Chapter 3
Bats as Potential Reservoir Hosts for Vector-Borne Diseases

Christian Melaun, Antje Werblow, Markus Wilhelm Busch, Andrew Liston, and Sven Klimpel

Abstract Bats are the only mammals with the capacity of powered flight. Nearly 1,000 species can be found all over the world except in the northern and southern polar areas. They perform important ecosystem services such as control of insects, reseeding of cut forests and pollination of plants, which provide food for humans and animals. On the other side, they are also recognized to be natural reservoir hosts of a large variety of zoonotic diseases with the ability to cross species barriers. To date, more than 80 virus species of different groups and various parasites, which can cause several diseases have been isolated or detected in bats. Especially their high population density and gregarious roosting behaviour increase the likelihood of intra- and inter-species transmission of infections. Another important factor, which enables pathogens to spread long distances, is the migratory habit of some bat species, resulting in a great dispersal capacity. The transmission of pathogens from bats to humans or other animals occurs by direct contact with infected animals, their blood and tissue or through vector species. One of the most important vector groups are insects. With more than a million described species, they are the most diverse group of animals. Especially haematophagous groups such as Cimicidae, Culicidae or Phlebotominae are known as vectors for a variety of diseases. These include bacteria, protozoan and metazoan parasites as well as viruses. We focused on blood-feeding insects, because the presence of certain viruses in them as well as in bats comprises a potential virus transmission from bats to humans through mosquitoes or other blood-feeding insects. For this chapter, we could find 20 viruses

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from four different families and two parasitic pathogens detected in all three groups of haematophagous insects.

Keywords Chiroptera • Haematophagous insects • Vectors • Virus • Diseases • Parasites

3.1 Introduction

Bats (order Chiroptera) are one of the most diverse, abundant and widely distributed groups of mammals and the only one with the capacity of powered flight (Li et al. 2010; Omatsu et al. 2007). Nearly 1,000 species are found worldwide, except in the northern and southern polar areas, representing approximately 20 % of all mammalian species (Omatsu et al. 2007; Teeling et al. 2005). Chiroptera can be divided into the two suborders Megachiroptera (old world fruit bats) and Microchiroptera (echolocating bats) (Jones et al. 2002). Analysis of 17 nuclear genes dated the origin of chiropterans up to 50 million years ago (Calisher et al. 2006). One major lineage of Microchiroptera was traced to Laurasia and one to Gondwana (Teeling et al. 2005). Derived ancient origins for certain zoonotic viruses in bats, such as lyssa and henipa viruses, suggest a long history of coevolution and cospeciation (Calisher et al. 2006). On the one hand, bats perform important ecosystem services, such as control of insects (Reiskind and Wund 2009, 2010; Rydell et al. 2002), reseeding of cut forests and pollination of plants that provide food for humans and animals. On the other hand, bats are recognized to be a natural reservoir of a large variety of zoonotic viruses, which can cross species barriers to infect humans and other domestic or wild animals (Li et al. 2010). To date, more than 80 virus species of different groups have been isolated or detected in bats. Bats have a great dispersal capacity and the migratory habits of some species provide a good opportunity for pathogens to spread long distances (Messenger et al. 2003). Further, different migration patterns can often be found within one species. These different patterns may allow the exchange of viruses or virus variants between subpopulations as well as members of other species, because several species may roost in the same place. Also, their high population densities and gregarious roosting behaviour increase the likelihood of intra- and inter-species transmission of viral infections (Calisher et al. 2006). The extreme longevity of bats may help to maintain the viruses, resulting in chronic infections, and increase the chances of transmission to other mammals or vertebrates. Calisher et al. (2006) suggest an explanation why some viruses, which are deadly for humans and other mammals, can persist in bats without proving being fatal: because bats form a very ancient lineage amongst the mammals, it is possible that their immune system with its innate acquired immune responses may differ significantly from those of other mammals. So far very little is known about bat immune systems, although some studies indicate similarities between bats immune responses and those of other mammals (Chakravarty and Sarkar 1994; McMurray et al. 1982; Sarkar and

Chakravarty 1991). The studies of Halpin et al. (2000), Lau et al. (2005) and Leroy et al. (2005) show the occurrence of virus-specific B- and T-cell responses despite persistent virus infection. One possible pathway of virus transmission involves the animal's ecology. Due to their flying habits, bats are constrained by the aerodynamics of flight and cannot therefore ingest huge amounts of food. Instead of swallowing whole fruits, bats chew these to extract sugars and other substances. The partially digested fruit is spat out and falls to the ground, where these remnants are fed on by other animals. Residual virus particles in the bat saliva on the fruit remnants may cause infection of the latter animals. Heavier body parts of insect prey are discarded in the same way and are also eaten by terrestrial foraging species (Dobson 2005).

Insects comprise the most diverse group of animals with more than a million described species. The estimated number of extant species is between four and six million (Chapman 2009; Novotny et al. 2002). Insects can be found in nearly all terrestrial environments. Some species have become specialized feeders on blood. Depending on the species, this haematophagous behaviour can be observed either in both males and females or just in females. In the latter case, blood proteins are essential for egg production. All haematophagous insects use modified extremities of the head and extensions of the head capsule as piercing-sucking mouthparts to obtain and feed on blood (Krenn and Aspöck 2012; Lehane 2005). Convergent evolution has led to the development of piercing proboscides in various haematophagous insect groups (Krenn and Aspöck 2010, 2012).

One group of haematophagous insects with a worldwide distribution is the family Cimicidae (bed and bat bugs), which contains more than 100 species. Balvín (2008) mentions that bats are generally considered to be the original hosts of the family. The same had long been thought about the bedbug *Cimex lectularius* (e.g. Sailer 1952; Usinger 1966), but new results suggest an early sympatric speciation on humans and bats for different populations of bed bugs (Balvín et al. 2012). Although various pathogens have been identified from Cimicidae (e.g. Burton 1963; Delaunay et al. 2011; Goddard and deShazo 2009), their role as vectors is still unclear.

