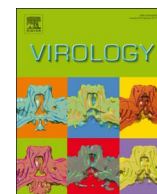




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## From fish to frogs and beyond: Impact and host range of emergent ranaviruses

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### ABSTRACT

Ranaviruses are pathogens of ectothermic vertebrates, including amphibians. We reviewed patterns of host range and virulence of ranaviruses in the context of virus genotype and postulate that patterns reflect significant variation in the historical and current host range of three groups of *Ranavirus*: FV3-like, CMTV-like and ATV-like ranaviruses. Our synthesis supports previous hypotheses about host range and jumps: FV3s are amphibian specialists, while ATVs are predominantly fish specialists that switched once to caudate amphibians. The most recent common ancestor of CMTV-like ranaviruses and FV3-like forms appears to have infected amphibians but CMTV-like ranaviruses may circulate in both amphibian and fish communities independently. While these hypotheses are speculative, we hope that ongoing efforts to describe ranavirus genetics, increased surveillance of host species and targeted experimental assays of susceptibility to infection and/or disease will facilitate better tests of the importance of hypothetical evolutionary drivers of ranavirus virulence and host range.

### 1. Background

Ranaviruses are large double-stranded DNA viruses of the family *Iridoviridae*, which infect amphibians, reptiles and fish (Duffus et al., 2015). They are considered important emergent pathogens and several lines of evidence point to humans playing a significant role in emergence: 1) disease outbreaks have occurred frequently in cultured amphibians and fish (Zhang et al., 2001), 2) ranavirus has been detected frequently infecting invasive populations of non-native species and traded animals in Europe, Asia and South America (Une et al., 2009; Sharifian-Fard et al., 2011; Soto-Azat et al., 2016) and 3) translocations by humans are thought to have facilitated range expansion on at least two continents (Picco and Collins, 2008; Price et al., 2016). The broad host range and role of people in emergence were key reasons behind the World Organisation for Animal Health's (OIE) decision to list ranaviruses as notifiable pathogens of amphibians (Schloegel et al., 2010) and fish (OIE, 2016). However, the ecological impacts of emergent ranaviruses on their ectothermic hosts, at the levels of individuals and populations, are highly variable. In some cases, emergent disease causes extensive mortality and drives host

populations into rapid demographic decline that can persist over multiple host generations. Alternatively, persistent disease dynamics may not be associated with observable population decline, and asymptomatic infections can also occur at high prevalence. Why host responses exhibit such variation, even within single host species is a subject of much debate and research effort.

Several ecological factors have been identified as correlates of mortality events. These factors can be broadly classified as: 1) age-dependent and host-specific susceptibility; 2) abiotic drivers, and; 3) host abundance and/or density. The difficulty with attribution is that many of these factors manifest coincidentally (Brunner et al., 2015). For example, outbreaks of *Epizootic haematopoietic necrosis virus* (EHNV) in red-finned perch (*Perca fluviatilis*) are age-specific and seasonal (Whittington et al., 2010), and mass mortality of adult common frogs may be linked to aggregation during breeding (Cunningham et al., 1996; Price et al., 2016). Attempting to completely disentangle the role of each factor is challenging due to interactions; temperature, for instance, can directly affect the outcome of ranavirus infections but also affects key aspects of the ecology of ectothermic vertebrates (Brunner et al., 2015).

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What is less explored is how systematic and pairwise variation in ranavirus genomes correlates with patterns of epidemic disease dynamics. However, research on *Frog virus 3* (FV3) has illustrated how the disease process is regulated by viral gene expression, ranaviruses evolve rapidly in single host species populations, and they recombine (Abrams et al., 2013; Epstein and Storfer, 2016; Price, 2016; Claytor et al., this issue). These findings, combined with evidence of heritable variation in host immunity to ranaviruses (Teacher et al., 2009; Echaubard et al., 2016), suggest that the emergence of epidemic disease dynamics (or lack thereof) must be governed to some degree by the genetic tools available to emergent ranaviruses. The specifics of gene conservation, expression and virulence are covered elsewhere, including in articles in this special issue. Here we review reports of ranavirus infection and epidemics in North and Central America, the region where ranavirus has been studied most intensively, and Europe, a region where a recently described ranavirus lineage is the cause of emerging disease, in the context of the phylogenetic identity of the causative ranaviruses. Where possible, we explore the relationships between ecological conditions and viral identity and comment on relative host ranges.

