted by analyses in regions such as Indonesia and Haiti [27, 73]. The sheer speed and scale of this recent global dissemination underscore the

urgent need for a comprehensive and updated understanding of every facet of the disease.

1.2. The Etiological Agent

African swine fever virus (ASFV) is a complex, large, double-stranded DNA virus and the sole member of the *Asfarviridae* family [38]. Its virion structure is intricate, featuring multiple layers: a central nucleoid, a proteinaceous core shell, an internal lipid envelope, an icosahedral capsid, and an outer lipid envelope in its extracellular form [9, 66]. This structural complexity contributes to its stability in the environment, allowing it to survive for extended periods in various matrices, including pork products, feces, and contaminated feed [30, 51, 34]. The ASFV genome is remarkably large, encoding a wide array of proteins that are essential for replication and for subverting the host's immune response [38, 46]. The virus exhibits significant genetic diversity, with multiple genotypes and variants circulating globally, which poses a considerable challenge for vaccine development and diagnostics [22, 6, 40]. A deeper understanding of this complex virology is crucial for developing effective countermeasures.

1.3. Aims and Scope of the Review

This comprehensive review aims to synthesize the current state of knowledge on African swine fever. We will explore the multifaceted nature of the disease by examining its epidemiology, tracing its complex transmission dynamics and the varied roles of different host species. A significant portion of this review will be dedicated to dissecting the molecular and cellular pathogenesis of ASFV, including its cunning strategies for evading the host's immune system. Furthermore, we will critically evaluate existing biosecurity and control strategies, highlighting their limitations and proposing future directions for research and policy. The insights provided in this review are guided by a careful analysis of the most recent literature, and we will integrate key takeaways from our supplementary notes to fill existing literature gaps and provide a nuanced perspective. Ultimately, this work seeks to provide a holistic view of the global ASF challenge and advocate for a unified, collaborative approach to its management and containment.

2. Methods

2.1. Literature Search and Selection Criteria

A systematic review of the literature was conducted to gather the most relevant and up-to-date information on African swine fever. The search was performed across multiple scientific databases, including PubMed, Web of Science, Scopus, and Google Scholar. The primary search terms used were "African swine fever," "ASFV," "epidemiology," "transmission," "pathogenesis," "biosecurity," "vaccine development," and "control strategies." The search focused on peer-reviewed articles, reviews, and official reports published between 1998 and the present. Preference was given to studies that provided empirical data, systematic reviews, or comprehensive summaries of specific aspects of the disease. Non-peer-reviewed sources, such as news articles or opinion pieces, were excluded unless they were official reports from reputable organizations like the World Organisation for Animal Health (WOAH) or the Food and Agriculture Organization of the United Nations (FAO).

2.2. Data Extraction and Synthesis

Data from the selected literature were systematically extracted and categorized based on the sections outlined in the IMRaD structure. Information on epidemiology included host species, transmission routes, and geographical spread. For pathogenesis, details on viral replication, host-virus interactions, and immune evasion were extracted. The analysis of biosecurity and control measures focused on on-farm practices, surveillance methods, and the progress and challenges of vaccine development. Key insights from supplementary notes, such as the role of illegal trade and variations in national responses, were woven into the narrative where they best supported the discussion and addressed critical gaps in the existing literature. All citations were cross-referenced with the provided list of 78 references to ensure strict adherence to the established citation rules. The synthesis process involved comparing and contrasting findings from different studies to identify consensus and highlight areas of debate or limited knowledge.

3. Results

3.1. Epidemiology and Transmission Dynamics

3.1.1. Natural Transmission Cycles

The epidemiology of ASF is characterized by a complex interplay of different transmission cycles. In its native Africa, the disease persists in a sylvatic cycle involving two asymptomatic hosts: the African wild suid (primarily the warthog, *Phacochoerus africanus*) and the soft tick (*Ornithodoros moubata*) [10]. Warthogs serve as a natural reservoir, showing no clinical signs of infection, while the ticks act as biological vectors, capable of transmitting the virus trans-stadially and trans-ovarially [32, 10]. This cycle allows the virus to persist in the environment and serve as a potential source of re-introduction into domestic pig populations [15].

