

# **One hundred years of African swine fever in Africa: where have we been, where are we now, where are we going?**

Mary Louise Penrith<sup>1\*</sup>; Fredrick Mathias Kivaria<sup>2</sup>

<sup>1</sup>Department of Veterinary Tropical Diseases, Faculty of Veterinary Science, University of Pretoria, Onderstepoort, South Africa

<sup>2</sup>Food and Agriculture Organization of the UN, Block P, Level 3, United Nations Complex, UN Avenue, Gigiri, Nairobi, PO Box: 30470, 00100, GPO, Nairobi, Kenya

\*Author to whom correspondence should be addressed

## **Summary**

One hundred years have passed since the first paper on African swine fever (ASF) was published by Montgomery in 1921. With no vaccine, ineffectiveness of prevention and control measures, and lack of common interest in eradicating the disease, ASF has proven to be one of the most devastating diseases because of its significant sanitary and socioeconomic consequences. The rapid spread of the disease on the European and Asian continents and its recent appearance in the Caribbean puts all countries at great risk because of global trade. The incidence of ASF has also increased on the African continent over the last few decades, extending its distribution far beyond the area in which the ancient sylvatic cycle is present with its complex epidemiological transmission pathways involving virus reservoirs in ticks and wild African Suidae. Both in that area and elsewhere, efficient transmission by infected domestic pigs and virus resistance in infected animal products and fomites mean that human driven factors along the pig value chain are the dominant impediments for its prevention, control, and eradication. Control efforts in Africa are furthermore hampered by the lack of information about the size and location of the fast-growing pig population, particularly in the dynamic smallholder sector that constitutes up to 90% of pig production in the region. A vaccine that will be both affordable and effective against multiple genotypes of the virus is not a short-term reality. Therefore, a strategy for management of ASF in sub-Saharan Africa is needed to provide a roadmap for the way forward for the continent. This review explores the progression of ASF and our knowledge of it through research over a century in Africa, our current understanding of ASF, and what must be done going forwards to improve the African situation and contribute to global prevention and control.

**Keywords:** African swine fever, history, century of research, sylvatic cycle, domestic cycles, prevention and control

## 1 Introduction

African swine fever (ASF) is one of the most important and feared diseases of domestic pigs. One hundred years have passed since the first paper on African swine fever was published (Montgomery, 1921). That first account described a highly fatal haemorrhagic disease of domestic pigs belonging to European settlers in East Africa that was in some way associated with warthogs. Over the last century, the disease has progressed from being a curiosity reported from most countries in eastern and southern Africa with an intriguingly complex epidemiology involving wild pigs and argasid ticks to a disease that has visited and is currently present in five continents and is arguably the most important threat to the global pig industry. This review traces its progression in Africa from the earliest decades to the present. It does not attempt to provide a detailed history, as that might take a century to write and another to read, but highlights important milestones and developments in sub-Saharan Africa and provides a vision for an African domestic pig population without ASF.

## 2 Where have we been?

African swine fever is believed to have evolved in Africa in the sylvatic cycle that occurs between common warthogs (*Phacochoerus africanus*) and argasid ticks of the *Ornithodoros moubata* complex that live in their burrows (Jori et al., 2013).

It is uncertain when domestic pigs (*Sus scrofa*) made their first appearance in sub-Saharan Africa. The concept that pigs were first introduced by European settlers and missionaries about 500 years ago has possibly been disproven by findings of what may be pig remains in the midden of an Early Iron Age human settlement in KwaZulu-Natal province, South Africa (Voigt & von den Driesch, 1984). In eastern and southern Africa, it is likely that ASF was already known to indigenous pig-keeping populations before the European settlers arrived, and that populations such as those in western Kenya and a triangle that includes adjacent districts in southern Malawi, north-western Mozambique and eastern Zambia (Chambaro et al., 2020; Haresnape, Lungu & Mamu, 1987; Penrith et al., 2004; Wilkinson et al., 1988) had already acquired a degree of resistance to the virus. In Angola, the pigs kept by the indigenous population were considered to be the source of infection for the settlers' pigs (Mendes, 1994).

### 2.1 The first decades (1900 – 1956)

Some 12 years before the publication of the first paper on ASF, a highly fatal disease of domestic pigs belonging to European settlers in Kenya came to the notice of R. Eustace Montgomery, who became the founding father of our knowledge of ASF. His paper described in detail the painstaking research that culminated in the author becoming certain that he was dealing with a viral disease (i.e., a disease caused by a filterable agent) that caused up to one hundred per cent mortality in domestic pigs and that was in some way associated with warthogs (Montgomery, 1921). Interestingly, at the same time that the disease was discovered in Kenya (then British East Africa) and also in German East Africa (now Tanzania) (Montgomery, 1921), it was also reported by a government veterinarian in Eastern Province of Zambia (Wilkinson et al., 1988). During the next decades, 'East African swine fever' was reported from South Africa (Steyn, 1928, 1932), Angola (Gago da Camará, 1933), Malawi (Matson, 1940; Turnbull, 1932-4), Democratic Republic of Congo (DRC) in 1939 (Colback, 1940; Saliki et al. 1985) and Mozambique in 1954 (Abreu, 1962).

In the decades before ASF virus reached Europe for the first time in 1957, research on ASF was concentrated in three African countries, namely Kenya, South Africa, and Angola.

Information about ASF in Angola and the research that was undertaken in that country is available in an excellent history of swine fever in Angola (Mendes, 1994) as well as many research publications in French and Portuguese. Research in East Africa was undertaken largely under the auspices of the East African Veterinary Research Association based at the laboratory in Muguga, Kenya. Researchers recruited from the USA and UK did pioneering work on ASF in the 1950s and 1960s that is reflected in many publications. In South Africa, research on ASF was carried out in the government veterinary laboratories at Onderstepoort, which evolved into the present-day ARC-Onderstepoort Veterinary Research Platform where ASF is one of the main research interests of the Transboundary Animal Diseases Programme. The research performed in these three countries formed a sound basis of knowledge on ASF that enabled rapid advances as new technology became available for the study of pathogens, culminating in molecular level research that informs our understanding today.

Research carried out in these countries before the virus reached Europe for the first time in 1957 and again in 1960 included various laboratory studies on the virus, studies on the pathology of the disease, and early attempts to immunise pigs by various means.

### *2.1.1 Differentiating African swine fever from classical swine fever*

In the very first publication on ASF Montgomery described unsuccessful attempts to protect pigs from ASF by inoculation of two different antisera to classical swine fever (CSF), also called hog cholera, obtained from England and Hungary (Montgomery, 1921). However, uncertainties persisted as to whether the virus that caused 'East African swine fever' was a more virulent form of the virus that caused classical swine fever or a different virus (De Kock, 1938; De Kock et al., 1940). The truth could have been discovered earlier, when Gago da Camara (1933) received samples from pigs that had died and was able to exclude erysipelas and concluded that he was dealing with swine fever. He intended to obtain antiserum to CSF to confirm his diagnosis and start immunising pigs, but for unknown reasons was not able to do this (Mendes, 1994).

In 1943, Dr Joaquim Monteiro de Conceição arrived in Angola. He was a noted pathologist, and shortly after his arrival he was able to investigate field outbreaks of disease with lesions that he considered similar to those described in East and South Africa. He obtained classical swine fever antisera from Europe and was able to confirm that they afforded no protection to pigs infected with the causative agent of the virus from the outbreaks in Angola and therefore concluded that the swine fever in Angola was the same as 'East African swine fever' (Conceição, 1949). In Kenya, Detray & Scott (1955) reported that hyperimmune serum against hog cholera from the USA failed to neutralise Kenyan ASF virus either *in vitro* or when inoculated into pigs that were inoculated at the same time with ASF virus.

### *2.1.2 Looking for a vaccine – the early attempts*

Predictably, attempts to inactivate ASF virus in order to immunise pigs were first described by Montgomery (1921), who found that heat killed ASF virus conferred no protection, while virus that had been heated sufficiently to reduce virulence but not to kill the virus could result in chronic disease with persistent infection of the pigs. Attempts in South Africa to immunise pigs with culture-sterile bile from pigs that died of ASF as well as with hyperimmune sera and virus treated with disinfectants were unsuccessful (Steyn, 1932). Attempts in Kenya to immunise pigs with virus attenuated by an array of different methods including heat and disinfectants failed, and simultaneous inoculation with hyperimmune serum and virus produced variable but generally only low grade and transitory protection (Walker, 1933). De Kock et al. (1940) reported that attempts to attenuate the South African virus with crystal violet to obtain a vaccine, as had been reported to be successful for CSF, failed to confer immunity against ASF.

However, the results gave some hope to researchers in Angola (Mendes, 1994). The growing demand for processed pork products after the end of the Second World War focused attention on the ideal conditions for growing maize and raising pigs in Angola but the latter was severely hampered by ASF. With the construction of a laboratory with a facility dedicated to research on ASF in 1952, serious attention was given to developing an ASF vaccine (Mendes, 1962; Mendes, 1994; Mendes & Daskalos, 1955). Similar to findings reported from East and South Africa, attenuation of the virus by addition of crystal violet or formalol failed to protect pigs, and results obtained using hyperimmune serum were sometimes encouraging but the results were variable at best (Mendes, 1994). Attenuation of the virus was achieved by numerous passages in rabbits, but the attenuated virus did not confer protection on pigs challenged with virulent ASF virus (Mendes, 1994; Mendes & Daskalos, 1955). Attempts to attenuate the virus in hen's eggs in South Africa and Angola were not successful, although some replication in eggs was observed in the South African experiments (McIntosh, 1952; Mendes, 1994).

## **2.2 The next decades (1957 – 1995)**

### *2.2.1 The first extra-African excursions of ASF*

In 1957 the first outbreaks of ASF outside the historically infected area in Africa occurred in Portugal in farms close to the international airport in Lisbon. The origin was assumed to be aeroplane galley waste from Angola, then an overseas province of Portugal, and the outbreak was quickly eradicated (Braço Forte, 1970; Wesley and Tuthill, 1984). However, in 1960 a new introduction occurred into Portugal that subsequently resulted in the disease becoming established in Portugal and Spain for more than 30 years, with spread to other countries in western Europe, the Caribbean and Brazil (Costard et al., 2009; Penrith, 2020). The impact on Africa of these events was twofold. Firstly, the surge in interest in ASF that arose from its devastating effect in countries with developed pig industries was the impetus for increased research from which Africa was also able to benefit. Secondly and unfortunately, changes in the way the disease manifested over time in Europe were accelerated and exacerbated by the premature release of unsafe vaccines in the Iberian Peninsula that resulted in chronic forms of the disease (Sánchez-Vizcaíno et al., 2015). These were for a long time attributed exclusively to natural changes in virus virulence, and the situation was extrapolated to Africa, although such manifestations are rare; to our knowledge no vaccines have ever been used in Africa outside of laboratories. The most serious problem about the observed attenuation of virulence was that the adaptation over centuries of exposure to ASF observed in certain pig populations in eastern Africa has been automatically attributed to circulation of viruses of low virulence, although there is ample evidence that these pigs are unaffected by highly virulent viruses belonging to more than one genotype (Penrith et al., 2004).

Although persistent low-grade disease and the presence of a domestic pig-tick cycle in the south-western parts of the Iberian Peninsula contributed to the lengthy presence of ASF in Spain and Portugal compared to other affected countries (Pérez-Sánchez et al., 1994; Sánchez Botija, 1963; Wilkinson, 1984), it became clear that ASF could persist in the absence of these factors. The island of Sardinia became infected in 1978, and in spite of high virulence of the virus and absence of ticks, that country is only now in the final stages of eradicating ASF (Laddomada et al., 2019; Loi et al., 2019; Mur et al., 2017; Rolesu et al., 2021). Similarly, ASF has persisted in Guinea-Bissau and its neighbours since the first reports of ASF in 1959 (Brown et al., 2018). The drastic approaches to eradication through culling of the entire pig population in Malta, Dominican Republic, and Haiti resulted in eradication of ASF in a relatively short time and supported the concept that this was the preferred method to deal with the disease (Arias & Sánchez-Vizcaíno, 2002; Balbo & Iannizzotto, 1983; Rivera, 1983; Sánchez Botija, 1982; Viltrop et al., 2021). The loss of the important local breed in Haiti (FAO, 2007), which

remains one of the poorest countries in the world, remains as an unwanted legacy and a warning against eradication of a single disease ahead of all other considerations.

Two major benefits to Africa that resulted from the virus reaching Europe were accelerated development of diagnostic techniques that do not involve inoculating pigs, and the discovery of the biological arthropod vector of ASF.

### 2.2.2 Advances in the diagnosis of ASF

Earlier studies required inoculation of pigs with blood from pigs showing signs of ASF. Failure of hyperimmune serum against classical swine fever to neutralise the effects of the virus was considered diagnostic for ASF (Sánchez Botija, 1982). The discovery by Malmquist and Hay (1960) that infection of macrophages in bone marrow or buffy coat cultures with ASF virus resulted in haemadsorption followed by cytopathic effects enabled differentiation of ASF virus from CSF virus without the need to infect pigs. During his 5-year stay in Kenya through the USDA project to support the East African Research Association, Leroy Coggins developed a modified haemadsorption-inhibition test and an agar diffusion precipitation test for ASF virus and antibody (Coggins, 1968a; Coggins and Heuschele, 1966) and also investigated the use of fluorescent antibodies to detect ASF virus (Heuschele et al., 1966), a test that is still recommended for the diagnosis of acute ASF, although reagents are becoming scarce (Gallardo et al., 2019). He also described finding a non-haemadsorbing ASF virus that could be identified by the cytopathic effect that it produced in cell cultures (Coggins, 1968b). Working at Onderstepoort in South Africa, Els and Pini (1977) described negative staining of a non-haemadsorbing strain of ASF virus.

### 2.2.3 The arthropod biological vector

In his first account of ASF, Montgomery (1921) raised the question of whether an arthropod vector might be involved in transmission of the ASF virus, because direct transmission of the virus through contact between domestic pigs and warthogs did not occur. In spite of this, many of the outbreaks on farms in Kenya could only be attributed to the presence of warthogs, because the farms were isolated and there was no history of introduction of pigs or their products. However, it was only in 1962 in Spain that the biological arthropod vector of ASF virus was unveiled when Sánchez Botija (1963) confirmed that *Ornithodoros erraticus*, a soft tick that lived in pig shelters, was able to maintain and transmit the ASF virus to pigs. This was followed by investigations by the East African researchers, who were able to demonstrate infection with ASF virus in *Ornithodoros moubata* complex ticks from animal burrows that had been occupied by warthogs in Tanzania (Plowright et al., 1969a). Plowright and his colleagues were further able to demonstrate proliferation of the virus in the ticks (Plowright, Perry, Peirce, & Parker, 1970), trans-stadial transmission in ticks (Plowright et al., 1969b), transovarial transmission in the ticks (Plowright, Perry, & Peirce, 1970) and sexual transmission from males to females (Plowright et al., 1974). Ticks of the *Ornithodoros moubata* complex are therefore competent biological vectors of the ASF virus. Plowright et al. (1969a) suggested, on the basis of common features of the virus with *Iridoviridae*, that the virus may have originated and evolved in the arthropod vector rather than in members of the pig family, which is supported by a recent molecular study that demonstrated the presence of ASF genome-like segments in archived specimens of ticks of the *Ornithodoros moubata* complex (Forth et al., 2020). Phylogenetic reconstruction and molecular clock analysis suggested that the integration of the ASF virus-like elements into the tick genome may have occurred more than 1.47 million years ago (Forth et al., 2020).

As the ticks are cryptic and spend most of their lives in the burrows, feeding rapidly and dropping off their hosts, transmission from warthogs to domestic pigs appeared to be an

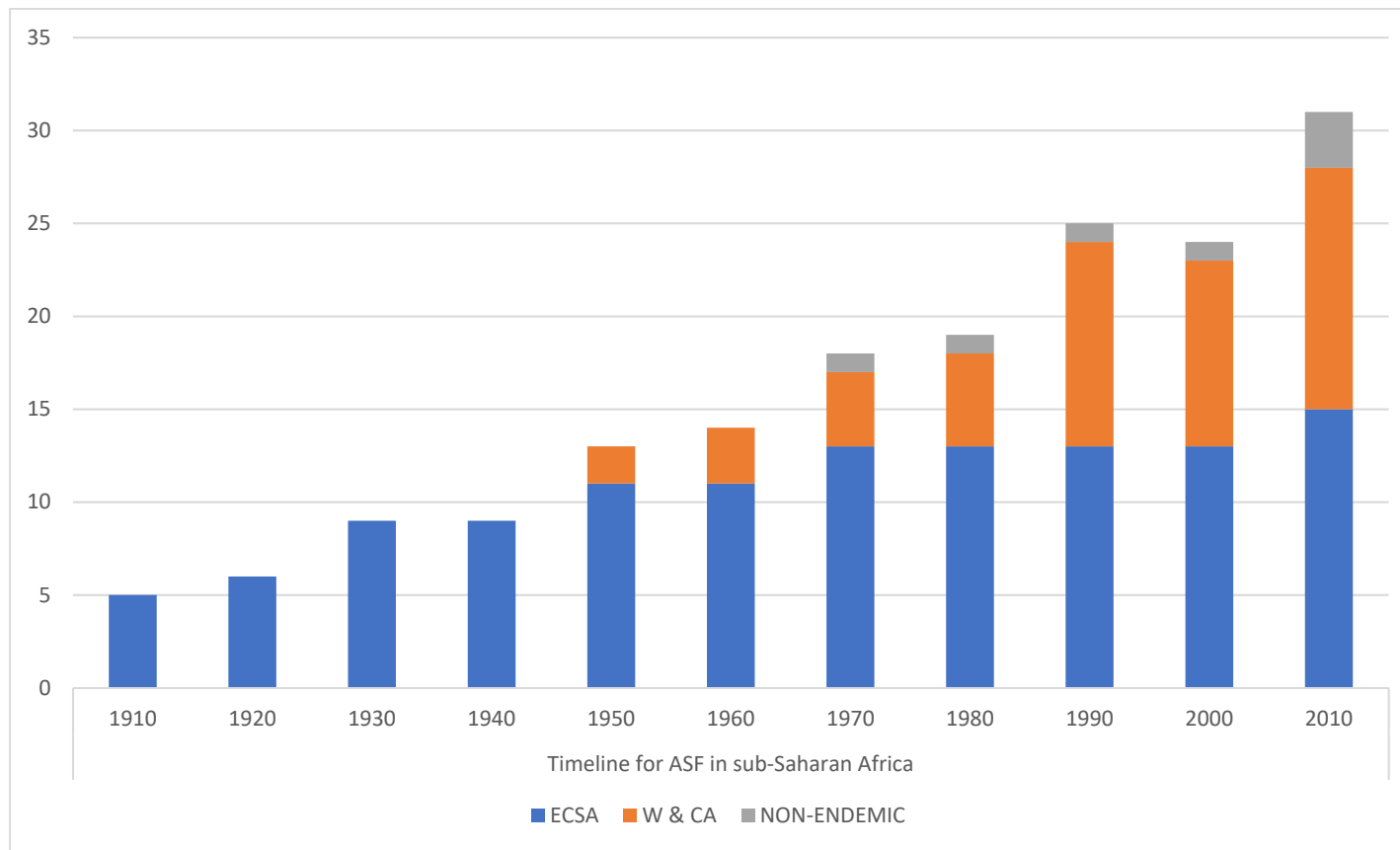
obstacle, but Plowright et al (1969a) noted that ticks were sometimes found on warthogs shot early in the morning. Later studies in Namibia and South Africa demonstrated that nymphs, sometimes in large numbers, were not infrequently found travelling on warthogs in ASF-endemic areas in Namibia and South Africa (Boomker et al., 1991; Horak et al., 1983; Horak et al., 1988).