Mosquitoes (Diptera: Culicidae) are a second group of blood-sucking insects. They are regarded worldwide as the major vectors of vector-borne diseases. Especially, species of the genus *Anopheles*, which are well known as vectors of malaria, can also impact human and animal health by their ability to transmit arboviruses (arthropod-borne viruses) as well as filarial parasites such as the elephantiasis-causing *Wuchereria bancrofti* and *Brugia malayi* (Gillies and Coetzee 1987; Sallum et al. 2000; Service 1993). Apart from *Anopheles* spp., numerous other species of mosquitoes are pests or vectors of pathogens that cause diseases in humans and animals (Reinert et al. 2004). Because of their adaptive abilities, mosquitoes are capable of inhabiting and surviving in a wide range of habitats. Worldwide, they colonize nearly every aquatic habitat. As a result of their large flight range, some floodwater mosquito species can become pests even in places located far away from their breeding sites (Mohrig 1969; Schäfer et al. 1997). Additionally, flood plains along coastal areas as well as tree holes are used as

breeding sites by certain species. Also impressive is the adaptive capacity of mosquitoes to extremes of, or changes in, climatic factors. This ecological flexibility is one of the reasons for the success of mosquitoes (Becker et al. 2010). With the exception of the tropical genus *Toxorhynchites*, in which both sexes subsist on carbohydrate-rich materials such as honeydew, nectar and plant fluids (Snodgrass 1959), the females consume blood, e.g. to obtain proteins necessary for egg production. The host is located mainly by their olfactory senses, by the odour of carbon dioxide or the use of visual contact (Becker et al. 2010). While some mosquito species have specialized on birds, amphibians and other animal groups, others feed on mammals. Especially species with the last feeding habits, or possibly hybrids between different species, can be responsible for zoonoses, because they act as vectors between reservoir hosts and humans. Phlebotomine sand flies (Diptera: Psychodidae: Phlebotominae) are small (ca. 3 mm) nematoceran dipterans (Ready 2013) and a third group of haematophagous insects. They are mainly distributed in the tropics, but there is also an important Palaearctic element (Lewis 1974). The group acts as vector of leishmaniasis, *Bartonella bacilliformis* as well as some arboviruses of the three different genera: *Phlebovirus* (family Bunyaviridae), *Vesiculovirus* (family Rhabdoviridae) and *Orbivirus* (family Reoviridae) (Depaquit et al. 2010). Known disease agents, who can be transmitted by insects and have a potential impact on bats include bacteria, viruses, fungi as well as protozoan and metazoan parasites. With a few exceptions, in this chapter we concentrate on viruses, which have been detected in bats, haematophagous insects and humans (short information see Table 3.1).

3.2 Pathogens in Bats, Humans and Haematophagic Insects

The most important pathogens causing viral infections in bats, humans and haematophagic insects belong to the families Togaviridae (genera *Alphavirus* and *Rubivirus*), Flaviviridae (genus *Flavivirus*), Bunyaviridae (genera *Orthobunyavirus* and *Phlebovirus*) and Arenaviridae (genus *Arenavirus*).

3.2.1 Bunyaviridae

The Bunyaviridae is the largest family of RNA viruses with over 300 serologically or molecular-genetically distinguishable strains (Elliott 1997; Soldan and González-Scarano 2005). It was characterized in 1975 (Soldan and González-Scarano 2005) and is now considered to contain five genera: *Tospovirus* (the only plant-infecting viruses in the group), *Hantavirus*, *Nairovirus*, *Phlebovirus* and *Orthobunyavirus* (Bowen et al. 2001; LeDuc and Kahlon 2012; Weidmann et al. 2003). The medically most important pathogens within this family are not only transmitted through the bite of infected mosquitoes but also by sand flies or

Table 3.1 Overview of the diseases mentioned in this review, further details incl. sources can be found in the particular chapters (AB = Antibodies, n.k. = not known)

virus family	genus	virus species	clinical features	disease occurence	bat species	common name	distribution infect. bat	vector	*vector species*
Arenaviridae	Arenavirus	Tacaribe virus (TACV)	haemorrhagic fever	South America	*Artibeus lituratus* *Artibeus jamaicensis* *Desmodus rotundus* (AB) *Platyrrhinus helleri* (AB) *Sturnira lilium* (AB)	Great fruit eating bat Jamaican fruit bat Common vampire bat Heller's broad-nosed bat Yellow-shouldered bat	Trinidad/Guatemala Trinidad n.k. n.k. n.k.	mosquito	n.k.
Bunyaviridae	Orthobunyavirus	Bwamba virus (BWAV)	fever headache myalgia slow pulse	Cameroon Kenya Nigeria Uganda	*Myotis lucifugus*	Little brown bat	infection only in the Laboratory	mosquito	*Aedes furcifer* *Anopheles coustai* *Anopheles funestus* *Anopheles gambiae* *Mansonia uniformis*
		Catú-virus (CATUV)	fever headache body pains weakness	Brazil	*Mollosus currentium*	Bonda mastiff bat	Brazil	mosquito	*Anopheles nimbus* *Culex* spp.
		Guamá-virus (GMAV)	fever headache muscle pain myalgia leukopenia	Brazil	unidentified	n.k.	Brazil	mosquito sandfly	*Culex* spp. n.k.
		Kaeng Khoi virus (KKV)	fibrile illness	Cambodia Thailand	*Chaerephon plicatus* *Taphozous theobaldi*	Wrinkle-lipped free-tailed bat Theobald's tomb bat	Thailand Cambodia	bedbugs	*Stricticimex parvus* *Cimex insuetus*
	Phlebovirus	Rift Valley fever virus (RVFV)	body pain flu-like fever loss of memory neck stiffness retinal lesions sensitivity to light vomitting	Egypt Kenya Madagascar Mauritania Saudi Arabia Somalia Yemen	*Epomops franqueti* *Glauconycteris argentata* *Hipposideros abae* *Hipposideros caffer* *Micropteropus pusillus* *Miniopterus schreibersii*	Franquet's epauletted fruit bat Silvered bat Aba roundleaf bat Sundevall's roundleaf bat Peter's dwarf epauletted fruit bat Schreiber's long-fingered bat	Guinea n.k. Guinea n.k. n.k. n.k.	mosquito sandfly	*Aedes dalzieli* *Aedes dentatus* *Aedes circumluteolus* *Culex antennatus* *Culex neavei* *Culex pipiens* *Phlebotomus duboscqi* *Phlebotomus papatasi*
		Toscana Virus (TOSV)	aseptic meningitis headache meningoencephalitis muscle aches neck stiffness strong fever	France Greece Italy Spain Sweden Swiss	*Pipistrellus kuhlii*	Kuhl's pipistrelle	n.k.	sandfly	*Phlebotomus perniciosus* *Phlebotomus perfiliewi*
Flaviviridae	Flavivirus	Dengue virus (DENV)	general indisposition headache haemorrhagic fever orbital pain	tropical and subtropical regions, especially in southeast and south Asia	*Artibeus jamaicensis* (AB) *Carollia perspicillata* *Molossus* sp. (AB) *Myotis nigricans* (AB) *Natalus stramineus* (AB) *Pteronotus parnellii* (AB) *Uroderma* sp.(AB)	Jamaican fruit-eating bat Seba's short-tailed bat n.k. Black myotis Mexican funnel-eared bat Parnell's mustached bat n.k.	Mexico French Guinea n.k. Mexico Mexico Mexico n.k.	mosquito	*Aedes aegypti* *Aedes albopictus*
		Ilheus virus (ILHV)	chills CNS pleocytosis fever photophobia asthenia	Bolivia Ecuador Panama Trinidad	unidentified	n.k.	n.k.	mosquito	*Culex* spp. *Haemagogus spp.* *Ochlerotatus spp.* *Psorophora ferox* *Sabethes spp.* *Trichoprospon spp.*

