Distribution and Host Range of Ranaviruses

**Amanda L.J. Duffus, Thomas B. Waltzek, Anke C. Stöhr,
Matthew C. Allender, Michael Gotesman, Richard J. Whittington,
Paul Hick, Megan K. Hines, and Rachel E. Marschang**

1 Introduction

The genus *Ranavirus* is a group of globally emerging pathogens infecting fish,
amphibians, and reptiles, impacting both captive and wild animals. Ranaviruses are
pathogens capable of infecting multiple species at a site (e.g., Mao et al. 1999a;

A.L.J. Duffus (✉)
Department of Biology, Gordon State College, Barnesville, GA, USA
e-mail: aduffus@gordonstate.edu

T.B. Waltzek • M. Gotesman
Department of Infectious Diseases and Pathology, College of Veterinary Medicine,
University of Florida, Gainesville, FL, USA
e-mail: tbwaltzek@ufl.edu; mgotesman@ufl.edu

A.C. Stöhr
Institute of Environmental and Animal Hygiene, University of Hohenheim,
Stuttgart, Germany
e-mail: anke.stoehr@freenet.de

M.C. Allender
Department of Comparative Biosciences, College of Veterinary Medicine,
University of Illinois, Urbana, IL, USA
e-mail: mcallend@illinois.edu

R.J. Whittington • P. Hick
Faculty of Veterinary Science, University of Sydney, Sydney, NSW, Australia
e-mail: richard.whittington@sydney.edu.au; paul.hick@sydney.edu.au

M.K. Hines
University of Wisconsin-Madison, School of Veterinary Medicine, Madison, WI, USA
e-mail: mkhines@wisc.edu

R.E. Marschang
Laboklin GmbH & Co. KG, Bad Kissingen, Germany
e-mail: rachel.marschang@gmail.com

Duffus et al. 2008), and can be transmitted between taxonomic classes of ectothermic vertebrates (e.g., Brenes et al. 2014a, b; Brunner et al. 2015). Ranaviruses are known to infect at least 175 species across 52 families of ectothermic vertebrates, and are found on all continents but Antarctica (Table 1; Figs. 1 and 2). Most of what is known

Table 1 The taxonomic distribution of ranavirus cases among amphibian, fish, and reptilian hosts

	Family	No. species affected
Amphibians	Alytidae	1
	Ambystomatidae	8[a]
	Bufonidae	8
	Centrolenidae	1
	Craugastoridae	3
	Cryptobranchidae	2
	Dendrobatidae	5
	Hylidae	15
	Hynobiidae	1
	Leptodactylidae	2[a]
	Megophryidae	1
	Myobatrachidae	2
	Pipidae	1
	Plethodontidae	21
	Ranidae	22[a]
	Rhacophoridae	1
	Salamandridae	8
	Scaphiopodidae	1
Fish	Acipenseridae	3
	Anguillidae	1
	Centrarchidae	9
	Channidae	1
	Catostomidae	1
	Cyprinidae	2
	Eleotridae	1
	Esocidae	2
	Gadidae	1
	Gasterosteidae	1
	Ictaluridae	2
	Labridae	1
	Latidae	1
	Lutjanidae	1
	Moronidae	3
	Percidae	2
	Poeciliidae	1
	Salmonidae	1
	Sciaenidae	1
	Scophthalmidae	1
	Serranidae	4
	Siluridae	1

(continued)

Table 1 (continued)

	Family	No. species affected
Reptiles	Agamidae	2
	Anguidae	1
	Boidae	1
	Dactyloidae	2
	Emydidae	4
	Gekkonidae	1
	Iguanidae	1
	Lacertidae	2
	Pythonidae	4
	Testudinidae	8
	Trionychidae	1
	Varanidae	1

[a]Some reports only include the genera
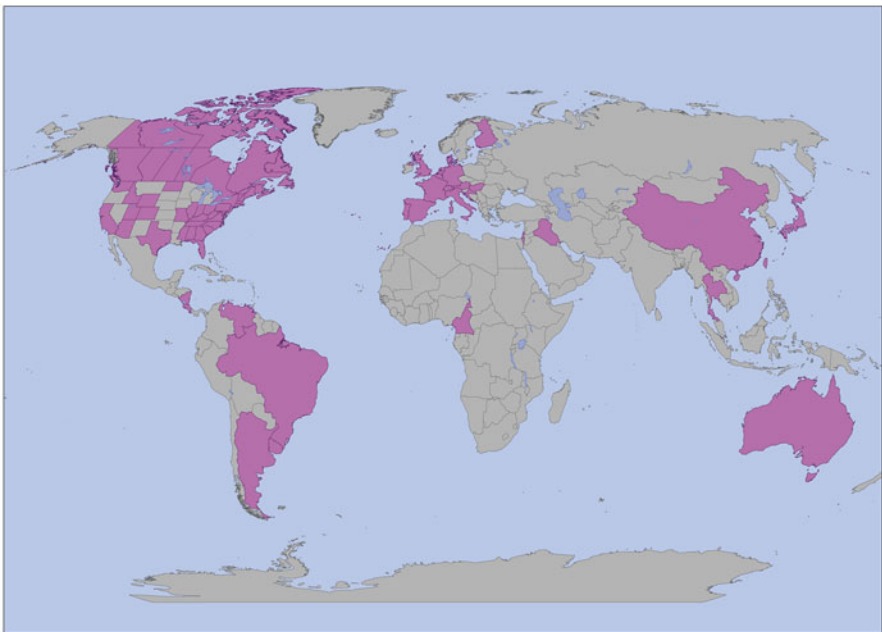
Fig. 1 Global distribution of ranavirus cases

about the epidemiology, geography, and host range of ranaviruses comes from investigations of obvious die-offs, sporadic surveillance efforts in small numbers of populations at one or two time points, and a few larger-scale surveillance efforts focused on a handful of species of economic importance or conservation interest (Grizzle and Brunner 2003; Gray et al. 2009b; Whittington et al. 2010; Miller et al. 2011; Gray et al. 2015). Because gross signs of infection may not be displayed, many host species are cryptic and difficult to detect, the lack of awareness of ranaviruses as significant pathogens, and occasional misdiagnosis, the known geographic distribution and host range of ranaviruses are likely underestimated.
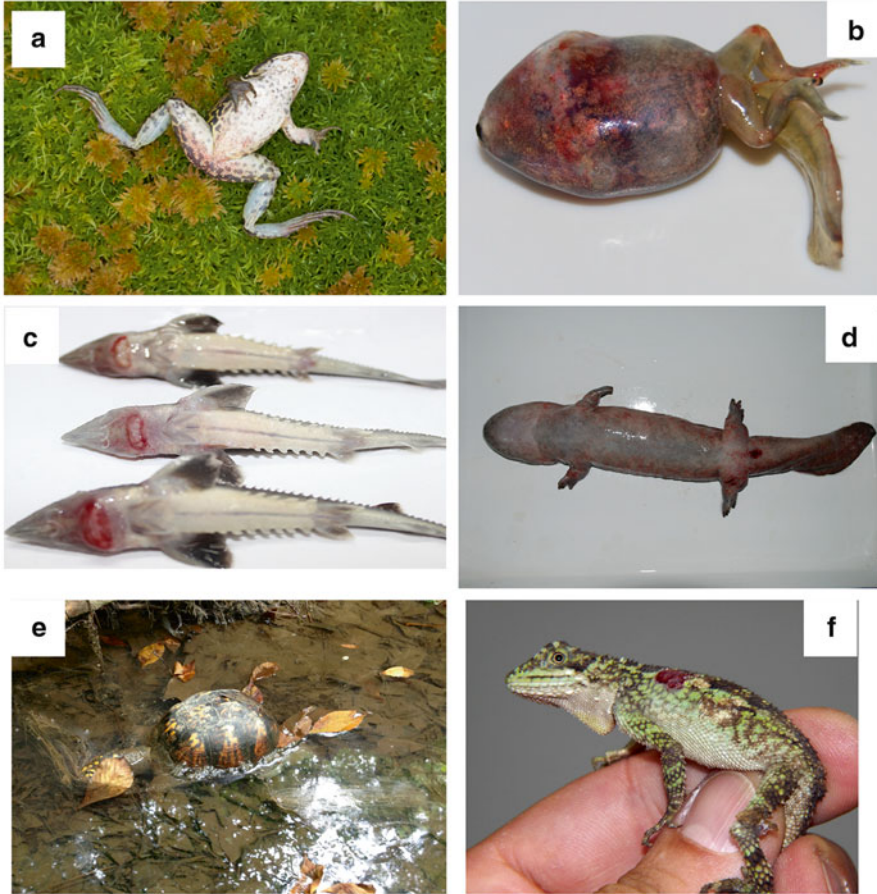
Fig. 2 Ranaviruses are known to cause disease in three ectothermic vertebrate classes. (**a**) Dead adult edible frog (*Rana esculenta*) in the Netherlands (credit=Jeiger Herder), (**b**) morbid plains spadefoot (*Spea bombifrons*) in the USA (credit=Drew Davis), (**c**) infected Amur sturgeon (*Acipenser schrenckii*) in China (credit=Yi Geng), (**d**) morbid juvenile Chinese giant salamander (*Andrias davidianus*) in China (credit=Lingbing Zeng), (**e**) dead eastern box turtle (*Terrapene carolina carolina*) in the USA (credit=Matthew Allender), and (**f**) infected green striped tree dragon (*Japalura splendida*) with ranavirus-associated dermatitis in Germany (credit=Helge Behncke)

Ranaviruses are classified as emerging pathogens, because their geographic distribution and host range appear to be expanding (Daszak et al. 1999). It is becoming evident that ranaviruses are frequently moved in the regional and international trade of animals. For example, barred tiger salamander (*Ambystoma mavortium*) larvae are sold as fishing bait in the southwestern USA, and as many as 100 % have been shown to be infected with the ranavirus, *Ambystoma tigrinum virus* (ATV; Picco and Collins 2008; Brunner et al. 2015). Amphibian ranaviruses have been found in animals that are traded over international borders for a variety of reasons, including human consumption and the pet trade (Schloegel et al. 2009; Kolby et al. 2014). Schloegel et al. (2009) found that 8.5 % of amphibians imported into the USA at three major port

cities were infected with ranavirus. Similarly, Kolby et al. (2014) found over 50 % of amphibians exported via Hong Kong International Airport were infected with ranavirus. Reptiles infected with ranaviruses also have been discovered in internationally traded animals (Hyatt et al. 2002; Stöhr et al. 2013b, 2015). Finally, internationally traded ornamental fishes have been shown to be infected with ranaviruses (Hedrick and McDowell 1995).

While the outcome of infection varies among hosts and strains of ranaviruses, it is clear that ranaviruses have the potential to cause population declines and extinctions (Teacher et al. 2010; Price et al. 2014; Earl and Gray 2014). They may present a significant threat to host species that are geographically isolated or exist at low abundance (Heard et al. 2013; Price et al. 2014; Earl and Gray 2014). Thus, highly susceptible host species that are rare may be at greatest risk (Earl and Gray 2014). However, common species also can be affected. For example, populations of the common frog (*Rana temporaria*) have declined on average 80 % in the UK where ranavirus die-offs have reoccurred (Teacher et al. 2010). It is therefore important to understand the geographic extent, host range, and phylogenetic relationships of these emerging pathogens (Jancovich et al. 2015).