One problem that remained to be solved was how the cycle between warthogs and ticks operated, because warthogs were never found with viraemia of sufficient levels to infect ticks. Feeding the tissues of acutely experimentally infected warthogs to domestic pigs resulted in infection of some of the pigs, but only after tissues including lymph nodes were liquidised in a blender (Thomson et al., 1980). This suggested that offal of free-living warthogs, in which virus is often limited to the lymph nodes, would not be a potent source of infection. The mystery was solved when it was found that neonatal warthogs, which spend the first weeks of their lives in the burrows where they are born, are fed on by the ticks and develop sufficient levels of viraemia to infect other ticks (Thomson et al., 1983; Thomson, 1985).

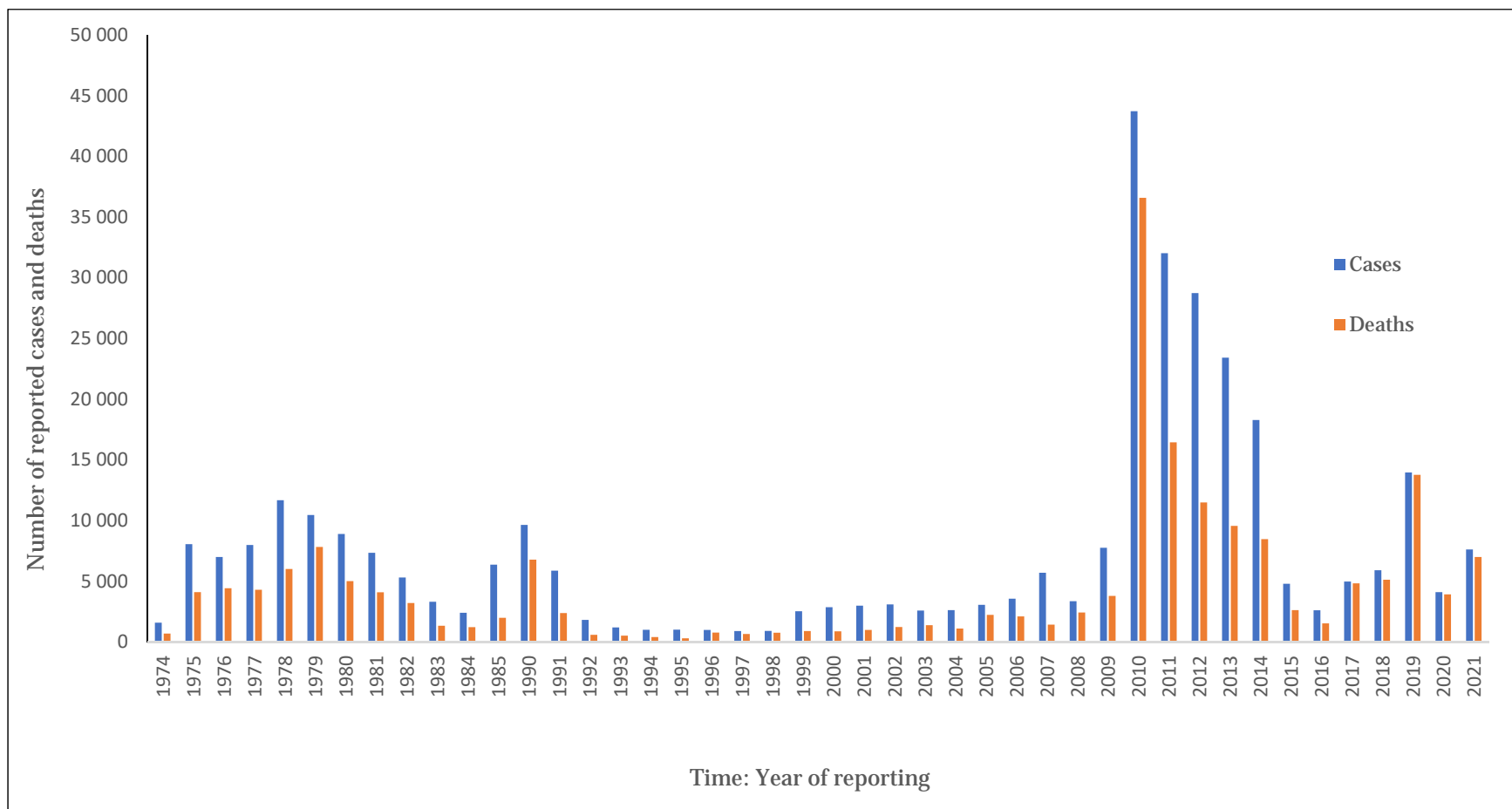
Also in the 1980s, researchers in Malawi discovered a domestic pig-tick cycle in an area where ASF outbreaks with relatively low mortality occurred regularly in domestic pigs. There were no warthogs in the area, and bushpigs that were sampled were negative for ASF (Haresnape, Lungu & Mamu, 1985; Haresnape, Wilkinson & Mellor, 1988). The ticks were found in both the shelters used by the pigs at night and the houses of their owners, where in both cases the mud and wood walls offered deep cracks in which the ticks could hide by day (Haresnape et al., 1988). The infection rates in the ticks were comparable with those reported from warthog burrows in East Africa, South Africa and Namibia (Haresnape et al., 1988). The endemic area in Malawi was found to be confined to the western part of the Mchinji District that borders on eastern Zambia and north-western Mozambique. Although the adjacent districts of Zambia and Mozambique are both endemic for ASF as well, to date the pig-associated ticks have not been found there (Penrith et al., 2004; Wilkinson et al., 1988).

#### *2.2.4 Introduction of ASF to previously uninfected areas in Africa*

Until the late 1950s, ASF had only been reported from countries in eastern and southern Africa, most of which had reported ASF by that time. The first confirmed report from West Africa, supported by a virus isolate Dakar/59, was from Senegal in 1959, but there were anecdotal reports of ASF between 1959 and 1961 in its neighbours Guinea Bissau and Cape Verde as well. Although reporting from these countries is sporadic, ASF is considered to be endemic at least in the Casamance province of Senegal (Etter, Seck et al., 2011; Sarr, 1990; Vial et al., 2007). Nigeria experienced an unconfirmed outbreak of disease in a pig farm in Ogun State in 1973 that was probably ASF (Babalobi et al., 2007; Isoun & Osunfisan et al., 1973), but it was rapidly eradicated. Warthogs from a conservation area in Nigeria were tested and found negative for antibodies to ASF (Taylor et al., 1977). In 1979 the Central African island nation of São Tomé e Príncipe suffered an outbreak of ASF that was eradicated by killing the entire pig population (Sanchez Botija, 1982). In 1982 Cameroon became the second previously unaffected Central African country to experience outbreaks of ASF after there had been an unprecedented expansion of the country's pig industry in the preceding decade (Nana-Nukechap et al., 1985). The disease became endemically established in the southern and central parts of the country where most of the pigs were raised (Ekue & Wilkinson, 1990, 2000). The introductions into Cameroon in northern Central Africa and into West Africa heralded continued spread in the continent with an increase in the number of countries infected (Fig. 1) as well as increased reported losses of pigs (Fig. 2), driven by exponential growth of the pig population in several countries as well as increased awareness and improved reporting of ASF (Penrith et al., 2013).



**Figure 1.** Timeline for reporting of ASF in Africa, based on reports to OIE and AU-IBAR as well as published literature. The dates below the columns represent the start date for the decade, thus the first column refers to the number of countries where infection was reported between 1910 and 1920 and the last column the number of reports from 2011 to 2020. Key: ECSA = East, Central and southern Africa; W & CA = West and Central Africa; Non-endemic = countries that have experienced ASF outbreaks but it has not become endemically established.



**Figure 2.** Cumulative number of ASF cases and deaths reported in Africa from 1974 to 2021. Source: FAO/Emergency Prevention System for Animal Health (EMPRES-AH)



### 2.2.5 Molecular epidemiology of the ASF virus

One of the most important advances in understanding the ASF virus was technology that enabled the study of the virus at the molecular level. The first studies were based on restriction fragment length polymorphism (RFLP) (Blasco et al., 1989; Wesley & Pan, 1982; Wesley & Tuthill, 1984). They revealed that all the isolates from outside Africa (Europe, the Caribbean and Brazil) were closely related to each other as well as to isolates from Angola and Senegal, although differences within the group were sufficient to confirm that the 1957 and 1960 outbreaks in Portugal were due to separate introductions (Blasco et al., 1989). On the other hand, the isolates from eastern and southern Africa studied showed marked differences from the European and western African isolates and amongst each other (Blasco et al., 1989; Wesley & Tuthill, 1984).

### 2.3 The interregnum – absence from most of Europe, expansion in Africa (1996-2006)

After the eradication of ASF from all countries outside Africa by 1994, with the exception of Sardinia and a single outbreak in Portugal in 1999 that was attributed to residual infection in *Ornithodoros erraticus* (Boinas et al., 2011), interest in ASF declined to a certain extent. However, from 1993 onwards Africa began to experience an upward trend, with new countries being infected as well as new areas in the long-time endemic countries. In 1993, for the first time in 30 years, outbreaks of ASF occurred in Kenya around the city of Nairobi that were attributed to infected pigs brought to Nairobi for slaughter from the western border area with Uganda, where ASF has long been endemic (M.-L. Penrith, unpublished report, 1996). In the following year, ASF was detected for the first time south of the Save River in pigs at the Veterinary Faculty of Eduardo Mondlane University in Maputo (Penrith et al., 2007). It was established that an ASF outbreak had occurred in Inhambane province in 1993 that was most probably the first outbreak south of the Save River, and the outbreaks in the three southern provinces continued until 2001 and reappeared September 2004, after which outbreaks have continued to be reported throughout the country (Penrith et al., 2007; World Organisation for Animal Health-WAHIS,2005-2021). In 1998, the Indian ocean island nation of Madagascar reported its first outbreaks of ASF, losing half of its pig population of about 2 million, and soon become endemic for ASF (Andriamanivo et al., 2015; Ravaomanana et al., 2011; Roger et al., 2001; Rousset et al., 2001).

In 1996, Côte d'Ivoire reported ASF for the first time (El Hicheri et al., 1998). By early 1997 the disease had been eradicated (Brown et al., 2018; El Hicheri et al., 1998), but in late 1997 Benin reported its first outbreaks of ASF, followed in rapid succession by neighbours Togo and Nigeria (Brown et al., 2018). All of these countries remained infected, with spread, and at the end of 1999 Ghana confirmed its first outbreak of ASF (Brown et al., 2018). In spite of it being eradicated in 2000, it was reintroduced in 2002 with subsequent endemic establishment, and in 2003 ASF was reported for the first time from Burkina Faso (Brown et al., 2018), where it also persists (Kouakou et al., 2016; Minoungou et al., 2021).

Molecular studies using RFLP undertaken to try to determine the origin of the outbreaks in São Tomé e Príncipe and Cameroon failed to pinpoint the origin of the viruses, which were closely related to those circulating in Europe at the time, and it was argued that they may have originated in Europe (Ekue & Wilkinson, 2000; Wesley & Tuthill, 1984), although Sanchez Botija (1982) attributed the introduction into São Tomé e Príncipe to meat imported from Angola, thought to have been where the viruses that were introduced into Portugal in 1957 and 1960 originated. The uncertainty surrounding the origin of the West African epidemic viruses was a major driver of further molecular advances in the study of ASF.

### *2.3.1 Molecular advances that resulted from the West African epidemic*

Based on the identification of variable and constant regions in the DNA of ASF viruses and the ability to classify 23 ASF viruses into five groups, four of which were comprised of African viruses and one of which also contained all of the available viruses from European and the American region (Blasco et al., 1989), a PCR-based method of genotyping ASF viruses was developed (Bastos et al., 2003). The results of this study agreed in broad terms with the RFLP study, yielding a single genotype, named genotype I, that contained all of the extra-African viruses as well as viruses from Angola, DRC, Namibia, western Zimbabwe, and Senegal and all the other affected West African countries, as well as nine other genotypes (II-X) that contained only African viruses, mainly from eastern and southern Africa (Bastos et al., 2003). The virus from Madagascar was unique, and was named genotype II, but in 1999 a genetically identical virus was isolated from an outbreak in pigs in north-western Mozambique in 1998 (Bastos et al., 2004), suggesting that the origin of the Madagascan virus was in eastern Africa.

Further molecular studies in South Africa revealed another twelve p72 genotypes (Boshoff et al., 2007; Lubisi et al., 2005) as well as a method of increasing the resolution at intragenotypic level by combined use of p72 and central variable region typing (Lubisi et al., 2007; Phologane et al., 2005).

Although these studies enabled a more detailed picture of relationships between various outbreak viruses, it was (and is) still not possible to determine the direction of transmission unless the finding can be reliably linked with particular events that may have led to transmission.

### *2.3.2 Advances in research into resistance to African swine fever*

Resistance to ASF had been reported in bushpigs since 1921, and in 1998 an experimental study of pathogenesis, resistance in and transmission by bushpigs was carried out in Zimbabwe (Anderson et al., 1998; Oura et al., 1998). Bushpigs experimentally infected with two virulent ASF viruses showed no clinical signs but did develop sufficient viraemia to infect ticks fed on them, which in turn were able to infect domestic pigs when feeding on them. Viraemia lasted in the bushpigs from 35 to 91 days, but levels declined between 35 and 70 days (Anderson et al., 1998). One of the viruses, which was isolated from a domestic pig, was able to infect an in-contact local breed pig, which subsequently infected a pen-mate, but the other virus, a tick isolate, was not transmitted to in-contact pigs during the experiment (Anderson et al., 1998). No virus was present in lymph nodes of bushpigs after 34 days. Warthogs in the same study were unable to infect in-contact pigs but transmission from viraemic warthogs via ticks to domestic pigs occurred. The virus persisted longer in lymph nodes of warthogs than in bushpigs but was not found after 56 weeks (Anderson et al., 1998). A comparative study of the pathogenesis in the bushpig and domestic pigs revealed more limited replication, mainly in the spleen, and more limited spread to other tissues in the bushpig (Oura et al., 1998). A high degree of apoptosis in B cells in lymph nodes was observed in the bushpig, leaving the T cells relatively unaffected, while in domestic pigs T cells are the major lymphocytes affected by ASF virus (Oura et al., 1998).

An investigation aimed to determine the nature of the resistance observed in a population of local breed pigs in Mozambique, where on average 40 percent of healthy pigs had antibodies to ASF virus, with up to 100 percent of the pigs in some villages investigated, was undertaken in South Africa (Penrith et al., 2004). Briefly, a group of pigs was brought to South Africa by air from the Angónia district of Tete province in Mozambique, which adjoins the Mchinji district in Malawi, and quarantined at the Onderstepoort Veterinary Institute (OVI). All of the 15 females and one of two boars were seropositive for ASF. Altogether 102 offspring derived

from these pigs were challenged with two virulent genotypes II and VIII ASF viruses that had been circulating in the area where the pigs were acquired, and only one survived without developing any clinical signs, while the rest died of severe acute ASF. These results suggested that the observed resistance was not simply inherited, and that further investigation including in the area of origin of the pigs was warranted. Other valuable findings were that the serologically positive imported pigs were not carriers, as the seronegative in-contact boar never became sick or seroconverted in spite of being in close contact with the rest of the group for more than two years, and that the survivor was fully resistant to both viruses (Penrith et al., 2004). The two viruses used were isolated from pigs that died of ASF within the first two weeks of quarantine, and it was found that the tissues of the affected pigs yielded one or other of the two co-circulating viruses, without co-infection in any of the pigs (Bastos et al., 2004).

### **3 Where are we now? (2007 to present)**

The period between 2007 and 2021 saw a major shift in the global ASF situation. In 2007 ASF was diagnosed in the Republic of Georgia in the Trans-caucasus region at the junction between Europe and Asia, and the virus turned out to be identical at genotype level to the genotype II virus thus far only diagnosed from outbreaks in Madagascar and Mozambique in 1998 and retrospectively from an outbreak in Zambia in 1989 (Rowlands et al., 2008). Within the same year, the disease spread to neighbouring Armenia as well as to wild boars in the Republic of Chechnya, which is part of the Russian Federation; an outbreak occurred in a village in Azerbaijan in January 2008 (Beltran Alcrudo et al., 2008). Spread occurred to wild boars in north-western Iran in December 2008 and January 2009 (Rahimi et al., 2010). Gradual northward spread in Russia occurred (Gogin et al., 2013), with ASF reported from Ukraine in 2012 and Belarus in 2013. Outbreaks in wild boars in Poland, Lithuania, Latvia, and Estonia in 2014 heralded unprecedented expansion of the infection to mainly EU member countries in Eastern and Central Europe, with wild boars in Belgium affected in 2018 (Linden et al., 2019) and in Germany in 2020 (Sauter-Louis et al., 2021). August 2018 saw what the world had been dreading, namely the first notification of ASF in China, and currently 16 countries in the Asia-Pacific region have reported ASF (Li & Tan, 2018; World Organisation for Animal Health-WAHIS, 2005-2021). Most recently, the genotype II virus has been reported from outbreaks in Dominican Republic and Haiti in the Caribbean, and in Lagos in Nigeria (Adedji et al., 2021; World Organisation for Animal Health-WAHIS, 2005-2021).

While global events have turned the spotlight away from ASF in Africa, the changing situation that was signalled by the incursions of ASF into several previously unaffected countries in West Africa as well as Madagascar in the preceding period continued and worsened, with ASF spreading to more countries. Outbreaks in domestic pigs have increased markedly, including in southern African countries where the disease in domestic pigs was previously largely confined to sporadic and isolated warthog-related events in poorly managed pigs (Penrith et al., 2019).

