Orthopoxviruses

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Zoonotic diseases, defined as diseases or infections that are naturally transmissible from vertebrate animals to humans, represent a significant threat to global health. Among the species recognized as pathogenic to humans, more than half originated in animals, and some have been characterized as emerging or re-emerging pathogens. Most zoonotic pathogens originated in wild and domesticated mammalian hosts such as bats, rodents, and primates. The analysis of global trends indicates that new zoonotic threats will continue to emerge at an accelerating rate, and are mainly associated with an growthing population, changes in land use, climate changes, increased intercontinental travel, and expanded trade networks. Poxviruses are among mankind's longest and best-known viruses mainly because of their most feared and lethal representative, Variola virus (VARV), the causative agent of smallpox. Orthopoxvirus is the most important and well-characterized poxvirus genus, mainly due to its impact on human and animal health. Orthopoxviruses are remarkable for their wide host spectrum, ranging from humans to domestic and wild animals.

Keywords: Orthopoxvirus ; Poxviridae ; zoonosis ; Monkeypox virus ; Cowpox virus ; Vaccinia virus ; host range ; wild and domestic animals ; emergent viruses ; outbreak

1. Poxvirus

Poxviruses are of great veterinary and human importance and infect numerous vertebrate and invertebrate animals, including humans. The Poxviridae family is divided into two subfamilies, namely: Chordopoxvirinae, which infect vertebrates, and Entomopoxvirinae (A–C), which infect invertebrates. The Chordopoxvirinae subfamily is further divided into 18 genera (Avipoxvirus, Capripoxvirus, Centapoxvirus, Cervidpoxvirus, Crocodylidpoxvirus, Leporipoxvirus, Macropopoxvirus, Molluscipoxvirus, Mustelpoxvirus, Orthopoxvirus, Oryzopoxvirus, Parapoxvirus, Pteropopoxvirus, Salmonpoxvirus, Sciuripoxvirus, Suipoxvirus, Vespertilionpoxvirus, and Yatapoxvirus), distinguishable by their serological reactions[1] [2]. The family Poxviridae comprises large, brick-shaped or ovoid enveloped viruses containing a linear, double-stranded DNA genome approximately 200 kilobase pairs in length [3][4]. Poxviruses are among mankind's longest and best-known viruses mainly because of their most feared and lethal representative, Variola virus (VARV), the causative agent of smallpox. Before its remarkable eradication in 1980, VARV represented a centuries-old threat to humans worldwide and killed approximately 300–500 million people during the 20th century [5]. The global eradication of smallpox marked the culmination of an intensive vaccination program and quarantine measures promoted by the World Health Organization (WHO) [6][7][8]. Although VARV was eradicated 40 years ago, many challenges regarding poxvirus infections persist, including the worrisome possibility of VARV reintroduction by accidental release, its use as a biological weapon, or biological weapon, or the emergence and re-emergence of zoonotic orthopoxviruses worldwide [9][10]. Among Poxviruses, the Orthopoxvirus genus is the most important and well-characterized, mainly due to its impact on human and animal health, and for its remarkable wide host spectrum, ranging from humans to domestic and wild animals [11][4] (Figure 1).