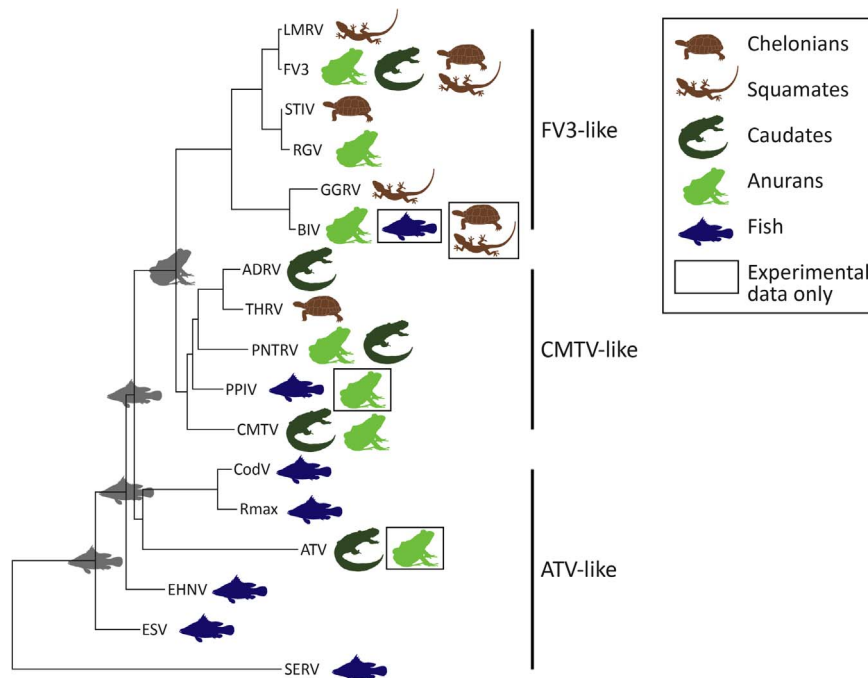
For our purposes, we will use terminology based on the phylogenetic analyses published in Jancovich et al. (2015), which identified four to five distinct *Ranavirus* lineages, but we will focus on the three associated with amphibians (frequently termed “amphibian-like ranaviruses” but hereon referred to as amphibian-associated ranaviruses): FV3-like ranaviruses, their sister group the common midwife toad virus (CMTV)-like variants, and the more basal *Ambystoma tigrinum virus* (ATV)-like group. These first two are monophyletic groups but for the purposes of this article we expand the ATV-like group to include all fish-associated forms at the base of the amphibian-like ranavirus phylogeny (Ariel et al., 2016; Subramaniam et al., 2016) which results in a paraphyletic group (Fig. 1). While there is significant variation encapsulated within these lineages (Echaubard et al., 2014), the deeper divisions described by these groups likely represent evolutionary steps

that involved changes in host range germane to our topic (Jancovich et al., 2010; Abrams et al., 2013). As more complete ranavirus genomes become available, we expect that ranavirus taxonomy and systematics will undergo further revision.

## 2. FV3-like ranaviruses in American herpetofauna

Fifty years after the serendipitous discovery of FV3 in the United States, FV3-like ranaviruses continue to cause mortality across the planet in wild and captive amphibians, chelonians, fish and squamate reptiles (Granoff et al., 1965; Duffus et al., 2015). The early work on FV3 presaged several interesting aspects of the biology of this virus. First, while experiments with this and closely related ranaviruses were often lethal to larval, and to a lesser extent adult amphibians, some individuals survived with persistent, asymptomatic infections (Clark et al., 1968, 1969; Tweedell and Granoff, 1968; Wolf et al., 1968). Second, the first FV3-like ranaviruses were isolated from animals purchased from biological suppliers (Clark et al., 1969), although there are few details of their particular origins (see Granoff et al., 1965). Third, it became clear, at least from cell culture experiments, that FV3 and related viruses have very broad host ranges (Granoff et al., 1966; Clark et al., 1968). Each of these patterns has been upheld in the five decades since.

Ranaviruses have been detected in amphibians across the United States and Canada (Fig. 2; Duffus et al., 2015). The vast majority of ranavirus detections have been FV3-like ranaviruses associated with mortality events, especially in larval amphibians (Green et al., 2002; Miller et al., 2011; Duffus et al., 2015). North American FV3-like ranaviruses have thus developed a reputation for high virulence, which has been supported by laboratory infection experiments (e.g., Pearman and Garner, 2005; Schock et al., 2008; Echaubard et al., 2016), though the outcome of exposure varies a great deal with host phylogeny and life history correlates, and virus genotype (Hoverman et al., 2010, 2011). Whilst episodic and recurrent mass mortality events attributed



**Fig. 1.** Phylogenetic perspective on host range of ranaviruses in the context of broad virus type (*Frog virus* (FV)3-like, common midwife toad virus (CMTV)-like, *Ambystoma tigrinum virus* (ATV)-like). Putative ancestral hosts (fish or amphibian) are denoted by gray host images at nodes. Host ranges of individual isolates serve as a guide only and do not control for observer effort. Hosts are summarised based on membership of five higher order taxonomic groups: chelonian, squamate, caudate, anuran and fish. The overall topology of the tree follows Fig. 3 of Stohr et al. (2007), which was simplified by removing tips for clarity of presentation. Isolate abbreviations: SERV, short-finned eel ranavirus; ESV, European sheatfish virus; EHNV, *Epizootic haematopoietic necrosis virus*; ATV, *Ambystoma tigrinum virus*; Rmax, *Ranavirus maximus*; CodV, *Cod iridovirus*; CMTV, common midwife toad virus; PPIV, pike-perch iridovirus; PNTRV, Portuguese newt and toad ranavirus; THRV, *Testudo hermanni* ranavirus; ADRV, *Andrias davidianus* ranavirus; BIV, *Bohle iridovirus*; GGRV, German gecko ranavirus; RGV, *Rana grylio* iridovirus; STIV, *Soft-shelled turtle iridovirus*; FV3, *Frog virus 3*; LMRV, *Lacerta monticola* ranavirus.

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