#### ***3.1 Major ASF events in Africa 2007 - 2021***

Throughout sub-Saharan Africa, the ASF situation appears to have worsened, although some of this may be due to improved reporting following the changes to the OIE platform with the launch of WAHID (World Animal Health Information Database) in 2005 as well as increased pressure from the African Union-Interafrican Bureau for Animal Resources (AU-IBAR) on countries to report transboundary animal diseases. Five countries reported ASF for the first time, and three countries that had previously only reported sporadic small outbreaks that were mostly due to contact with the sylvatic cycle experienced domestic pig-related outbreaks that affected larger numbers of pigs. In spite of this, according to FAOSTAT data up to 2018, Africa

as a whole experienced steady growth of the pig population and several of the countries where ASF is endemic showed a marked increase in pig numbers during this period (<http://www.fao.org/faostat/en/#data/QA>).

### *3.1.1 West Africa*

Only two countries in West Africa, Côte d'Ivoire and Ghana, were able to eradicate ASF after its introduction in 1996 and 1999 respectively, but Ghana was rapidly reinfected in 2002 and the disease became endemic (Brown et al., 2018). Côte d'Ivoire remained free of ASF from 2007 until 2014, when an incursion occurred in the port city of San Pedro, which had escaped infection in 1996. Carelessly disposed galley waste from the port at an open landfill frequented by livestock was most likely responsible for the deaths of the first pigs, and the virus was found to be a genotype I virus most closely related to a variant circulating in Cameroon (Couacy-Hymann et al., 2018). The outbreak was eradicated, but in 2016 outbreaks were recorded close to the northern border with Burkina Faso, an area that a risk assessment had suggested could be at high risk (Kouakou et al., 2016). Also, in 2016, Mali experienced its first outbreak of ASF close to its southern border shared with Burkina Faso (World Organisation for Animal Health-WAHIS, 2005-2021). Both outbreaks were eradicated, but since 2018 further ASF outbreaks have been experienced in the northern parts of Côte d'Ivoire as well as in two districts in the south-western part of the country (World Organisation for Animal Health-WAHIS, 2005-2021). The first outbreaks of ASF in Sierra Leone were reported in 2019 (Wadoum et al., 2020). The AU-IBAR yearbook includes an unconfirmed report of an outbreak in Liberia in 2011 (African Union-Interafrican Bureau for Animal Resources, 2012).

### *3.1.2 Central Africa*

Two additional Central African countries reported first introductions of ASF, both linked to an outbreak in previously unaffected northern Cameroon. Although ASF has been endemic in Cameroon since soon after its introduction in 1982, the disease remained limited to the South, Southwest and Central provinces where the majority of commercial pigs were produced until 2010 when, for the first time, outbreaks in the North and Far North provinces were recorded, followed rapidly by the first outbreaks in Chad and Central African Republic (Bidjeh, Ban-Bo, Nadjilem et al., 2015; Mouiche et al., 2021; Ngwa et al., 2020; Wade et al., 2019; World Organisation for Animal Health-WAHIS, 2005-2021). A study in the two adjacent districts of Mayo-Danay in the North West province of Cameroon and Mayo-Kebbi in south-western Chad in the Logone Basin that were affected by ASF revealed that pigs were kept in a free-ranging husbandry system (Assana et al., 2001). The 2010 ASF outbreak was attributed to infected pork brought into Chad from Cameroon; according to descriptions of demography, pig husbandry and trade in the area, the people on either side of the border are closely related and exchange of pigs is common (Bidjeh, Ban-Bo, Nadjilem et al., 2015; Koussou & Duteurtre, 2002). Since then both Chad and Central African Republic have periodically submitted reports of ASF outbreaks to OIE, suggesting that the disease may have become endemic, also suggested by a serological study undertaken in Chad (Bidjeh, Ban-Bo, & Mopate Logtene, 2015). Recent studies have also provided more information on the ASF situation in Cameroon (Mouiche et al., 2021; Ngwa et al., 2020; Wade et al., 2019), Congo Republic (Gallardo, Anchuelo et al., 2011) and DRC (Bisimwa et al., 2019; Bisimwa, Machuka et al., 2020; Bisimwa, Ongus, Tiambo et al., 2020; Mulumba-Mfumumu et al., 2017).

The last decades have provided more information about ASF in two long-time infected Central African countries. Viruses from outbreaks in the DRC between 2005 and 2012 confirmed that most of the outbreaks were caused by genotype I viruses, but genotype IX was recorded from an outbreak near the eastern border, while genotype XIV, previously only known from the

sylvatic cycle in Zambia, had caused outbreaks in pigs in the south-western part of the country (Mulumba-Mfumumu et al., 2017). Genotypes IX and X have been reported from outbreaks in the South-Kivu province on the eastern side of the DRC (Bisimwa, Ongus, Tiambo et al., 2020; Bisimwa, Ishara et al., 2021). Gallardo, Anchuelo et al. (2011) reported genotypes I and IX from Republic of Congo. A 1978 report of an ASF-positive warthog in Congo exists (Plowright et al., 1994) but it is now believed that warthogs are extinct in Congo (De Jong et al., 2016). However, Congo has reported ASF outbreaks to OIE almost every year since 2005. One of the genotype I viruses reported by Gallardo, Anchuelo et al. (2011) was similar to viruses isolated in Angola in 1972 and DRC in 1967, but there are no recent publications on ASF in Angola, although reporting to the OIE shows that ASF remains endemic (World Organisation for Animal Health-WAHIS, 2005-2021).

### *3.1.3 Eastern and southern Africa*

There have been concerning developments in ASF in eastern and southern Africa, with two eastern African countries reporting ASF infection for the first time, three countries in southern Africa experiencing a shift from sporadic warthog-related outbreaks to more severe and larger outbreaks involving only domestic pigs, and several other countries experiencing a marked increase in outbreaks in domestic pigs. Some countries, notably Tanzania and Uganda, experienced remarkable growth of their pig populations during this period, which undoubtedly contributed to the increase in reported ASF (Mulumba-Mfumumu et al., 2019; Penrith et al., 2013).

In 2007, the island nation of Mauritius experienced its first outbreak of ASF. At first, CSF was suspected, as the island had experienced several brief incursions of CSF from neighbouring Madagascar, and like in Madagascar, efforts to vaccinate the pigs probably contributed to the spread of the virus (Lubisi et al., 2009). The outbreaks were caused by the genotype II virus circulating in Madagascar and Mozambique as well as the Caucasus, and the most likely source was harbour waste fed to pigs as swill (Lubisi et al., 2009). The outbreak was declared over by 12 July 2008, and after an extensive serological survey that revealed no positive results, as well as a risk assessment (Etter, Penrith et al., 2011), a “self-declaration of freedom from ASF” was published in the Bulletin of the OIE (World Organisation for Animal Health, 2012).

In 2011 Ethiopia reported its first outbreaks to AU-IBAR (African Union-Interafrican Bureau for Animal Resources, 2012). Pig keeping in Ethiopia had been unusual owing to the fact that few of the population will eat pork, but it was suggested as a source of income for poor households (Tekle et al., 2013). Isolation of the virus from outbreaks that occurred between 2011 and 2014 yielded two intragenotypic variants of a new p72 genotype ASF virus, genotype XXIII, suggesting that Ethiopia, which has two species of warthogs, may be part of the area where the warthog-tick sylvatic cycle occurs (Achenbach et al., 2017).

Studies in western Kenya have revealed pig populations in which ASF circulates endemically and largely without causing marked outbreaks (Abworo et al., 2017; Okoth et al., 2013; Thomas et al., 2016). Interestingly, a genetic study on pigs from this area showed that the local pigs appeared to have a higher ASF survival rate and were genetically more similar to European wild boars than hybrid pigs in the same population (Mujibi et al., 2018). These pig populations are situated along the Kenya-Uganda border and studies indicated cross-border trade and an important role for traders as well as free-range husbandry systems in the spread of ASF (Dione et al., 2016; Lichoti et al., 2016, 2017; Nantima et al., 2015, 2016).

The smallholder pig sector in Uganda has received considerable recent attention through research projects aimed at examining transmission at the wildlife interface (Kukielka et al., 2016; Payne et al., 2018; Ståhl et al., 2014) as well as ways to improve pig production and mitigate the risks of ASF in some of the poorest districts (Atuhaire, Ochwo et al., 2013; Chenais

et al., 2015; Chenais et al., 2017, Chenais et al., 2019; Dione et al., 2016; Dione et al., 2017, Dione et al., 2020; Nantima et al., 2015; Nantima et al., 2016).

Tanzania has a long association with ASF, as mentioned by Montgomery (1921), and ASF infected *Ornithodoros moubata* complex ticks from warthog burrows were first reported from Tanzania (Plowright et al., 1969a). However, reports of ASF in domestic pigs were scarce. Reports of outbreaks of ASF in domestic pigs were documented at a scientific meeting in Tanzania in 1988, and an absence of outbreaks for the decade preceding the millennium was reported (Wambura et al., 2006). Since 2001, increasing numbers of outbreaks in domestic pigs have been reported, with the emergence since 2010 of the genotype II virus in the Southern Highlands (Chang'a et al., 2019; Fasina et al., 2020; Yona et al., 2020). A study of the socio-economic effects of ASF in the Rombo district of Tanzania showed that the disease caused severe financial losses to pig farmers and other pig value chain actors (Swai & Lyimo, 2014).

Although ASF is considered endemic in Burundi and viruses isolated from pigs in Burundi in 1984 and 1990 have been recorded (Bastos et al., 2003; Hakizimana, Nyabongo et al., 2020; Lubisi et al., 2005), the first publication on ASF outbreaks in Burundi appeared in 2020 (Hakizimana, Nyabongo et al., 2020). Apart from sporadic reports of large numbers of ASF outbreaks to the OIE, the only published information on ASF in Rwanda is that in pigs tested for ASF at an abattoir in Bukavu, eastern DRC, infection with ASF virus was less prevalent in pigs from Rwanda than in those obtained locally (Bisimwa et al., 2019). It is probable that the warthog-tick sylvatic cycle is or was present in both countries, but that has never been investigated.

The first recorded outbreak of ASF in Zambia occurred in the Eastern Province in 1912 (Wilkinson et al., 1988). By 1965 it was recognised that ASF was endemic in free-roaming pigs in the Eastern Province, which shares borders with the highly endemic areas in Malawi and Mozambique (Haresnape et al., 1985; Penrith et al., 2007; Wilkinson et al., 1988). This endemicity in pigs has been confirmed in a recent study (Chambaro et al., 2020) that revealed 50.9 percent of pigs were positive for antibodies to ASF virus and 11.7 per cent were positive for ASF genome; unfortunately, the presence of ticks in those areas was not investigated. However, previous investigations revealed the presence of ASF virus in ticks from warthog burrows in the Eastern Province, as well as in national parks and wildlife management areas in other parts of Zambia, but did not find ticks in two villages in the Eastern Province that were investigated (Wilkinson et al., 1988). The first outbreak of ASF outside the Eastern Province occurred in Kabwe in the Central Province in 1989 and was traced to infected pork from the Eastern Province (Samui et al., 1991). Despite stringent restrictions on the movement of pigs and pork from the Eastern Province, outbreaks of ASF occurred in Lusaka and the Southern Province in 1993, 2001-2002 and 2004-2006 (Simulundu et al., 2017). Following unofficial reports of suspicious deaths of pigs in 2006, ASF was diagnosed for the first time in the Northwestern Province in 2007 (Simulundu et al., 2017). Between 2013 and 2015 six provinces in Zambia experienced outbreaks of ASF that appeared to be linked to trade routes but did not originate in the Eastern Province, calling into question the value of restrictions imposed upon that province alone (Simulundu et al., 2017).

Mozambique has reported outbreaks of ASF since the 1950s and viruses belonging to four genotypes have been responsible (Bastos et al., 2004; Penrith et al., 2007), but the warthog-tick sylvatic cycle has only been confirmed recently (Quembo et al., 2016; Quembo et al., 2018). Warthogs are not (or no longer) present in the highly endemic area in Tete Province (Penrith et al., 2004), similar to the adjacent Mchinji district in Malawi (Haresnape et al., 1988). However, research in the Gorongosa area, where there is an interface between domestic pigs and warthogs in the buffer zone around the Gorongosa National Park, revealed high rates of

seropositivity in warthogs as well as infection in ticks from warthog burrows. Infected ticks were also found in pig shelters in the same area (Quembo et al., 2016; Quembo et al., 2018). Samples from both burrow and pig shelter ticks yielded a novel genotype, bringing the number of known genotypes to 24 (Quembo et al., 2018). It is likely that the sylvatic cycle is present elsewhere where warthogs are present, mainly if not exclusively in conservation areas, but domestic pig-related outbreaks of ASF predominate throughout the country and are driven by movements of infected pigs and pork (Penrith et al., 2007).

From the 1930s until this period, Botswana, Namibia, South Africa, and Zimbabwe had experienced ASF outbreaks that were usually limited to a single farm or herd and most often linked to contact with warthogs (Janse van Rensburg, Etter et al., 2020; Mulumba-Mfumum et al., 2019). Botswana has a small and mainly well-confined pig population, with free-ranging pigs reported from a single village (Nsoso et al., 2006). Serologically positive warthogs were reported from Botswana (Simpson & Drager, 1979), but very few outbreaks in pigs have been documented, in 1953, 1987 and 1999 (Plowright et al., 1994; World Organisation for Animal Health-OIE Handistatus II, 1996-2004). However, since 2009 Namibia has reported ASF outbreaks on the northern border with Angola, with spread in villages in a pattern unusual with the typical isolated event linked to warthogs (World Organisation for Animal Health-WAHIS, 2005-2021), and as the people on either side of the border are related, with many having originated from Angola, it seems likely that these outbreaks could be an extension of the endemic ASF situation that has prevailed in Angola for a long time (Mendes, 1971, 1994). Zimbabwe has a relatively small pig population, and the majority of pigs are farmed commercially, but free-ranging local breed pigs are kept, most in traditional free-ranging systems, in the north-eastern part of Zimbabwe that shares a border with the Tete province of Mozambique (Mashatise et al., 2005). No ASF outbreaks were reported in Zimbabwe from 1993 to 2014, but in 2015 ASF was reported for the first time in these free-ranging pigs at the Mozambique border, caused by the genotype II virus currently circulating in Europe and Asia as well as several south-eastern African countries (van Heerden et al., 2017). The outbreak was characterised by very high mortality, with all of the infected pigs believed to have died of ASF, only 591 out of 3,427 pigs having been spared due to the fact that they were confined and had no contact with infected pigs or material (van Heerden et al., 2017). No warthogs were present in the area, and it was likely that the outbreak was linked to an outbreak in the adjacent area in Mozambique (Dr R.M. Spargo, personal communication, 2016). In 2018 another incursion of ASF occurred in the same area (World Organisation for Animal Health-WAHIS, 2005-2021).

South Africa proclaimed a Controlled Area for ASF in 1935 based on the distribution of outbreaks of 'East African swine fever', and until 2012 very few outbreaks occurred outside that area, mostly close to its border (Janse van Rensburg, Etter et al., 2020; Magadla et al., 2016). Outbreaks within the Controlled Area occurred sporadically when pigs were allowed to roam freely on farms where warthogs were present or were insecurely penned in these areas. However, in 2012 pigs with signs confirmed to be ASF were detected at an abattoir in Gauteng province, distant from the Controlled Area, and were traced to a sales yard in Mpumalanga province, also outside the Controlled Area, to which sick pigs from the Controlled Area had been illegally moved for sale (Geertsma et al., 2012). Although spread had occurred in both provinces, relatively small numbers of pigs were involved, and the outbreak was eradicated within a short time (Geertsma et al., 2012; Janse van Rensburg, van Heerden et al., 2020).

Outbreaks outside the Controlled Area were registered in 2016 and 2017 in three provinces and with considerable spread and larger numbers of pigs involved. These outbreaks all involved variants of the genotype I virus and no specific link to warthogs has been demonstrated, with most of the outbreaks having been linked to illegal movement of pigs and pork and swill

feeding (Janse van Rensburg, van Heerden et al., 2020). Since 2018, rolling outbreaks have been experienced, affecting all the provinces except KwaZulu-Natal, and mostly involving a genotype II virus. The great majority of outbreaks have occurred among smallholder pigs and the patterns of spread have been typical of a domestic pig cycle. Examples of this are an outbreak that occurred in Gauteng Province in July 2020 that could be linked with some confidence to recent outbreaks in an area about 90 km away (Amar et al., 2021) and the first outbreaks in the Western Cape province, which occurred in 2021 (World Organisation for Animal Health-WAHIS, 2005-2021), caused by an identical virus to one that had been circulating in the Eastern Cape province since 2020 (Dr L. Heath, personal communication, 2021), and appearing in a settlement close to the highway connecting the two provinces. Many of the settlements around Cape Town are populated by immigrants from the Eastern Cape province who maintain strong links with their original homes.

### ***3.2 Exponential growth of research in Africa***

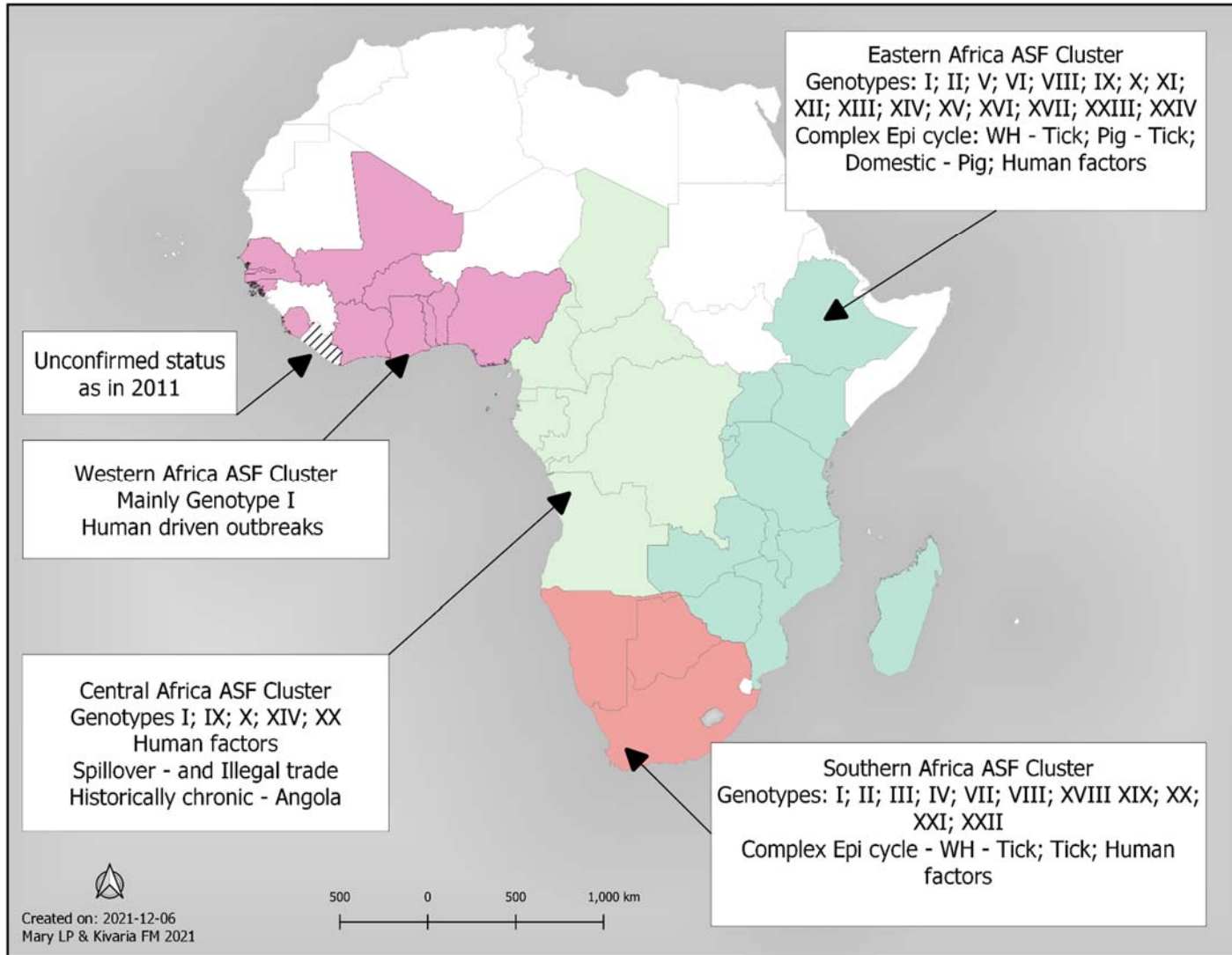
The trend for published research on ASF in Africa is similar to the global trend as indicated by the timeline provided on PubMed from 1955 to the present, which shows exponential growth in the number of publications during the last few years. The trends are event-related. In Africa, the number of publications grew steadily from 1921 to 2021 but peaks were evident after the 1960 outbreaks in Europe and the 2018 introduction into China.