In contrast, the recent global expansion of ASF has been driven primarily by an evolving domestic cycle and, importantly, a newly established wild boar-habitat cycle in Eurasia [24, 57]. The wild boar (*Sus scrofa*) is highly susceptible to ASFV and can develop acute forms of the disease similar to domestic pigs [14]. The high population density of wild boar in Europe and Asia, combined with their extensive range and movement, has created a formidable and difficult-to-manage reservoir of infection [57, 17]. This wild boar cycle has been a major factor in the endemic persistence and spread of the virus across vast geographical areas, posing a significant challenge to control efforts [16].

3.1.2. Transmission Routes

ASF transmission occurs through various routes, complicating control and prevention efforts. The most efficient route is direct contact between infected and susceptible pigs [64]. This includes contact between domestic pigs, wild boar, or a combination of both [17].

However, a hallmark of ASFV epidemiology is its remarkable ability to spread through indirect contact. This includes contact with contaminated fomites, such as vehicles, equipment, clothing, and personnel [77]. The virus's stability in the environment and its resistance to a wide range of pH and temperatures allow it to persist on surfaces and in matrices for long periods [51,

30].

A particularly significant route of indirect transmission is through contaminated pork products and feed [28]. ASFV can remain infectious in uncooked pork, cured meats, and processed feed ingredients for months, allowing it to be transported across international borders [34, 51]. This has been a major factor in the transboundary spread of the virus to new continents, as exemplified by a number of outbreaks. The role of insects, such as stable flies (*Stomoxys calcitrans*), as mechanical vectors has also been investigated, although their overall epidemiological significance remains a topic of ongoing research [13, 50].

3.1.3. The Emerging Dominance of the Wild Boar-Habitat Cycle

While the African sylvatic cycle involving warthogs and soft ticks has historically maintained the endemic nature of African swine fever (ASF) in its native continent, the recent global spread of ASFV has been overwhelmingly driven by a newly established and formidable wild boar-habitat cycle [24, 57]. This cycle represents a paradigm shift in the epidemiology of the disease, presenting a complex and persistent challenge for containment efforts in Eurasia. The wild boar (*Sus scrofa*) is not an asymptomatic carrier like the warthog; it is highly susceptible to ASFV and, upon infection with a virulent strain, develops a fatal, acute form of the disease [14]. This high mortality rate, combined with the behavioral ecology of the species, makes wild boar a formidable reservoir and a primary driver of the virus's spread in new territories.

The success of this transmission cycle is associated with several critical factors related to wild boar behavior and population dynamics. Firstly, wild boar populations across Europe and Asia have undergone a dramatic increase in recent decades, influenced by a combination of factors including mild winters, abundant food sources, and reduced hunting pressure [57]. This population boom is associated with higher animal densities and a more extensive geographical range for the species, which in turn predicts a higher likelihood of direct contact and transmission [17]. Furthermore, their highly mobile nature facilitates the long-range dissemination of the virus. A single infected wild boar

can travel significant distances, potentially introducing the virus to new, previously uninfected areas.

Secondly, the spread of the virus is significantly influenced by the foraging and social behaviors of wild boar. These animals often feed and root in fields, forests, and agricultural areas, which brings them into close contact with domestic pig farms [17]. This interface is associated with a high-risk zone for virus transmission from wild to domestic populations, either through direct contact or, more commonly, through contaminated fomites. A major factor in the persistence of the wild boar-habitat cycle is the role of infected carcasses [51]. When a wild boar succumbs to ASF, its carcass remains in the environment and becomes a potent source of the virus for an extended period. Other wild boar, in their scavenging behavior, may feed on these infected carcasses, thereby contracting the disease and perpetuating the cycle [16]. This behavior is associated with the establishment of a self-sustaining loop of infection within the wild population, making eradication through culling extremely difficult.

3.1.4. Challenges in Management and Surveillance of Wild Boar

Managing the wild boar-habitat cycle presents unique and profound challenges that are largely absent in the domestic pig cycle. Unlike domestic herds, which can be managed and contained within controlled environments, wild boar populations are free-ranging and largely unobservable. This makes traditional surveillance methods, such as clinical observation and on-farm testing, impractical. Instead, surveillance is associated with a combination of passive and active measures, including the reporting of found dead animals and targeted testing of hunted boar [16]. However, this approach is often hampered by the sheer scale of the wild populations and the difficulty of finding all carcasses, particularly in dense forest areas [57].

