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Review

Paramyxoviruses in reptiles: A review

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ABSTRACT

In 1972, an outbreak of neurorespiratory disease in a Swiss serpentarium formed the basis for the first description of a paramyxovirus isolated from a reptile. In the forty years since this outbreak, there have been over 50 published reports about reptilian paramyxoviruses from all over the world. The majority of these investigations have concerned themselves with ferlaviruses (sometimes previously referred to as ophidian paramyxoviruses, or OPMV). The biology of these viruses is reviewed and this is followed by a review of the clinical findings that are associated with ferlaviral infection and the various diagnostic tests that are used to identify infected reptiles. Recently, a second, and highly divergent, reptilian paramyxovirus, Sunshine virus, was described in Australian pythons, so it is an opportune time to reflect on the paramyxoviruses that infect reptiles.

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1. Introduction

A wide range of viruses have been detected in reptiles throughout the world and the interested reader is referred to the reviews by Wellehan and Johnson (2005), Jacobson (2007), Marschang (2011) and Ariel (2011) for more general overviews of these viruses. This review will focus on the paramyxovirus infections of reptiles. Since an outbreak of neurorespiratory disease in a Swiss serpentarium that was associated with a paramyxovirus (Folsch and Leloup, 1976), reptilian paramyxoviruses have been described in other regions of Europe (Ahne et al., 1987; Blahak, 1995; Manvell et al., 2000; Franke et al., 2001), USA (Jacobson et al., 1980; Jacobson et al., 1981; Potgieter et al., 1987; Richter et al., 1996) and Brazil (Nogueira et al., 2002; Kolesnikovas et al., 2006). Most recently, a novel paramyxovirus, named Sunshine virus, was described in Australian pythons (Hyndman et al., 2012a,b) and so it is important to review the established and emerging areas in this field.

2. Taxonomy of reptilian paramyxoviruses

Members of the family *Paramyxoviridae* are currently divided into two subfamilies: *Pneumovirinae* and *Paramyxovirinae* (ICTV, 2013). *Paramyxovirinae* currently contains seven genera, one of which is the genus *Ferlavirus*. Prior to the discovery of Sunshine virus, all phylogenetically-characterised reptilian paramyxoviruses have clustered within *Ferlavirus* (Marschang et al., 2009). Sunshine virus clusters within *Paramyxoviridae* but outside of both subfamilies and therefore broadens our understanding of the diversity of paramyxoviruses that infect reptiles (Hyndman et al., 2012a).

2.1. *Ferlavirus*

The literature has not shown conformity in how it refers to ferlaviruses. Since the first characterisation of a snake paramyxovirus that was named Fer de Lance Virus (FDLV) (Clark et al., 1979), the term ophidian paramyxovirus (often abbreviated to OPMV or oPMV) has also been used to describe the paramyxoviruses found in snakes (Lloyd and Flanagan, 1991; Homer et al., 1995; Jacobson et al., 1997; Manvell et al., 2000; Kindermann et al., 2001; Oros et al., 2001; Nogueira et al., 2002; Kolesnikovas et al., 2006). In 2009, a proposal was put forward by Kurath to the International Committee on Taxonomy of Viruses (ICTV) to create the new genus *Ferlavirus* with *Fer-de-Lance paramyxovirus* (the same virus as FDLV) as its type species. This proposal has been accepted by the ICTV (2013) and all future work should refer to these viruses as ferlaviruses. By avoiding the general term "ophidian paramyxovirus", Sunshine virus and the ferlaviruses of snakes can be unambiguously delineated.

Folsch and Leloup (1976) produced the first report of a reptilian paramyxovirus following an outbreak of neurorespiratory disease in a Swiss serpentarium. The physicochemical traits of this first isolate were then characterised and described by Clark et al. (1979). The origin of the ferlaviruses is unknown but one reference provides further insight. A personal communication mentioned in a paper by Kolesnikovas et al. (2006) states that the Brazilian lancehead vipers (*Bothrops moojeni* but incorrectly referred to as Fer-de-Lance vipers [*B.atrox*] in earlier works) in the Swiss serpentarium originated from Brazil. No further information is provided.

The entire genome of *Fer-de-Lance paramyxovirus* has been sequenced (Kurath et al., 2004). The genome is 15,378 nucleotides long and is made up of seven distinct genes: 3′–Nucleocapsid (N)–Unknown (U)–Phosphoprotein/Protein V (P/V)–Matrix (M)–Fusion (F)–Haemagglutinin-Neuraminidase (HN)–RNA-dependent RNA polymerase (L). The fusion gene has been analysed by others (Franke et al., 2006). Several authors have analysed the phylogenetic relationships that exist between ferlaviruses (Ahne et al., 1999b; Franke et al., 2001; Kindermann et al., 2001; Marschang et al., 2009; Papp et al., 2010a,b; Abbas et al., 2011) while others have compared the ferlaviruses to other paramyxoviruses (Junqueira de Azevedo et al., 2001; Kurath et al., 2004; Marschang et al., 2009). These studies support the classification of the squamate ferlaviruses as a single genus containing at least three distinct genogroups (A, B and C). The clinical significance and serodiagnostic implications of the different genotypes remains undefined.

The serological relatedness of ferlaviruses to other paramyxoviruses has been reported by several authors (Clark et al., 1979; Potgieter et al., 1987; Blahak, 1995; Richter et al., 1996; Ahne et al., 1999b). Clark et al. (1979) titrated antisera against 19 myxoviruses (16 paramyxoviruses and 3 orthomyxoviruses) against *Fer-de-Lance paramyxovirus* and then did the reverse by titrating ferlavirus antisera against the same suite of myxoviruses. No cross-reactivity was detected. Richter et al. (1996) showed that the antisera specific for eight paramyxoviruses did not inhibit the haemagglutinating ability of three ferlaviral isolates. Ahne et al. (1999b) was also unable to demonstrate any cross-reactivity between ferlaviral antisera and a range of paramyxoviruses.

In contrast to these findings, serological relationships between ferlaviruses and other paramyxoviruses have been shown by other authors. Blahak (1995) demonstrated a serological relationship between ferlavirus and *Avian paramyxovirus* types 1 and 7 (aPMV-1 and -7), while Gravendyck et al. (1998) reported on the cross-reactivity of a paramyxovirus from a monitor (*Varanus prasinus*) with aPMV-7. Later, Manvell et al. (2000) classified two isolates of ferlavirus as "ophidian paramyxovirus type 1 (PMV-1) and ophidian paramyxovirus type 7 (PMV-7)" based on the strength of their serological cross-reactivity with antisera against aPMV-1 and -7. In another report, Potgieter et al. (1987) used immunohistochemical staining to detect ferlavirus in a section of infected snake lung after the lung had been treated with the fluorescently-labelled antisera of *Parainfluenza virus* type 2.

The incongruence that exists in the conclusions of the studies on ferlaviral serological relatedness could be explained by a serological *un*relatedness between the various ferlaviral isolates used in these studies. Serological unrelatedness between ferlaviral isolates has been shown in at least two studies (Marschang et al., 2002; Allender et al., 2008). In general, however, it seems reasonable to