### ***3.3 Molecular advances***

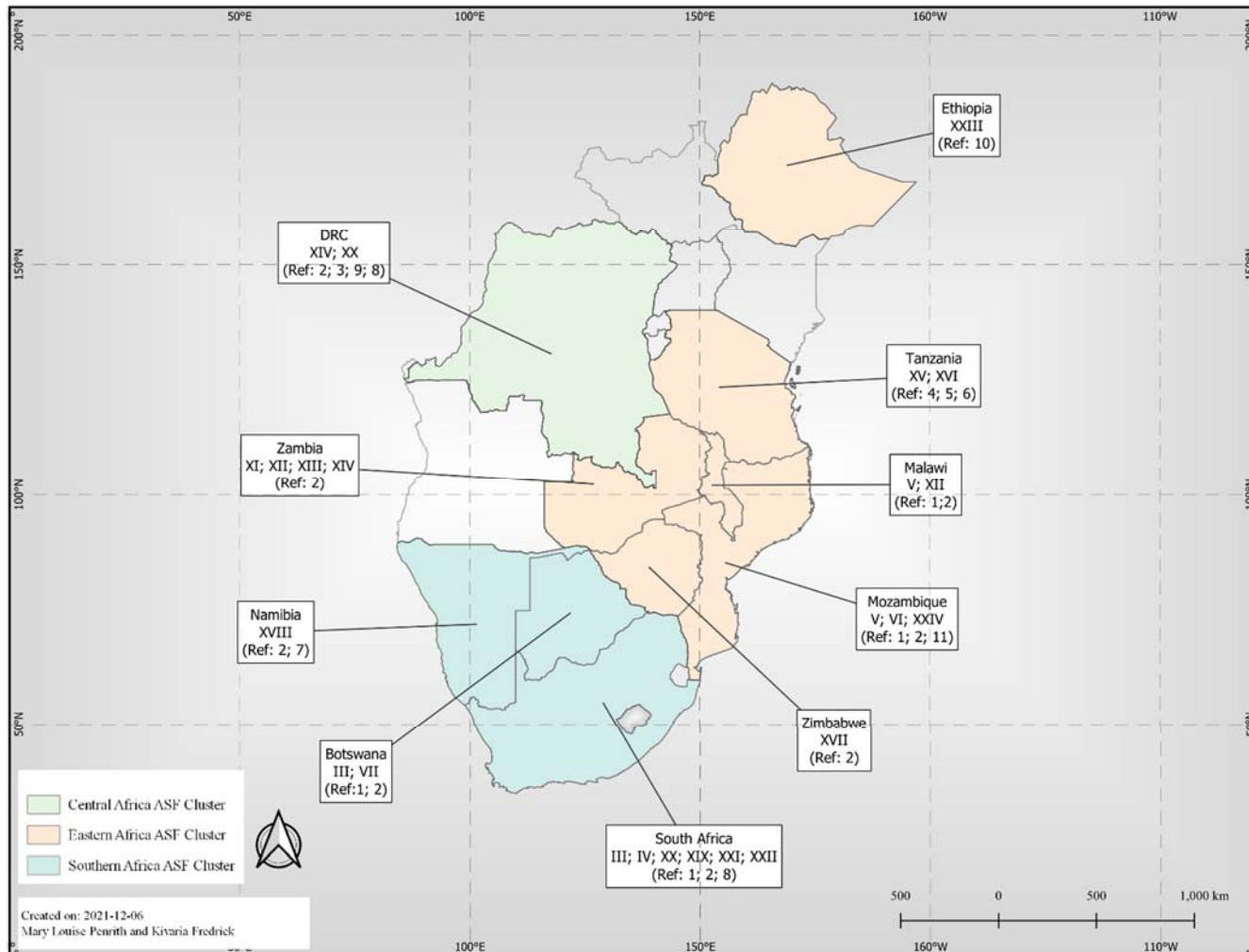
The last decade and a half have seen remarkable advances in molecular studies on ASF virus, including in Africa. Since the wide acceptance of the p72 genotype classification proposed by Bastos and co-workers (2003), molecular genetic characterisation of ASF viruses has exponentially increased our understanding of the molecular epidemiology of ASF globally and in Africa. All of the 24 p72 genotypes identified to date are present in the area where the ancient sylvatic cycle is present in eastern central and southern Africa (Achenbach et al., 2017; Bastos et al., 2003; Boshoff et al., 2007; Lubisi et al., 2005; Misinzo et al., 2010; Misinzo, Jumapili et al., 2012; Misinzo et al., 2014; Mulumba-Mfumumu et al., 2017; Quembo et al., 2018; Simulundu, Chambaro et al., 2018). In the remaining African countries where ASF is endemic, apart from the recent introduction of the genotype II virus into Nigeria (Adedeji et al., 2021) only one genotype is present, with genotype I in western Africa from Cape Verde and Senegal to Cameroon (Bastos et al., 2003; Couacy-Hymann et al., 2018; Luka et al., 2017; Wade et al., 2019) and genotype II in Madagascar (Bastos et al., 2003). The genotype II ASF virus recently reported from an outbreak on a pig farm in Lagos state, Nigeria shares 99-100% similarity with viruses recently isolated in Vietnam and China (Adedeji et al., 2021). Given the propensity for transboundary spread demonstrated by the genotype II virus originally introduced into the Republic of Georgia in 2007 (Rowlands et al., 2008), its introduction into both the Caribbean region and a ‘new’ part of Africa, possibly from Asia, is not unduly surprising.

Several of the known genotypes have only been isolated from the sylvatic cycle or from isolated outbreaks in pigs that were clearly related to the sylvatic cycle (Boshoff et al., 2007; Janse van Rensburg, Etter et al., 2020; Lubisi et al., 2005; Quembo et al., 2018). Five genotypes have been widely reported from outbreaks in domestic pigs and can be considered pig-related. Genotypes I and II are the most striking examples of pig-related ASF viruses, although both have also been isolated from ticks and/or African wild suids (Lubisi et al., 2005; Quembo et al., 2018). Genotypes VIII, IX and X, although they have a more restricted distribution, spanning several countries in eastern and Central Africa (Atuhaire, Afayoa et al., 2013; Atuhaire, Ochwo et al., 2013; Bishop et al., 2015; Bisimwa, Ongus, Tiambo et al., 2020; Bisimwa, Ongus, Steinaa et al., 2021; Chang’a et al., 2019; Gallardo, Anchuelo et al., 2011;





**Figure 3.** Key epidemiological features of the different regions and spatial distribution of the ASF genotypes in Africa. Epi = epidemiological, WH = warthog



## References

1. Bastos *et al.*, 2003
2. Boshoff *et al.*, 2007
3. Mulumba-Mfumu *et al.*, 2017
4. Lubisi *et al.*, 2005;
5. Misinzo *et al.*, 2010;
6. Peter *et al.*, 2021
7. Molini *et al.*, 2020
8. Janse van Rensburg, Etter *et al.*, 2020
9. Hakizimana *et al.*, 2021
10. Achenbach *et al.*, 2017
11. Quembo *et al.*, 2018

**Figure 4.** Spatial distribution of genotypes with a limited known range of distribution in Africa

Hakizimana, Nyabongo et al., 2020; Hakizimana et al. 2021; Misinzo, Jumapili et al., 2012; Misinzo et al. 2014; Mulumba-Mfumum et al., 2017) are also well adapted to pigs (Lubisi et al., 2005). These viruses may also be candidates for extra-African ventures. The distribution of the widespread genotypes and those with a more limited range is shown in Figures 3 and 4.

Intragenotypic classification of subgroups enables a better understanding of relationships between outbreak viruses and the evolution of outbreaks and has been used widely in Africa (Chang'a et al., 2019; Couacy-Hymann et al., 2018; Gallardo et al., 2009; Lubisi et al., 2007; Minoungou et al., 2021; Mulumba-Mfumum et al., 2017; Mwiine et al., 2019; Nix et al., 2006; Onzere et al., 2018; Owolodun et al., 2010; Phologane et al., 2005; Simulundu, Sinkala et al., 2018; Wade et al., 2019). Most recently, full genome sequencing has been published for several African ASF virus isolates belonging to genotypes I, II, III, IV, VIII, IX, X, XX and XXII, derived from domestic pigs, warthog, *Ornithodoros moubata* complex ticks, and a European wild boar in South Africa. It is hoped that this technology will eventually be able to provide much more information about the molecular relationships between viruses and could possibly be linked to their biological characteristics (Bishop et al., 2015; Bisimwa, Ongus, Steinaa et al., 2021; de Villiers et al., 2010; Masembe et al., 2018; Ndlovu, Williamson, Heath et al., 2020; Ndlovu, Williamson, Malesa et al., 2020; Njau et al., 2021).

### *3.3.1 Application of molecular genetic information*

As indicated previously, molecular characterization of ASF viruses is useful in investigating the relatedness of outbreaks, bearing in mind that without sufficient history about the context in which the outbreaks occurred it is rarely possible to pinpoint the source or even determine the direction of transmission. However, molecular studies are always informative and can contribute to understanding the disease as well as control. The major excursions of ASF from Africa to other parts of the world could be traced to their area of origin in Africa (Bastos et al., 2003; Rowlands et al., 2008). Although the two viruses were closely related, RFLP studies reflected a difference in length of the right terminal fragment of the ASF virus genome of the 1957 and 1960 isolates from outbreaks in Lisbon, showing that there were two separate introductions of ASF (Blasco et al., 1989; Ekue & Wilkinson, 2000). The 1957 Lisbon virus shared this characteristic with isolates from Katanga (DRC) in 1967 and Angola in 1970 (Blasco et al., 1989; Ekue & Wilkinson, 2000). While numerous studies have shown that the viruses involved in the widespread outbreaks of ASF from 1959/1960 in the Western Hemisphere in the last century and the even more widespread outbreaks throughout Europe and Asia that began in 2007 were due to single introductions from Africa, the situation in Africa is more complicated. The first outbreak isolates from Senegal in 1959 coincided temporally with the second introduction into Portugal and the viruses were identical (Bastos et al., 2003). On balance of probabilities, the virus reached both Senegal and Portugal from Angola, probably arriving in Senegal first, but later incursions into São Tomé e Príncipe in 1978 and Cameroon in 1982 could on molecular genetic grounds have come either from Europe or the Caribbean or from Africa (Wesley & Tuthill, 1984). The assertion by Sanchez Botija (1982) that the virus entered São Tomé e Príncipe in meat imported from Angola is certainly plausible. However, the origin of the introduction into Cameroon has never been established with any certainty, and some variability amongst Cameroon isolates from 1982 to 1986 raised the possibility of more than one introduction from countries in the region (Ekue & Wilkinson, 2000). This was supported by a recent study of virus isolates in Cameroon between 2010 and 2018 using the most up-to-date technology (Wade et al., 2019). The outbreak of ASF in the port of San Pedro, Côte d'Ivoire in 2014 was caused by a genotype I virus most closely related to genotype I strains from Cameroon that differed at intragenotypic level from the 1996 Côte d'Ivoire strains (Couacy-Hymann et al., 2018). The recent study of Minoungou and co-workers (2021)

confirmed the finding by Bastos and co-workers (2003) that the 1996 epidemic in West Africa was not related to the endemic situation in Senegal and its neighbours, although a single variant isolated in Côte d'Ivoire in 1996 clustered with the Senegal group (Phologane et al., 2005).

As one would expect, most of the ASF viruses isolated have come from outbreaks in domestic pigs, but the majority have been confirmed in sylvatic cycle as well. The countries in which infection has been confirmed in warthogs and/or *Ornithodoros moubata* complex ticks from either warthog burrows or tick shelters are summarised in Table 1. Table 2 summarises the hosts from which ASF viruses have been isolated in the region.

**Table 1. Countries with confirmed warthog-associated (WH) and/or pig-associated *Ornithodoros moubata* complex ticks infected with ASF and/or seropositive warthogs for ASF**

Country	ASF +ve WH ticks	ASF +ve pig ticks	ASF virus or sero+ve WH	References
Botswana	-	-	+	Simpson & Drager, 1970
Kenya	+	-	+	Gallardo, Okoth et al., 2011; Thomson, 1985
Madagascar	-	+	-	Ravaomanana et al., 2010
Malawi	-	+	-	Haresnape et al., 1988
Mozambique	+	+	+	Quembo et al., 2016, 2018
Namibia	+	-	+	Thomson, 1985
South Africa	+	-	+	Thomson, 1985
Tanzania	+	-	+	Plowright et al., 1969a; Thomson, 1985
Uganda	+	-	+	Thomson, 1985
Zambia	+	-	-	Wilkinson et al., 1988
Zimbabwe	-	-	+	Thomson, 1985

**Table 2. Summary of host associations of African swine fever genotypes.**

Host	Genotype	Reference
Domestic pig	I; II; III; IV; V; VI; VII; VIII; IX; X; XII; XIV; XV; XVI; XVII; XVIII; XIX; XX; XXI; XXII; XXIII	Achenbach et al., 2017; Boshoff et al., 2007; Janse van Rensburg, Etter et al., 2020; Lubisi et al., 2005; Mulumba-Mfumum et al., 2017
European wild boar (South Africa)	XX	Ndlovu, Williamson, Heath et al., 2020
Common warthog	IV ; V ; VI ; VII ; IX ; X ; XI ; XIII ; XIV ; XX ; XXI	Boshoff et al., 2007; Hakizimana et al., 2021; Janse van Rensburg, Etter et al., 2020; Lubisi et al., 2005; Ndlovu, Williamson, Heath et al., 2020
Eastern bushpig	I	Lubisi et al., 2005
<i>Ornithodoros</i> ticks	I; II; III; VII; VIII; X; XI; XII; XIII; XIV; XV; XIX; XX; XXI; XXII; XXIV	Boshoff et al., 2007; Janse van Rensburg, Etter et al., 2020; Lubisi et al., 2005 ; Quembo et al., 2018

### 3.3.2 *The pig-adapted ASF viruses*

Genotype I remains the most widespread genotype in Africa, having been reported from 20 countries throughout sub-Saharan Africa (Bastos et al., 2003; Boshoff et al., 2007; Gallardo, Anchuelo et al., 2011), and is endemic in most of them. It has been reported in recent outbreaks in domestic pigs in Côte d'Ivoire (Couacy-Hymann et al., 2019), Cameroon (Wade et al., 2019), Congo Republic (Gallardo, Anchuelo et al., 2011), DRC (Mulumba-Mfumu et al., 2017), Namibia (Molini et al., 2020), South Africa (Amar et al., (2021); Janse van Rensburg, Etter et al., 2020), and Zambia (Simulundu et al., 2017; Simulundu, Chambaro et al., 2018; Thoromo et al., 2016).

The genotype II virus that is currently dominant in the world was first isolated from outbreaks in 1998 in Madagascar, shortly followed by outbreaks in Mozambique in December 1998 (Bastos et al., 2004). Retrospective studies showed identity with a virus isolated an outbreak in Lusaka, Zambia in 1993 (Rowlands et al., 2008). Although both the 1998 isolate from Mozambique and the Lusaka isolate come from inland localities, the virus caused outbreaks in Maputo between 2002 and 2005 (Penrith et al., 2007) and this is the most likely source of the infection in Georgia in 2007 as the busy port of Maputo generates provisions for ships that would contribute to galley waste.

Published reports of genotype II were confined to outbreaks in domestic pigs until it was found to be the dominant isolate from warthog burrow ticks in Mozambique (Quembo et al., 2018). Since the first report of the virus from Mozambique (Bastos et al., 2004) and the historical report from Zambia (Rowlands et al., 2008), the virus spread widely in Mozambique (Penrith et al., 2007), and caused outbreaks in Mauritius in 2007 (Lubisi et al., 2009). It was first reported from outbreaks in Tanzania in 2010 (Misinzo, Kasanga et al., 2012). Since the historical finding of genotype II isolate from an outbreak in Lusaka, several variants of genotype II have been identified from recent outbreaks in Zambia (Simulundu et al., 2017; Simulundu, Chambaro et al., 2018; Simulundu, Sinkala et al., 2018). Recently the first full genome sequence of an African genotype II virus isolate from an outbreak in Rukwa, Tanzania in 2017 has been published (Njau et al., 2021). Genotype II has been reported from 8 countries in the African region (Bastos et al., 2003; Bastos et al., 2004; Hakizimana, Kamwendo et al., 2020; Lubisi et al., 2005; Misinzo, Kasanga et al., 2012; van Heerden et al., 2017), most recently and likely due to an introduction from Asia, Nigeria (Adedeji et al., 2021).

Genotypes IX and X are widespread in East Africa in both the sylvatic cycle and in outbreaks in domestic pigs (Lubisi et al., 2005). Genotype IX has been reported from Kenya, Tanzania, Uganda, DRC and Congo Republic (Bastos, 2003; Gallardo, Anchuelo et al., 2011; Gallardo . Okoth et al., 2011; Lubisi et al., 2005; Mulumba-Mfumu et al., 2017). Genotype X has been reported from Burundi, DRC, Kenya, Tanzania and Uganda (Bastos et al., 2003; Bisimwa, Ongus, Tiambo et al., 2020; Gallardo, Okoth et al., 2011; Hakizimana. Nyabongo et al., 2020).