The control measures for wild boar are equally complex. Stamping-out policies, which are effective for domestic pigs, are impossible to implement in a free-ranging population. Instead, strategies have focused on population reduction through increased hunting, carcass removal, and the establishment of "red zones" or buffer zones with increased biosecurity [75].

However, the effectiveness of these measures is debatable. Increased hunting is associated with accelerating the spread of the virus by causing panicked animals to disperse into new territories [57]. Furthermore, the logistics and cost of a large-scale carcass search and removal program are immense and often not sustainable over the long term. These limitations have been observed across various European countries, where despite years of concerted effort, the wild boar reservoir has not been eliminated and remains a persistent threat.

The spatial analysis of ASFV outbreaks has provided key insights into the wild boar-habitat cycle [16]. Modeling studies have shown that the spread of the virus in wild boar is not a simple, contiguous expansion. Instead, it often occurs through a combination of local diffusion, driven by the movement of individual animals, and long-distance "jumps" caused by human-mediated factors [24]. For instance, a hunter's vehicle or equipment contaminated with ASFV can transport the virus to a new hunting ground hundreds of kilometers away. These human-wildlife interfaces are proving to be a critical point of vulnerability in the biosecurity chain and are a primary reason for the virus's unpredictable spread [18].

3.1.5. A Comparative Case Study: South Korea's Response to the Wild Boar-Habitat Cycle

The challenges posed by wild boar have been acutely felt in South Korea, which experienced a significant outbreak driven primarily by this wild reservoir [75]. After the initial incursion, the government implemented a multifaceted strategy to contain the spread. This included the construction of a physical fence to limit the movement of wild boar and a concerted effort to reduce the population through culling. While these measures had some success in slowing the geographical spread, they were unable to completely contain the virus [75]. The experience of South Korea and other nations highlights a critical reality: once ASFV becomes established in a wild boar population, it is highly likely to become endemic. This underscores the need for a proactive, long-term management approach rather than a purely reactive one.

The persistence of the virus in wild boar populations has also raised new questions about cross-protection and

vaccine development [20]. Oral vaccination is being investigated as a potential tool to manage the disease in wild boar, but challenges remain in ensuring the efficacy of the vaccine, particularly in a non-uniform field setting. The need for an oral vaccine that is both effective and safe for consumption by non-target species is a complex scientific hurdle [35].

The findings from these analyses predict that the lack of a unified global strategy and significant variations in national responses can hinder effective control [29]. The disparity in resources and political will among nations is particularly evident in their approach to managing wild boar populations. Countries with high population densities and less-developed biosecurity protocols face an uphill battle. The fragmented nature of the response is associated with the virus exploiting weak links in the chain of containment, which is associated with perpetuating the cycle of outbreaks and economic devastation. This highlights the need for international cooperation and a shared, evidence-based approach to managing this evolving threat.

In summary, the wild boar-habitat cycle has become the most significant epidemiological challenge in the global fight against ASFV. The behavioral traits of wild boar, combined with their population explosion, are associated with the creation of a persistent reservoir of infection that is resilient to conventional control methods. Addressing this challenge requires a coordinated, international strategy that combines population management with advanced surveillance technologies and a nuanced understanding of wild boar ecology.

3.2. Pathogenesis and Host-Virus Interaction

3.2.1. Cellular and Molecular Mechanisms

The pathogenesis of ASF begins with the entry of ASFV into the host, primarily targeting cells of the monocyte-macrophage lineage [40, 65]. The virus uses a complex process of endocytosis, including both dynamin- and clathrin-dependent pathways, to gain entry into the cell [67]. Once inside, the virion undergoes a series of uncoating and disassembly steps within multivesicular endosomes, ultimately releasing its core into the cytoplasm [68, 41].

ASFV replication is a sophisticated process that occurs exclusively in the cytoplasm of infected cells, a rare characteristic for a DNA virus [38]. The virus encodes its own DNA polymerase and other enzymes necessary for replication and transcription [41]. The assembly of new virions is equally complex, with viral polyproteins (e.g., pp220 and pp62) assembling into the core shell and other structural proteins (e.g., p54, p30) contributing to the formation of the outer layers [7, 74, 59]. The final virions are then transported to the cell surface, where they can be released through budding or cell lysis [76]. This complex replicative cycle ensures the production of a large number of progeny viruses, leading to a massive systemic infection [40].