2 Ranaviruses Infecting Amphibians

The first ranaviruses were isolated from northern leopard frogs (*Lithobates pipiens*) from the Midwest USA in the 1960s (Granoff et al. 1965; Clark et al. 1968). One of these viruses, isolated from a frog with adenocarcinoma, was designated *Frog virus 3* (FV3; Granoff et al. 1965), and became the type species of the genus, *Ranavirus*. While many aspects of FV3 virology were well characterized in the following decades (Chinchar 2002), there were few reports of ranaviral disease associated with amphibians so the pathogen received little attention. A second species of *Ranavirus*, *Bohle iridovirus* (BIV), was not isolated from amphibians until the early 1990s. This virus was detected in captive animals in Australia (Speare and Smith 1992). About the same time, epizootic die-offs were being recorded in the southwestern USA and the UK (Collins et al. 1988; Cunningham et al. 1993), but it was not until the mid-1990s that the etiology of the disease was determined to be a ranavirus (Drury et al. 1995; Cunningham et al. 1996; Jancovich et al. 1997, Fig. 2). Reports of ranavirus-related mortality and infection in amphibians have grown exponentially, with over 90 % of reports occurring after 2010. Although greater awareness and more surveillance for the pathogen have impacted this trend, the increase in ranavirus cases is likely not solely a sampling artifact. We now realize that the distribution of amphibian ranaviruses is global, and die-offs are occurring in places where these viruses were previously undetected.

Ranaviruses have a global distribution (Fig. 1; Table 2), and have been identified as threats to amphibian populations (e.g., Duffus and Cunningham 2010; Teacher et al. 2010; Miller et al. 2011). Amphibian ranaviruses have been reported in at least 105 species of amphibians in 18 families in 25 countries (Fig. 3; Table 2). These numbers are likely underestimated because many amphibians are cryptic in nature or rare, gross signs

Table 2 Distribution of ranavirus infections or mortality in wild and captive amphibians, including the location of origin for imported animals; table adapted from Miller et al. (2011)

Continent	Nation	Origin[a]	State/Province[a]	Family	Latin name	I, M[b]	W, C[c]	References
Africa	Cameroon	–	–	Pipidae	*Xenopus longipes*	I	W	Docherty-Bone et al. (2013)
Asia	China	–	–	Cryptobranchidae	*Andrias davidanus*	M	C	Geng et al. (2011), Zhou et al. (2013), Ma et al. (2014)
		–	–	Ranidae	*Rana dybowskii*	I	W	Xu et al. (2010)
		–	–		*Rana grylio*	M	C	Zhang et al. (1996, 2001)
		–	–		*Hoplobatrachus tigerinus* Formerly: *Rana tigrina*	M	C	Weng et al. (2002)
	Japan	–	–	Hynobiidae	*Hynobius nebulosus*	M	C	Une et al. (2009a)
		–	–	Ranidae	*Lithobates catesbieanus* Formerly: *Rana catesbieana*	M	W	Une et al. (2009b)
	Thailand	–	–	Ranidae	*Hoplobatrachus tigerinus*	M	C	Kanchanakhan (1998)
Australia	Australia	–	–	Hylidae	*Litoria caerulea*	M	W, C	Cullen and Owens (2002), Weir et al. (2012)
		–	–		*Litoria splendida*	M	C	Weir et al. (2012)
		–	–	Myobatrachidae	*Limnodynastes ornatus*	M	C	Speare and Smith (1992)
		–	–		*Pseudophryne corieacea*	M	C	Cullen and Owens (2002)
Europe	Belgium	–	–	Bufonidae	*Bufo bufo*	I	W	Martel et al. (2012)
		–	–	Ranidae	*Lithobates catesbieanus*	I	W	Sharifian-Fard et al. (2011)
		CN[d]	–	Salamandridae	*Tylototriton kweichowensis*	M	C	Pasmans et al. (2008)
	Croatia	–	–	Ranidae	*Pelophylax esculenta*	M	W	Fijan et al. (1991)
	Denmark	–	–	Ranidae	*Pelophylax esculenta*	M	W	Ariel et al. (2009)

Country		Family	Species			Reference
France	–	Ranidae	*Rana temporaria*	M	W	C. Miaud (personal communication)
Germany	CH, CZ, PL, SK	Ranidae	*Pelophylax esculenta*	M	C	Stöhr et al. (2013a)
	Iraq	Salamandridae	*Neurergus crocatus*	M	C/W	Stöhr et al. (2013c)
Israel	–	Bufonidae	*Pseudepidalea viridis*	I	W	Miller et al. (2011)
Italy	–	Ranidae	*Pelophylax esculenta*	–	–	Ariel et al. (2010)
Netherlands	–	Dendrobatidae	*Dendrobates auratus*	M	C	Kik et al. (2012)
			Phyllobates bicolor	M	C	Kik et al. (2012)
			Phyllobates vittatus	M	C	Kik et al. (2012)
	–	Ranidae	*Pelophylax spp.*	M	W	Kik et al. (2011)
	–	Salamandridae	*Lissotriton vulgaris*	M	W	Kik et al. (2011)
Portugal	–	Alytidae	*Alytes obstetricans*		W	R. Marschang (personal communication)
	–	Salamandridae	*Lissotriton boscai*		W	R. Marschang (personal communication)
	–		*Triturus marmoratus*	M	W	Alves de Matos et al. (2008)
	–		*Triturus boscai*	M	W	Alves de Matos et al. (2008)
Spain	–	Alytidae	*Alytes obstetricans*	M	W	Balseiro et al. (2009)
	–	Salamandridae	*Ichthyosaura alpestris*	M	W	Balseiro et al. (2010)
Switzerland	–	Ranidae	*Pelophylax ridibunda*	M	C	Stöhr et al. (2013a)
UK	–	Alytidae	*Alytes obstetricans*	M	W	Duffus et al. (2014)
	–	Bufonidae	*Bufo bufo*	M	W	Hyatt et al. (2000), Duffus et al. (2014)
	–	Ranidae	*Rana temporaria*	M	W	Cunningham et al. (1993), Drury et al. (1995), Cunningham et al. (1996), Teacher et al. (2010), Duffus et al. (2013)
	–	Salamandridae	*Lissotriton vulgaris*	I	W	Duffus et al. (2014)

(continued)

Table 2 (continued)

Continent	Nation	Origin[a]	State/Province[a]	Family	Latin name	I, M[b]	W, C[c]	References
North America	Canada	–	AB, SK, MB	Ambystomatidae	*Ambystoma mavortium*	M	W	Bollinger et al. (1999), Schock et al. (2008), Miller et al. (2011)
		–	ON		*Ambystoma* spp.	I	W	Duffus et al. (2008)
		–	ON	Hylidae	*Hyla versicolor*	I	W	Duffus et al. (2008)
		–			*Pseudacris crucifer*	M	W	Miller et al. (2011)
		–	ON		*Pseudacris* spp.	I	W	Duffus et al. (2008)
		–	ON, PEI	Ranidae	*Lithobates clamitans*	I, M	W	St Amour et al. (2008), Miller et al. (2011), Forzán and Wood (2013)
		–	SK, ON, QU		*Lithobates pipiens*	I, M	W, C	Greer et al. (2005) Schock et al. (2008), Echaubard et al. (2010), Paetow et al. (2011)
		–	AB, NU, NWT, ON, QC, SK		*Lithobates sylvaticus*	I, M	W	Greer et al. (2005) Duffus et al. (2008) Schock et al. (2008), Miller et al. (2011), Schock et al. (2010); D. Lesbarreres (personal communication), D. Schock (personal communication)
		–	BC		*Rana pretiosa*	M	C	D. Schock et al. (2008)
		–	ON	Salamandridae	*Notophthalmus viridescens*	I	W	Duffus et al. (2008)
	Costa Rica	–	–	Bufonidae	*Rhaebo haematiticus*	I	W	Whitfield et al. (2013)
		–	–		*Rhinella marina/Bufo marinus*	I	W, C	Speare et al. (1991), Whitfield et al. (2013)
		–	–	Hylidae	*Scinax elaeochroa*	I	W	Whitfield et al. (2013)
		–	–		*Smilisca baudinii*	I	W	Whitfield et al. (2013)
		–	–	Centrolenidae	*Teratohyla spinosa*	I	W	Whitfield et al. (2013)

Country		State	Family	Species		W/C	Reference
	–		Craugastoridae	*Craugastor bransfordii*	I	W	Whitfield et al. (2013)
	–			*Craugastor fitzingeri*	I	W	Whitfield et al. (2013)
	–			*Craugastor megacephalus*	I	W	Whitfield et al. (2013)
	–		Dendrobatidae	*Oophaga pumilio*	I	W	Whitfield et al. (2013)
Nicaragua	–		Hylidae	*Agalychnis callidryas*	M	W	Stark et al. (2014)
	–		Ranidae	*Lithobates forreri*	M	W	Stark et al. (2014)
USA	–		Ambystomatidae	*Ambystoma jeffersonianum*	M	W	Miller et al. (2011)
	–			*Ambystoma macrodactylum*	M	W	Miller et al. (2011)
	–	MA, ME, NC, NY, OH, TN		*Ambystoma maculatum*	I, M	W	Green et al. (2002), Petranka et al. (2003), Gahl and Calhoun (2010), Todd-Thompson (2010), Brunner et al. (2011), O'Bryan et al. (2012), Homan et al. (2013)
	–	AZ, ND		*Ambystoma mavortium*	I, M	W	Jancovich et al. (1997, 2005), Docherty et al. (2003), Picco and Collins (2008), Greer et al. (2009)
	–	TN		*Ambystoma opacum*	M	W	Todd-Thompson (2010)
	–	TN		*Ambystoma talpoideum*	I	W	O'Bryan et al. (2012)
	–	CO, ID, ND, UT, WY		*Ambystoma tigrinum*	I, M	W, C	Green et al. (2002), Hoverman et al. (2012a)
	–		Bufonidae	*Anaxyrus americanus*	I	W	Hoverman et al. (2012a)
	–			*Anaxyrus boreas boreas*	I, M	C	Cheng et al. (2014)
		NJ		*Anaxyrus fowleri*	M	W	Monson-Collar et al. (2013)
				Melanophryniscus stelzneri	I	C	Cheng et al. (2014)

(continued)

Table 2 (continued)

Continent	Nation	Origin[a]	State/Province[a]	Family	Latin name	I, M[b]	W, C[c]	References
		–	TN	Cryptobranchidae	*Cryptobranchus alleganiensis alleganiensis*	I	W	Souza et al. (2012)
		–		Dendrobatidae	*Dendrobates auratus*	I	C	Miller et al. (2008)
		–			*Phyllobates terribilis*	I	C	Miller et al. (2008)
		–		Hylidae	*Acris crepitans*	I	W	Hoverman et al. (2012b)
		–			*Hyla chrysoscelis*	I, M	W, C	Miller et al. (2011), Driskell et al. (2009)
		–	TN		*Hyla chrysoscelis*/*Hyla versicolor* Complex	I	W	O'Bryan et al. (2012)
		–			*Hyla cinerea*	M	W	Green and Converse (2005)
		–	TX		*Pseudacris clarkii*	M	W	Torrence et al. (2010)
		–	TN, ME		*Pseudacris crucifer*	M	W	Green et al. (2002), Gahl and Calhoun (2010), Todd-Thompson (2010)
		–	TN		*Pseudacris feriarum*	I, M	W	Todd-Thompson (2010), Hoverman et al. (2012a)
		–			*Pseudacris regilla*	M	W	Miller et al. (2011)
		–	ID		*Pseudacris sierra*	M	W	Russell et al. (2011)
				Megophryidae	*Megophrys nasuta*	I	C	Cheng et al. (2014)
		–	TN	Plethodontidae	*Desmognathus conanti*	I	W	Gray et al. (2009a)
		–	GA, NC		*Desmognathus folkertsi*	I	W	Rothermel et al. (2013)
		–	VA		*Desmognathus fuscus*	I	W	Davidson and Chambers (2011), Hamed et al. (2013)
		–	TN		*Desmognathus imitator*	I	W	Gray et al. (2009a, b)