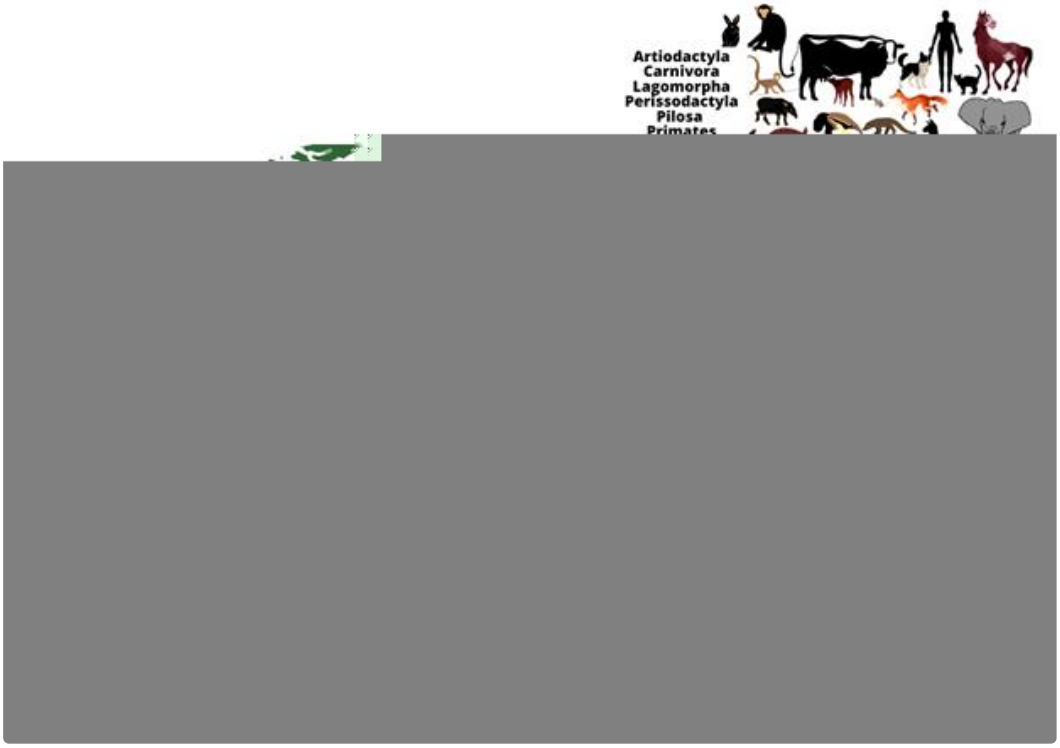

Figure 1: The worldwide distribution and host range of monkeypox, cowpox and vaccinia viruses. The image shows the range of animal hosts (represented by orders) that have been demonstrated to be naturally infected by some Orthopoxvirus species, according to different regions of the world (except by Monkeypox virus in the United States of America, represented by imported cases). Orthopoxvirus infections have been demonstrated in animals belonging to different orders, using different methods (virus isolation, molecular detection of viral genomes or serological screening for antibodies against orthopoxviruses). The occurrence of some zoonotic orthopoxviruses has already been confirmed (by virus isolation or molecular detection of the viral genome) in some geographical regions (indicated by colored dots: blue: vaccinia virus (including buffalopox and rabbitpox viruses) in South America, Europe, Asia, and the Middle East; brown: monkeypox virus in Africa and North America; orange: cowpox virus in Europe and Asia).

2. Orthopoxvirus

The Orthopoxvirus genus comprises VARV, vaccinia (VACV) and vaccinia-like, cowpox (CPXV), monkeypox (MPXV), camelpox, and Akhmeta viruses, and other species with zoonotic potential. All orthopoxviruses share significant DNA sequence similarity and are immunologically cross-reactive and cross-protective. Infection with any orthopoxvirus is considered to generate protection against exposure or re-exposure to any other member of the genus [12][13]. Orthopoxvirus species are named primarily according to the hosts from which they were first isolated and identified; however, the name does not necessarily represent its natural reservoir or complete host range [6][14][15][16]. Despite a large number of studies, little is known about the primary hosts and reservoirs of zoonotic orthopoxviruses in nature, or their transmission and maintenance cycles [17]. Regarding the host range, orthopoxviruses can be both highly specialized and host restricted or generalists with a broad host range. For instance, VARV is a highly specialized virus that infects only humans, whereas MPXV, CPXV, and VACV are examples of generalist zoonotic orthopoxviruses that can infect several mammalian host species and also spillover into humans [17]. The evolution of generalist pathogens requires the successful crossing of host transmission barriers [18]. These include geographical, ecological, and behavioral constraints that separate a virus from its possible recipient hosts; virus-host cell incompatibility, such as tissue tropism, differences in receptor binding, genome replication, production, and shedding of infectious particles; and host immunity evasion, which includes cellular barriers or responses that restrict the infection and/or evasion of a virus from the innate immune system of its host [19]. To overcome these barriers, orthopoxviruses have different biological features that can synergistically contribute to the transmission to, and exploitation of, a broad range of new hosts species as observed for CXPV, MPXV, and VACV.

Orthopoxviruses can cause both local lesions on the skin and systemic infections, resulting in direct and indirect transmission routes. When accompanied by viral particle stability in the environment, this can increase the likelihood of potential hosts being exposed to the virus independently of direct contact with infected hosts. In addition, orthopoxviruses can infect a variety of mammalian cells in a manner that is mostly independent of species-specific receptors and have large genomes that carry the information essential for viral replication, thereby increasing the possibility of successful infection in a new cell/host. Although the double-stranded DNA genomes of orthopoxviruses have low mutation rates when