3.2.2. Evasion of Host Immune Response

One of the most remarkable aspects of ASFV pathogenesis is its ability to effectively evade the host's immune response, a key factor associated with its high virulence [39]. The virus achieves this through a variety of mechanisms. It actively interferes with the host's innate immune signaling pathways, such as the type I interferon response, by encoding proteins that block the detection of viral DNA or inhibit downstream signaling [39, 70]. ASFV also modulates the cell cycle of infected cells to create an optimal environment for its replication [12]. The widespread destruction of immune cells, including lymphocytes and macrophages, in lymphoid tissues such as the tonsils and lymph nodes, further cripples the host's ability to mount a protective response [47, 60]. This immunosuppression is a major reason why infected pigs succumb to the disease and why a natural protective immune response is so difficult to achieve [53].

3.2.3. Clinical Manifestations and Pathology

ASF presents with a wide range of clinical signs, from peracute to chronic forms, depending on the virulence of the viral strain. Acute ASF is the most common form and is characterized by high fever, anorexia, lethargy, and widespread hemorrhages [14]. Externally, this presents as reddening of the skin, particularly on the ears and abdomen. Internally, there is extensive hemorrhage in multiple organs, including the lymph nodes, spleen, and kidneys [60, 61]. The spleen can become massively enlarged and friable, a

pathognomonic sign of the disease [60]. The widespread hemorrhages and tissue damage are a result of the virus infecting endothelial cells and macrophages throughout the body, leading to cell death and a systemic inflammatory response [44]. The severe, multi-organ damage is associated with the rapid mortality linked to highly virulent strains [14].

3.3. Biosecurity and Control Strategies

3.3.1. On-Farm Biosecurity

Biosecurity is the cornerstone of ASF prevention and control. The FAO and WOAHA have developed comprehensive guidelines for good biosecurity practices in the pig sector [52]. These measures are designed to create a physical barrier between susceptible pigs and potential sources of the virus. Key components include: strict access control for personnel and vehicles, thorough cleaning and disinfection of facilities and equipment, controlled sourcing of feed and animals, and proper disposal of carcasses and waste [77]. Implementing these measures is particularly crucial for commercial farms, but a major challenge remains in applying them consistently in smallholder and backyard farming systems, which often lack the necessary resources and infrastructure.

3.3.2. Surveillance, Detection, and Response

Effective surveillance and early detection are paramount to containing outbreaks. Surveillance involves a combination of clinical monitoring and laboratory testing. The gold standard for ASFV detection is real-time polymerase chain reaction (RT-PCR) which can identify the viral genome with high sensitivity [69, 43]. Serological assays, which detect antibodies against ASFV, are also used for surveillance in populations or to determine the history of exposure [62].

Rapid and coordinated response protocols are essential once an outbreak is detected. This typically includes a stamping-out policy, where all pigs in an infected premises are culled to prevent further spread, followed by rigorous disinfection [64]. However, the effectiveness of this approach is highly dependent on the speed of detection and the ability to accurately delineate the outbreak zone. In regions with dense wild boar

populations, culling and carcass removal from the environment are often part of the control strategy, but this is a complex and resource-intensive task [75].

3.3.3. Challenges in Vaccine Development

Despite decades of intensive research, a commercially available ASF vaccine remains elusive [11]. The development of a safe and effective vaccine is complicated by the virus's size and complexity, its unique replication cycle, and its ability to modulate the host immune system [38, 39]. Most current research focuses on live attenuated vaccines (LAVs), subunit vaccines, and genetically modified viruses [20, 35]. A key challenge is achieving durable, protective immunity without causing adverse side effects or reverting to virulence. The development of DIVA (Differentiating Infected from Vaccinated Animals) tests is also crucial to ensure that vaccinated animals can be distinguished from naturally infected animals, which is essential for trade and surveillance [62]. Until a safe and effective vaccine is available, biosecurity and culling remain the only viable control measures.

3.4. Socio-Economic Impacts and Global Spread

The global spread of ASF has been driven by a confluence of biological and anthropogenic factors, with devastating socio-economic consequences. The disease has led to the culling of hundreds of millions of pigs, causing immense economic losses to farmers, processors, and related industries [27]. In Asia, where swine production is a cornerstone of the agricultural economy, the impact has been catastrophic, destabilizing rural livelihoods and threatening food security [72].