	Location	Family	Species			Reference
–	GA, NC		*Desmognathus marmoratus*	I	W	Rothermel et al. (2013)
–	GA, NC, TN, VA		*Desmognathus monticola*	I	W	Gray et al. (2009a, b), Davidson and Chambers (2011), Hamed et al. (2013), Rothermel et al. (2013)
–	GA, NC, TN		*Desmognathus ocoee*	I	W	Gray et al. (2009a, b) Rothermel et al. (2013)
–	VA		*Desmognathus orestes*	I	W	Hamed et al. (2013)
–	VA		*Desmognathus organi*	I	W	Hamed et al. (2013)
–	GA, NC, TN, VA		*Desmognathus quadramaculatus*	I	W	Gray et al. (2009a, b), Davidson and Chambers (2011), Hamed et al. (2013), Rothermel et al. (2013)
–	TN		*Desmognathus santeetlah*	I	W	Gray et al. (2009a, b)
–	TN		*Desmognathus wrighti*	I	W	Gray et al. (2009a, b)
–	VA		*Eurycea cirrigera*	I	W	Davidson and Chambers (2011)
–	VA		*Eurycea longicauda*	I	W	Davidson and Chambers (2011)
–	VA		*Eurycea lucifuga*	I	W	Davidson and Chambers (2011)
–	TN		*Eurycea wilderae*	I	W	Gray et al. (2009a, b)
–	TN		*Gyrinophilus porphyriticus*	I	W	Gray et al. (2009a, b)
–	VA		*Plethodon glutinosus complex*	I	W	Davidson and Chambers (2011)
–	TN		*Plethodon jordani*	I	W	Gray et al. (2009a, b)
–	VA		*Plethodon montanus*	I	W	Hamed et al. (2013)
–	VA		*Plethodon welleri*	I	W	Hamed et al. (2013)
–		Ranidae	*Lithobates blairi*	M	W	Miller et al. (2011)

(continued)

Table 2 (continued)

Continent	Nation	Origin[a]	State/Province[a]	Family	Latin name	I, M[b]	W, C[c]	References
		–	FL, OH, MA, ME, NC, TN, VA		*Lithobates catesbeianus*	I, M	W, C	Wolf et al. (1969) Green et al. (2002), Gray et al. (2007), Majji et al. (2006), Miller et al. (2007; 2009), Gahl and Calhoun (2010), Davidson and Chambers (2011), Homan et al. (2013), Landsberg et al. (2013)
		–	MA, ME, NJ, OH, TN		*Lithobates clamitans*	I, M	W	Green et al. (2002), Gahl and Calhoun (2010), Gray et al. (2007), Johnson et al. (2007), Miller et al. (2009), Homan et al. (2013), Monson-Collar et al. (2013)
		–	MA, NH, TN, VA		*Lithobates palustris*	I, M	W	Green et al. (2002), Hoverman et al. (2012b), Davidson and Chambers (2011)
		–	MA, MN, VT		*Lithobates pipiens*	I, M	W	Granoff et al. (1965), Clark et al. (1968), Green et al. (2002), Uyehara et al. (2010)
		–	MA, MN		*Lithobates septentrionalis*	M	W	Green et al. (2002)
		–	NJ, TN, FL		*Lithobates sphenocephalus*	I, M	W	Johnson et al. (2007), Miller et al. (2011), Hoverman et al. (2012a), O'Bryan et al. (2012), Landsberg et al. (2013), Monson-Collar et al. (2013)

	Country		Location	Family	Species	[a][b]	[c]	References
		–	CT, MA, ME, MN, NC, ND, NY, TN		Lithobates sylvaticus	I, M	W	Green et al. (2002), Petranka et al. (2003), Harp and Petranka (2006), Gahl and Calhoun (2010), Todd-Thompson (2010), Uyehara et al. (2010), Brunner et al. (2011), T. Rittenhouse (personal communication)
		–			Pyxicephalus adspersus	M	C	Miller et al. (2007)
		–	CA		Rana aurora	M	W	Mao et al. (1999a)
		–			Rana draytonii	M	W	Miller et al. (2011)
		–			Rana heckscheri	M	W	Miller et al. (2011)
		–	ID		Rana luteiventris	M	W	Converse and Green (2005), Green and Converse (2005), Russell et al. (2011)
		–			Rana mucosa	M	W	Converse and Green (2005)
		–		Rhacophoridae	Rhacophorus dennysi	M	C	Miller et al. (2008)
			KY	Salamandridae	Notophthalmus viridescens	I, M	W	Granoff et al. (1965), Green et al. (2002), Glenney et al. (2010), Richter et al. (2013)
		–		Scaphiopodidae	Scaphiopus holbrookii	I, M	W	Miller et al. (2011)
South America	Argentina	–		Leptodactylidae	Atelognathus patagonicus	M	W	Fox et al. (2006)
	Brazil	–		Ranidae	Lithobates catesbeianus	M	C	Mazzoni et al. (2009)
	Uruguay	–		Ranidae	Lithobates catesbeianus	I	C	Galli et al. (2006)
	Venezuela	–		Bufonidae	Rhinella marina/Bufo marinus	I	W	Zupanovic et al. (1998a)
		–		Leptodactylidae	Leptodactilus spp.	I	W	Zupanovic et al. (1998b)

[a] Provided when available

[b] I infection with no gross signs of ranaviral disease, M Mortality due to ranaviral disease

[c] W wild population, C Captive populations including zoological and ranaculture facilities, it does not include controlled virus challenge studies

[d] It is thought that these animals were imported from China
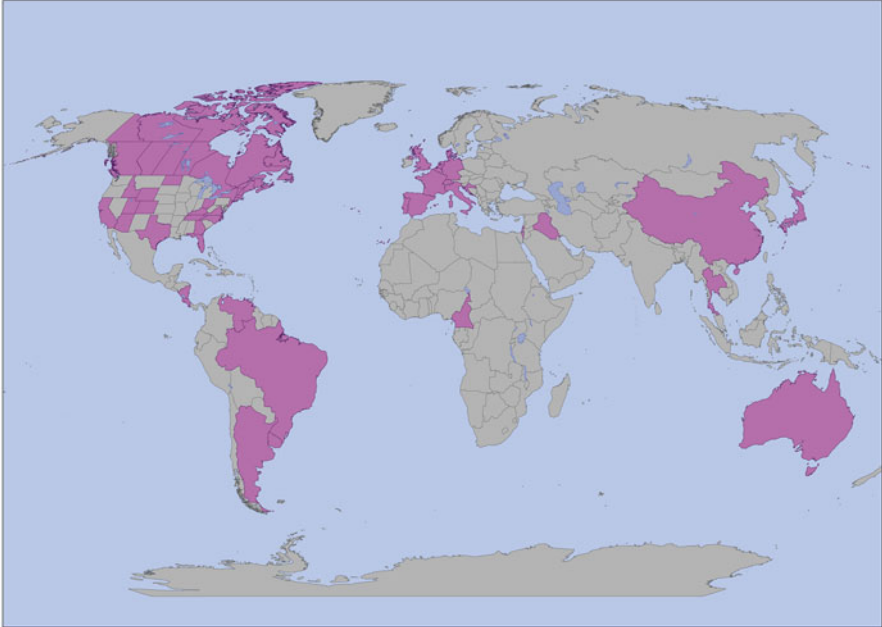
Fig. 3 Distribution of ranavirus cases involving amphibians
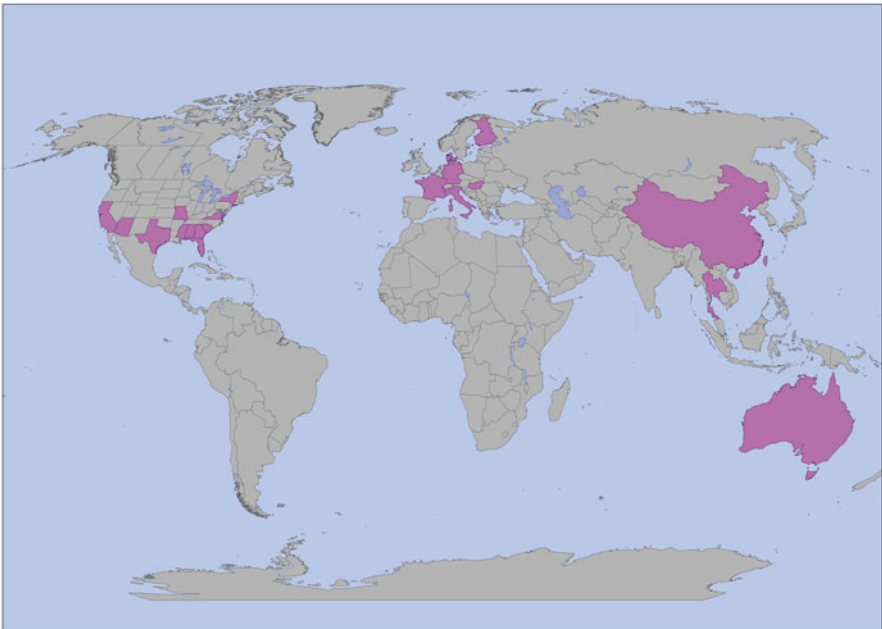
Fig. 4 Distribution of ranavirus cases involving fish
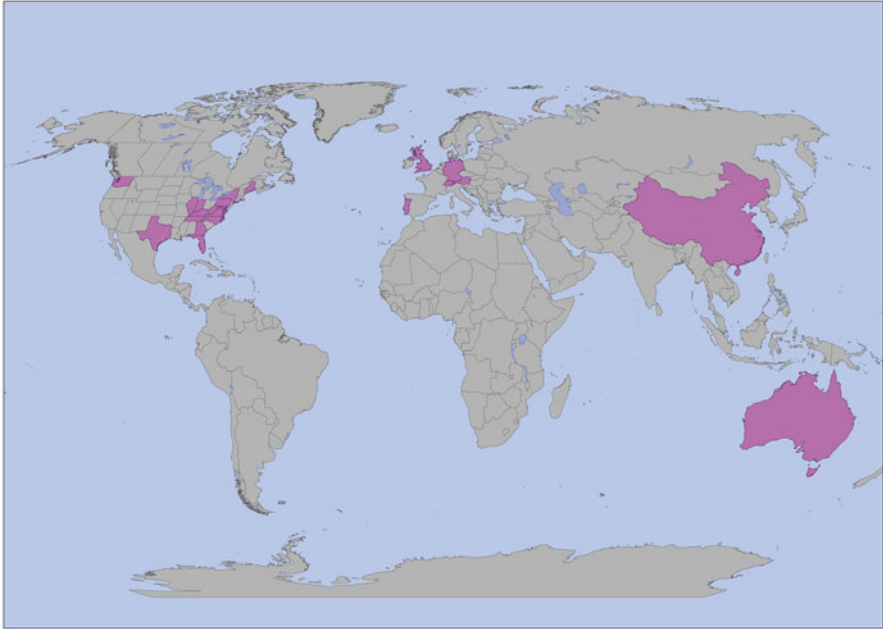
Fig. 5 Distribution of ranavirus cases involving reptiles

of ranavirus infection are not always apparent and can be confused with other factors, and mortality events are not easily observed due to their rapid progression and the fast decomposition of dead hosts (Brunner et al. 2015; Miller et al. 2015). It is perhaps not surprising that caecilians, which are fossorial and as a group poorly studied, are the only amphibian family with no reports of ranavirus infection. To our knowledge, no one has tested the susceptibility of caecilians to ranavirus or performed surveillance in wild populations.

There are three recognized species of ranaviruses that are known to infect amphibians: FV3, ATV, and BIV. Also, there are several other ranaviruses that have been isolated from amphibians (e.g., common midwife toad virus, CMTV; Balseiro et al. 2009), but are not currently recognized as ranavirus species. As discussed in Jancovich et al. (2015), declaring a given isolate as a unique viral species is complex, and compounded by the fact that there is considerable sequence conservation, often greater than 95 % at the amino acid level among many ranavirus isolates. A challenge for the future is identifying genetic sequences that allow for unique characterization of ranaviruses in an evolutionary context. Below, we discuss what is known about some of the ranaviruses that infect amphibians.