Genotype VIII has been reported from Malawi, Mozambique, South Africa, Zambia and Zimbabwe (Bastos et al., 2003; Bastos et al., 2004; Boshoff et al., 2007; Janse van Rensburg, Etter et al. 2020; Lubisi et al, 2007).

## **4 Where are we going?**

Recent FAOSTAT figures indicate that pig production is of growing importance in sub-Saharan Africa (FAOSTAT 2018). There is no doubt that pig production has unparalleled potential to alleviate poverty and to improve intake of high-quality protein in Africa. However,

ASF is also increasing as pig numbers rise (Penrith et al., 2013), and there is increasing pressure to manage it better. A strategy for management of ASF in sub-Saharan Africa (FAO/AU-IBAR/ILRI, 2017) that is currently being updated should provide a roadmap for the way forward for the continent. Efforts are hampered by the lack of information about the size and location of the pig population, particularly in the dynamic smallholder sector that constitutes up to 90 per cent of pig production in the region. While traditional free-range pig production in rural areas is probably relatively stable, smallholder pig production in and around rapidly expanding African cities is highly dynamic, driven by demand for pork by city populations and the need for income by migrants to cities among whom unemployment is often high. These pig keepers are subject to losses due to ASF that result from poor biosecurity and management practices. African swine fever is increasingly recognised as a socio-economic rather than a purely veterinary problem that requires multi-disciplinary and inclusive approaches to obtain the cooperation of pig keepers and the communities to which they belong (Barnes, Alvaran et al., 2020; Barnes, Morais et al., 2020; Fischer et al., 2020). Using participatory approaches to develop feasible and practical biosecurity measures could go a long way towards preventing ASF and improving the quality and quantity of pork (Barongo et al., 2016; Chenais et al. 2017, 2019; Penrith et al., 2021). However, in most areas more information is needed about the structure and economic drivers of pig value chains as well as resources available to support better biosecurity.

Pigs have a long history in Africa and the importance of conserving hardy local breeds that can produce pork under less-than-optimal conditions of management and nutrition is increasingly recognised (Darfour-Oduro et al., 2009; Halimani et al., 2010, 2013, 2020; Kiendrebiogo et al., 2012; Madzimure et al., 2013; Nsoso et al., 2006). While modern, high-producing breeds are used for commercial production, smallholder farmers who cannot afford commercial rations and may not have access to unlimited supplies of water need more forgiving breeds that can nevertheless provide them with a good income (Chiduwa et al., 2008; Madzimure et al., 2013; Mashatise et al., 2005). For aspirant small scale commercial farmers, acquiring a good boar to use with hardy local sows can be a good option to improve productivity without losing the good qualities of the local breed pigs (Chimonyo et al., 2010; Ncube et al., 2003; Verhulst, 1998). The option of artificial insemination could be a good alternative to maintaining a boar, although it is not widely practised by small-scale farmers in Africa currently. It would also assist in reducing the practice of sharing boars, which can contribute to ASF transmission.

A number of local breed pig populations have been identified in long-time ASF-endemic areas in which ASF circulates without causing major losses, although from time-to-time notable outbreaks may be experienced (Abworo et al., 2017; Haresnape et al., 1985, 1987; Penrith et al., 2004; Thomas et al., 2016). This opens up a potentially interesting field of research into the immune responses of these pigs, as well as their potential as genetic resources in ASF endemic areas. Since there is no evidence that these pigs become long-term carriers of ASF virus and the majority of them are reared and traded locally, the possibility exists to exploit this resistance (Penrith et al., 2004; Ståhl et al., 2019). Studies to find the genetic basis of the observed resistance are limited (Mujibi et al., 2018) but should be expanded to find markers and perhaps enable selective breeding (Penrith et al., 2021).

The importance of genetic studies covering the plethora of ASF virus genotypes and probably serotypes that are found in the ancient endemic region of eastern and southern Africa cannot be over-emphasised. Such studies might support advanced new generation vaccine development. Currently the main focus on vaccine development globally is to produce a vaccine that will be effective against the genotype II viruses that are becoming ever more widespread outside Africa but are also endemic in a growing number of African countries

(Borca et al., 2020; Rock, 2021). However, the degree to which such a vaccine would provide cross protection across multiple genotypes is unknown. High quality full genome sequencing of a wide selection of African viruses could enable the identification of shared genes of antigenic importance and might enable the development of multivalent vaccines. Bearing in mind the existence of an increasing number of pig-adapted ASF viruses that might develop increased invasive potential and spread to other regions, a multivalent vaccine might find application beyond the borders of Africa (Rock, 2021).

Although a deeper understanding of the virus is important to support control, in particular through vaccine development, an in-depth understanding of the hosts and vectors of the virus and the environment in which the disease flourishes is of even greater importance. The development and implementation of an appropriate strategy to improve management of ASF is crucial. This should be a dynamic document that can be adapted to changing conditions in pig production and patterns of ASF occurrence. It will focus on smallholder and traditional pig farming, using a farmer-based, One Health approach that takes into consideration socioeconomics and the environment and involves multiple stakeholders. At the same time, it will propose measures such as compartmentalisation of pig farms at all levels where it is achievable and vertical integration of the pig sector to the greatest extent possible to raise the profile of pig production in Africa and increase its contribution to GDP in lower- and middle-income countries. While a vaccine would be an extremely valuable tool in managing ASF in sub-Saharan Africa, it may be a long time before it can be incorporated into the strategy, and even with a vaccine biosecurity will remain the cornerstone of efficient pig production.

It is hoped that the next decades will bring sub-Saharan Africa closer to realising the vision of ‘an African continent where ASF no longer impedes sustainable pig production and rural development and threatens livelihoods’ (FAO/AU-IBAR/ILRI, 2017). In brief, this could be summarised as Healthy Pigs, Healthy People, Healthy Livelihoods.

## References

- Abreu, E.F. de, Valadão, F.B., Limpo Serra, J.J.B., Ornelas Mário, R., & Sousa Montenegro, A. (1962). Peste suína africana em Moçambique. *Anais dos Serviços Veterinários de Moçambique*, 8, 105–123.
- Abworo, E. Okoth, Onzere, C., Oluoch-Amimo, J., Riitho, V., Mwangi, W., Davies, J., Blome, S., & Bishop, R.P. (2017). Detection of African swine fever virus in the tissues of asymptomatic pigs in smallholder farming systems along the Kenya-Uganda border: implications for transmission and surveillance in endemic areas in East Africa. *Journal of General Virology*, 98, 1806-1814. doi: 10.1099/jgv.0.000848.
- Achenbach, J.E., Gallardo, C., Nieto-Pelegri, E., Rivera-Arroyo, B., Degefa-Negi, T., Arias, M., Jenberie, S., Mulisa, D.D., Gizaw, D., Gelaye, E., Chibssa, T.R., Belaye, A., Loitsch, A., Forsa, M., Yami, M., Diallo, A., Soler, A., Lamien, C.E., & Sánchez-Vizcaino, J.M. (2017). Identification of a new genotype of African swine fever virus in domestic pigs from Ethiopia. *Transboundary and Emerging Diseases*, 64(5), 1393-1404 doi: 10.1111/tbed.12511.
- Adedeji, A.J., Luka, P.D., Atai, R.B., Olubade, T.A., Hambolu, D.A., Ogunleye, M.A., Muwanika, V.B., & Masembe, C. (2021). First time presence of African swine fever virus genotype II in Nigeria. *Microbiology Resource Announcements*, 10, e00350-21. doi: 10.1128/MRA.00350-21.
- African Union-Interafrican Bureau for Animal Resources. (2012). *Panfrican Animal Health Yearbook 2011*. AU-IBAR, Nairobi, Kenya.

- Amar, S., De Boni, L., de Voux, A., Heath, L., & Geertsma, P. (2021). An outbreak of African swine fever in small-scale pigs, Gauteng, South Africa, July 2020. *International Journal of Infectious Diseases*, *110*, Suppl. 1, S44-S49. doi: 10.1016/j.ijid.2021.04003.
- Anderson, E.C., Hutchings, G.H., Mukarati, N., & Wilkinson, P.J. (1998). African swine fever virus infection of the bushpig (*Potamochoerus porcus*) and its significance in the epidemiology of the disease. *Veterinary Microbiology*, *62*, 1–15.
- Andriamanivo, H.R., Randriamananjara, D., Ralalarison, R.A., Nomenjanahary, L.A., Razafindraibe, N.P., Andria-Mananjara, E.D., Rakotomanana, D.O., Fenozara, P.S., Biarmann, M., Halm, A., Razafimandimby, H., Flachet, L., & Cardinale, E. (2019). How could an African swine fever outbreak evolve in an enzootic context? The case of Imerintriosika, Madagascar in 2015. *PLoS ONE*, *14*, e0221928. <https://doi.org/10.1371/journal.pone.0221928>.
- Arias, M., & Sánchez-Vizcaíno, J.M. (2002). African swine fever eradication: The Spanish model. In: A. Morilla, K.J. Yoon, & J.J. Zimmerman (eds.) *Trends in Emerging Viral Infections of Swine*, vol. 1, pp. 133-139, Iowa State Press, Ames.
- Assana, E., Zoli, P.A., Sadou, H.A., Nguekam, Vondou, L., Pouedet, M.S.R., Dorny, P., Brandt, J., & Geerts, S. (2001). Prévalence de la cysticerose porcine dans le Mayo-Danay (Nord Cameroun) et Mayo-Kebbi (sud-ouest du Tchad). *Revue d'Élevage et de Médecine Vétérinaire des Pays tropicaux*, *54*(2), 123-127.
- Atuhaire, D.K., Afayoa, M., Ochwo, S., Mwesigwa, S., Okuni, J.B., Olaho-Mukani, W., & Ojok, L. (2013). Molecular characterization and phylogenetic study of African swine fever isolates from recent outbreaks in Uganda (2010 – 2013). *Virology Journal*, *10*, 247. doi: 10.1189/1743-422X-10-247.
- Atuhaire, D.K., Ochwo, S., Afayoa, M., Mwiine, F.N., Kokas, I., Arinaitwe, E., Ademun-Okurut, R.A., Okuni, J.B., Nanteza, A., Ayebazibwe, C., Okedi, L., Olaho-Mukani, W., & Ojok, L. (2013). Epidemiological overview of African swine fever in Uganda (2001 – 2012). *Journal of Veterinary Medicine*, *2013*, Article 939648.
- Babalobi, O.O., Olugasa, B.O., Oluwayelu, D.O., Ijagbone, I.F., Ayoade, G.O., & Agbede, S.A. (2007). Analysis and mortality losses of the 2001 African swine fever outbreak, Ibadan, Nigeria. *Tropical Animal Health and Production*, *39*(7), 533-542. doi: 10.1007/s11250-007-9038-9.
- Balbo, S., & Iannizzotto, G. (1983). Epidemiological investigation, prophylaxis and eradication of African swine fever in Malta. In Wilkinson, P.J. (ed) *African Swine Fever*, pp.42-48. EUR 8466 EN. Commission of the European Communities.
- Barnes, T. S., Alvaran, P. J. J., Lantican, T. L. D., Lapuz, E. L., Ignacio, C.; Baluyut, A. S., Parke, C.R., Palaniappan, G., Cameron, D., Ancog, R.C., Mananggit, M.R., de Castro, R., Meers, J., Palmieri, C., Turni, C., Villar, E.C., & Blackall, P.J. (2020). Combining conventional and participatory approaches to identify and prioritise management and health-related constraints to smallholder pig production in San Simon, Pampanga, Philippines. *Preventive Veterinary Medicine*, *178*, 104987. doi: 10.1016/j.prevetmed.2020.104987
- Barnes, T.S. Morais, O. Cargill, C. Parke, C.R., & Urlings, A. (2020). First steps in managing the challenge of African swine fever in Timor-Leste. *One Health*, *10*, 100151. doi: 10.1016/j.onehlt.2020.100151.
- Barongo, M.B., Bishop, R.P., Fèvre, E.M., Knobel, D.L., & Ssematimba, A. (2016). A mathematical model that simulates control options for African swine fever virus (ASFV). *PLoS ONE*, *11*(7), e0158658. doi: 10.1371/journal.pone.0158658.
- Bastos, A.D.S., Penrith, M.-L., Crucière, C., Edrich, J.L., Hutchings, G., Roger, F., Couacy-Hyman, E., & Thomson, G.R. (2003). Genotyping field strains of African swine fever



- virus by partial p72 gene characterisation. *Archives of Virology*, 148(4), 693-706. doi: 10.1007/s00705-002-0946-8.
- Bastos, A.D.S., Penrith, M.-L., Macome, F., Pinto, F., & Thomson, G.R. (2004). Co-circulation of two genetically distinct viruses in an outbreak of African swine fever in Mozambique: no evidence for individual co-infection. *Veterinary Microbiology*, 103(3-4), 169-182. doi: 10.1016/j.vetmic.2004.09.003.
- Beltrán Alcrudo, D., Lubroth, J., Depner, K., & De la Rocque, S. (2008). African swine fever in the Caucasus. EMPRES Watch, April 2008. Food and Agriculture Organization of the United Nations, Rome.
- Bidjeh, K., Ban-Bo, B.A., & Mopate Logtene, Y. (2015). Factors contributing to the introduction and the spread of African swine fever in Chad. *International Journal of Current Microbiology and Applied Sciences*, 4, 607-613.
- Bidjeh, K., Ban-Bo, B.A., Nadjilem, D., Tchari, D., Golwa, D., & Maho, A.J. (2015). Serological study of African swine fever in traditional pig farms in Chad. *Animal and Veterinary Sciences*, 3, 149-152. doi:10.11648/j.avs.20150306.11.
- Bishop, R.P., Fleischauer, C., de Villiers, E.P., Okoth, E.A., Arias, M., Gallardo, C., & Upton, C. (2015). Comparative analysis of the complete genome sequences of Kenyan African swine fever isolates within p72 genotypes IX and X. *Virus Genes*, 50(2), 303-309. doi: 10.1007/s11262-014-1156-7.
- Bisimwa, P.N., Ishara, L.K., Wasso, D.S., Bantuzeko, F., Tonui, R., & Bwihangane, A.B. (2021). Detection and characterization of the African swine fever virus (ASFV) in clinically infected pigs in two districts in South Kivu Province, Democratic Republic of Congo. *Heliyon*, 7, e06419 doi: 10.1016/j.heliyon.2021.06419.
- Bisimwa, P.N., Machuka, E.M., Githae, D., Banswe, G., Amimo, J.O., Ongus, J.R., Masembe, C., Bishop, R.P., Steinaa, L., Djikeng, A., & Pelle, R. (2020). Evidence for the presence of African swine fever virus in apparently healthy pigs in South-Kivu Province of the Democratic Republic of Congo. *Veterinary Microbiology*, 240, 108521. <https://doi.org/10.1016/j.vetmic.2019.108521>.
- Bisimwa, P.N., Ongus, J.R., Steinaa, L., Bisimwa, E.B., Bochere, E., Machuka, E.M., Entfellner, J.-B. D., Okoth, E., & Pelle, R. (2021). The first complete genome sequence of the African swine fever virus genotype X and serogroup 7 isolated in domestic pigs from the Democratic Republic of Congo. *Virology Journal*, 18, 23 doi: 10.1186/s12985-021-01497-0.
- Bisimwa, P.N., Ongus, J.R., Tiambo, C.K., Machuka, E.M., Bisimwa, E.B., Steinaa, L., & Pelle, R. (2020). First detection of African swine fever (ASF) virus genotype X and serogroup 7 in symptomatic pigs in the Democratic Republic of Congo. *Virology Journal*, 17, 135; doi: 10.1186/s12985-020-01398-8.
- Bisimwa, P.N., Wasso, S.D., Ntakundi, M.T., Bwihangane, T.A., Bisimwa, B.E., Mushagalusa, N.G., Katcho, K., & Baluku, B. (2019). Evidence of African swine fever virus in pigs slaughtered at Muhanzi Municipal Abattoir in Bukavu City, Eastern of Democratic Republic of Congo. *International Journal of Microbiology and Biotechnology*, 4, 1-7. doi: 10.11648/j.ijmb.20190401.11.
- Blasco, R., Agüero, M., Almendral, A.M., & Viñuela, E. (1989). Variable and constant regions in African swine fever virus DNA. *Virology*, 168(2), 330-338. doi: 10.1016/0042-6822(89)90275-0.
- Boinas, F.S., Wilson, A.J., Hutchings, G.H., Martins, C., & Dixon, L.K. (2011). The persistence of African swine fever virus in field-infected *Ornithodoros erraticus* during the ASF endemic period in Portugal. *PLoS ONE*, 6, e20383. doi: 10.1371/journal.pone.0020383.