(continued)

Table 3.1 (continued)

virus family	genus	virus species	clinical features	disease occurence	bat species	common name	distribution infect. bat	vector	*vector species*
Flaviviridae	Flavivirus	Japanese encephalitis virus (JEV)	CNS pleocytosis CNS signs fever headache prostration	Asia northern Australia	*Miniopterus schreibersi* *Myotis mystacinus* (AB) *Plecotus auritus* (AB) *Pipistrellus abramus* (AB) *Rhinolophus pusillus*	Schreiber's long-fingered bat Whiskered bat Brown big-eared bat Japanese Pipistrelle Least horseshoe bat	Japan n.k. n.k. n.k. Japan	mosquito	*Culex annulirostris* *Culex gelidus* *Culex pipiens* *Mansonia uniformis* *Ochleorotatus japonicus*
		St. Louis encephalitis (SLEV)	fever headache meningoencephalitis	Canada Central/South America USA	*Eptesicus fuscus* (AB) *Myotis lucifugus* (AB)	Big brown bat Little brown bat	USA USA	mosquito	*Aedes aegypti* *Culex nigripalpus* *Culex quinquefasciatus* *Culex tarsalis*
		West Nile virus (WNV)	coma fever headache neck stiffness paralysis tiredness	Africa Asia Middle East Europe	*Eptesicus fuscus* (AB) *Myotis lucifugus* (AB) *Myotis septentrionalis* (AB) *Rousettus aegyptiacus* *Rousettus leschenaultii* *Tadarida brasiliensis* (AB)	Big brown bat Little brown bat Northern myotis Fruit bat Leschenault's rousette Brazilian free-tailed bat	India New York n.k. Uganda/Israel India n.k.	mosquito	*Coquillettidia richiardii* *Culex modestus* *Culex pipiens* *Culex quinquefasciatus* *Culex univittatus* *Culex vishnui*
		Yellow fever virus (YFV)	body aches chills fever headache nausea vomiting	Africa Latin America	*Eidolon* sp. *Rousettus* sp.	n.k. n.k.	East Africa	mosquito	*Aedes* spp. *Haemogogus spp.*
		Zika virus (ZIKV)	diarrhea dizziness fever headache joint pain rash	Gaboon Sierra Leone Tanzania Thailand Uganda Yap Island	*Myotis lucifugus*	Little brown bat	infection only in the Laboratory	mosquito	*Aedes aegypti* *Aedes africanus* *Aedes apicoargenteus* *Aedes furcifer* *Aedes luteocephalus* *Aedes vittatus*
Togaviridae	Alphavirus	Chikungunya virus (CHIK)	fever headache haemorrhagic signs leukopenia lyphadenopathy	Africa south and southeast Asia	*Chaerephon pumilus* *Hipposideros caffer* *Rousettus leschenaultia* *Scotophilus* sp.	Little free-tailed bat Sundevall's leaf-nosed bat Leschenault's rousette Asiatic yellow bat	China China China Senegal	mosquito	*Aedes aegypti* *Aedes albopictus*
		Eastern equine encephalitis virus (EEV)	abdominal pain fever cyanosis lethargy seizures	Eastern USA	*Artibeus lituratus* (AB) *Artibeus jamaicensis* (AB) *Eptesicus fuscus* *Lasiurus cinereus* *Myotis lucifugus* *Tadarida brasiliensis* (AB)	Great fruit-eating bat Jamaican fruit-eating bat Big brown bat Hawaiian hoary bat Little brown bat Brazilian free-tailed bat	Guatemala Guatemala New Jersey New Jersey New Jersey n.k.	mosquito	*Aedes vexans* *Coquillettidia perturbans* *Culiseta melanura* *Culex erraticus* *Uranotaenia sapphirina*
		Ross River virus (RRV)	arthralgia/arthritis fever paraesthesia rash	Am. Samoa Australia Fiji New Guinea Solomon Is. S. Pacific Is	*Pteropus conspicillatus*	Spectacled flying-fox	Australia	mosquito	*Aedes camptorhynchus* *Aedes vigilax* *Culex annulirostris*
		Sindbis virus (SINV)	headache itchy exanthema joint pain mild fever nausea	Africa Asia Australia Europe	*Hipposideridae* sp. *Rhinolophidae* sp.	Old world leaf-nosed bat Horseshoe bat	Venezuela Mexiko	mosquito	*Aedes* spp. *Culiseta morsitans* *Culex pipiens* *Culex torrentium* *Ochleorotatus* spp.

Togaviridae	Alphavirus	Venezuelan equine encephalitis virus (VEEV)	ataxia chills coma fever headache malaise nuchal rigidity paralysis sore throats	Belize Colombia Ecuador El Salvador Guatemala Honduras Mexico Panama Venezuela	*Artibeus lituratus* *Artibeus jamaicensis* (AB) *Artibeus phaeotis* (AB) *Desmodus rotundus* (AB) *Glossophaga commissarisi* (AB) *Myotis nigricans* (AB) *Uroderma bilobatum* (AB)	Great fruit-eating bat Jamaican fruit-eating bat Pygmy fruit-eating bat Common vampire bat Commissaris's long-tongued bat Black myotis Tent-making bat	Guatemala	mosquito	*Aedes serratus* *Culex* spp. *Mansonia titilans* *Ochleorotatus taeniorhynchus*
		Western equine encephalitis (WEEV)	fever headache manifestations in CNS somnolence	North America	*Artibeus lituratus* (AB) *Artibeus jamaicensis* (AB)	Great fruit-eating bat Jamaican fruit-eating bat	Guatemala Haiti	mosquito	*Aedes campestris* *Aedes dorsalis* *Culex tarsalis* *Ochleorotatus melanimon*