2.1 Frog Virus 3

Since its initial isolation from the leopard frog, cases of FV3 and FV3-like infections and disease have been confirmed in a growing number of amphibian species (as well as fish and reptiles, Sects. 3 and 4). Infected animals include some that were

visibly diseased or dying, and several cases from apparently healthy individuals. Outbreaks of FV3 and FV3-like viruses in amphibians have occurred across large sections of North America and have been found in many different species of anurans and urodeles in eastern North America. In both the USA and Canada, the number of infections caused by FV3 or FV3-like viruses is unknown, because many researchers do not report the strain of ranavirus detected in their studies. There have been no reports of ranavirus infections in Mexico, likely due to a lack of investigation. In Central America, an FV3-like ranavirus has been detected in a minimum of ten amphibian species. Specifically, in Costa Rica, at least eight species are known to have been infected with an FV3-like ranavirus (Whitfield et al. 2013), and in Nicaragua, an FV3-like ranavirus has been detected in at least two species (Stark et al. 2014). Cases of FV3 infection and disease in South America have been primarily associated with American bullfrog (*L. catesbeianus*) farms (Mazzoni et al. 2009), but a single case of infection in a wild amphibian population of Patagonia frogs (*Atelognathus patagonicus*) was reported (Fox et al. 2006).

In Europe, the first outbreaks of FV3-like viruses occurred in the southeastern UK in common frogs (Cunningham et al. 1993, 1996; Drury et al. 1995). The emergence of these viruses in common frogs was followed quickly by their emergence in common toads (*Bufo bufo*; Hyatt et al. 2000; Cunningham et al. 2007). Since then, FV3-like infections have been documented in common newts (*Lissotriton vulgaris*) and common midwife toads (*Alytes obstetricans*; Duffus et al. 2014). FV3-like viruses have also been detected in amphibians in continental Europe (e.g., Ariel et al. 2009; Stöhr et al. 2013c). In total, FV3-like ranaviruses have been documented in a minimum of five amphibian species in Europe.

In Asia, there have been several reports of FV3-like viruses in both wild and captive populations of amphibians. In China, an FV3-like virus was found across Heilongjiang Province in 5.7 % of adult and 42.5 % of larval *R. dybowskii* surveyed (Xu et al. 2010). In Japan, an FV3-like ranavirus was responsible for a mass mortality of American bullfrog tadpoles, an introduced species (Une et al. 2009a). In this case, adult bullfrogs and fish (*Gnathopogon* spp.) that were present in the pond did not die or appear moribund, but ranavirus was documented in the livers of the fish (Une et al. 2009b), suggesting interclass transmission. The single case of ranavirus infection in Africa reported by Docherty-Bone et al. (2013) is also likely to be an FV3-like virus. The primers used were those developed for the major capsid protein of FV3, but the PCR products were of poor quality and could not be sequenced (Docherty-Bone et al. 2013). In general, surveillance data for ranaviruses in Asia and Africa have been slower to accumulate than for North America or Europe, which are essential to understanding the distribution, host range, and threat of ranaviruses.

As mentioned, FV3 and FV3-like ranaviruses have affected many aquaculture facilities. In Japan, a ranavirus with 99 % homology to the major capsid protein of FV3 was isolated from a mass mortality event in cultured Japanese clouded salamanders (*Hynobius nebulosus*, Une et al. 2009a). In the Americas, FV3-like viruses have also been documented in association with mass mortality events in aquaculture facilities. In the USA, FV3-like viruses have been responsible for mass mortalities

of tadpoles and recently metamorphosed American bullfrogs in culture facilities (Majji et al. 2006; Miller et al. 2007). In Brazil, FV3-like ranaviruses have been responsible for mass mortality events at several aquaculture facilities that rear American bullfrogs (Mazzoni et al. 2009). There is some evidence that suggests that the FV3-like viruses that are present in aquaculture facilities are more virulent than those found in natural populations (Majji et al. 2006; Hoverman et al. 2010, 2011).

2.2   Ambystoma Tigrinum Virus

Ambystoma tigrinum virus was first described in larval Sonora tiger salamanders (*Ambystoma tigrinum stebbinsi*) collected from the San Rafael Valley in Arizona, USA in 1995 (Jancovich et al. 1997). This virus was isolated from a population that had both apparently healthy and visibly diseased salamander larvae (Jancovich et al. 1997). The virus that was later isolated was successfully transmitted to healthy individuals via the water, as well as through the feeding of body parts of infected animals to healthy individuals in the laboratory (Jancovich et al. 1997). After fulfilling Koch's Postulates, it was determined that ATV was the causative agent of the disease found in the tiger salamander larvae and the likely cause of recurrent epizootics first described in 1985 (Collins et al. 1988).

Ambystoma tigrinum virus in the wild appears to be restricted to western North America (Jancovich et al. 2005; Ridenhour and Storfer 2008). Phylogeographic studies of ATV strains suggest local range expansion and long-distance colonization events, which may be attributed to anthropogenic spread (Jancovich et al. 2005). ATV is found in tiger salamander larvae sold commercially as fish bait (Picco and Collins 2008), providing an anthropogenic explanation for range expansion.

Because of the potential for introduction, ATV may be a threat to naïve urodeles of conservation concern. In the lab, the endangered California tiger salamander (*Ambystoma californiense*) is susceptible to ATV and experienced mortality associated with infection (Picco et al. 2007). There have been no reports of ATV infections or associated mortality in wild California tiger salamanders, probably due in part to the ban on importation of non-native Ambystomatidae into the state.

Patterns of ATV infection are more similar among ponds in the same year, rather than between years (Greer et al. 2009). In natural populations of tiger salamanders located on the Kaibab Plateau in the Northern Kaibab National Forest in Arizona, outbreaks of ATV appear to be synchronous (Greer et al. 2009). Interestingly, despite four years of observation, no visible signs of disease were seen, even in cases where the infection rate in the pond was greater than 50 % (Greer et al. 2009). It is thought that the lack of observed morbidity and mortality in these populations is due to coevolution between ATV and the host (Greer et al. 2009). This may be the case as there is evidence of local adaptation in ATV strains isolated from the western USA (Ridenhour and Storfer 2008).

2.3   Bohle Iridovirus

Bohle iridovirus was first described in the early 1990s and was isolated from recently metamorphosed ornate burrowing frogs (*Limnodynastes ornatus*) in Australia that had been raised in captivity and suddenly died (Speare and Smith 1992). Using sequences from the major capsid protein, BIV was determined to be most closely related to *Epizootic hematopoietic necrosis virus* (EHNV), a fish ranavirus that had also been isolated in Australia (Hyatt et al. 2000). Subsequent experimentation showed that BIV was pathogenic in additional species of Australian anurans and was involved in mortality events in captive and wild settings (Cullen et al. 1995; Cullen and Owens 2002).

Until recently, BIV and BIV-like viruses were known only from Australian anurans. Then, in 2010, a BIV-like virus was isolated from boreal toads (*Anaxyrus boreas boreas*) held in an Iowa, USA aquarium that experienced a mass mortality. The virus, tentatively designated Zoo Ranavirus (ZRV), was found to have high sequence homology with BIV (Cheng et al. 2014). These toads had been housed with multiple species, some of which were collected in the wild from Southeast Asia, suggesting a potential route of introduction. Other species that were infected with ZRV but did not experience mortality in the outbreak included a Malayan horned frog (*Megophrys nasuta*) and a bumblebee toad (*Melanophryniscus stelzneri*, Cheng et al. 2014). At present, it is unknown whether ZRV represents a novel North American isolate of BIV, or the transmission of BIV from another captive animal.

2.4   Other Amphibian Ranaviruses

Common midwife toad virus (CMTV) was first isolated from common midwife toad tadpoles experiencing a mass mortality event in 2007 in northern Spain (Balseiro et al. 2009). A second mass mortality event during 2008 in the same region of Spain involving CMTV affected common midwife toad tadpoles and juvenile alpine newts (*Mesotriton alpestris*; Balseiro et al. 2010). A long-term study in Spain reported six amphibian species experiencing die-offs due to CMTV at several sites, with population declines documented in three species (Price et al. 2014). CMTV infections have also been found in invasive populations of American bullfrogs in Belgium (Sharifian-Fard et al. 2011), and in both captive and wild animals in the Netherlands (Kik et al. 2011, 2012). CMTV appears to be the most common ranavirus in continental Europe, but has not been found elsewhere. This virus appears to be evolutionarily unique from other ranaviruses (Mavian et al. 2012); thus, species designation may be warranted.

Another possibly unique ranavirus was isolated recently from the endangered Chinese giant salamander (*Andrias davidianus*; Geng et al. 2011; Chen et al. 2013; Ma et al. 2014). The virus was isolated from captive populations, and in all cases resulted in high morbidity and mortality (Geng et al. 2011; Chen et al. 2013;

Ma et al. 2014). Phylogenetic analyses have shown that it is most closely related to CMTV (Chen et al. 2013). Dr. Lingbing Zeng has been working with several Chinese giant salamander farms, and has documented the virus across 11 Chinese provinces (L. Zeng and J. Ma, Yangtze River Fisheries Institute, unpublished data). The emergence of this ranavirus in China is a serious conservation threat (Cunningham et al. 2015).

There are several other ranaviruses that have been isolated from amphibians and named, but are not considered unique species. *Rana grylio* virus (RGV) was isolated in the mid-1990s in China (Zhang et al. 1996), and appears to be closely related to FV3 (Lei et al. 2012). The tiger frog virus (TFV) was isolated in 2000 from Chinese amphibians involved in a mass mortality event at a ranaculture facility (Weng et al. 2002). Both of these ranaviruses may be a threat to aquaculture facilities in Asia.

3 Ranaviruses Infecting Fish

Ranaviruses can cause severe systemic diseases in finfish in both marine and freshwater environments (Whittington et al. 2010). EHNV was the first ranavirus associated with fish die-offs, and was isolated in 1985 in Australia (Langdon et al. 1986b). A genetically distinct, but closely related ranavirus, *European catfish virus* (ECV), was detected soon after in Europe (Ahne et al. 1989). The *Santee-Cooper ranavirus* (SCRV), known informally as largemouth bass virus (LMBV) and currently classified by the International Committee on the Taxonomy of Viruses (ICTV) as a ranavirus, was associated with wild fish epizootics in the USA (Plumb et al. 1996). Although typically associated with morbidity in amphibians and reptiles, FV3 also has been isolated from a moribund threespine stickleback (*Gasterosteus aculeatus*) during a sympatric epizootic in the northern red-legged frog (*Rana aurora*; Mao et al. 1999a). There are three species of ranavirus recognized by the ICTV that primarily infect fish: EHNV is not known to occur naturally in any country except Australia; ECV appears to be confined to Europe; and SCRV has primarily been detected in North American fishes.

While both EHNV and ECV have impacted aquaculture (Whittington et al. 2010), BIV appears to be restricted to a single outbreak in hatchery-reared Nile tilapia fry (*Oreochromis niloticus*) in Australia (Ariel and Owens 1997). Recently, SCRV and FV3 have been repeatedly detected among hatchery-reared freshwater fishes in North America and Asia (Woodland et al. 2002b; Prasankok et al. 2005; Deng et al. 2011; George et al. 2014; Chinchar and Waltzek 2014; Waltzek et al. 2014). Two genetically distinct but related ranaviruses, Singapore grouper iridovirus (SGIV) and grouper iridovirus (GIV), have negatively impacted grouper mariculture in Asia since the 1990s (Chua et al. 1994; Murali et al. 2002; Qin et al. 2003). The reasons for the emergence of ranaviruses as pathogens of finfish within both natural and managed populations are unknown. However, the repeated detection of the same finfish ranaviruses (e.g., SCRV) around the globe suggests that the international movement of live

animals and their products likely plays an important role in the occurrence of these epizootics (Hedrick and McDowell 1995; Plumb and Zilberg 1999a; Grant et al. 2005; Schramm and Davis 2006; Deng et al. 2011; George et al. 2014).

