One hundred years of African swine fever: A tribute to R. Eustace Montgomery

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One hundred years ago, the first scientific publication on "a form of swine fever" that occurred in East Africa was published by R. Eustace Montgomery in the *Journal of Comparative Pathology and Therapeutics* (Montgomery, 1921). Now known as African swine fever (ASF), this disease has, over the last century, been reported from all five continents and is dreaded by pig industries worldwide (Liang et al., 2020; Penrith, 2020). It is hoped that this tribute will contribute to ensuring that the great legacy of Montgomery's research is not forgotten. Table 1 lists his key findings that remain valid today.

Robert Eustace Montgomery was born in 1880 in the United Kingdom and graduated in 1903 from the Royal (Dick) Veterinary College in Edinburgh. His research on African swine fever was undertaken during the period from 1909 to 1918 when he was the pathologist for the East African Protectorate. He left East Africa in 1918 for South Africa to replace Sir Arnold Theiler as Director of Veterinary Research at the Onderstepoort Laboratory (later the Onderstepoort Veterinary Institute), but left again for East Africa when Theiler was re-appointed. He died on June 11, 1932 while serving as veterinary adviser to the Colonial Office (S2A3 Biographical Database of Southern African Science, 2020).

The monumental paper describing Montgomery's painstaking research was published in two parts that appeared three months apart. This is clearly reflected in the Web of Science database CAB Abstracts, but some databases only reflect the first part, or alter the title to include "Part I" and "Part II," which is incorrect and has always resulted in errors of citation. Furthermore, the format of the paper does not make for easy reading. A footnote to the first page explains that the report consists of laboratory records, which the author had planned to revise and process further into a formal publication. The First World War and subsequent changes in location and duties of the author delayed the publication, and rather than lose the information the laboratory records were simply published. These are extremely valuable and reflect the detailed investigation of the important aspects of the disease with all the means that existed at the time.

TABLE 1. Key findings described by Montgomery[1]

	Montgomery's observations	Subsequent confirmation
1	Outbreaks in domestic pigs were associated with the presence of warthogs	Warthogs have been confirmed in numerous studies as the natural reservoir of the ASF virus (reviewed by Plowright et al., 1994)
2	Warthogs and bushpigs show no ill effects after infection with ASF infective material	Confirmed by experimental studies (Anderson et al., 1998; Thomson et al., 1983
3	Members of the pig family are the only species that are naturally susceptible to ASF	Numerous studies have failed to find evidence for susceptibility of other species in nature (reviewed by Plowright et al., 1994)
4	Infective materials in pigs included blood, organs, body cavity fluids, urine, faeces, bile	Widespread presence of the virus in in pigs that have died of ASF has been confirmed often (reviewed by Plowright et al., 1994)
5	Pigs could be infected by inoculation, direct contact, and ingestion of infective materials	All of these routes of infection have been confirmed in many studies (reviewed by Plowright et al., 1994)
6	The agent is not transmitted by passing through air	The virus is only transmitted over distances of a few metres in closed housing (de Carvalho Ferreira et al., 2013; Wilkinson et al., 1977)
7	The infectious agent was filterable, i.e. a virus	The agent was accepted to be a virus in all subsequent studies
8	The agent remained viable for long periods in a protein environment	Persistence of the virus in a protein environment has been confirmed frequently (reviewed by Plowright et al., 1994)
9	The agent was relatively resistant to decomposition	Persistence of ASF viral DNA in decomposed carcasses has been helpful for surveillance in wild boar in Europe (Carlson et al., 2018; Zani et al., 2020)
10	Heating at 60°C for 10, 15, or 20 minutes inactivated the agent	This temperature/time ratio remains valid although longer periods at higher temperatures are usually recommended as a precaution
11	Pig sties in which pigs had died of ASF were safe for pigs introduced after 5.5 days without cleaning or disinfection	Pig sties in which pigs had died of ASF were safe for pigs introduced after 3 days without cleaning or disinfection (Olesen et al., 2018; Steyn, 1932)

The report by Montgomery is no longer widely available and probably not widely read, but the research it described was ground breaking, and the key findings have been confirmed in research over the subsequent decades up to the present time. As a tribute to R. Eustace Montgomery, the discoverer and founding father of research on ASF, we provide a summary of his key findings that have stood the test of time and advanced technology.

The paper provides the first description of the disease as it occurred against the background of the way the settlers' pigs were farmed and traded. It describes the clinical signs and macroscopic pathology of natural and experimental cases. Pigs were raised either for home consumption or direct movement to a bacon factory and each outbreak occurred independently. Although circumstantial evidence suggested involvement of warthogs in the transmission of the disease to pigs, attempts to infect pigs by direct contact with warthogs consistently failed. However, inoculation of pigs with the blood of either warthogs or bushpigs that were experimentally infected, resulted in infection of the domestic pigs for up to or a little longer than two weeks post infection of the wild pigs (Montgomery, 1921).

The second part of the paper described investigations into immunity to the disease in domestic pigs. Efforts to produce immunity through the use of serum against classical swine fever obtained from England failed to protect pigs against the East African virus. A pig that was immune to the classical swine fever virus developed severe clinical signs and died when inoculated with the East African virus. However, limited experiments with serum from one pig that survived infection with the East African virus as well as serum from bush pigs did

not demonstrate protection in inoculated pigs from subsequent infection with the East African virus. Using heated virus, Montgomery found that one pig inoculated with the virus that had been heated to the temperature required to destroy the virus was immune, but pigs inoculated with virus heated to below the virus death point developed chronic forms of the disease that resembled classical swine fever[1]. Similar chronic forms of ASF have been described elsewhere particularly in the Iberian Peninsula after the 1960 incursion and were ascribed to naturally attenuated viruses. However, this phenomenon has rarely been observed in other endemic areas. Vaccination of pigs with inadequately attenuated ASF virus is also likely to have played a role (Sánchez-Vizcaíno et al., 2015).

In spite of the fact that there was no cross protection with classical swine fever antiserum, the differences in the manifestation of the disease and the fact that classical swine fever virus was markedly more resistant to heating than ASF virus, Montgomery preferred to consider the East African virus to be a particularly virulent variety of the virus that caused classical swine fever until proven otherwise by further investigation. It was only in the 1940s that this topic ceased to be controversial (Conceição, 1949; De Kock et al., 1940; Verge, 1944).

Since the initial attempts by Montgomery to immunize pigs against ASF, great efforts by researchers in many countries have gone into developing a safe, efficacious vaccine but the results so far have largely been disappointing. In recent times considerable progress has been made particularly towards identifying promising candidates for a vaccine against the East African ASF virus currently circulating widely in Europe and Asia (Rock, 2021), but despite the available technology today which is beyond anything that Montgomery could have dreamed of, the truth is that a broad spectrum, guaranteed safe and efficacious vaccine against ASF in all its epidemiological scenarios has not become a reality. Therefore one hundred years after the discovery, the world is still grappling with the ASF virus. Thus the struggle continues on all fronts.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

ETHICAL APPROVAL

The authors confirm that the ethical policies of the journal, as noted on the journal's author guidelines page, have been adhered to. No ethical approval was required as this is a review article with no research data.

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