disease	**parasite**	**species**	**symptoms**	**occurence**	**bat species**	**common name**	**distribution bat**	**vector**	***vector species***
Chagas-disease	Flagellates	*Trypanosoma cruzi*	fever swelling around the site of inoculation inflammation of heart, muscle or brain	Central and South America	*Artibeus lituratus* *Carollia perspicillata* *Desmodus rotundus* *Glossophaga soricina* *Molossus molossus* *Phyllostomus hastatus*	Great fruit-eating bat Seba's short-tailed bat Common vampire bat Pallas's long-tongued bat Pallas's mastiff bat Greater spear-nosed bat	infection under controlled conditions, but also natural	triatomine bug	*Rhodnius prolixus* *Triatoma dimidiata* *Triatoma infestans*
Malaria	Apicomplexa	*Plasmodium* sp. *Hepatocytis* sp. *Polychromophilus* sp.	fever headache death	Africa Mediterranean South-East Asia	*Eptesicus serotinus* *Kerivoula hardwickii* *Megaderma spasma* *Miniopterus gleni* *Myotis daubentonii* *Myotis goudoti* *Myotis myotis* *Nyctalus noctula* *Pteropus poliocephalus*	Serotine Hardwicke's woolly bat Lesser false vampire Glen's long-fingered bat Daubenton's myotis Malagasy mouse-eared bat Greater mouse-eared bat Noctule Grey-headed flying fox	Switzerland Cambodia Cambodia Madagascar Switzerland Madagascar Switzerland Switzerland Australia	mosquito biting-midges bat flies	*Anopheles* spp. *Culicoides nubecolusus* *Nycteribia kolenatii*

possibly by bedbugs (Darai et al. 2011; Elliott and Blakqori 2011). The largest of the five genera is the genus *Orthobunyavirus*, containing 174 known viruses (Elliott and Blakqori 2011). Within this group, up to half of the potential 60 Bunyaviridae viruses that cause disease in humans belong to *Orthobunyavirus* (Soldan and González-Scarano 2005) including the prototype bunyavirus, Bunyamwera virus. It was first isolated in 1943 from *Aedes* mosquitoes in Uganda and gave its name to the family Bunyaviridae and the genus *Bunyavirus*. In 2005, Bunyavirus was renamed *Orthobunyavirus* (Bowen et al. 2001; Elliott and Blakqori 2011). The first virus within this genus is the **Bwamba virus** (BWAV), which is a member of the Bwamba serogroup (Lambert and Lanciotti 2008). It is transmitted by mosquitoes including *Aedes furcifer, Anopheles coustani, Anopheles funestus, Anopheles gambiae* and *Mansonia uniformis* (Lee et al. 1974; Lutwama et al. 2002). According to Gonzales and Georges (1988), the principal anthropophilic vector species are *An. funestus* and *An. gambiae*. The first encounter with Bwamba fever was in 1937 among construction workers in Western Uganda (Smithburn et al. 1941). Today, Bwamba virus is endemic in Nigeria, Cameroon, Central African Republic, Kenya, Tanzania and South Africa, but due to the mild symptoms it is often mistaken for malaria (Lutwama et al. 2002; Moore et al. 1975; Smithburn et al. 1941). In a laboratory study by Reagan et al. (1955), the cave bat *Myotis lucifugus* was successfully infected after intraperitoneal, intradermal, intracerebral and intrarectal injection of the virus, although the bats were not susceptible to the virus after intranasal exposure. The second virus is the **Kaeng Khoi virus** (KKV), which was first isolated in Thailand in 1969 from the bat species *Chaerephon plicata* (wrinkle-lipped bat) and *Taphozous theobaldi* (Theobald's bat). Both species can be found across the Indian subcontinent and Southeast Asia. (Hutson et al. 2001) In 1976 and 2003, the virus was found again in *C. plicata* in Thailand and for the first time in Cambodia (Osborne et al. 2003; Williams et al. 1976). Apart from bats, Williams et al. (1976) found the virus also in bedbugs *(Stricticimex parvus* and *Cimex insuetus*) that inhabit caves together with other haematophagous arthropods, which attack humans. The virus might be a public health concern, because serum analysis found neutralizing antibody in 29 % of the population. The symptoms of the virus in bats and humans are unknown, but a survey of the population indicated that they believe that bedbug bites were the cause of an influenza-like illness, which is typical of infection by members of *Orthobunyavirus* (Osborne et al. 2003). Also known to occur in bats and humans are the **Guamá and Catú viruses**, which are members of the Guamá serotype group and are transmitted by species of *Culex* mosquitoes (Darai et al. 2011; Löscher and Burchard 2008). Both were isolated from humans and mosquitoes in the Amazon area (Causey et al. 1961) and Catú virus also from humans in Trinidad (Tikasingh et al. 1974). However, Catú virus was also isolated in Brazil from the bat *Molossus currentium* and Guamá virus from an unidentified bat (Calisher et al. 2006; Karabatsos 1985). The symptoms of both viruses show considerable variation such as fever, headache, general body pains, weakness or dizziness and photophobia (Causey et al. 1961).

Another group of viruses that may be transmitted by bats is the genus ***Phlebovirus***, including nine species with 37 viruses (Bouloy 2011), distributed in

Africa, Asia, North and South America and the Mediterranean region (McMullan et al. 2012). Many phleboviruses are transmitted by sandflies or other arthropods such as mosquitoes or ticks. The first pathogen in this genus that has to be considered in connection with bats is the **Rift Valley fever virus** (RVFV). It is primarily transmitted by mosquitoes of the genus *Aedes* (e.g. *Ae. cumminsii, Ae. circumluteolus, Ae. mcintoshi* or *Ae. vexans*) or *Culex* (e.g. *Cx. pipiens*, *Cx. tritaeniorhynchus* or *Cx. neavei*), but it has been shown that sandflies (*Phlebotomus duboscqi* and *P. papatasi*) might also be potential vectors (Dohm et al. 2000; Fontenille et al. 1998; Pepin et al. 2010). RVFV can be transmitted into mosquito offspring transovarially (Ikegami and Makino 2011). Outbreaks of RVF are associated with heavy rainfalls during the El Niño/Southern Oscillation (ENSO) phenomenon (Miller et al. 2002; WHO 2013a) because the floods create optimal breeding conditions (Bowen et al. 2001; Fontenille et al. 1998; Woods et al. 2002). After the first identification of the virus in the Rift Valley of Kenya in 1930, numerous outbreaks of RVF have been reported in many regions of Africa (Fig. 3.1a) (Daubney and Hudson 1931; Fontenille et al. 1998). The largest occurred in Egypt in 1977–1978 with 200,000 estimated human infections, 18,000 cases of illness and 600 deaths (Ikegami 2012). The first detected outbreak of RVF outside the African continent was in 2000 in Saudi Arabia and Yemen. The latest outbreak of RVF was 2012 in Mauritania with 34 cases and 17 deaths reported (WHO 2012). The clinical symptoms range from flu-like fever, muscle pain or headache to neck stiffness, retinal lesions, loss of memory and even death (Ikegami 2012; WHO 2013b). However, RVF occurs not only in humans. Outbreaks can also result in devastating economic losses when livestock is infected (Woods et al. 2002). In 1991, the virus was also isolated from bats in West Africa (Fontenille et al. 1998). Calisher et al. (2006) suggest the bat species *Micropteropus pusillus*, *Epomops franqueti, Hipposideros abae*, *H. caffer, Miniopterus schreibersii* and *Glauconycteris argentata* as potential hosts for the RVFV. They are all distributed in West, East and Central Africa except for *M. schreibersii*, which occurs primarily in southern and middle Europe (e.g. Portugal, Italy (Sardinia, Sicily), Turkey, Switzerland and Serbia) (IUCN red list 2012). The effect on potential vectors (e.g. *Aedes vexans*) of climate changes may enable this bat to spread the virus to European countries. The second pathogen within the *Phlebovirus* genus that has been linked with bats is the **Toscana virus**, a serotype of Sand fly fever distributed in the Mediterranean region (Fig. 3.1b) (Charrel et al. 2005; Cusi et al. 2010). In 1971, the Toscana virus was isolated for the first time from the sand fly *Phlebotomus perniciosus* in Monte Argentario, Toscana (Braito et al. 1997; Cusi et al. 2010; Valassina et al. 2003; WHO 2004). Later the virus was also isolated from the sand fly *P. perfiliewi* (Valassina et al. 2003). However, *P. perniciosus* is probably the most common insect vector of the Toscana virus, being one of the most abundant sand flies in southern Europe (Maroli et al. 1994; Sanbonmatsu-Gámez et al. 2005). With tourists, returning from Mediterranean countries, the virus has been imported to further European countries such as Germany, Sweden and Switzerland (Cusi et al. 2010). The only known vertebrate hosts beside humans are bats. Accordingly, the virus has been isolated from the bat