- Boomker, J., Horak, I.G., Booyse, D.G., & Meyer, S. (1991). Parasites of South African wildlife. VIII. Helminth and arthropod parasites of warthogs, *Phacochoerus aethiopicus*, in the eastern Transvaal. *Onderstepoort Journal of Veterinary Research*, 58, 195-202.
- Borca, M.V., Ramirez-Medina, E., Silva, E., Vuono, E., Rai, A., Pruitt, S., Holinka, L.G., Velazquez-Salinas, L., Zhu, J., & Gladue, D.P. (2020). Development of a highly effective African swine fever virus vaccine by deletion of the I177L gene results in sterile immunity against the current epidemic Eurasia strain. *Journal of Virology*, 94(7), e02017-19. doi: 10.1128/JVI.02017-19.
- Boshoff, C.I., Bastos, A.D.S., Gerber, L.J., & Vosloo, W. (2007). Genetic characterisation of African swine fever viruses from outbreaks in southern Africa (1973 – 1999). *Veterinary Microbiology*, 121(1-2), 45-55.
- Braço Forte Junior, M. da C. (1970). Peste suína africana em Portugal. *Anais de Escola Superior de Veterinária*, 12, 37-69.
- Brown, A.-A., Penrith, M.-L., Fasina, F.O., & Beltran-Alcrudo, D. (2018). The African swine fever outbreak in West Africa, 1996-2002. *Transboundary and Emerging Diseases*, 65(1), 64-76. doi: 10.1111/tbed.12673.
- Chambaro, H.M., Sasaki, M., Sinkala, Y., Gonzalez, G., Squarre, D., Fandamo, P., Lubaba, C., Mataa, L., Shawa, M., Mwape, K.E., Gabriël, S., Chembensofu, M., Carr, M.J., Hall, W.W., Qiu, Y., Kajihara, M., Tajada, A., Orba, Y., Simulundu, E., & Sawa, H. (2020). Evidence of exposure of asymptomatic domestic pigs to African swine fever virus during an inter-epidemic period in Zambia. *Transboundary and Emerging Diseases*, 67(,) 2741-2752. doi: 10.1111/tbed.13630.
- Chang'a, J.S., Mayenga, C., Settypalli, T.B.K., Achenbach, J.E., Mwanandota, J.J., Magidanga, B., Cattoli, G., Jeremiah, M., Kamigwe, A., Guo, S., Kalabi, D., Mranba, F., & Lamien, C.E. (2019). Symptomatic and asymptomatic cases of African swine fever in Tanzania. *Transboundary and Emerging Diseases*, 66(6), 2402-2410. doi: 10.1111/tbed.13296.
- Chenais, E., Boqvist, S., Emanuelson, U., von Brömssen, C., Ouma, E., Aliro, T., Masembe, C., Ståhl, K., & Sternberg-Lewerin, S. (2017). Quantitative assessment of the social and economic impact of African swine fever outbreaks in northern Uganda. *Preventive Veterinary Medicine*, 144, 134-148.
- Chenais, E., Sternberg-Lewerin, S., Boqvist, S., Emanuelson, U., Aliro, T., Tejla, E., Cocca, G., Masembe, C., & Ståhl, K. (2015). African swine fever in Uganda: qualitative evaluation of three surveillance methods with implications for other resource-poor settings. *Frontiers in Veterinary Science*, 2, 51. doi: 10.3389/fvets.2015.00051
- Chenais, E., Sternberg-Lewerin, S., Boqvist, S., Ståhl, K., Alike, S., Nokorach, B., & Emanuelson, U. (2019). Smallholders' perceptions on biosecurity and disease control in relation to African swine fever in an endemically infected area in Northern Uganda. *BMC Veterinary Research*, 15, 279. <https://doi.org/10.1186/s12917-019-2005-7>.
- Chiduwa, G., Chimonyo, M., Halimani, T.E., Chisambara, S.R., & Dzama, K. (2008). Herd dynamics and contribution of indigenous pigs to the livelihoods of rural farmers in a semi-arid area of Zimbabwe. *Tropical Animal Health and Production*, 40, 125-136. doi: 10.1007/s11250-007-9071-8.
- Chimonyo, M., Dzama, K., & Mapiye, C. (2010). Growth performance and carcass characteristics of indigenous Mukota pigs of Zimbabwe. *Tropical Animal Health and Production*, 42, 1001-1007. doi: 10.1007/s11250-009-9522-5.
- Coggins, L. (1968a). A modified hemadsorption-inhibition test for African swine fever virus. *Bulletin of the Office international des Épizooties* 16(1), 61-64.

- Coggins, L. (1968b). Segregation of a nonhemadsorbing African swine fever virus in tissue culture. *Cornell Veterinarian* 58(1), 12-20.
- Coggins, L., & Heuschele, W.P. (1966). Use of agar diffusion precipitation test in the diagnosis of African swine fever. *American Journal of Veterinary Research* 27(117), 485-488.
- Colback, H.R.F. (1940). Congo Belge: Gouvernement general. Rapport veterinaire 1939.
- Conceição, J.M. (1949). Estudo das zoonoses porcinas de Angola. Primeiro relatório. A zoonose porcina Africana de virus filtrável. *Pecuária: Anais dos Serviços Pecuários da Colônia de Angola*, 1, 217-245.
- Costard, S., Wieland, B., de Glanville, W., Jori, F., Rowlands, E., Vosloo, W., Roger, F., Pfeiffer, D.U., & Dixon, L.K. (2009). African swine fever: how can global spread be prevented? *Philosophical Transactions of the Royal Society B*, 364, 2683-2696. doi: 10.1098/rstb.2009.0098.
- Couacy-Hymann, E., Kouakou, K.V., Achenbach, J.E., Kouadio, L., Koffi, Y.M., Godji, H.P., Adjé, K.E., Oulai, J., Pell-Minhiaud, H.G., & Lamien, C.E. (2018). Re-emergence of genotype I of African swine fever virus in Ivory Coast. *Transboundary and Emerging Diseases*, 66(2), 882-896. doi: 10.1111/tbed.13098.
- Darfour-Oduro, K.A., Naazie, A., Ahunu, B.K., & Aboagye, G.S. (2009). Genetic parameter estimates of growth traits of indigenous pigs in northern Ghana. *Livestock Science*, 125, 187-191. doi: 10.1016/j.livsci.2009.04.007.
- De Jong, Y.A., Cumming, D., d'Huart, J., & Butynski, T. (2016). *Phacochoerus africanus*. The IUCN red list of threatened species 2016: e.T41768A109669842. Retrieved from <https://doi.org/10.2305/iucn.uk.2016-2.rlts.t4176a44140445>.
- De Kock, G. (1938). Recent research regarding tropical and subtropical diseases in the Union of South Africa. *Report, 13th International Veterinary Congress, 1938*, 2, 734-751.
- De Kock, G., Robinson, E.M., Keppel, J.J.G. (1940). Swine fever in South Africa. *Onderstepoort Journal of Veterinary Science and Animal Industry*, 14, 31 – 93.
- DeTray, D.E., & Scott, G.R. (1955). The effect of hyperimmune hog cholera serum on the virus of African swine fever. *Journal of the American Veterinary Association* 126(937), 313-314.
- de Villiers, E.P., Gallardo, C., Arias, M., da Silva, M., Upton, C., Martin, R., & Bishop, R.P. (2010). Phylogenomic analysis of 11 complete African swine fever virus genome sequences. *Virology*, 400(1), 128-136. doi: 10.1016/j.virol.2010.01.019.
- Dione, M.M., Akol, J., Roesel, K., Kungu, J., Ouma, E.A., Wieland, B., & Pezo, D. (2017). Risk factors for African swine fever in smallholder pig production systems in Uganda. *Transboundary and Emerging Diseases*, 64(3), 872-882. doi: 10.1111/tbed.12542.
- Dione, M.M., Dohoo, I., Ndiwa, N., Poole, J., Ouma, E., Amia, C., & Wieland, B. (2020). Impact of participatory training of smallholder farmers on knowledge, attitudes and practices regarding biosecurity for the control of African swine fever in Uganda. *Transboundary and Emerging Diseases*, 67(6), 2482-2493 doi: 10.1111/tbed.13587.
- Dione, M., Ouma, E., Opio, F., Kawuma, B., & Pezo, D. (2016). Qualitative analysis of the risks and practices associated with the spread of African swine fever within the smallholder pig value chains in Uganda. *Preventive Veterinary Medicine*, 135, 102-112. doi: 10.1016/j.prevetmed.2016.11.001.
- Ekue, N.F., & Wilkinson, P.J. (1990). Absence of *Ornithodoros moubata*, the vector of African swine fever virus, from the main pig producing area of Cameroon. *Tropical Animal Health and Production*, 22(2), 127 – 131. doi: 10.1007/BF02239840.
- Ekue, N. F., Wilkinson, P.J. (2000). Comparison of genomes of African swine fever virus isolates from Cameroon, other African countries and Europe. *Revue d'Élevage et de Médecine Vétérinaire des Pays Tropicaux*, 53, 229-236.

- El Hicheri, K., Gomez-Tejedor, C., Penrith, M.-L., Davies, G., Douati, A., Edoukou, G., & Wojciechowski, K. (1996). L'épizootie de peste porcine africaine de 1996 en Côte d'Ivoire. *Revue scientifique et technique, Office International des Épizooties*, 17(3), 660 – 673.
- Els, H.J., & Pini, A. (1977). Negative staining of a non-haemadsorbing strain of African swine fever virus. *Onderstepoort Journal of Veterinary Research* 44(1), 39-46.
- Etter, E.M.C., Penrith, M.L., Meenowa, D., Munstermann, S., & Jori, F. (2011). Risk assessment of the re-emergence of African swine fever in Mauritius. Sixth International Symposium on Emerging and Re-emerging Pig Diseases, Barcelona, Spain, 12-15 June, 2011, p.290.
- Etter, E.M.C., Seck, I., Grosbois, V., Jori, F., Blanco, E., Vial, L., Akakpo, A.J., Bada-Alhambédi, R., Kone, P., & Roger, F.L. 2011. Seroprevalence of African swine fever in Senegal, 2006. *Emerging Infectious Diseases*, 17(1), 49 – 54. doi: 10.3201/eid1701.100896.
- Fasina, F.O., Kissinga, H., Mlowe, F., Mshang'a, S., Matogo, B., Mrema, A., Mhagama, A., Makungu, S., Mtui-Malamsha, N., Sallu, R., Misinzo, G., Magidanga, B., Kivaria, F., Bebay, C., Nong'ona, S., Kafeero, F., & Nonga, H. (2020). Drivers, risk factors and dynamics of African swine fever outbreaks, southern highlands, Tanzania. *Pathogens*, 9, 155. doi: 10.3390/pathogens9030155.
- Fischer, K., Schulz, K., & Chenais, E. (2020). “Can we agree on that”? Plurality, power and language in participatory research. *Preventive Veterinary Medicine*, 180, 104991. doi: 10.1016/j.prevetmed.2020.104991
- Food & Agriculture Organization of the United Nations. (2007). *The State of the World's Animal Genetic Resources for Agriculture*. Rischkowsky, B., & Pilling, D. (eds). Food & Agriculture Organization of the United Nations, Rome.
- Food & Agriculture Organization of the United Nations/African Union-Interafrican Bureau for Animal Resources/International Livestock Research Institute. (2017). *Regional Strategy for the Control of African Swine Fever in Africa*. FAO/AU-IBAR/ILRI, Accra, Ghana. <http://www.fao.org/3/cb2118en/cb2118en.pdf>.
- Forth, J.H., Forth, L.H., Lycett, S., Bell-Sakyi, L., Keil, G.M., Blome, S., Calvignac-Spencer, S., Wissgott, A., Krause, J., Höper, D., & Beer, M. (2020). Identification of African swine fever virus-like integrated elements in the soft tick genome provides insights into the virus' evolution. *BMC Biology*, 18(1), 136; doi: 10.1186/s12915-020-00865-6
- Gago da Câmara, N.J. (1933). História da peste suína em Angola. *Pecuária: Anais dos Serviços Pecuários da Colônia de Angola 1932*, 1, 25-40.
- Gallardo, C., Anchuelo, R., Pelayo, V., Poudevigne, F., Tati, L., Nzoussi, J., Bishop, R., Pérez, C., Soler, A., Nieto, R., Martín, H., & Arias, M. (2011). African swine fever virus p72 genotype IX in domestic pigs, Congo, 2009. *Emerging Infectious Diseases*, 17(8), 1556-1558. doi: 10.3201/eid1708.101877.
- Gallardo, C., Fernández-Pinero, J., & Arias, M.L. (2019). African swine fever (ASF) diagnosis, an essential tool in the epidemiological investigation. *Virus Research*, 271, 197676. doi: 10.1016/j.virusres.2019.197676.
- Gallardo, C., Mwaengo, D.M., Macharia, J.M., Arias, M., Taracha, E.A., Soler, A., Okoth, E., Martín, E., Kasiti, J., & Bishop, R.P. (2009). Enhanced discrimination of African swine fever virus isolated through nucleotide sequencing of p54, p72 and pB602L (CVR) genes. *Virus Genes*, 38, 85-95. doi: 10.1007/s11262-008-0293-2.
- Gallardo, C., Okoth, E., Pelayo, V., Anchuelo, R., Martín, E., Simón, A., Llorente, A., Nieto, R., Soler, A., Martín, R., Arias, M., Bishop, R.P. (2011). African swine fever viruses with two different genotypes, both of which occur in domestic pigs, are associated

- with ticks and adult warthogs, respectively, at a single geographical site. *Journal of General Virology*, 92, 432-444. doi: 10.1099/vir.0.025874-0.
- Geertsma, P.J., Mpofo, D., & Walters, J. (2012). Investigation and control of an outbreak of African swine fever in the Gauteng Province in 2012. *Proceedings of the 10th Annual Congress of the Southern African Society for Veterinary Epidemiology and Preventive Medicine*, 1-3 August 2012, Farm Inn, South Africa, pp. 17-21.
- Gogin, A., Gerasimov, V., Malogolovkin, A., & Kolbasov, D. (2013). African swine fever in the North Caucasus region and the Russian Federation in the years 2007-2012. *Virus Research*, 173(1), 198-203. doi: 10.1016/j.virusres.2012.12.0007.
- Hakizimana, J.N., Kamwendo, G., Chulu, J.L.C., Kamana, O., Nauwynck, H.J., & Misinzo, G. (2020). Genetic profile of the African swine fever virus responsible for the 2019 outbreak in northern Malawi. *BMC Veterinary Research*, 16, 316. doi: 10.1186/s12917-020-02536-8.
- Hakizimana, J.N., Ntirandekura, J.B., Yona, C., Nyabongo, L., Kamwendo, G., Chulu, J.L.C., Ntakirutimana, D., Kamana, O., Nauwynck, H., & Misinzo, G. (2021). Complete genome analysis of African swine fever virus responsible for outbreaks in domestic pigs in 2018 in Burundi and in 2019 in Malawi. *Tropical Animal Health and Production*, 53, 438. doi: 10.1007/s11250-021-02877-y.
- Hakizimana, J.N., Nyabongo, L., Ntirandekura, J.B., Yona, C., Ntakirutimana, D., Kamana, O., Nauwynck, H.J., & Misinzo, G. (2020). Genetic analysis of African swine fever virus from the 2018 outbreak in south-eastern Burundi. *Frontiers in Veterinary Science*, 7, 578474. doi: 10.3389/fvets.2020.578474.
- Halimani, T.E., Mapiye, O., Marandure, T., Januarie, D., Imbayarwo-Chikosi, V., & Dzama, K. (2020). Domestic free-range pig genetic resources in southern Africa: progress and prospects. *Diversity*, 12, 68. doi:10.3390/d01200068.
- Halimani, T.E., Muchadeyi, F.C., Chimonyo, M., & Dzama, K. (2010). Pig genetic resource conservation: The southern African perspective. *Ecological Economics*, 69, 944-951. doi: 10.1016/j.ecolcon.2010.01.005.
- Halimani, T.E., Muchadeyi, F.C., Chimonyo, M., & Dzama, K. (2013). Opportunities for conservation and utilization of local pig breeds in low-input production systems in Zimbabwe and South Africa. *Tropical Animal Health and Production*, 45, 81-90. doi: 10.1007/s11250-012-0177-2.
- Haresnape, J.M., Lungu, S.A.M., & Mamu, F.D. (1985). A four-year survey of African swine fever in Malawi. *Journal of Hygiene*, 95(2), 309 – 322. doi: 10.1017/s0022172400062732.
- Haresnape J.M., Lungu, S.A.M., & Mamu, F.D. (1987). An updated survey of African swine fever in Malawi. *Epidemiology and Infection*, 99(31), 723–732. doi: 10.1017/s0950268800066589.
- Haresnape, J.M., Wilkinson, P.J., & Mellor, P.S. (1988). Isolation of African swine fever virus from ticks of the *Ornithodoros moubata* complex (Ixodoidea: Argasidae) collected within the African swine fever enzootic area of Malawi. *Epidemiology and Infection*, 101(1), 173 – 185. doi: 10.1017/s0950268800029332.
- Heuschele, W.P., Coggins, L., & Stone, S.S. (1966). Fluorescent antibody studies on African swine fever virus. *American Journal of Veterinary Research*, 27, 477-484.
- Horak, I.G., Biggs, H.C., Hanssen, T.S., & Hanssen, R.E. (1983). The prevalence of helminth and arthropod parasites of warthog, *Phacochoerus aethiopicus*, in South West Africa/Namibia. *Onderstepoort Journal of Veterinary Research*, 50, 145-148.
- Horak, I.G., Boomker, J., De Vos, V., & Potgieter, F.T. (1983). Parasites of domestic and wild animals in South Africa. XXIII. Helminth and arthropod parasites of warthogs,

- Phacochoerus aethiopicus*, in the eastern Transvaal lowveld. *Onderstepoort Journal of Veterinary Research*, 55, 145-152.
- Isoun, T.T., & Osunfisan, T.J. (1973). An outbreak of fatal diseases: acute septicaemia with meningoencephalitis in a piggery in western state of Nigeria. *Nigerian Veterinary Journal*, 2, 69-73.
- Janse van Rensburg, L., Etter, E., Heath, L., Penrith, M.-L., & van Heerden, J. (2020). Understanding African swine fever outbreaks in domestic pigs in a sylvatic endemic area: the case of the South African controlled area between 1977 – 2017. *Transboundary and Emerging Diseases*, 67(6), 2753-2769. doi: 10.1111/tbed.13632.
- Janse van Rensburg, L., van Heerden, J., Penrith, M.-L., Heath, L., Rametse, T., & Etter, E. (2020). Investigation of African swine fever outbreaks in domestic pigs outside the controlled areas of South Africa, 2012 – 2017. *Journal of the South African Veterinary Association*, 91, a1997. doi: 10.4102/jsava.v91i0.1997.
- Jori, F., Vial, L., Penrith, M.-L., Pérez-Sánchez, R., Etter, E., Albina, E., Michaud, V., & Roger, F. (2013). Review of the sylvatic cycle of African swine fever in sub-Saharan Africa and the Indian Ocean. *Virus Research* 173(1), 212-227. doi: 10.1016/j.virusres.2012.10.005.
- Kiendrebogo, T., Mopate Logtene, Y., Kondombo, S.R., & Kabore-Zoungrana, C.Y. (2012). Characterization and importance of pig breeds in the pork industry of the zone of Bobo-Dioulasso, Burkina Faso. *International Journal of Biology and Chemistry Sciences*, 6, 1535-1547. <http://dx.doi.org/10.4314/ijbcs.v6i4.13>.
- Kouakou, K.V., Michaud, V., Biego, H.G., Gnabro, H.P.G., Kouakou, A.V., Mossoun, A.M., Awuni, J.A., Minoungou, G.L., Aplogan, G.L., Awoumé, F.K., Albina, E., Lancelot, R., & Couacy-Hymann, E. (2017). African and classical swine fever situation in Ivory-Coast and neighbouring countries, 2008-2013. *Acta Tropica*, 166, 241-248. doi: 10.1016/j.actatropica.2016.10.027.
- Koussou, M.O., & Duteurtre, G. (2002). Les facteurs compétitivité de la filière porcine dans la Bassin du Logone. Communication au colloque 'Systèmes agro-alimentaires localisés', CIRAD, Montpellier, France, 16-18 Oct. 2002, [http://pigtrop.cirad.fr/subjects/socio\\_economy\\_in\\_pig\\_production\\_sector/filiere\\_porcin\\_au\\_nord\\_cameroun](http://pigtrop.cirad.fr/subjects/socio_economy_in_pig_production_sector/filiere_porcin_au_nord_cameroun).
- Kukielka, E.A., Jori, F., Martínez-López, B., Chenais, E., Masembe, C., Chavernac, D., & Ståhl, K. (2016). Wild and domestic pig interactions at the wildlife-livestock of Murchison Falls National Park, Uganda, and the potential association with African swine fever. *Frontiers in Veterinary Science*, 3, 31. doi: 10.3389/fvets.2016.00031.
- Laddomada, A., Rolesu, S., Loi, F., Cappai, S., Oggiano, A., Madrau, M.P., Sanna, M.L., Pilo, G., Bandino, E., Brundu, D., ... & Sgarangella, F. (2019). Surveillance and control of African swine fever in free-ranging pigs in Sardinia. *Transboundary and Emerging Diseases*, 66(3), 1114-1119. doi: 10.1111/tbed.13138.
- Li, X., & Tian, K. (2018). African swine fever in China. *Veterinary Record*, 183(9), 300-301. doi: 10.1136/vr.k3774.
- Lichoti, J.K., Davies, J., Kitala, P.M., Githigia, S.M., Okoth, E., Maru, Y., Bukachi, S.A., & Bishop, R.P. (2016). Social network analysis provides insights into African swine fever epidemiology. *Preventive Veterinary Medicine*, 126, 1-10. doi: 10.1016/j.prevetmed.2016.01.019.
- Lichoti, J.K., Davies, J., Maru, Y., Kitala, P.M., Githigia, S.M., Okoth, E., Bukachi, S.A., Okuthe, S., & Bishop, R.P. (2017). Pig traders' networks on the Kenya-Uganda border highlight potential for mitigation of African swine fever virus transmission and improved ASF disease risk management. *Preventive Veterinary Medicine*, 140, 87-96.