compared with other viruses, such as RNA viruses, orthopoxviruses possess a genetic arsenal comprising several immune-regulatory, virulence, and host range genes [17]. The variety of host-genes among poxviruses enables them to express different viral proteins with important roles in cell tropism, as well as in the modulation of host signaling pathways and immunomodulatory responses, thereby establishing optimal cellular conditions for viral replication [20]. Finally, many of the strategies employed by orthopoxviruses to evade host immune defenses target conserved elements of the immune system in different potential hosts [17]. Combined, these features altogether are crucial for virus-cell and virus-host interactions and can contribute to the success of viral replication and transmission. Despite the eradication of smallpox, the possibility of its re-emergence or the emergence of other orthopoxviruses in human and animal populations is a relevant global health issue. As smallpox vaccination is no longer mandatory, most of the world's population that is under 40 years of age lacks immunity against orthopoxviruses [21][22]. This scenario is highlighted by numerous reports in recent years of human diseases caused by zoonotic orthopoxviruses such as MPXV [23][24][25][26][27][28][29][30], CPXV [31][32][33][34][35][36][37][38], VACV-like [39][40][41][42][43][44][45][46], and Akhmeta virus [16]. To date, the circulation of orthopoxviruses among wild and domestic animals has been recorded in different regions of the world, including South America, Africa, Europe, the Middle East, and Asia [24][37][39][47][48][49][50][51][52][53][54][55]. These facts raise concerns regarding the host ranges and distribution of orthopoxviruses, as well as their potential to cause outbreaks in animals and human populations, thereby further impacting animal and public health.

2.1. Monkeypox Virus

Monkeypox virus isolates are subdivided into two clades, namely, the West African and the Congo Basin clades, based on genetic and phenotypic (virulence) differences [56]. Notably, several studies have indicated that the clinical signs are similar between infections caused by viruses from either clade[57]. The first observation of MPXV infection was reported in 1958 during an outbreak of pustular rash illness in cynomolgus macaques (*Macaca fascicularis*) arriving in Copenhagen, Denmark, from Singapore [58]. Despite being named after the first described host, non-human primates are accidental hosts for MPXV [59]. In 2003, an MPXV outbreak occurred in the United States of America (USA). Human infection was associated with direct contact with ill pet prairie dogs that were kept near to infected exotic animals imported from Ghana, West Africa [60]. This episode, as well as the infection of rodents, heightened concerns regarding the introduction of MPXV into the Americas. Meanwhile, the susceptibility of several African rodents to MPXV raised worries about the transmission of the virus to humans, as these animals are sometimes kept as pets [61][62]. Although humans are also accidental hosts [59], MPXV became the most significant pathogenic zoonotic orthopoxvirus for humans since the eradication of smallpox, given its associated morbidity (systemic infection) and lethality. The natural source of MPXV and its maintenance cycle in nature remains unknown as the virus has only been isolated twice in nature (wild animals): once from the rope squirrel (*Funisciurus anerythrus*), Zaire, in 1985 [63], and once from the sooty mangabey (*Cercocebus atys*), Côte d'Ivoire, in 2012 [64]. To date, naturally occurring MPXV infections remain confined to the forest regions of West and Central Africa [65]. Consequently, a higher proportion of human MPXV cases are reported in regions (mainly African villages) where humans and non-human primates live in close proximity. The consumption, hunting, and handling of meat derived from non-human primates, rodents, and other small mammals have also been associated with human cases of MPXV infection [66][67][68][69][70]. Close contact with rodents has also been implicated as a source of human infection [71][72]. As monkeypox is an emerging zoonotic disease with epidemic potential and much of its host range and maintenance cycle in nature remains obscure, advances are urgently needed to better understand the natural cycle of MPXV.

2.2. Cowpox Virus

Edward Jenner was the first to document CPXV infection after observing local lesions on the teats of cows, which he called "cow-pox". Then, in 1798, Jenner demonstrated the efficacy of "true cow-pox" scarification in inducing immunity against smallpox [73][74]. There were frequent reports of bovine cowpox cases until the early 1970s in Europe, with sporadic transmission to humans, mainly milkers, occurring via contact with infected cows [75]. CPXV is currently mostly found in Europe and northern and central Asia where cases of infections in rodents, cats, and humans continue to be reported. In Great Britain, CPXV is endemic in rodents such as bank voles (*Myodes glareolus*) and wood mice (*Apodemus sylvaticus*), while in Turkmenistan and Russia CPXV was isolated in the laboratory as well as in wild rodents [76]. Furthermore, serological surveys have also detected orthopoxvirus infections in France, Austria, and Norway in voles and wood mice [76]. Antibodies against orthopoxviruses were also detected in red foxes *(Vulpes vulpes*) in Western Europe being possibly related to CPXV infection, although red foxes are also known to be susceptible to ectromelia virus [76][77]. These reports of CPXV infection have occurred alongside an increasing number of reported infections in different animal species, leading to the designation of CPXV as an emerging health threat [78]. Cats are the most affected domestic animals, mainly due to their predatory behavior against rodents, which are the CPXV reservoir in domestic and peridomestic environments [13][79][80][81][82]. However, the exact prevalence of feline cowpox is uncertain. CPXV infections in cats are mostly observed after increases in the rat population density [82][13]. The infection of pet rats and domestic cats