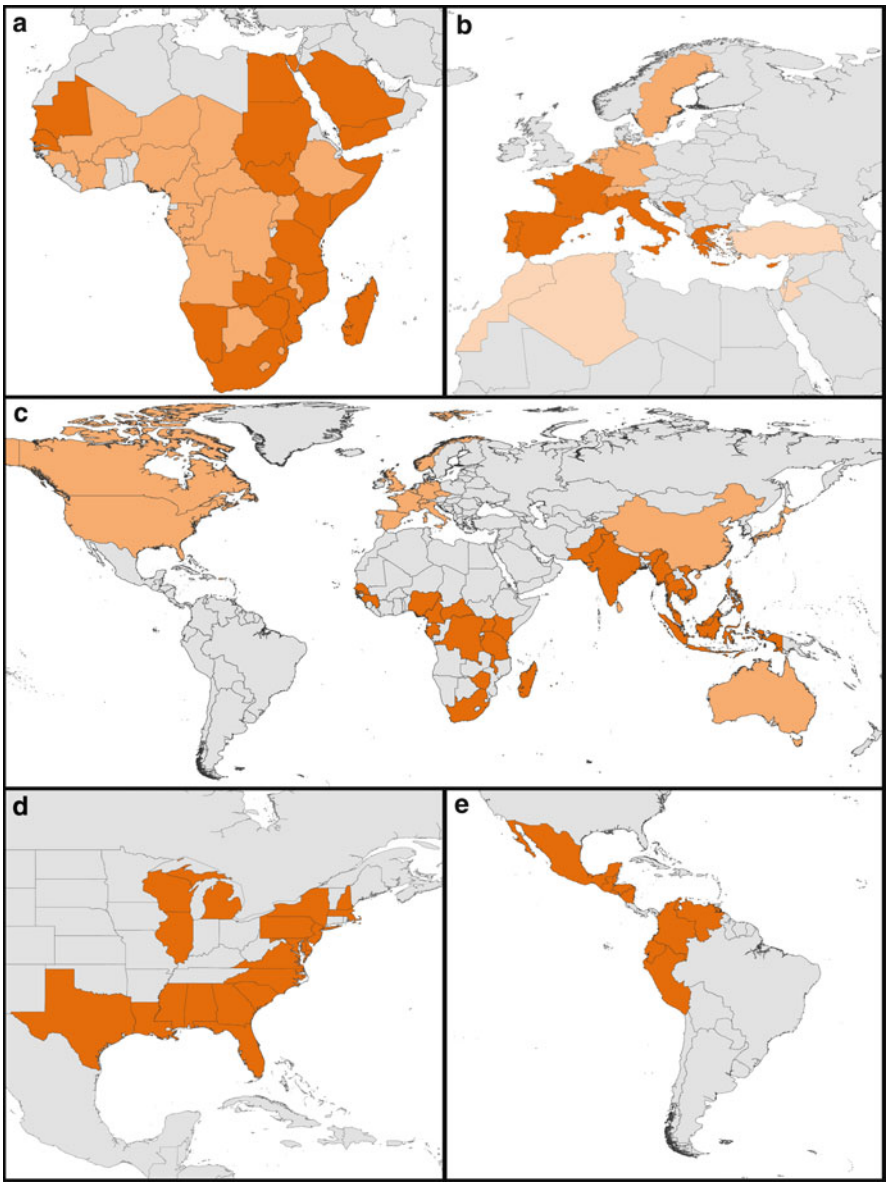

Fig. 3.1 Virus distribution (**a**) Rift Valley fever: *dark orange* (do)—epizootic and epidemic areas; *light orange* (lo)—serological evidence or virus isolation (Ikegami 2012). (**b**) Toscana virus: do—native infections; *middle orange* (mo)—imported cases; lo—seropositive cases in population (Cusi et al. 2010). (**c**) Chikungunya virus: do—endemic or epidemic areas; lo—imported cases (Powers and Logue 2007). (**d**) Eastern equine encephalitis: reported cases between 1964 and 2010 (CDC 2010). (**e**) Venezuelan equine encephalitis: major outbreaks regions (Weaver et al. 2004)

Pipistrellus kuhlii in regions where the insect vectors were present (Charrel et al. 2005; Valassina et al. 2003). The role of bats as virus reservoirs is not yet definitely clarified (Valassina et al. 2003). Most infections are recorded during summertime and cause high fever, headaches, muscle aches, neck stiffness and aseptic meningitis with a non-fatal course or a mild meningoencephalitis, but asymptomatic infections are also possible (Baldelli et al. 2004; Braito et al. 1997; Hemmersbach-Miller et al. 2004). Studies in central Italy showed that 52 % of aseptic meningitis cases were caused by Toscana virus (Charrel et al. 2005). Studies of Sanbonmatsu-Gámez et al. (2005) in Spain, where 979 persons were probed for their seroprevalence, indicated that Toscana virus occurs more often in rural areas (26.7 %) than in urban (20.6 %).