- Linden, A., Licoppe, A., Volpe, R., Paternostre, J., Lesenfants, C', Cassart, D., Garigliany, M., Tignon, M., van den berg, T., Desmecht, D., & Cay, A.B. (2019). Summer 2018: African swine fever virus hits north-western Europe. *Transboundary and Emerging Diseases*, 66(1), 54-55. doi:10.1111/tbed.13047.
- Loi, F., Cappai, S., Coccollone, A., & Rolesu, S. (2019). Standardized risk analysis approach to evaluate the last African swine fever eradication program performance, in Sardinia. *Frontiers in Veterinary Science*, 6, 299. doi: 10.3389/fvets.2019.00299.
- Lubisi, B.A., Bastos, A.D.S., Dwarka, R.M., & Vosloo, W. (2005). Molecular epidemiology of African swine fever in East Africa. *Archives of Virology*, 150(12), 2439-2452. doi: 10.1007/s00705-005-0602-1.
- Lubisi, B.A., Bastos, A.D.S., Dwarka, R.M., & Vosloo, W. (2007). Intra-genotypic resolution of African swine fever viruses from an East African domestic pig cycle: a combined p72-CVR approach. *Virus Genes*, 35(3), 729-735. doi: 10.1007/s11262-007-0148-2.
- Lubisi, B.A., Dwarka, R.M., Meenowa, D., & Jaumally, R. (2009). An investigation into the first outbreak of African swine fever in the Republic of Mauritius. *Transboundary and Emerging Diseases*, 56(5), 178 – 188. doi:10.1111/j.1865-1682.2009.01078.x.
- Luka, P.D., Achenbach, J.E., Mwiine, F.N., Lamien, C.E., Shamaki, D., Unger, H., & Erume, J. (2017). Genetic characterization of circulating African swine fever viruses in Nigeria (2007-2015). *Transboundary and Emerging Diseases*, 64(5), 1598-1609, doi: 10.1111/tbed.12553.
- Madzimure, J., Chimonyo, M., Zander, K.K., & Dzama, K. (2013). Potential for using indigenous pigs in subsistence-oriented and market-oriented small-scale farming systems of southern Africa. *Tropical Animal Health and Production*, 45, 135-142. doi: 10.1007/s11250-012-01843.
- Magadla, N.R., Vosloo, W., Heath, L., & Gummow, B. (2016). The African swine fever control zone in South Africa and its current relevance. *Onderstepoort Journal of Veterinary Research*, 83, a1034. doi: 10.4102/ojvr.v83i1.1034.
- Malmquist, W.A., & Hay, D. (1960). Hemadsorption and cytopathic effect produced by African swine fever virus in swine bone marrow cells and buffy coat cultures. *American Journal of Veterinary Research*, 21, 104-108.
- Masembe, C., Phan, M.V.T., Robertson, D.L., & Cotton, M. (2021). Increased resolution of African swine fever virus genome patterns based on profile HMM protein domains. *Virus Evolution*, 6, veaa044. doi: 10.1093/ve/veaa044.
- Masembe, C., Sreenu, V.B., Da Silva Felipe, A., Wilkie, G.S., Ogweng, P., Mayega, F.J., Muwanika, V.B., Biek, R., Palmarini, M., & Davison, A.J. (2018). Genome sequences of five African swine fever genotype IX isolates from domestic pigs in Uganda. *Microbiology Resource Announcements*, 7(13), e01018-18. doi: 10.1128/MRA.01018.18.
- Mashatise, E., Hamudikuwanda, H., Dzama, K., Chimonyo, M., & Kanengoni, A. (2005). Socio-economic roles, traditional management systems and reproductive patterns of mukota pigs in semi-arid north-eastern Zimbabwe. *Bunda Journal of Agriculture, Environmental Science and Technology*, 3, 97-105.
- Matson, B.A. (1960). An outbreak of African swine fever in Nyasaland. *Bulletin of Epizootic Diseases in Africa*, 8, 305–308.
- McIntosh, B.M. (1952). The propagation of African swine fever virus in the embryonated hen's egg. *Journal of the South African Veterinary Medical Association*, 23, 217-220.
- Mendes, A.M. (1962). The lapinization of the virus of African swine fever. *Bulletin de l'Office International des Épizooties*, 58, 699–705.

- Mendes, A.M. (1971). Algumas doenças dos animais em Angola e Moçambique e sua importância na higiene das carnes. *Revista Portuguesa de Ciências Veterinárias*, 66, 271–286.
- Mendes, A.M. (1994). A história da peste suína africana em Angola. *Revista Portuguesa de Ciências Veterinárias*, 89, 110–120.
- Mendes, A.M., & Daskalos, A.M. (1955). Studies on the lapinization of African swine fever virus in Angola. *Bulletin of Epizootic Diseases of Africa*, 3, 9-14.
- Minoungou, G.L., Diop, M., Dakouo, M., Ouattara, A.K., Settypalli, T.B.K., Lo, M.M., Sidibe, S., Kanyala, E., Kone, Y.S., Diallo, M.S.,... & Simpoire, J. (2021). Molecular characterisation of African swine fever viruses in Burkino Faso, Mali, and Senegal 1989-2016. *Transboundary and Emerging Diseases*, 68(5), 2842-2852. doi: 10.1111/tbed.14240.
- Misinzio, G., Jumapili, F., Ludosha, M., Mafie, E., Silialis, J., Mushi, R., Viaene, W., & Van Doorselaere, J. (2012). Genotyping of African swine fever virus from an outbreak in Tanzania in 2009. *Research Opinions in Animal and Veterinary Sciences*, 2(5), 334-338.
- Misinzio, G., Kasanga, C.J., Mpelumbe-Ngeleja, C., Masambu, J., Kitambi, A., & Van Doorselaere, J. (2012). African swine fever virus, Tanzania, 2010-2012. *Emerging Infectious Diseases*, 18(12), 2081-2083. doi: 10.3201/eid1812.121083.
- Misinzio, G., Kwavi, D.E., Sikombe, C.D., Makange, M., Peter, E., Muhairwa, A.P., & Madege, M.J. (2014). Molecular characterization of African swine fever virus from domestic pigs in northern Tanzania during an outbreak in 2013. *Tropical Animal Health and Production*, 46(7), 1199-1207. doi: 10.1007/s11250-014-0628-z.
- Misinzio, G., Magambo, J., Masambu, J., Yongolo, M.G., Van Doorselaere, J., & Nauwynck, H.J. (2010). Genetic characterization of African swine fever viruses from a 2008 outbreak in Tanzania. *Transboundary and Emerging Diseases*, 58(1), 86-92. doi: 10.1111/j.1865-1682.2010.01177.x.
- Molini, U., Mushonga, B., Settypalli, T.B.K., Dundon, W.G., Khaiseb, S., Jago, M., Cattoli, G., & Lamien, C.E. (2020). Molecular characterization of African swine fever virus from outbreaks in Namibia in 2018. *Transboundary and Emerging Diseases*, 67(2), 1008-1014. doi: 10.1111/tbed.13399.
- Montgomery, R.E. (1921). On a form of swine fever occurring in British East Africa (Kenya Colony). *Journal of Comparative Pathology and Therapeutics*, 34, 159-191, 243-262.
- Mouiche, M.M.M., Noumedem, R.N.G., Namegni, R.P., Feussom, J.M.K., Moffo, F., Okah-Nnane, N.H., Njifon, H.L.M., Wade A., & Awah-Ndukum, J. (2021). African swine fever in the northern regions of Cameroon: seroprevalence survey and spatiotemporal analysis of outbreaks from 2010 to 2017. *Tropical Animal Health and Production*, 53(2), 214. doi: 10.1007/s11250-021-02641-2.
- Mujibi, F.D., Okoth, E., Cheruiyot, E.K., Onzere, C., Bishop, R.P., Fèvre, E.M., Thomas, L., Masembe, C., Plastow, G., & Rothschild, M. (2018). Genetic diversity, breed composition and admixture of Kenyan domestic pigs. *PLoS ONE*, 13, e0190080. doi: 10.1371/journal.pone.0190080.
- Mulumba-Mfumumu, L.K., Achenbach, J.E., Mauldin, M.R., Dixon, L.K., Tshilenge, C.G., Thiry, E., Moreno, N., Blanco, E., Saegerman, C., Lamien, C.E., & Diallo, A. (2017). Genetic assessment of African swine fever isolates involved in outbreaks in the Democratic Republic of Congo between 2005 and 2012 reveals co-circulation of p72 genotypes I, IX and XIV, including 19 variants. *Viruses*, 9, 31. doi: 10.3390/v9020031.
- Mulumba-Mfumumu, L.K., Saegerman, C., Dixon, L.K., Madimba, K.C., Kazadi, E., Mukalakata, N.D., Oura, C.A.L., Chenais, E., Masembe, C., Ståhl, K., Thiry, E., &



- Penrith, M.-L. (2019). African swine fever: update on Eastern, Central and Southern Africa. *Transboundary and Emerging Diseases*, 66(4), 1462-1480. DOI: 10.1111/tbed.13187.
- Mur, L., Iscaro, C., Cocco, M., Jurado, C., Rolesu, S., De Mia, G.M., Feliziani, F., Pérea-Sánchez, R., Oleaga, A., & Sánchez-Vizcaíno, J.M. (2017). Serological surveys and direct field searching reaffirm the absence of *Ornithodoros erraticus* ticks role in African swine fever cycle in Sardinia. *Transboundary and Emerging Diseases*, 64(4), 1322-1328. doi: 10.1111/tbed.12485.
- Mwiine, F.N., Nkamwesiga, J., Ndekezi, C., & Ochwo, S. (2019). Molecular characterization of African swine fever viruses from outbreaks in peri-urban Kampala, Uganda. *Advances in Virology*, 2019 Article ID 1463245. doi: 10.1155/2019/1463245.
- Nana-Nukechap, M.F., & Gibbs, E.P.J. (1985). Socioeconomic effects of African swine fever in Cameroon. *Tropical Animal Health and Production*, 17(3), 183 – 184. doi: 10.1007/BF02356970,
- Nantima, N., Davies, J., Dione, M., Ocaido, M., Okoth, E., Mugisha, A., & Bishop, R. (2016). Enhancing knowledge and awareness of biosecurity practices among smallholder pig farmers in four districts along the Kenya – Uganda border. *Tropical Animal Health and Production*, 48(4), 727-734. doi: 10.1007/s11250-016-1015-8.
- Nantima, N., Ocaido, M., Ouma, E., Davies, J., Dione, M., Okoth, E., Mugisha, A., & Bishop, R. (2015). Risk factors associated with occurrence of African swine fever outbreaks in smallholder pig farms in four districts along the Uganda-Kenya border. *Tropical Animal Health and Production*, 47(3), 589-595. doi: 10.1007/s11250-015-0768-9.
- Ncube, M., Dzama, K., Chimonyo, M., Kanengoni, A., & Hamudikuwanda, H. (2003). Effect of boar genotype on reproductive performance of the local sows of Zimbabwe. *Livestock Research for Rural Development*, 15(2). <http://www.lrrd.org/lrrd15/2/ncub152.htm>.
- Ndlovu, S., Williamson, A.-L., Heath, L., & Carulei, O. (2020). Genome sequences of three African swine fever viruses of genotypes IV and XX from Zaire and South Africa, isolated from a domestic pig (*Sus scrofa domesticus*), a warthog (*Phacochoerus africanus*), and a European wild boar (*Sus scrofa*). *Microbiology Resource Announcements*, 9, e00341-20; doi: 10.1128/MRA.00341-20.
- Ndlovu, S., Williamson, A.-L., Malesa, R., van Heerden, J., Boshoff, C.L., Bastos, A.D.S., Heath, L., & Carulei, O. (2020). Genome sequences of three African swine fever viruses of genotypes I, III, and XXII and XX from South Africa and Zambia, isolated from *Ornithodoros* soft ticks. *Microbiology Resource Announcements*, 10, e01376-19; doi: 10.1128/MRA.01376-19.
- Ngwa, V.N., Abouna, A., Zoli, A.P., & Attili, A.-R. (2020). Epidemiology of African swine fever in piggeries in the Center, South and South-West of Cameroon. *Veterinary Sciences*, 7, 123. doi: 10.3390/vetsci7030123.
- Nix, R.J., Gallardo, C., Hutchings, G., Blanco, E., & Dixon, L.K. (2006). Molecular epidemiology of African swine fever virus studied by analysis of four variable genome regions. *Archives of Virology*, 151(12), 2475 – 2494. doi: 10.1007/s00705-006-0794-z.
- Njau, E.P., Entfellner, J.-B.D., Machuka, E.M., Bochere, E.N., Cleaveland, S., Shirima, G.N., Kusiluka, L.J., Upton, C., Bishop, R.P., Pellee, R., & Okoth, E.A. (2021). The first genotype II African swine fever virus isolated in Africa provides insight into the current Eurasian pandemic. *Scientific Reports*, 11, 13081. doi: 10.1038/s41598-021-92593-2.

- Nsoso, S.J., Mannathoko, G.G., & Modise, K. (2006). Monitoring production, health and marketing of indigenous Tswana pigs in Ramotswa village of Botswana. *Livestock Research for Rural Development*, 18(9), <http://www.lrrd.org/lrrd18/9/nsos18125.htm>.
- Okoth, E., Gallardo, C., Macharia, J.M., Omore, A., Pelayo, V., Bulimo, D.W., Arias, M., Kitale, P., Baboon, K., Lekolol, I., Mijeje, D., & Bishop, R.P. (2013). Comparison of African swine fever virus prevalence and risk in two contrasting pig-farming systems in South-west and Central Kenya. *Preventive Veterinary Medicine*, 110, 198-205. doi: 10.1016/j.prevetmed.2012.11.012.
- Onzere, C.K., Bastos, A.D., Okoth, E.A., Lichoti, J.K., Bochere, E.N., Owido, M.G., Ndambuki, G., Bronsvoort, M., & Bishop, R.P. (2018). Multi-locus sequence typing of African swine fever viruses from endemic regions of Kenya and eastern Uganda (2011-2013) reveals rapid B602L central variable region evolution. *Virus Genes*, 54(1), 111-123. doi: 10.1007/s11262-017-1521-4.
- Oura, C.L., Powell, P.P., Anderson, E.C., & Parkhouse, R.M.E. (1998). The pathogenesis of African swine fever in the resistant bushpig. *Journal of General Virology*, 79(6), 1439-1443. doi: 10.1099/0022-1317-79-6-1439.
- Owolodun, O.A., Bastos, A.D.S., Antiabong, J.F., Ogedengbe, M.E., Ekong, P.S., & Yakubu, B. (2010). Molecular characterisation of African swine fever viruses from Nigeria (2003-2006) recovers multiple virus variants and reaffirms CVR epidemiological utility. *Virus Genes*, 41(3), 361-368. doi: 10.1007/s11262-009-0444-0.
- Payne, A., Ogweng, P., Ojok, A., Etter, E.M., Gilot, E., Masembe, C., Ståhl, K., & Jori, F. (2018). Comparison of three methods to assess the potential for bushpig-domestic pig interactions at the livestock-wildlife interface in Uganda. *Frontiers in Veterinary Science*, 5, 295. doi: 10.3389/fvets.2018.00295.
- Penrith, M.-L. (2020). Current status of African swine fever. *CABI Agriculture and Bioscience*, 1, 11. doi: 10.1186/s43170-020-00011-w.
- Penrith, M.L., Bastos, A.D., & Chenais, E. (2021). With or without a vaccine - complementary and alternative approaches to managing African swine fever in resource-constrained smallholder settings. *Vaccines*, 9, 116. doi: 10.3390/vaccines9020116.
- Penrith, M.-L., Bastos, A.D., Etter, E.M.C., & Beltrán-Alcrudo, D. (2019). Epidemiology of African swine fever in Africa today: sylvatic cycle versus socio-economic imperatives. *Transboundary and Emerging Diseases*, 66(1), 672-686. doi: 10.1111/tbed.13117.
- Penrith, M.-L., Lopes Pereira, C., Lopes da Silva, M.M.R., Quembo, C., Nhamusso, A., & Banze, J. (2007). Overview of African swine fever in Mozambique: risk factors and potential for control. *Onderstepoort Journal of Veterinary Research*, 74, 149-160.
- Penrith, M.-L., Thomson, G.R., Bastos, A.D.S., Phiri, O.C., Lubisi, B.A., Botha, B., Esterhuysen, J., Du Plessis, E.C., Macome, F., & Pinto, F. (2004). An investigation into natural resistance to African swine fever in domestic pigs from an endemic area in southern Africa. *Revue scientifique et technique, Office International des Épizooties*, 23, 665-677. doi : 10.20506/rst.23.3.1533.
- Penrith, M.-L., Vosloo, W., Jori, F., & Bastos, A.D.S. (2013). African swine fever virus eradication in Africa. *Virus Research*, 173(1), 228-246. doi: 10.1016/j.virusres.2012.10.011.
- Pérez-Sánchez, R., Astigarraga, A., Oleaga-Pérez, A., & Encinas-Grandes, A. (1994). Relationship between the persistence of African swine fever and the distribution of *Ornithodoros erraticus* in the province of Salamanca, Spain. *Veterinary Record*, 135(9), 207-209. doi: 10.1136/vr.135.9.207.