3.1 Epizootic Haematopoietic Necrosis Virus

The first ranavirus to be associated with systemic infection and mass mortality in any vertebrate species was EHNV. It was identified as the cause of epizootic mortality of redfin perch (*Perca fluviatilis*) and rainbow trout (*Oncorhynchus mykiss*) in Australia in 1985 (Langdon et al. 1986b, 1988; Langdon and Humphrey 1987). The source of the outbreak was not determined. A survey to detect viral infections of salmonids conducted in Australia between 1981 and 1984 did not identify any viruses (Langdon et al. 1986a), so EHNV may not have been present in trout prior to these first mortality events. Although redfin perch populations were not surveyed, there was no record of prior mass mortality (Whittington et al. 1996). To date, there have been no other known cases of EHNV mortality in the wild other than redfin perch, despite the fact that at least 14 additional species are known to be susceptible to this ranavirus according to experimental challenges (Whittington et al. 2010; Becker et al. 2013). Perhaps the difficulty of observing free-living finfish species combined with unreliable reporting of clinical disease is responsible for the current lack of EHNV detection in Australia.

The impact of EHNV on aquaculture has been limited to farmed rainbow trout in southeastern Australia; salmonid populations of Tasmania and western Australia remain free of EHNV infection. EHNV infection is endemic in wild redfin perch populations throughout southeastern Australia, excluding Tasmania. Redfin perch are highly susceptible to EHNV, while rainbow trout are relatively resistant (Whittington and Reddacliff 1995). In affected trout farms, EHNV tends to occur in only a small proportion of fish (Whittington et al. 1994, 1999), with total mortality generally ≤4 % across all age classes. While few fish become infected, the mortality rate of infected individuals appears to be high (Whittington et al. 1994, 1999). In contrast, EHNV causes severe disease in redfin perch, affecting high proportions of populations of fingerlings and juveniles in endemic areas, and also naïve adults that enter new areas (Langdon et al. 1986b; Langdon and Humphrey 1987; Whittington et al. 1996). Anecdotal evidence suggests that redfin perch populations exposed to EHNV can recover over a few years. There is some evidence based on virus isolation and serology that both redfin perch and rainbow trout are capable of living with subclinical infections of EHNV, thus possibly function as reservoirs for the pathogen (Whittington et al. 2010).

In redfin perch, there has been progressive spread of EHNV into river systems, possibly due to natural fish migration, fish releases, and avifauna (Whittington et al. 1996). Waterborne infection and ingestion of infected fish are transmission routes of EHNV between susceptible hosts within a population, but longer distance spread is likely a result of human activity, particularly by movement of infected trout

fingerlings in aquaculture (Langdon et al. 1988; Whittington et al. 1994, 1999). Annual outbreaks on trout farms may be due to persistence of the virus in the local environment or reinfection from wild redfin perch.

Natural epizootics in redfin perch occur most often in summer, and there is evidence of a positive relationship between EHNV pathogenicity and water temperature. Redfin perch are not susceptible to EHNV below 10 °C, and incubation periods for the virus are shorter at higher temperatures (Whittington and Reddacliff 1995). In rainbow trout, EHNV outbreaks have occurred between 11 and 20 °C (Whittington and Reddacliff 1995; Whittington et al. 1994, 1999). Temperature-dependent pathogenicity may be related to viral replication rates (Ariel et al. 2009).

The first transmission studies with EHNV were conducted by Langdon (1989) who identified a wide range of susceptible hosts, a factor that contributed to the listing of EHNV by the International Office of Epizootics (OIE). Although there are recognized deficiencies in laboratory challenge models to determine the susceptibility of host fish to virus isolates under natural conditions, a potential increase in the host range of EHNV infections has been predicted. In three separate challenge studies, black bullhead (*Ameiurus melas*), pike (*Esox Lucius*), and pike-perch (*Sander lucioperca*) experienced significant mortality following bath exposure to EHNV (Bang-Jensen et al. 2009, 2011a; Gobbo et al. 2010). On the other hand, goldfish (*Carassius auratus*), common carp (*Cyprinus carpio*), and European sheatfish (*Silurus glanis*) did not experience significant mortality following bath exposure to EHNV (Bang-Jensen et al. 2011b; Leimbach et al. 2014). Like other ranaviruses, the outcome of EHNV infection may depend on various viral, host, and environmental factors including: virus concentration and route of delivery, viral strain, host genetics, host density and age, and water temperature (Brunner et al. 2015). For example, lower mortality was observed when European redfin perch stocks were challenged with EHNV, but it was these individuals that caused transmission of the pathogen to and extensive mortality in Australian redfin perch that were cohoused with them (Ariel and Bang-Jensen 2009).

3.2   European Catfish Virus

European catfish virus is the most important ranavirus that causes disease of fish in Europe. It was referred to as European sheatfish virus (ESV) prior to its formal classification. This pathogen has triggered epizootics in cultivated sheatfish in Germany (Ahne et al. 1989, 1991) and wild black bullheads in France and Italy (Pozet et al. 1992; Bovo et al. 1993; Bigarré et al. 2008). Evidently, the virus is endemic in some locations (e.g., Lake le Bourget and Lake Apremont in France; Bigarré et al. 2008). In Italy, the disease occurs in both farmed and wild black bullhead and in farmed brown bullhead (*A. nebulosus*), and affects production of these species (Ariel et al. 2010). An ECV outbreak was detected in brown bullheads in Hungary in 2008 (Juhász et al. 2013).

The host range, geographic distribution, and diversity of ECV strains in Europe is incompletely understood. The virus is readily transmitted to catfish via a range of challenge methods including bath exposure, cohabitation, and intramuscular injection (Ahne et al. 1990; Pozet et al. 1992), and results in only a small proportion of exposed catfish surviving (Pozet et al. 1992). Interestingly, Gobbo et al. (2010) found different patterns of susceptibility based on closely related ranavirus strains, as black bullheads were susceptible to ECV, but not to the ESV isolate used in this study. More recent experiments have demonstrated variable pathogenicity of different isolates of ECV, and a strong impact of water temperature on disease outcome, with mortality varying between 8 and 10 % among challenged sheatfish (Leimbach et al. 2014). In three separate experimental challenge studies, black bullhead, pike, and sheatfish experienced significant mortality following bath exposure to strains of ECV (Bang-Jensen et al. 2009; Gobbo et al. 2010; Leimbach et al. 2014). Goldfish, common carp, and pike-perch did not experience significant mortality following bath exposure to ECV strains (Bang-Jensen et al. 2011a, b).

3.3   *Santee-Cooper Ranavirus*

The discovery of an iridovirus from largemouth bass (*Micropterus salmoides*) was reported from a 1995 epizootic that occurred in the Santee-Cooper Reservoir, South Carolina, USA (Plumb et al. 1996). Accordingly, the authors named the pathogen LMBV based on the host. Subsequent genetic analyses confirmed LMBV to be a unique member of the genus *Ranavirus* (Mao et al. 1997, 1999b), and nearly identical to doctor fish virus (DFV) and guppy virus 6 (GV6), which had previously been isolated from imported ornamental fishes originating in Southeast Asia (Hedrick and McDowell 1995). The designation of LMBV later as SCRV was based on the location where the virus was isolated. However, Grizzle et al. (2002) disputed the change in name citing the fact that the LMBV had previously (1991) been isolated in largemouth bass from Lake Weir, Florida, USA (Francis-Floyd 1992). The aforementioned studies and more recent phylogenetic analyses support LMBV, GV6, and DFV as strains of the same species that is formally known by the ICTV as the SCRV (Holopainen et al. 2009). Importantly, it has been argued based on the genetic sequence analyses as well as epidemiological and pathobiological characteristics that SCRV may be too divergent to be included within the genus *Ranavirus* (Hyatt et al. 2000; Whittington et al. 2010; Jancovich et al. 2015).

Epizootics attributable to SCRV have been repeatedly reported among wild populations of North American largemouth bass (Grizzle and Brunner 2003; Plumb and Hanson 2011). Although SCRV virulence appears variable in natural and experimental settings, typical outbreaks involve adult fish observed during summer at the surface with buoyancy or equilibrium problems. In general, the factors responsible for SCRV epizootics remain unknown, and may be case-specific. However, genetic background of the largemouth bass population, SCRV exposure history within that population, SCRV strain, and environmental factors (e.g., low dissolved oxygen

associated with warmer water temperatures) have been argued as potential factors contributing to emergence (Grizzle and Brunner 2003; Plumb and Hanson 2011). Experimental infections of SCRV in largemouth bass and striped bass (*Morone saxatilis*) revealed a direct correlation between virus titer and mortality by both injection and immersion; however, striped bass experienced lower overall cumulative mortality (Plumb and Zilberg 1999b; Zilberg et al. 2000). Experimental transmission of SCRV in largemouth bass via oral administration resulted in infection of the skin and internal organs (e.g., swim bladder) without mortality (Woodland et al. 2002a).

In the USA, SCRV has also been isolated from a wide range of wild asymptomatic freshwater fishes (6 families and 17 species) in 31 states ranging as far south as Florida to as far west as Arizona, and to the northern states of Wisconsin, Michigan, New York, Vermont, and Delaware (Goldberg 2002; Woodland et al. 2002b; Groocock et al. 2008; USFWS 2011; Iwanowicz et al. 2013; Table 3). Most recently, a SCRV strain was isolated from the exotic Northern snakehead (*Channa argus*) recently introduced into the Chesapeake Bay watershed (Iwanowicz et al. 2013). Asian strains of SCRV (DFV/GV6) were shown experimentally to infect and induce low mortality in rainbow trout and chinook salmon (*Oncorhynchus tshawytscha*), but not channel catfish (*Ictalurus punctatus*; Hedrick and McDowell 1995). A SCRV strain isolated from moribund hatchery-reared largemouth bass reared in China was found to be highly lethal to largemouth bass (Deng et al. 2011); however, little or no mortality was observed in seven other species tested including koi (*Cyprinus carpio*; Table 3). In contrast, a recent mass mortality event among farmed koi in southern India was attributed to a strain of SCRV (George et al. 2014), although the authors did not provide a detailed description of viral-induced pathology.

It seems likely that SCRV has been disseminated across the USA and globally through the unrestricted movement of live fish and their products associated with the ornamental (Hedrick and McDowell 1995; Deng et al. 2011; George et al. 2014), food (Plumb and Zilberg 1999a), and angling industries (Grant et al. 2005; Schramm and Davis 2006). For example, in the USA, largemouth bass angling tournaments may contribute to the spread of SCRV to naïve fish by placing infected and uninfected fish in close proximity; however, the stress associated with angling has not been shown to greatly increase SCRV-associated mortality (Grant et al. 2005; Schramm and Davis 2006). Given that SCRV remains infectious in frozen tissues, the import/export of frozen fish tissues may represent another mechanism by which the virus can be spread (Plumb and Zilberg 1999a). Future concerted surveillance efforts are needed to confirm the risk that the aforementioned industries play in the global dissemination of SCRV.