3.2.2 Togaviridae

Within this second large virus family, the two genera *Alphavirus* and *Rubivirus* are known (Rolle and Mayr 2007). It can be characterized as a group of positive stranded RNA viruses, which possess a cubically symmetric capsid. All vector-borne togaviruses, which are medically important, belong to *Alphavirus* that contains 26 different viruses (Laine et al. 2004). The first of five viruses associated with bats, human and haematophagous insects is the **Western equine encephalitis virus,** which is eponymous for the western equine encephalitis antigenic complex and an important pathogen not only in human but also in veterinary medicine (Reisler et al. 2012). It was isolated in 1930 from a horse brain although epidemics had already been described in 1912 and 1919 (Johnson 1964). The natural vertebrate hosts of WEEV are passerine and domestic birds (Eklund 1954) where it maintains an enzootic cycle with the mosquito vectors. The main vector is *Culex tarsalis*, of which hybrid strains have evolved that are highly resistant to WEEV infection (Hardy et al. 1978). Other vectors are *Aedes campestris, Ae. dorsalis* and *Ochlerotatus melanimon* (Zacks and Paessler 2010). In early experiments, transmission could also be shown in *Ae. aegypti* (Kelser 1933; Merrill and Ten Broeck 1935; Merrill et al. 1934), *Ae. albopictus* (Simmons et al. 1936), *Ae. nigromaculis* (Madsen and Knowlton 1935; Madsen et al. 1936), *Ae. sollicitans* (Merrill et al. 1934), *Ae. taeniorhynchus* (Kelser 1937, 1938) and *Ae. vexans* (Kelser 1937, 1938; Knowlton and Rowe 1935). *Culiseta* spp. is mentioned as vector by Whitley and Gnann (2002) without mentioning the species or the source of the information.

The connection between Western equine encephalitis and human disease was proven in 1938, when the virus was recovered from a child's brain that died of encephalitis (Griffin 2001). Nevertheless in North America, WEEV is a rare cause of encephalitis and only seven cases were reported from 1987 to 2002 (CDC 2002; Romero and Newland 2003). The virus has caused encephalitis epidemics in emus, humans and horses with fatality rates of 10 % for emus and humans and 20–40 % for horses (Ayers et al. 1994; Nalca et al. 2003). The patients suffer a 2- or 3-day

period with fever, headache, vomiting, nausea, somnolence and irritability before manifestations in the CNS begin (Nalca et al. 2003). Constantine (1970) mentions that WEEV has been isolated from bats and Western equine encephalitis N antibodies were detected in *Artibeus jamaicensis* from Haiti (McLean et al. 1979) and *Artibeus lituratus* from Tikal, Guatemala (Ubico and McLean 1995). The latter authors postulate that bats may become infected, especially during epizootics in other hosts. The prototype virus of the genus *Alphavirus* is the **Sindbis virus** (SINV), which belongs together with the Highland J, Fort Morgan, Buggy Creek and Aura virus to the Western equine encephalomyelitis antigenic complex (Hubálek 2008; Lundström and Pfeffer 2010; Netolitzky et al. 2000). It was first recognized and isolated from *Culex pipiens* and *Cx. univittatus* in 1952 in Egypt (Jöst et al. 2010; Kurkela et al. 2008; Laine et al. 2004). The first record of Sindbis virus in European countries was in 1975 (Laine et al. 2004). Today, Sindbis virus is one of the most widely distributed viruses, having been isolated in Europe (e.g. Sweden, Finland and Italy (Sicily)), Africa (e.g. Egypt, Kenya and South Africa), Asia (e.g. China, Malaysia and Lebanon) and Australia (Lundström and Pfeffer 2010; Norder et al. 1996; Tesh 1982). Nucleotide sequencing of SINV strains isolated around the globe has shown that the majority of SINV strains are geographically distinct genotypes and that migrating birds may carry the virus over long distances (Modlmaier et al. 2002; Strauss and Strauss 1994). Together with a wide distribution, the virus also has a broad host range and has been isolated from frogs, ticks, humans and numerous mosquito species (Kurkela et al. 2008; Modlmaier et al. 2002). Furthermore, Blackburn et al. (1982) isolated the virus from the organs of the Microchiropteran bats *Hipposideros* spp. and *Rhinolophus* spp. Vectors of SINV are ornithophilic mosquitoes *Cx. torrentium* or *Cx. pipiens*, *Culiseta morsitans* and *Ochlerotatus* spp. or *Aedes* spp. (Hubálek 2008; Jöst et al. 2010). The first description of symptoms caused by Sindbis virus infection is from Uganda in 1961 (Laine et al. 2004). They range from itchy exanthema, mild fever and joint pain in wrists, hips, knees and ankle to nausea, headache and muscle pain (Kurkela et al. 2005). Together with other mosquito-borne diseases like the Ross River virus, Mayaro-, onyong-nyong-, Bebaru-, Getah and Semliki forest virus, the **Chikungunya virus** is a member of the Semliki forest antigenic complex (Burt et al. 2012). The first isolation of the virus from an infected patient was carried out by Ross in 1952/1953 during an outbreak in Tanzania (Diallo et al. 1999; Tesh 1982; Tiawsirisup 2011). Today, the geographic distribution of this enzootic virus includes the tropical and subtropical areas of Africa, and southern or southeast Asia, including India, Sri Lanka, Myanmar, Thailand, Indonesia, Malaysia and the Philippines (Fig. 3.1c) (Burt et al. 2012; Krishna et al. 2006; Sam et al. 2006). The virus is transmitted by *Aedes* spp. mosquitoes and exhibits two different transmission cycles. *Aedes aegypti* as well as *Ae. albopictus* are the main vectors in Asia and transmit the virus to humans directly in an urban transmission cycle. Virus isolation from non-human primates or vertebrates like bats in Africa suggests the occurrence of a sylvatic transmission cycle. The main vectors of CHIKV in Africa are *Ae. furcifer-taylori*, *Ae. africanus*, *Ae. luteocephalus* and *Ae. aegypti* (Higgs 2006; Krishna et al. 2006). In the last