- Peter, E., Machuka, E., Githae, D., Okoth, E., Cleaveland, S., Shirima, G., Kusilika, L., & Pelle, R. (2021). Detection of African swine fever virus genotype XV in a sylvatic cycle in Saadani National Park, Tanzania. *Transboundary and Emerging Diseases*, 68(2), 813-823. doi: 10.1111/tbed.13747.
- Phologane, S.B., Bastos, A.D.S., & Penrith, M.-L. (2005). Intra- and inter-genotypic size variation in the central variable region of the 9RL open reading frame of diverse African swine fever viruses. *Virus Genes*, 31(3), 357-360, doi: 10.1007/s11262-005-3254-z.
- Plowright, W., Parker, J.A., & Peirce, M.A. (1969a). African swine fever virus in ticks (*Ornithodoros moubata* Murray) collected from animal burrows in Tanzania. *Nature*, 221, 1071-1073.
- Plowright, W., Parker, J., & Peirce, M.A. (1969b). The epizootiology of African swine fever in Africa. *Veterinary Record*, 85, 668-674.
- Plowright, W., Perry, C.T., & Greig, A. (1974). Sexual transmission of African swine fever virus in the tick, *Ornithodoros moubata* porcinus Walton. *Research in Veterinary Science*, 17, 106-113.
- Plowright, W., Perry, C.T., Peirce, M.A., & Parker, J. (1970). Experimental infection of the argasid tick, *Ornithodoros moubata* porcinus, with African swine fever virus. *Archiv für die gesamte Virusforschung*, 31, 33-50.
- Plowright, W., Perry, C.T., & Peirce, M.A. (1970). Transovarial infection with African swine fever virus in the argasid tick, *Ornithodoros moubata* porcinus Walton. *Research in Veterinary Science*, 11, 582-584.
- Plowright, W., Thomson, G.R., & Naser, J.A. (1994). African swine fever. In: Coetzer, J.A.W., Thomson, G.R., & R.C. Tustin (eds.), *Infectious diseases of livestock, with special reference to southern Africa*, Vol. 1, pp. 568-599, Oxford University Press, Cape Town.
- Quembo, C.J., Jori, F., Heath, L., Pérez-Sánchez, R., & Vosloo, W. (2016). Investigation into the epidemiology of African swine fever virus at the wildlife-domestic interface of the Gorongosa National Park, central Mozambique. *Transboundary and Emerging Diseases*, 63(4), 443-451. doi: 10.1111/tbed.12289.
- Quembo, C.J., Jori, F., Vosloo, W., & Heath, L. (2018). Genetic characterisation of African swine fever isolates from soft ticks at the wildlife/domestic interface in Mozambique and identification of a novel genotype. *Transboundary and Emerging Diseases*, 65(2), 420-431. doi: 10.1111/tbed.12700.
- Rahimi, P., Sohrabi, A., Ashrafihelan, J., Edalat, R., Alamdari, M., Masoudi, M., Mostofi, S., & Azadmanesh, K. (2010). Emergence of African swine fever virus, Northwestern Iran. *Emerging Infectious Diseases*, 16, 1946-1948. doi: 10.3201/eid1612.100378.
- Ravaomanana, J., Jori, F., Vial, L., Pérez-Sánchez, R., Blanco, E., Michaud, V., & Roger, F. (2011). Assessment of interactions between African swine fever virus, bushpigs (*Potamochoerus larvatus*), *Ornithodoros* ticks and domestic pigs in north-western Madagascar. *Transboundary and Emerging Diseases*, 58(3), 247-254. doi: 10.1111/j.1865-1682.2011.01207.x.
- Ravaomanana, J., Michaud, V., Jori, F., Andriatsimahavandy, A., Roger, F., Albina, E., Vial, L. (2010). First detection of African swine fever virus in *Ornithodoros porcinus* ticks in Madagascar and new insights into tick distribution and taxonomy. *Parasites and Vectors*, 3, 115. doi: 10.1186/1756-3305-3-115.
- Rivera, E.M. (1983). African swine fever in the Dominican Republic. In: Wilkinson, P.J. (ed) *African Swine Fever*, pp.17-24. EUR 8466 EN. Commission of the European Communities.

- Rock, D.L. (2021). Thoughts on African swine fever vaccines. *Viruses*, 13, 943. doi: 10.3390/v13050943.
- Roger, F., Ratovonjato, J., Vola, P., & Uilenberg, G. (2001). *Ornithodoros porcinus* ticks, bushpigs, and African swine fever in Madagascar. *Experimental and Applied Entomology*, 25(3), 263 – 269. doi:10.1023/a:1010687502145.
- Rolesu, S., Mandas, D., Loi, F., Oggiano, A., Del Giudici, S., Franzoni, G., Guberti, V., & Cappai, S. (2021). African swine fever in smallholder Sardinian farms: last ten years of network transmission reconstruction and analysis. *Frontiers in Veterinary Science*, 8, 692448. doi: 10.3389/fvets.2021.692448.
- Rousset, D., Randriamparany, T., Maharavo Rahantamalala, C.Y., Randriamahefa, N., Zeller, H., Rakoto-Andrianarivelo, M., & Roger, F. (2001). Introduction de la peste porcine africaine à Madagascar, histoire et leçons d'une émergence. *Archives de l'Institut Pasteur de Madagascar*, 67(1-2), 31-33.
- Rowlands, R.J., Michaud, V., Heath, L., Hutchings, G., Oura, C., Vosloo, W., Dwarka, R., Onashvili, T., Albina, E., & Dixon, L.K. (2008). African swine fever isolate, Georgia, 2007. *Emerging Infectious Diseases*, 14(12), 1870-1874. doi: 10.3201/eid1412.080591.
- Saliki, J.T., Thiry, E., & Pastoret, P.P. (1985). La peste porcine africaine (African swine fever). *Études et Synthèses de l'Institut d'Élevage et de Médecine Vétérinaire des Pays Tropicaux*, No. 11, Paris.
- Samui, K.L., Mwanaumo, B., & Chizyuka, H.G.B. (1991). African swine fever in Zambia – report on the first outbreak outside the endemic zone. *Proceedings of the 6th International Symposium on Veterinary Epidemiology and Economics*, available at [www.sciquest.org.nz](http://www.sciquest.org.nz).
- Sánchez Botija, C. (1963). Reservorios del virus de la peste porcina africana – Investigación del virus de la P.P.A. en los artrópodos mediante la prueba de la hemoadsorción. *Bulletin, Office international des Épidémiologies*, 60, 895-899.
- Sánchez Botija, C. (1982). African swine fever. New developments. *Revue scientifique et Technique de l'Office International des Épidémiologies*, 1, 1065-1094.
- Sánchez-Vizcaíno, J.M., Mur, L., Gomez-Villamandos, J.C., & Carrasco, L. (2015). An update on the epidemiology and pathology of African swine fever. *Journal of Comparative Pathology*, 152, 9-21. doi: 10.1016/j.jcpa.2014.09.003.
- Sarr, J. (1990). Etude de la peste porcine Africaine au Sénégal. Rapport final. Programme de recherche financé par le Commission des Communautés Européennes, Direction Générale de la Science, de la Recherche et de la Développement. Unpublished report. Laboratoire de l'Élevage et de Recherches Vétérinaires, Dakar-Hann, Sénégal.
- Sauter-Louis, C., Forth, J.H., Probst, C., Staubach, C., Hlinak, A., Rudovsky, A., Holland, D., Schlieben, P., Göldner, M., Schatz, J.,... Blome, S. (2021). Joining the club: First detection of African swine fever in wild boar in Germany. *Transboundary and Emerging Diseases*, 68(4), 1744-1752. doi: 10.1111/tbed.13890.
- Simulundu, E., Chambaro, H.M., Sinkala, Y., Kajihara, M., Ogawa, H., Mori, A., Ndebe, J., Dautu, G., Mataa, L., Lubaba, C.H., Simuntala, C., Fandamu, P., Simuunza, M., Pandey, G.S., Samui, K.L., Misinzo, G., Takada, A., & Mweene, A.S. (2018). Co-circulation of multiple genotypes of African swine fever viruses among domestic pigs in Zambia (2013-2015). *Transboundary and Emerging Diseases*, 65(1), 114-122. DOI: 10.1111/tbed.12635.
- Simulundu, E., Lubaba, C.H., van Heerden, J., Kajihara, M., Mataa, L., Chambaro, H.M., Sinkala, Y., Munjita, S.M., Munang'andu, H.M., Nalubamba, K.S., Samui, K., Pandey, G.S., Takada, A., & Mweene, A.S. (2017). The epidemiology of African

- swine fever in "non-endemic" regions of Zambia (1989-2015): implications for disease prevention and control. *Viruses*, 9, 236. doi: 10.3390/v9090236.
- Simulundu, E., Sinkala, Y., Chambaro, H.M., Chinyemba, A., Banda, F., Mooya, L.E., Ndebe, J., Chitanga, S., Makungu, C., Munthali, G., Fandamu, P., Takada, A., & Mweene, A.S. (2018). Genetic characterisation of African swine fever virus from 2017 outbreaks in Zambia: identification of p72 genotype II variants in domestic pigs. *Onderstepoort Journal of Veterinary Research*, 85(1), a1562. doi: 10.4102/ojvr.v85i1.1562.
- Simpson, V.R., & Drager, N. (1979). African swine fever antibody detection in warthogs. *Veterinary Record*, 105(3), 61. doi: 10.1136/vr.105.3.61.
- Ståhl, K., Ogweng, P., Okoth, E., Aliro, T., Muhangi, D., LeBlanc, N., Atimmedi, P., Berg, M., Bishop, R.P., Rasmussen, H.B., & Masembe, C. (2014). Understanding the dynamics and spread of African swine fever virus at the wildlife-livestock interface: insights into the potential role of the bushpig, *Potamochoerus larvatus*. *Suiform Soundings*, 13, 24-28.
- Ståhl, K., Sternberg-Lewerin, S., Blome, S., Viltrop, A., Penrith, M.-L., & Chenais, E. (2019). Lack of evidence for long-term carriers of African swine fever virus - a systematic review. *Virus Research*, 272, 197725, doi: 10.1016/j.virusres.2019.197725.
- Steyn, D.G. (1928). Preliminary report on a South African virus disease amongst pigs. 13th and 14th Reports of the Director of Veterinary Education and Research, Union of South Africa pp. 415 – 428.
- Steyn, D.G. (1932). East African virus disease in pigs. 18th Report of the Director of Veterinary Services and Animal Industry, Union of South Africa 1: 99 – 109.
- Swai, E.S., & Lyimo, C.J. (2014). Impact of African swine fever epidemics in smallholder pig production units in Rombo district of Kilimanjaro, Tanzania. *Livestock Research for Rural Development*, 26 (2), Article #32.
- Taylor, W.P., Best, J.R., & Couquhoun, I.R. (1977). Absence of African swine fever from Nigerian warthogs. *Bulletin of Animal Health and Production in Africa*, 25(2), 196 – 197.
- Tekle, T., Tesfay, A., & Kifleyohannes, T. (2013). Smallholder pig production and its constraints in Mekelle and southern zone of Tigray region, North Ethiopia. *Livestock Research for Rural Development*, 25(10). <http://www.lrrd.org/lrrd25/10/tek125184.htm>.
- Thomas, L.F., Bishop, R.P., Onzere, C., McIntosh, M.T., Lemire, K.A., de Glanville, W.A., Cook, E.A.J., & Fèvre, E.M. (2016). Evidence for the presence of African swine fever virus in an endemic region of Western Kenya in the absence of any reported outbreak. *BMC Veterinary Research*, 12, 192. doi: 10.1186/s12917-016-0830-5
- Thomson, G.R. (1985). The epidemiology of African swine fever: the role of free-living hosts in Africa. *Onderstepoort Journal of Veterinary Research*, 52(3), 201–209.
- Thomson, G.R., Gainaru, M., Lewis, A., Biggs, H., Nevill, E., van der Pypekamp, H., Gerber, L., Esterhuysen, J., Bengis, R., Bezuidenhout, D., & Condy, J. (1983). The relationship between African swine fever virus, the warthog and *Ornithodoros* species in southern Africa. In Wilkinson, P.J. (ed) *African Swine Fever*, pp.85-100. EUR 8466 EN. Commission of the European Communities.
- Thomson, G.R., Gainaru, M.D., & Van Dellen, A.F. (1980). Experimental infection of warthogs (*Phacochoerus aethiopicus*) with African swine fever virus. *Onderstepoort Journal of Veterinary Research*, 47(1), 19-22.
- Thoromo, J., Simulundu, E., Chambaro, H.M., Mataa, L., Lubaba, C.H., Pandey, G.S., Takada, A., Misinzo, G., & Mweene, A.S. (2016). Diagnosis and genotyping of

- African swine fever viruses isolated from 2015 outbreaks in Zambia. *Onderstepoort Journal of Veterinary Research*, 83, a1095. doi: 10.4102/ojvr.83i1.1095.
- Turnbull, D.O. (1932). Nyasaland. Swine fever. Annual Report of the Veterinary Department, 1931.
- Turnbull, D.O. (1933). Nyasaland. Swine fever. Annual Report of the Veterinary Department, 1932.
- Turnbull, D.O. (1934). Nyasaland. Swine fever. Annual Report of the Veterinary Department, 1933.
- van Heerden, J., Malan, K., Gadaga, B.M., & Spargo, R.E. (2017). Reemergence of African swine fever in Zimbabwe, 2015. *Emerging Infectious Diseases*, 23(5), 860-861. doi: 10.3201/eid2305.161238.
- Verhulst, A. (1990). Lessons from field experience in the development of monogastric animal production. In: Mack, S. (ed.). *Strategies for sustainable animal agriculture in developing countries*. Proceedings of the FAO Expert Consultation held in Rome, Italy, 10-14 December 1990. FAO Production and Health Paper 107, pp. 261-271. <http://www.fao.org/3/t0582e/T0582E27.htm> (accessed 7 June 2020).
- Vial, L., Wieland, B., Jori, F., Etter, E., Dixon, L., & Roger, F. (2007). African swine fever virus in soft ticks, Senegal. *Emerging Infectious Diseases*, 13(12), 1928-1931. doi: 10.3201/eid1312.071022.
- Viltrop, A., Boinas, F., Depner, K., Jori, F., Kolbasov, D., Laddomada, A., Ståhl, K., & Chenais, E. (2021). 9. African swine fever epidemiology, surveillance and control. In: Iacolina, L., Penrith, M.-L., Bellini, S., Chenais, E., Jori, F., Montoya, H., Ståhl, K., Gavier-Widén, D. (eds). *Understanding and combatting African swine fever – A European perspective*. pp.229-261. doi: 10.3920/978-90-8686-910-7\_9. Wageningen Academic Publishers, Netherlands.
- Voigt, E.A., & von den Driesch, A. (1984). Preliminary report on the faunal assemblages from Ndongondwane, Natal. *Annals of the Natal Museum*, 26, 95-104.
- Wade, A., Achenbach, J.E., Gallardo, C., Settypalli, T.B.K., Souley, A., Djonwe, G., Loitsch, A., Dauphin, G., Ngang, J.J.E., Boyomo, O., Cattoli, G., Diallo, A., & Lamien, C.E. (2019). Genetic characterization of African swine fever virus in Cameroon, 2010-2018. *Journal of Microbiology* 57(4), 316-324. doi: 10.1007/s12275-019-8457-4.
- Wadoum, R.E.G., Lichoti, J.K., Nantima, N., Austine, B., Amara, L., Sesay, A.K., JoJo, D.H., Conteh, A.M., Leigh, M.H., Marah, J., Sesay, H.M., Caulker, G., Kanu, S.T., Sesay, B.H., Turay, J.A., & BoBo, G. (2020). Quantitative outcomes of a One Health approach to investigate the first outbreak of African swine fever in the Republic of Sierra Leone. *Global Journal of Medical Research: K Interdisciplinary*, 20(1), Version 1,0 Year 2020.
- Walker, J.S. (1933). *East African swine fever*. Institute of Veterinary Pathology, University of Zurich, Zurich, Switzerland.
- Wambura, P.N., Masambu, J., & Msami, H. (2006). Molecular diagnosis and epidemiology of African swine fever outbreaks in Tanzania. *Veterinary Research Communications*, 30(6), 667-672. doi: 10.1007/s11259-006-3280-x.
- Wesley, R.D., & Pan, I.C. (1982). African swine fever virus DNA: restriction endonuclease cleavage patterns of wild type, Vero cell-adapted and plaque-purified virus. *Journal of General Virology*, 63(2), 383-391. doi: 10.1099/0022-1317-63-2-383.
- Wesley, R.D., & Tuthill, A.E. (1984). Genome relatedness among African swine fever field isolates by restriction endonuclease analysis. *Preventive Veterinary Medicine*, 2, 53-62. doi: 10.1016/0167-5877(84)90048-5.

- Wilkinson, P.J. (1984). The persistence of African swine fever in Africa and the Mediterranean. *Preventive Veterinary Medicine* 2, 71-82. doi: 10.1016/0167-5877(84)90050-3.
- Wilkinson, P.J., Pegram, R.G., Berry, B.D., Lemche, J., & Schels, H.F. (1988). The distribution of African swine fever virus isolated from *Ornithodoros moubata* in Zambia. *Epidemiology and Infection*, 101(3), 547-564. doi: 10.1017/S0950268800029423.
- World Organisation for Animal Health, (2021). OIE Handistatus II, Tanzania 1996 – 2004. [https://web.oie.int/hs2/sit\\_pays\\_mald\\_pl.asp?c\\_pays=30&c\\_mald=13](https://web.oie.int/hs2/sit_pays_mald_pl.asp?c_pays=30&c_mald=13).
- World Organisation for Animal Health. (2021). OIE Handistatus II, Botswana 1996 – 2004. [https://web.oie.int/hs2/sit\\_pays\\_mald\\_pl.asp?c\\_pays=193&c\\_mald=13](https://web.oie.int/hs2/sit_pays_mald_pl.asp?c_pays=193&c_mald=13)
- World Organisation for Animal Health-WAHIS. (2005-2021). <https://wahis.oie.int/#/home>.
- World Organisation for Animal Health. (2012). Self-declaration by Mauritius of regaining its freedom from African swine fever. Bulletin, No. 2012-3, 37-38. [https://www.oie.int/fileadmin/Home/eng/Publications\\_%26\\_Documentation/docs/pdf/bulletin/Bull\\_2012-3-ENG.pdf](https://www.oie.int/fileadmin/Home/eng/Publications_%26_Documentation/docs/pdf/bulletin/Bull_2012-3-ENG.pdf)
- Yona, C.M., Vanhee, M., Simulundu, E., Makange, M., Nauwynck, H.J., & Misinzo, G. (2020). Persistent domestic circulation of African swine fever virus in Tanzania, 2015-2017. *BMC Veterinary Research*, 16, 369. doi: 10.1186/s12917-020-02588-w.