3.4   Frog Virus 3

Although only a single case of FV3 infection has been reported in wild fish (Mao et al. 1999a), a number of cases of piscine infection with FV3 have been reported among captive/cultured fish. In the former, an FV3-like virus was recovered from a

Table 3 Distribution of ranavirus infections or mortality in wild and captive fish, including the location of origin for imported animals

Continent	Nation	Origin[a]	State/Province[a]	Family	Latin name	I, M[b]	W, C[c]	References
Asia	China	–	Guangdong	Centrarchidae	*Micropterus salmoides*	M	C	Deng et al. (2011)
	India	–		Cyprinidae	*Cyprinus carpio*	M	C	George et al. (2014)
	Singapore	–		Serranidae	*Epinephelus tauvina*	M	C	Chua et al. (1994), Qin et al. (2003)
	Taiwan	–		Centrarchidae	*Micropterus salmoides*	–	C	Huang et al. (2011)
		–		Latidae	*Lates calcarifer*	–	C	Huang et al. (2011)
		–		Lutjanidae	*Lutjanus erythropterus*	–	C	Huang et al. (2011)
		–		Serranidae	*Epinephelus awoara*	M	C	Murali et al. (2002), Huang et al. (2011)
		–			*Epinephelus coioides*	–	C	Huang et al. (2011)
		–			*Epinephelus lanceolatus*	–	C	Huang et al. (2011)
	Thailand	–	Nakompathom	Eleotridae	*Oxyeleotris marmoratus*	M	C	Prasankok et al. (2005)
Australia	Australia	–	NSW, SA, Vic	Percidae	*Perca fluviatilis*	M	W	Whittington et al. (2010)
		–	NSW, SA, Vic	Salmonidae	*Oncorhynchus mykiss*	M	C	Whittington et al. (2010)
Europe	Denmark	–	–	Gadidae	*Gadus morhua*	I	W	Ariel et al. (2010)
		–	–	Scophthalmidae	*Scophthalmus maximus*	M	C	Ariel et al. (2010)
	Finland	–	–	Percidae	*Sander lucioperca*	I	W	Tapiovaara et al. (1998)
	France	–	–	Ictaluridae	*Ictalurus melas*	M	W	Pozet et al. (1992), Bigarré et al. (2008)
	Germany	–	–	Siluridae	*Silurus glanis*	M	C	Ahne et al. (1989, 1991)
	Hungary	–	–	Ictaluridae	*Ameiurus nebulosus*	M	W	Juhász et al. (2013)
	Italy	–	–	Ictaluridae	*Ictalurus melas*	M	W	Bovo et al. (1993)
	Italy	New Zealand	–	Anguillidae	*Anguilla australis*	–	W	Bovo et al. (1999)

North America	USA	Asia			Family	Species	Reference
North America	CA	Asia	–	–	Labridae	Labroides dimidiatus	Hedrick and McDowell (1995)
	VA	Asia	I	W	Channidae	Channa argus	Iwanowicz et al. (2013)
	MN	–	–	–	Centrarchidae	Ambloplites rupestris	USFWS (2011)
	MD, TN	–	–	–	Centrarchidae	Lepomis auritus	USFWS (2011)
	GA, IL, MN, OH	–	–	–	Centrarchidae	Lepomis macrochirus	Woodland et al. (2002a), USFWS (2011)
	AR	–	–	–	Centrarchidae	Lepomis megalotis	USFWS (2011)
	AZ, KY, MI, MN, NY, OH, OK, PA, WI, WV	–	M	W	Centrarchidae	Micropterus dolomieu	Groocock et al. (2008), USFWS (2011)
	FL	–	–	–	Centrarchidae	Micropterus notius	USFWS (2011)
	AL, AR, GA, KY, LA, MI, OK, TN	–	–	–	Centrarchidae	Micropterus punctulatus	USFWS (2011)
	AL, AR, AZ, CT, DE, FL, GA, IA, IL, KS, KY, LA, MD, MI, MN, MO, MS, NC, NJ, NY, OH, OK, PA, SC, TN, TX, VA, VT, WI	–	I, M	W, C	Centrarchidae	Micropterus salmoides	Grant et al. (2005), Groocock et al. (2008), Grizzle et al. (2002), Hanson et al. (2001), Mao et al. (1999b), Neal et al. (2009), Plumb et al. (1996, 1999), Southard et al. (2009), USFWS (2011), Woodland et al. (2002b)
	WI	–	–	–	Centrarchidae	Pomoxis nigromaculatus	USFWS (2011)
	KY	–	–	–	Catostomidae	Minytrema melanops	USFWS (2011)
	NC	–	–	–	Cyprinidae	Nocomis leptocephalus	USFWS (2011)

Table 3 (continued)

Continent	Nation	Origin[a]	State/Province[a]	Family	Latin name	I, M[b]	W, C[c]	References
		–	IL	Esocidae	Esox masquinongy	–	–	USFWS (2011)
		–	–	Esocidae	Esox niger	–	–	Goldberg (2002)
		–	SC	Moronidae	Morone americana	–	–	USFWS (2011)
		–	KS	Moronidae	Morone chrysops	–	–	USFWS (2011)
		–	AZ	Moronidae	Morone mississippiensis	–	–	USFWS (2011)
		–	MN, OH	Sciaenidae	Aplodinotus grunniens	–	–	USFWS (2011)
		Asia	CA	Poeciliidae	Poecilia reticulata	–	–	Hedrick and McDowell (1995)
		–	CA	Gasterosteidae	Gasterosteus aculeatus	M	W	Mao et al. (1999a)
		–	GA	Acipenseridae	Acipenser gueldenstaedtii	M	C	Waltzek et al. (2014)
		–	CA	Acipenseridae	Acipenser transmontanus	M	C	Waltzek et al. (2014)
		–	MO	Acipenseridae	Scaphirhynchus albus	M	C	Waltzek et al. (2014)

[a]Provided when available

[b]I infection with no gross signs of ranavirus disease, M Mortality due to ranavirus disease

[c]W wild population, C Captive populations including zoological and fish culture facilities, it does not include controlled virus challenge studies

single moribund threespine stickleback that was coinfected with myxozoan parasites, obscuring the role of the virus in the disease (Mao et al. 1999a). However, FV3-like ranaviruses have been isolated from captive fishes on several occasions. A ranavirus displaying 98–99 % nucleotide identity to FV3 over a portion of the major capsid gene has been reported among cultured marbled sleeper goby (*Oxyeleotris marmoratus*) in Thailand (Prasankok et al. 2005). Furthermore, FV3 outbreaks have impeded efforts to restore populations of the critically endangered pallid sturgeon (*Scaphirhynchus albus*) in the Missouri River Basin of the USA (Waltzek et al. 2014). High-mortality epizootics were reported among young-of-the-year pallid sturgeon in 2001, 2009, and 2013 at the Blind Pony Hatchery in Sweet Springs, Missouri, USA (Chinchar and Waltzek 2014; Waltzek et al. 2014). Experimental transmission of the 2009 isolate recreated the same high-mortality disease in naïve juvenile pallid sturgeon following bath exposure (Waltzek et al. 2014). Furthermore, an FV3 strain isolated from moribund hatchery-reared Russian sturgeon (*Acipenser gueldenstaedtii*) was found to be lethal to both Russian and lake (*A. fluvescens*) sturgeon following intraperitoneal injection (Waltzek et al. 2014). Finally, an FV3-like ranavirus was isolated from juvenile white sturgeon (*A. transmontanus*) on a California, USA, farm during an unusual mortality event in 1998 (Waltzek et al. 2014).

Experimental transmission studies using FV3-like viruses isolated from a diversity of ectothermic vertebrate classes have been shown to infect black bullhead (*Ameiurus melas*), northern pike, pike-perch, mosquito fish (*Gambusia affinis*), and bluegill (*Lepomis macrochirus*), although little or no mortality was observed in these species (Gobbo et al. 2010; Bang-Jensen et al. 2009, 2011a, b; Brenes et al. 2014a). Similarly, recent North American fish health surveys resulted in the isolation of FV3 from healthy appearing fathead minnow (*Pimephales promelas*), walleye (*Sander vitreus*), and northern pike (Waltzek et al. 2014). Although preliminary, these data suggest that imperiled sturgeon may be predisposed to infections with FV3-like viruses; whereas, other fishes may simply act as viral carriers or dead-end hosts. Future studies are needed to explore the importance of FV3-like viruses across a wider range of wild and captive fish species as well as the potential role of aquaculture in the global dissemination of these important pathogens.

3.5   Bohle Iridovirus

As indicated above, BIV was first isolated from diseased ornate burrowing frog tadpoles (*Limnodynastes ornatus*) in Australia. Although designated as a distinct species by the ICTV, the sequence of the MCP gene is 97.8 % identical to that of EHNV, which is endemic in a different part of the continent (Marsh et al. 2002). As with FV3, laboratory challenge studies demonstrated that BIV is also pathogenic to fish, in this case to barramundi (*Lates calcarifer*), a popular sport fish in Australia (Moody and Owens 1994). On just one occasion, BIV may have been associated with high mortality in hatchery-reared Nile tilapia fry in Australia (Ariel and Owens 1997). Although the authors did not genetically characterize the iridovirus, feeding

the moribund tilapia fry to barramundi fingerlings reproduced disease similar to what had been reported following challenge studies of barramundi to BIV (Moody and Owens 1994).

3.6 Taxonomically Unassigned Ranaviruses That Affect Fish

Although ranaviruses infecting freshwater fishes are relatively well characterized, less is known about the significance of ranaviruses infecting cultured or feral populations of marine fishes. Exceptions include two related ranaviruses, SGIV and GIV, which significantly impact grouper mariculture in Asia (Chua et al. 1994; Murali et al. 2002; Qin et al. 2003). Phylogenetic analysis based on the 26 conserved iridovirus genes demonstrated that GIV and SGIV are each other's closest relatives; however, these viruses are genetically divergent from other ranaviruses (Eaton et al. 2007). Therefore, GIV/SGIV may need to be considered as a new genus within the family *Iridoviridae* (Jancovich et al. 2015).

SGIV was first identified following a mass mortality event of net-cage farmed brown-spotted grouper (*Epinephelus tauvina*) in Singapore in 1994 (Chua et al. 1994). The authors referred to the epizootic as Sleepy Grouper Disease; however, they failed to isolate or genetically characterize the virus. In 1998, the same disease was again observed in Singapore farms following imports of brown-spotted grouper fry from Taiwan (Qin et al. 2003). These authors genetically characterized the virus as a novel ranavirus, and named it SGIV (Qin et al. 2003). Similarly, GIV has negatively impacted production of yellow grouper (*Epinephelus awoara*) in Taiwan (Murali et al. 2002). Delivery of the virus to yellow grouper by injection resulted in 100 % mortality during experimental challenges (Murali et al. 2002). A recent study reported the isolation of SGIV and GIV strains from grouper and non-grouper species cultured in Taiwan (Huang et al. 2011, Table 3). This study illustrates the apparent expanding host range of SGIV/GIV including the first isolation of these viruses in freshwater (largemouth bass) and catadromous (barramundi) fishes.

Other partially characterized ranaviruses from wild marine fishes include cod ranavirus (CoIV) isolated from Danish Atlantic cod (*Gadus morhua*; Ariel et al. 2010) and the short-finned eel ranavirus (SERV) isolated from short-finned eel (*Anguilla australis*) off the coast of New Zealand (Bang-Jensen et al. 2009). Ranaviruses isolated from seemingly healthy cultivated freshwater and marine fishes include the pike-perch iridovirus (PPIV) isolated from Finnish pike-perch fingerlings (Tapiovaara et al. 1998) and Ranavirus maxima (Rmax) isolated from Danish turbot (*Scophthalmus maximus*) fry (Ariel et al. 2010). Preliminary phylogenetic analyses of these fish viruses have revealed they represent previously unknown ranaviruses, warranting more comprehensive study into their biology and potential impact on cultivated and wild populations (Holopainen et al. 2009; Jancovich et al. 2015).

4 Ranaviruses Infecting Reptiles

Although ranaviral disease has been described in reptiles in a number of cases, it is likely that these disease events are underreported (Daszak et al. 1999; Johnson et al. 2010; Allender 2012) due to lack of awareness, few long-term research studies, and lack of disease monitoring in biological studies. It is notable that reports of ranavirus infections in reptiles have markedly accelerated over the past decade. The rising awareness of these viruses in chelonians as important infectious agents may have contributed to the high number of case reports in these species as well as increasing the awareness of these viruses as pathogens in reptiles in general (Shaver 2012). It has also been surmised that the global trade of reptiles and amphibians in combination with the wide host range of ranaviruses is contributing to its emergence (Stöhr et al. 2013a). This is of significant importance for wild and captive reptiles as well as amphibians and fish.