50 years, numerous outbreaks of CHIKV were reported (Schwartz and Albert 2010). One of the last large-scale epidemics began in 2004 in Kenya and spread to several islands in the Indian Ocean (Powers and Logue 2007). On La Réunion, nearly 34 % of the total island population was infected and 237 people died (Schwartz and Albert 2010; Tsetsarkin et al. 2007). It was a noteworthy outbreak because *Ae. albopictus* was recognized as the major vector for the first time (Reiter et al. 2006). In July to September 2007, the first autochthonous epidemic outbreak of CHIKV with 248 cases was reported in Italy. The vector responsible for this outbreak was also *Ae. albopictus* (Rezza et al. 2007; Sambri et al. 2008). An infection with CHIKV can cause acute, subacute and chronic diseases. Especially in areas that also suffer outbreaks of Dengue virus, CHIKV can easily be mistaken for Dengue and both viruses can occur in one patient. Dengue has much more potential for causing infections with serious outcomes (PAHO 2011; Tiawsirisup 2011). An acute disease is characterized by fever and joint pain, while other symptoms may include headache, myalgia, nausea, vomiting, polyarthritis, rash and conjunctivitis (PAHO 2011). Apart from humans, bats can also be carriers of the virus. Diallo et al. (1999) isolated it from bats of the genus *Scotophilus* sp. in Senegal. Other surveys suggest *Rousettus aegyptiacus* (Egyptian rousette), *Hipposideros caffer* (Sundevall's leaf-nosed bat) as well as *Chaerephon pumilus* (little free-tailed bat) to be vertebrate hosts for the virus (Calisher et al. 2006). **Ross River virus** (RRV) causes a disease known as epidemic polyarthritis, which is regarded with 2,000–8,000 notified cases per annum as the most common cause of arboviral disease in humans in Australia (Russell 2002; Smith et al. 2011). The first reported outbreak of an infection with RRV was in 1928 during epidemics in New South Wales (Mackenzie et al. 1994; Russell 2002). Today, human infections are also documented for New Guinea, Solomon Islands, Fiji and American Samoa (Meyer 2007; Tesh 1982). It is believed that the virus was introduced to these islands by viraemic air travellers from Australia (Smith et al. 2011). The first isolation of the virus from a mosquito (*Ae. vigilax*) was by Doherty et al. in 1959 (Harley et al. 2001). In 1979, the virus was isolated for the first time from the serum of a patient with epidemic polyarthritis (Mackenzie et al. 1994). The virus was also isolated from a *Pteropus* bat in Australia (Doherty et al. 1966; Messenger et al. 2003). Serological surveys and virus isolation by Harley et al. (2000) from mosquitoes trapped near a flying fox camp suggested the flying fox *Pteropus conspicillatus* as a potential reservoir host. These authors also suggest that other vertebrates living in the flying fox camp could also be important reservoir hosts (Harley et al. 2000, 2001). On the other hand, Ryan et al. (1997) showed that the grey-headed flying fox (*Pteropus poliocephalus*) does not produce a viraemia of sufficient magnitude to be very competent vertebrate hosts of RRV (Ryan et al. 1997). Within 9 years (1991–2000), more than 47,000 laboratory-notified cases were reported by national authorities (Russell 2002). Typical symptoms are various combinations of arthralgia and arthritis, muscle and joint pains, myalgia, lethargy, headache or fever. To return to full physical activity, most of the patients need up to 6 months (Mackenzie et al. 1994; Smith et al. 2011; Weinstein et al. 2011). So far, RRV has been isolated from 27 mosquito species. In Australia,

these include the major vectors *Aedes vigilax*, *Ae. camptorhynchus* and *Cx. annulirostris* (Harley et al. 2000; Hu et al. 2006; Mackenzie et al. 1994). There is also evidence that *Ae. aegypti* can be infected with and transmit the virus, but it has not been isolated from this species in the field (Harley et al. 2000). The **Eastern equine encephalitis virus** (EEEV) is placed as the only species in the Eastern equine encephalitis complex (EEE) and is distributed in North America (Fig. 3.1d) (Calisher et al. 1980). Originally, it was divided into North and South American varieties based on antigenic properties (Casals 1964). Following further antigenic studies four different subtypes have been distinguished, which correspond to four genetic lineages (I–IV) (Arrigo et al. 2010; Brault et al. 1999). EEEV was first recognized as a horse disease in the northeastern USA in 1831 (Hanson 1957; Nalca et al. 2003; Scott and Weaver 1989). The most severe outbreak of EEEV was recorded from Texas and Louisiana in 1947, causing 14,344 cases with 11,722 horse deaths (Chang and Trent 1987; Nalca et al. 2003). However, suspected EEEV could not be linked to humans till an outbreak in 1938 (Fothergill et al. 1938; Getting 1941). In humans, the virus causes severe meningoencephalitis, sometimes causing focal brain lesions. Morse et al. (1992) report the fatality rate in humans of all ages as 30 %, and in affected children up to 75 %. A prodrome of fever, headache, confusion, lethargy, myalgias, vomiting and abdominal pain, which lasts 1–3 weeks, precedes the onset of neurologic symptoms. The onset of illness is characterized by fever, altered mental condition, seizures, vomiting and cyanosis (Deresiewicz et al. 1997; Hart et al. 1964; Romero and Newland 2003). In a study made in Alabama, several mosquito species were found to be carriers of the virus: *Culiseta melanura, Aedes vexans, Coquillettidia perturbans, Culex erraticus* and *Uranotaenia sapphirina*. Interestingly, these species were infected at different times: *Aedes vexans* at the beginning of the season; *Cx. erraticus* and *Cs. melanura* from June till mid-September (Cupp et al. 2003). In most publications, the ornithophilic mosquito *Cs. melanura* is mentioned as the main vector of EEEV, but *Cx. erraticus* is an important bridge vector between birds and mammals in the mid-south USA, because of frequent virus isolations and abundance of this mosquito species in bottomland swamps, flood plains, permanent standing water, recreation areas near rivers or ponds and water impoundments (Jacob et al. 2010). However, EEEV has been isolated from a wide range of species of *Aedes, Anopheles, Coquillettidia, Culex, Ochlerotatus* and *Uranotaenia*, though not all of the species involved can be regarded as competent vectors (more specific e.g. in Armstrong and Andreadis 2010; Arrigo et al. 2010). In surveying for the natural vector of EEEV, Merrill et al. (1934) mention *Ae. cantator* and even more *A. sollicitans* and *A. aegypti*. Regarding the latter species, they conclude with Kelser (1933) that it could not be the transmitting species at it did not occur sufficiently far northwards. Generally, epizootics of EEE occur every 5–10 years and are associated with increased mosquito populations resulting from heavy rainfall and warm weather (Grady et al. 1978; Letson et al. 1993; Mahmood and Crans 1998; Nalca et al. 2003). Although birds seem to be the main reservoir hosts of EEEV, the virus has also been detected in bats. During 1969 and 1970, it was found in ten bat individuals caught in the wild in New Jersey, belonging to three