by CPXV brings a higher risk of exposure to humans in the domestic environment, but rural or wild areas may be important as the source of infection [33]. Even though human cowpox cases are usually self-limiting and not lethal, most people are susceptible to the disease, particularly children who are more often in close contact with pet animals [34][83]. The zoonotic potential of CPXV and its capacity to cause infection in wild and domestic environments are well established; however, many aspects of its natural maintenance cycle remain unknown.

2.3. Vaccinia Virus and Related Viruses

Although VACV is the most extensively studied orthopoxvirus, its origin remains unknown [84]. Vaccinia virus, the prototype species of the Orthopoxvirus genus, is best known as the live attenuated virus used worldwide by the WHO in the smallpox vaccine [85][86][87]. Despite the successful use of VACV as a vaccine, several vaccine strain-dependent complications have been reported, including progressive vaccinia, eczema vaccinatum, vaccinia gangraenosum, and neurological complications [88][89]. During smallpox eradication campaigns, various VACV strains with different degrees of virulence were used. The highly attenuated and modified VACV Ankara is a well-stablished third-generation smallpox vaccine [90][91]. For a long time, VACV vaccine strains were assumed to be incapable of establishing a natural cycle due to their attenuation in the laboratory. However, several VACVs have been isolated from different host species, and in different locations around the world [39][92][93][94]. Similarly, sub-lineages of VACV (as buffalopox virus (BPXV) and rabbitpox virus (RPXV)) have been consistently isolated in different countries and from a wide range of hosts [12][13][14][95][96]. In India, BPXV was first described in 1934 and was responsible for infections that mainly affected domestic buffaloes (Bubalus bubalis), but also cows and humans [97]. Since its first description, outbreaks of BPXV have been reported in India, Pakistan, Nepal, Egypt, Bangladesh, Indonesia, Russia, and Italy [13][98][51][99][100]. Humans become infected with BPXV through close contact with infected animals and no human-to-human transmission has been reported to date. Additionally, a variety of animal species, such guinea pigs, BALB and white Swiss mice, cows, buffalo calves, rabbits, and chickens have been experimentally demonstrated to be susceptible to BPXV. Nevertheless, the role of these species in BPXV transmission and maintenance in nature remains unknown [41][101] and requires clarification. RPXV is another VACV described as affecting different animal species worldwide. RPXV was first described between 1930–1933 after outbreaks in laboratory rabbits in the United States of America. Additional outbreaks were later reported in 1941 in the Netherlands, while several other cases were also reported in Europe and the USA [102][103]. To date, no human transmission has been described for RPXV [102][104]. Different VACV isolates also circulate in South American countries, including Uruguay, Argentina, Colombia, and Brazil [52][53][54][105]. In the last few decades, several outbreaks of VACV infection have occurred in Brazil where the disease caused by VACV is popularly known as “bovine vaccinia”, due to its association with dairy cattle [106][39]. Bovine vaccinia is characterized by vesiculopustular exanthematous disease in cattle and dairy workers who have direct contact with infected animals [107][108][109]. Initially, VACV outbreaks were described as affecting dairy cattle and humans in rural environments. Consequently, the epidemiology of the bovine vaccine in Brazil is associated with economic losses resulting from compromised milking herds [39][109][110][111]. Nevertheless, VACV circulation in Brazil has already been documented for all the regions, affecting farm animals other than cattle, as well as wild animals [39]. Although VACV is known to have a broad range of hosts, many aspects of its natural history remain unknown. Although VACV infection is usually self-limiting and not lethal, the disease profile in immunocompromised individuals may be differentially affected, presenting with severe and generalized manifestation [112], similar to that observed for cowpox. Although farm animals are important sources of infection, the commercialization and consumption of dairy products could be alternative routes of zoonotic VACV transmission. In addition, VACV circulation in domestic animals such as cats and dogs bring the risk of viral transmission to humans in the domestic environment. The urban emergence of VACV could be an important health burden due to the unpreparedness of healthcare professionals to correctly identify and handle emerging cases [113].

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