There is an increasing amount of information available on ranaviruses capable of infecting reptiles. The majority of ranaviruses detected in reptiles so far have been FV3-like (Huang et al. 2009; Allender et al. 2011). In addition, ECV-, BIV-, and CMTV-like viruses have been detected in several reptile species in captivity (Marschang et al. 2013; Stöhr et al. 2015). Characterization of these viruses has most often been based on partial MCP gene sequences, but additional sequence data are becoming available to help understand relationships between the ranaviruses found in reptiles. In the USA, only FV3-like viruses have been detected in reptiles so far, which is the most commonly reported ranavirus for anurans. In Europe, a wider range of ranavirus types has been described, including both FV3-like viruses as well as ECV, BIV, and CMTV representatives. A fully sequenced ranavirus from chelonians in Asia (soft-shelled turtle iridovirus, STIV) has been shown to be closely related to FV3 (Huang et al. 2009).

4.1 History of Reptile Cases

In the 1980s, two cases of iridovirus infections in tortoises were described in Switzerland (Heldstab and Bestetti 1982; Müller et al. 1988). Due to the described clinical, histological, and electronmicroscopical findings, these animals are believed to have been infected with a ranavirus and are therefore the first documented cases of ranaviral infection and disease in reptiles. A low number of proven detections of ranavirus infection in reptiles were documented in captive and wild chelonians in the late 1990s (Table 4). The first cases of ranavirus infections in reptiles from which data were available on the viral genome were from a box turtle (*Terrapene c. carolina*) and a tortoise (*Testudo horsfieldii*) from North America. Both appeared to be FV3-like based on partial MCP gene sequences and restriction endonuclease analysis (Mao et al. 1997). No clinical information on those two chelonians was

Table 4 Distribution of ranavirus infections or mortality in wild and captive reptiles, including the location of origin for imported animals

Continent	Nation	Origin[a]	State/Province[a]	Family	Latin name	I, M[b]	W, C[c]	References
Asia	China	–	–	Trionychidae	Pelodiscus (Trionyx) sinensis	M	C	Chen et al. (1999)
Australia	Australia	Indonesia	–	Pythonidae	Morelia (Chondropython) viridis	M	C/W	Hyatt et al. (2002)
Europe	Austria	Ethiopia	–	Testudinidae	Stigmochelys (Geochelone) pardalis	M	C	Benetka et al. (2007)
	Germany	Asia via FL	–	Agamidae	Japalura splendida	M	C/W	Behncke et al. (2013)
		–	–		Pogona vitticeps	I, M	C	Stöhr et al. (2013b), Marschang et al. (2013)
		Asia	–	Anguidae	Dopasia gracilis	M	C/W	Stöhr et al. (2013a)
		–	–	Boidae	Eunectes sp.	I	C	Marschang et al. (2013)
		USA	FL	Dactyloidae	Anolis sagrei	M	C/W	Stöhr et al. (2013b)
		USA	FL		Anolis carolinensis	M	C/W	Stöhr et al. (2013b)
		–	–	Emydidae	Emys orbicularis	I	C	Stöhr et al. (2013d)
		–	–		Trachemys scripta elegans	I	C	Marschang et al. (2013)
		–	–	Gekkonidae	Uroplatus fimbriatus	M	C	Marschang et al. (2005)
		–	–	Iguanidae	Iguana iguana	M	C	Stöhr et al. (2013b)
		–	–	Testudinidae	Testudo graeca	I	C	Marschang et al. (2013)
		–	–		Testudo hermanni	M	C	Blahak and Uhlenbrok (2010)
		–	–		Testudo horsfieldii	I	C	Marschang et al. (2013)
		–	–		Testudo kleinmanni	M	C	Blahak and Uhlenbrok (2010)
		–	–		Testudo marginata	M	C	Blahak and Uhlenbrok (2010)
		–	–		Stigmochelys pardalis	I	C	Marschang et al. (2013)

(continued)

Table 4 (continued)

Continent	Nation	Origin[a]	State/Province[a]	Family	Latin name	I, M[b]	W, C[c]	References
		ID	–	Pythonidae	*Python brongersmai*	M	C/W	Stöhr et al. (2015)
		–	–		*Python regius*	I	C	Marschang et al. (2013)
		–	–		*Python molurus*	I	C	Marschang et al. (2013)
		–	–	Varanidae	*Varanus macraei*	I	C	Marschang et al. (2013)
	Portugal	–	–	Lacertidae	*Lacerta monticola*	I	W	Alves de Matos et al. (2011)
	Switzerland	Yugosl-avia	–	Testudinidae	*Testudo hermanni*	M	C/W	Müller et al. (1988)
		–	–		*Testudo hermanni*	M	C	Heldstab and Bestetti (1982), Marschang et al. (1999)
	United Kingdom	–	–	Lacertidae	*Lacerta agilis*	I	W	Marschang et al. (2013)
		–	–	Testudinidae	*Testudo hermanni*	M	C	Marschang et al. (2013)
North America	USA	–	RI, VA, WA	Emydidae	*Chrysemys picta*	I, M	W	USGS (2005, 2008), Goodman et al. (2013)
		–	FL		*Terrapene carolina bauri*	M	C, W	Johnson et al. (2008)
		–	IL, IN, KY, MD, NC, NY, PA, TN, TX, VA, WV		*Terrapene carolina carolina*	I, M	C, W	Mao et al. (1997), De Voe et al. (2004), Allender et al. (2006), Johnson et al. (2008), Ruder et al. (2010), Farnsworth (2012), Sim et al. (2012), Allender (personal communication), Currylow et al. (2014), Kimble et al. (2014)
		–	–		*Trachemys scripta elegans*	I	W	Allender (personal communication)
		–	GA	Testudinidae	*Geochelone platynota*	M	C	Johnson et al. (2008)
		–	–		*Gopherus polyphemus*	M	W	Westhouse et al. (1996), Johnson et al. (2008)
		–	–		*Testudo horsfieldii*	–	C	Mao et al. (1997)

[a]Provided when available
[b]I infection with no gross signs of ranaviral disease, M Mortality due to ranaviral disease
[c]W wild population, C Captive populations including zoological and breeding facilities, it does not include controlled virus challenge studies

published. Recently, there has been an increase in the number of reports and cases in chelonians worldwide, especially box turtles (*Terrapene* sp.) in the USA (De Voe et al. 2004; Allender et al. 2006; Johnson et al. 2008; Allender 2012, Table 4). Although ranavirus detection in chelonians has been reported most frequently, detection of these viruses in lizards and snakes has been increasing, mostly from captive populations (Stöhr et al. 2013b; Behncke et al. 2013; Marschang et al. 2013). The causes for increased detection of ranaviruses in wild and captive reptiles may include increased awareness or surveillance, improved testing methods, or actual emergence of the pathogen.

4.2   Outbreaks in Chelonians

Adult chelonians have been more commonly reported to develop FV3-like infections than juveniles (Johnson 2006). However, recent surveillance in eastern box turtles demonstrated that juveniles are more likely to be FV3 positive (Allender 2012). Therefore, it is likely that susceptibility of chelonians to ranaviruses differs among developmental stages similar to amphibians (Haislip et al. 2011). Some outbreaks in box turtles have involved translocation events that congregate many individuals, resulting in high infection prevalence and death (Belzer and Seibert 2011; Farnsworth and Seigel 2013; Kimble et al. 2014). In a multiyear survey of box turtles in the USA, ranavirus prevalence has not been reported above 5 % in a population without abnormal mortality events (Allender et al. 2013).

Reports of single cases and outbreaks in reptiles so far have mainly involved box turtles within North America (De Voe et al. 2004; Allender et al. 2006; Johnson et al. 2008, 2010; Ruder et al. 2010; Allender 2012; Kimble et al. 2014). While eastern box turtles are primarily terrestrial, they have been shown to spend a considerable amount of time in temporary ponds (Donaldson and Echternacht 2005), which may expose them to ranavirus through water or sympatric amphibians (Belzer and Seibert 2011; Currylow et al. 2014). Some studies have indicated that increased ranaviral mortality in box turtles may correlate with increased exposure to infected sympatric amphibians, possibly via predation on infected amphibians, exposure to water containing ranavirus shed by amphibians, or via hematophagous insects (Belzer and Seibert 2011; Kimble et al. 2014). A study of wild Eastern painted turtles, an aquatic species, in Virginia, USA, reported infection prevalence of 4.8–31.6 % in different ponds, with no apparent disease (Goodman et al. 2013).

Koch's postulates have been fulfilled for ranaviral disease in chelonians, including box turtles. Experimental challenge with FV3-like isolates from either Burmese star tortoises (*Geochelone platynota*) or eastern box turtles has resulted in high mortality in red-eared sliders (Johnson et al. 2007; Allender 2012). Characteristic clinical signs of nasal discharge and oral plaques were seen, but were inconsistent among individuals. Mortality rate and the presence of clinical signs were observed to be significantly greater in turtles exposed at 22 °C compared to 28 °C, with corresponding increased viral copy number and shorter median survival time at lower temperatures (Allender et al. 2013).

In addition to the box turtle cases described above, several other reports of FV3-like infections have been seen in captive chelonians (Marschang et al. 1999; De Voe et al. 2004; Benetka et al. 2007; Johnson et al. 2008; Blahak and Uhlenbrok 2010, Table 4). Ranavirus infections were described in two juvenile diseased Hermann's tortoises (*Testudo hermanni*) in Germany using PCR. All seven animals in the affected group died with similar signs (Marschang et al. 1999). The associated virus was first described as FV3-like, but has since been shown to be more closely related to CMTV (Stöhr et al. 2015). A leopard tortoise (*Stigmochelys* (*Geochelone*) *pardalis pardalis*) with nasal discharge, stomatitis, and lethargy had concurrent ranavirus and herpes virus infection confirmed by PCR (Benetka et al. 2007). Ranaviruses have also been detected in association with mortality events in captive Hermann's tortoises, Egyptian tortoises (*T. kleinmanni*), and marginated tortoises (*T. marginata*) in Germany. Affected animals developed stomatitis as well as splenic necrosis, enteritis, hepatitis, pancreatitis, and dermatitis in some cases (Blahak and Uhlenbrok 2010). Analysis of the genomes of the viruses associated with these outbreaks (tortoise ranavirus 1 and 2, ToRV-1 and -2) shows that sequence analysis clusters them closely with FV3, while their genomic arrangement resembles that of CMTV (Stöhr et al. 2015). Captive farmed soft-shelled turtles in China developed "red neck disease" associated with a ranavirus (Chen et al. 1999). Soft shell turtle iridovirus was the first reptilian ranavirus to be fully sequenced, demonstrating that it is FV3-like (Huang et al. 2009). Comparative studies of ranaviruses infecting chelonians have shown that both FV3- and CMTV-like strains occur, and that strains from different outbreaks differ from one another and are often more closely related to previously described amphibian ranaviruses than to other reptile-derived ranaviruses (Stöhr et al. 2015).

The short- and long-term impacts of ranaviruses on chelonian populations are unknown. Population stability in the face of ranavirus outbreaks has been debated, particularly regarding vulnerable Eastern box turtles. Due to the low reproductive rate and long time to sexual maturation of these animals, loss of adult females due to this disease will likely lead to significant population declines over time (Farnsworth and Seigel 2013).