A key insight is the role of **illegal trade and inadequate surveillance as a major driver of the pandemic-like spread of ASFV**. The movement of infected pigs, contaminated pork products, and feed, often through informal or illegal channels, is a significant vector for the virus, and is associated with its rapid spread across borders [28, 71]. This has been particularly evident in Asia, where outbreaks in one country are associated with a domino effect in others. This lack of robust surveillance and enforcement in many regions is associated with localized outbreaks escalating into

regional and global crises [55, 72]. This contrasts sharply with previous outbreaks that were more confined due to stricter containment measures, which highlights a new and more insidious mode of global spread.

4. Discussion

4.1. Synthesis of Findings

This review has demonstrated that African swine fever is a highly complex and multifaceted disease, and its recent global expansion is associated with a perfect storm of factors. The virus's inherent biological characteristics—its environmental stability, multiple transmission routes, and sophisticated immune evasion strategies—are associated with it being an extraordinarily difficult pathogen to control [51, 39]. The establishment of a new, self-sustaining wild boar-habitat cycle in Eurasia has created a permanent reservoir of infection that will be nearly impossible to eradicate [57, 16]. This necessitates a long-term, strategic approach that accounts for both domestic and wild pig populations. The current reliance on biosecurity and stamping-out policies, while essential, is clearly insufficient to contain a disease that can spread through contaminated products and feed [28, 34].

4.2. Limitations of Current Control Models

A critical finding from our analysis is that current control models are fundamentally limited by the lack of a unified global strategy and significant variations in national responses. The reliance on reactive culling and blanket movement restrictions is associated with an expensive and often ineffective way to manage the disease, especially in regions with high densities of wild boar or fragmented smallholder farming systems [17, 75]. The disparity in resources, political will, and biosecurity standards among different countries is associated with a fragmented and inconsistent global defense [23, 29]. Some countries have implemented robust surveillance and control programs, while others, particularly those with less developed agricultural sectors, have struggled to respond effectively. This is associated with a patchwork of policies where an outbreak in one country can re-infect a neighbor, even if the latter has a more effective response in place [71, 55]. This fragmentation is associated with a truly global containment strategy

being impossible. Unlike cooperative efforts against other animal diseases, the global response to ASF is associated with being hindered by a lack of coordinated, well-funded initiatives among international organizations. This suggests that without a cohesive, harmonized global strategy, ASF will continue to persist and pose a recurring threat.

4.3. Future Directions

The global ASF pandemic is associated with a shift in focus toward more innovative and collaborative solutions. A top priority must be the development of a safe, effective, and field-ready vaccine. Continued research into novel vaccine candidates, including subunit and vector-based options, is crucial. The focus should be on creating a vaccine that is not only effective but also easy to produce and deploy, particularly in resource-limited settings [11].

Concurrently, there is an urgent need for the development of rapid, point-of-care diagnostic tools that can be used on farms or in the field to enable real-time detection and response [43]. This would allow for more targeted and efficient control measures, reducing the need for large-scale, indiscriminate culling.

Perhaps most importantly, a **'One Health' approach** is necessary to effectively manage ASF. This involves recognizing the interconnectedness of human, animal, and environmental health. ASF is not just an animal health problem; it is a human problem influenced by trade, travel, biosecurity practices, and human-wildlife interactions. A 'One Health' strategy would be associated with requiring enhanced collaboration between veterinary services, public health officials, wildlife management agencies, and government bodies [21]. It would necessitate a paradigm shift from a purely reactive, disease-specific response to a proactive, integrated, and holistic approach.

4.4. Conclusion

In conclusion, the global resurgence of African swine fever represents one of the most significant challenges to animal agriculture in the 21st century. The disease's successful dissemination is a testament to the virus's tenacity and the vulnerabilities in our current global

systems of biosecurity and surveillance. While significant progress has been made in understanding its epidemiology and pathogenesis, the absence of a vaccine and the limitations of fragmented national responses mean that ASF will likely remain a persistent and evolving threat. Only through coordinated international efforts, continued scientific innovation, and the adoption of a unified 'One Health' framework can we hope to effectively mitigate and ultimately contain this devastating disease.

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