4.3   Outbreaks in Squamates

Until recently, ranaviruses were only rarely reported in squamate reptiles (snakes and lizards). The first report of ranaviruses in these animals was in a group of ten juvenile green tree pythons (*Morelia* (*Chondropython*) *viridis*) imported into Australia from Papua New Guinea with oral and hepatic lesions. A ranavirus that was 97 % homologous to FV3 was isolated from pooled necropsy tissues (Hyatt et al. 2002). An FV3-like ranavirus was isolated from several organs of a red blood python (*Python brongersmai*) with similar pathology imported into Germany from Indonesia. The isolated ranavirus was most closely related to TFV, originally described in China (Stöhr et al. 2015). A leaf-tailed gecko (*Uroplatus fimbriatus*) died unexpectedly and was diagnosed with a BIV-like ranavirus infection

(Marschang et al. 2005, Stöhr et al. 2015). In Portugal, a ranavirus was isolated from a wild-caught Iberian mountain lizard (*Lacerta monticola*) that did not show any clinical signs of disease. This isolate was closely related to FV3; a coinfection with erythrocytic necrosis virus was also found (Alves de Matos et al. 2011). In a study describing virological screening of samples from lizards (Stöhr et al. 2013b), ranaviral infections were detected in five species: brown anoles (*Anolis sagrei*), Asian glass lizards (*Dopasia gracilis*), green anoles (*Anolis carolinensis*), green iguanas (*Iguana iguana*), and a central bearded dragon (*Pogona vitticeps*). All of the infected lizards had skin lesions. Sequencing part of the MCP gene of each virus showed that the five detected viruses were distinct from one another and were 98.4–100 % identical to the corresponding portion of the FV3 genome. However, the ranavirus detected in the green iguana was 100 % identical to ECV, whereas the ranavirus found in the bearded dragon was identical to a ranavirus detected in tortoises in Germany (ToRV-1), which is most closely related to FV3 (Stöhr et al. 2015). Further analysis of the genomes of the isolated viruses demonstrated that the ranaviruses detected in anoles were closely related to FV3, whereas the isolate from the Asian glass lizard clustered phylogenetically to TFV (Stöhr et al. 2015). A ranavirus was also detected in green striped tree dragons (*Japalura splendida*) imported from southwestern China via Florida into Germany during a mass mortality event. The ranavirus appeared to be closely related to FV3 (Behncke et al. 2013). During a study in Germany, different reptilian samples submitted for virological testing were screened for the presence of ranavirus, with an increasing number of infections detected from 2010 to 2013. Affected species included various chelonian and squamate species (Table 4). Some of the detected ranaviruses were most closely related to ECV, others clustered together with the previously detected ranaviruses in European amphibians or reptiles, and one virus was FV3-like (A. Stöhr, unpublished data). This increase in detection of ranaviruses in reptiles may reflect either true emergence of these viruses in reptiles or increased surveillance. The genomic differences found in the viruses studied indicate that there is not a single strain of ranavirus that has adapted to reptiles as hosts, but rather that multiple transmissions of ranaviruses from amphibians and fish to reptiles may have taken place (Jancovich et al. 2010), and may continue to occur. Interestingly, studies have shown that within the legal international trade of reptiles, the largest numbers are traded through Europe and that these include both captive bred and wild-caught animals (Bush et al. 2013). The majority of reptile infections with genetically diverse ranaviruses have also been reported in Europe, often with a connection to the pet trade (Stöhr et al. 2013b; Stöhr et al. 2015). The role of illegal trade in exotic pets for the epidemiology of ranaviral infections in reptiles has not been studied, although there is some indication that this has played a role in ranaviral outbreaks in pet reptiles as well (S. Blahak, CVUA-OWL, personal communication). Wild-caught and farmed reptiles that are globally traded are often in contact with other animal species (reptiles and amphibians), and are not regularly tested for the presence of infections. Another aspect of increased surveillance and reporting of ranaviral infections in reptiles is the increased finding of co-infections with other pathogens, making diagnosis of ranaviral disease in some cases difficult.

5 Interclass Transmission of Ranaviruses

Ranaviruses, as described above, are pathogens that affect a wide variety of hosts across three classes of ectothermic vertebrates (Amphibia, Reptilia, and Osteichthyes). It has long been suspected that interclass transmission of this group of viruses was possible, but it has only recently been demonstrated experimentally under controlled laboratory conditions (Brenes et al. 2014a). Evidence exists that interclass transmission may occur in wild populations for at least BIV, ATV, and FV3.

The first evidence for interclass transmission of ranaviruses was provided by Moody and Owens (1994). Barramundi (*Lates calcarifer*) were exposed to BIV, an isolate derived from amphibians, by water bath exposure or injection. The exposed fish developed disease and experienced 100 % mortality (Moody and Owens 1994). BIV has also successfully been transmitted to juvenile short-necked turtles (*Emydura macquarii krefftii*) and saw-shelled turtles (*Myuchelys* (*Elseya*) *latisternum*), but adult turtles of the same species as well as juvenile crocodiles (*Crocodylus johnstoni*) were not successfully infected. Transmission studies with three species of snakes (brown tree snakes, *Boiga irregularis*, common green tree snakes, *Dendrelaphis punctulatus*, and keelback snakes, *Tropidonophis* (*Amphiesma*) *mairii*) did not induce disease in any of the animals, but BIV was reisolated from one of the brown tree snakes four weeks after inoculation (Ariel 1997). The isolation of BIV so long after initial infection without clinical signs suggests that this species may be a viable reservoir (Ariel 1997).

Although originally thought to be restricted to urodeles (Jancovich et al. 2001), ATV was later shown to be pathogenic to anurans (Schock et al. 2008). Experimental infection of largemouth bass was successful, but inoculated animals experienced no mortality or disease (Picco et al. 2010). There is also evidence that multiple FV3-like and ATV-like strains may circulate in ponds and may affect both urodeles and anurans (Schock et al. 2008). To date, no experimental infections of ATV in reptiles have been attempted.

An additional study by Bayley et al. (2013) has shown that a ranavirus originally isolated from fish (PPIV) is capable of causing mortality in common frog tadpoles. Common frog tadpoles were exposed to a panel of six fish-derived ranavirus isolates via water bath. However, only one of the six ranavirus isolates, PPIV, caused mortality. This was the first case where exposure to a fish-derived isolate caused death in an amphibian. Subsequent experiments by Brenes et al. (2014a) have shown transmission of an FV3-like isolate from fish to amphibians.

FV3-like viruses have been detected in fish, amphibians, and reptiles and there is evidence from wild populations, captive settings, and from experimental transmission studies that these viruses have a very wide host range. Mao et al. (1999a) found identical ranavirus isolates from a threespine stickleback and a northern red-legged frog (*Rana aurora*) tadpole from the same area. FV3-like viruses have been isolated from moribund marbled sleeper gobies (*Oxyeleotris marmoratus*) cultivated in Thailand (Prasankok et al. 2005) and several hatchery-reared sturgeon species during epizootics in the USA (Waltzek et al. 2014); however, the role of the virus in disease was only thoroughly studied and confirmed in pallid sturgeon.

Brenes et al. (2014a) demonstrated water-bath transmission of an FV3-like virus, originally isolated from a moribund pallid sturgeon to amphibians (Cope's gray treefrog, *Hyla chrysoscelis*), fish (mosquito fish) and reptiles (red-eared sliders). In a similar experiment, three chelonians (Florida soft-shelled turtle, *Apalone ferox*; eastern river cooters, *Pseudemys concinna*; Mississippi map turtles, *Graptemys pseudogeographica kohnii*) were assessed for susceptibility to the same FV3-like virus, an FV3-like isolate from an eastern box turtle and a third FV3-like isolate from an American bullfrog, from the USA (Brenes et al. 2014b). While no disease or mortality was observed in these experiments, infections were documented in soft-shelled turtles that were exposed to the fish isolate and those that were exposed to the turtle isolate (Brenes et al. 2014b). Infections were also observed in the Mississippi map turtles that were exposed to the turtle isolate (Brenes et al. 2014b). These results demonstrate the possibility that reptiles, fish, and amphibians may act as reservoirs for FV3-like ranaviruses for other taxa.

The role of different host classes in the epidemiology of ranaviruses remains to be studied. A number of field studies have indicated that ranavirus infections in one group of hosts can affect the health and survival of sympatric ectothermic vertebrates, but the role of various hosts as long-term carriers of virus and in the dynamics of transmission is yet unknown. The fact that several studies have shown that different viruses may have vastly different effects on various hosts is also important for the assessment of infection status in clinically healthy animals, both in the wild and in captivity, especially in trade. Healthy infected animals in which ranaviruses are not suspected could be a source of infection via direct contact or environmental contamination for other susceptible species of other animal classes. All of these findings underscore the need to reassess our understanding of ranaviruses as multispecies pathogens, not only as pathogens of specific groups of animals.

6   Summary and Conclusions

Ranavirus infections in amphibians, fish, and reptiles are widespread and affect a diverse suite of species within these vertebrate classes (Table 1, Fig. 6). The species affected include some that are economically important (e.g., rainbow trout, soft-shelled turtle, bullfrogs), but also several that are of conservation concern (e.g., Chinese giant salamander, gopher tortoise, dusky gopher frog, pallid sturgeon). The economic and conservation risk of these multispecies pathogens is dependent upon many factors, including characteristics of the host species. One thing is certain – some host species are highly susceptible to ranavirus, and these species are most likely to be affected during outbreaks. Thus, understanding host susceptibility to different ranaviruses is key to quantifying risk. Host–pathogen interactions between ranaviruses and amphibians are the best characterized. Research in this area needs to continue, but there also needs to be greater attention on the role of reptiles and fish in ranavirus epizootic events.

Fig. 6 Sites of ranavirus outbreaks include seemingly undisturbed sites, such as (**a**) Maine, USA (credit = Nathaniel Wheelwright) and (**b**) Dwingelderveld, Netherlands (credit = Jeiger Herder), (**c**) constructed ponds in urban environments (credit = Jeiger Herder), and (**d**) aquaculture facilities (credit = Rolando Mazzoni). High host density and environmental stressors likely contribute to outbreaks, especially in captive facilities (e.g., (**e**) bullfrog farm in Brazil; credit = Rolando Mazzoni). Some highly endangered species (e.g., *Andrias davidianus*) have been affected (**f**), credit = Yi Geng

All three classes of vertebrate hosts are intensively farmed in different regions of the world. The conditions of captive culture facilities that often maintain high densities of genetically similar individuals may be conducive to repeated outbreaks of ranaviral disease (Pearman and Garner 2005; Fig. 6). Additionally, conditions that favor transmission can lead to increased virulence, according to the virulence trade-off hypothesis (Alizon et al. 2009). Thus, captive facilities with recurring ranavirus outbreaks may facilitate evolution of ranavirus types that are more virulent than wild types (Brunner et al. 2015).

The commercial trade of ranavirus hosts is likely a significant factor facilitating the global distribution of ranaviruses, as well as interclass transmission of the pathogen. If novel strains of ranaviruses are introduced into naïve populations, experimental evidence suggests that there could be devastating effects (e.g., Pearman et al. 2004; Storfer et al. 2007; Hoverman et al. 2010). With the trade in animals being truly global and ranaviruses accompanying them (e.g., Schloegel et al. 2009; Kolby et al. 2014), it is important to understand what ranaviruses are being transported and where they end up.

Understanding the geographical distribution and host range of ranaviruses is becoming increasingly important as the World Health Organization for Animals has declared that EHNV and ranaviruses that infect amphibians are "reportable infections of wildlife" (OIE 2008). This designation requires countries that have agreed to OIE policies to screen a sample of ranavirus hosts that are crossing international borders for the presence of ranaviruses (Schloegel et al. 2010). However, few countries have yet taken steps to implement import policies that require declaration of ranavirus-free animals. Moreover, infection of fish by ranaviruses (other than EHNV) and reptiles (for any ranavirus species) are not included in the OIE regulations.

We are just beginning to understand the distribution and host range of ranaviruses. Continued surveillance of wild and captive populations, as well as, commercially traded animals combined with the characterization of the ranavirus strains are necessary to fully understand the distribution and host diversity of ranaviruses. Therefore, when ranavirus studies are undertaken, sufficient funding should be obtained to at least partially characterize the virus if detected. This approach will require that researchers work in interdisciplinary groups.

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