species: one *Lasiurus cinereus*, two *Myotis lucifugus* and seven *Eptesicus fuscus* (Main 1979a). Antibodies have been detected in the previously mentioned species, *Tadarida brasiliensis* and an unidentified bat (Daniels et al. 1960; Hayes et al. 1964; Karstad and Hanson 1958). The survey by Main (1979a) showed that EEE neutralizing antibodies were detectable in a small percentage of the tested adult hibernating animals (0.3 % of *Myotis keenii*) but significantly more in non-hibernating animals (3.4 % in *M. lucifugus, M. keenii* and *E. fuscus*). In experimentally infected bats, the virus could be detected in the blood, mammary glands, brown fat, lung, kidney, brain, pancreas, heart, salivary glands, liver and ovary, with the highest percentage in blood and mammary glands (Main 1979b). In a serological survey of Guatemalan bats, antibodies neutralizing EEEV were found in *Artibeus intermedius, A. jamaicensis, A. lituratus, Glossophaga soricina, Rhynchonycteris naso* and *Sturnira lilium* (Ubico and McLean 1995). The **Venezuelan equine encephalitis virus** (VEEV) belongs to the VEE complex, which consists of six subtypes which have been identified in North, Central and South America (Fig. 3.1e) (Fine et al. 2007; Weaver et al. 1992). The first isolation of VEEV was in 1938 from the brain of a Venezuelan animal (Beck and Wyckhoff 1938). It is the most important pathogen among the New World alphaviruses affecting humans and horses. It not only remains a naturally emerging disease but is also a highly developed biological weapon (Colpitts et al. 2007), because it can be also spread by aerosol infection. Since 1938, sporadic outbreaks have involved hundreds of thousands of people (Weaver et al. 2004). During an epidemic in Colombia, more than 75,000 human cases were reported (Rivas et al. 1997). The symptoms in humans include malaise, sore throats, headaches, fever and chills, persisting for 4–6 days and followed by 2 or 3 weeks of generalized weakness. Encephalitis occurs mainly in children (in about 4 % of cases). Other symptoms range from mild nausea, vomiting with decreased sensorial capability, nuchal rigidity, ataxia and convulsions, to coma and paralysis. The fatality rate in humans is about 1 % (Johnson and Martin 1974; Johnson et al. 1968; Nalca et al. 2003; Pittman et al. 1996). Currently, no vaccine for VEEV is publicly available and the experimental military vaccine has poor efficacy (Colpitts et al. 2007; Russell 1999). In nature, VEEV is maintained in a cycle between mosquitoes and small rodents (Grayson and Galindo 1968; Nalca et al. 2003; Scherer et al. 1972). Epidemic outbreaks of the epizootic strains occur in 10–20-year intervals in the ranch areas in Peru, Venezuela, Colombia and Ecuador after heavy rainfall, which lead to increased mosquito populations (Rivas et al. 1997). Enzootic strains are transmitted by *Culex* species, whereas the main vector of the epizootic strains seems to be *Ochlerotatus taeniorhynchus* and possibly also *Psorophora confinnis*, but nearly all mosquito species have been found to be infected during epizootics (Rivas et al. 1997; Smith et al. 2008; Zacks and Paessler 2010). Weaver et al. (1992) list *Culex cedeci, Cx. ocossa, Cx. panocossa, Cx. portesi, Cx. taeniopus* and cliff swallow bugs *Oeciacus vicarius* as vectors. Other natural enzootic vectors are *Cx. accelerans, Cx. adamesi, Cx. amazonicus, Cx. ferreri*, *Cx. nigripalpus, Cx. pedroi, Cx. spissipes, Cx. vomerifer, Aedes serratus* and *Mansonia titillans* (Ferro et al. 2003). In the laboratory, *Aedes aegypti* and *Culex aikenii* could additionally

be infected (Kramer and Scherer 1976; Sudia et al. 1971). By testing haemagglutination inhibition antibody titres in Guatemalan bats, antibodies against enzootic VEEV strains were detected in seven bat species: *Artibeus jamaicensis, A. lituratus, A. phaeotis, Desmodus rotundus, Glossophaga commissarisi, Myotis nigricans* and *Uroderma bilobatum*, and it was noted that the insectivorous *M. nigricans* may become infected by eating infected mosquitoes and the vampire bat *D. rotundus* by feeding on viraemic cattle (Seymour et al. 1978a). Experimental infection studies showed that bat genera respond differently to infection, e.g. *Artibeus jamaicensis* and *A. lituratus* showed longer VEEV viraemias than *Phyllostomus discolor*, which had a faster, higher and longer lasting immune response to epizootic strains than to enzootic ones. *Phyllostomus discolor* may not serve as a host for enzootic VEEV strains, while the circulating virus levels in *Artibeus jamaicensis, A. lituratus* and *Sturnira lilium* seemed to be high enough to permit the infection of *Culex* vectors (Seymour et al. 1978b).

3.2.3 Flaviviridae: *Flavivirus*

The family Flaviviridae can be divided into the three genera *Pestivirus*, *Hepacivirus* and *Flavivirus* (Cook and Holmes 2006). The last named contains the largest number of viruses with the potential to cause diseases in bats and humans and may be spread by haematophagous insects. *Flavivirus* currently consists of 70 serologically related, single-strand, positive-sense RNA viruses (Hoshino et al. 2009; Mackenzie and Williams 2008; Tajima et al. 2005). All members of the genus can be found around the world and are most often transmitted by arthropods. The most important mosquito-borne diseases caused by flaviviruses are Yellow fever, Japanese Encephalitis, West Nile fever, Dengue fever and St. Louis encephalitis (Mackenzie and Williams 2008). **Yellow fever** is an acute haemorrhagic disease and is endemic in tropical areas of Africa and Latin America with an incidence of 200,000 cases and 30,000 deaths each year (Fig. 3.2b). The symptoms range from mild to severe illness (WHO 2000). Yellow fever transmission depends on arthropods as vectors, e.g. several mosquito (Culicidae) species belonging to *Aedes* in Africa and *Haemogogus* in South America (Ellis and Barrett 2008; WHO 2000). As long ago as the first half of the twentieth century, scientists tried to detect a connection between the yellow fever virus and bats. Williams et al. (1964) emphasized the potential and importance of bats in the wild cycle of arboviruses, e.g. yellow fever virus. In the experiments of Kumm (1932), Brazilian bats (*Molossus molossus obscurus* and *M. rufus*) were exposed to unfed *Aedes aegypti*. The mosquitoes willingly took blood, but no transmission of the disease from the infected mosquitoes to the bats resulted. The author concluded that bats play little part in the life cycle of this disease. Contrastingly, Simpson and O'Sullivan (1968) stated that in East Africa, yellow fever virus circulated in the fruit bat genera *Eidolon* and *Rousettus*. However, the virus did not produce demonstrable viraemia in the tested fruit bats (Simpson and O'Sullivan 1968). Marinkelle

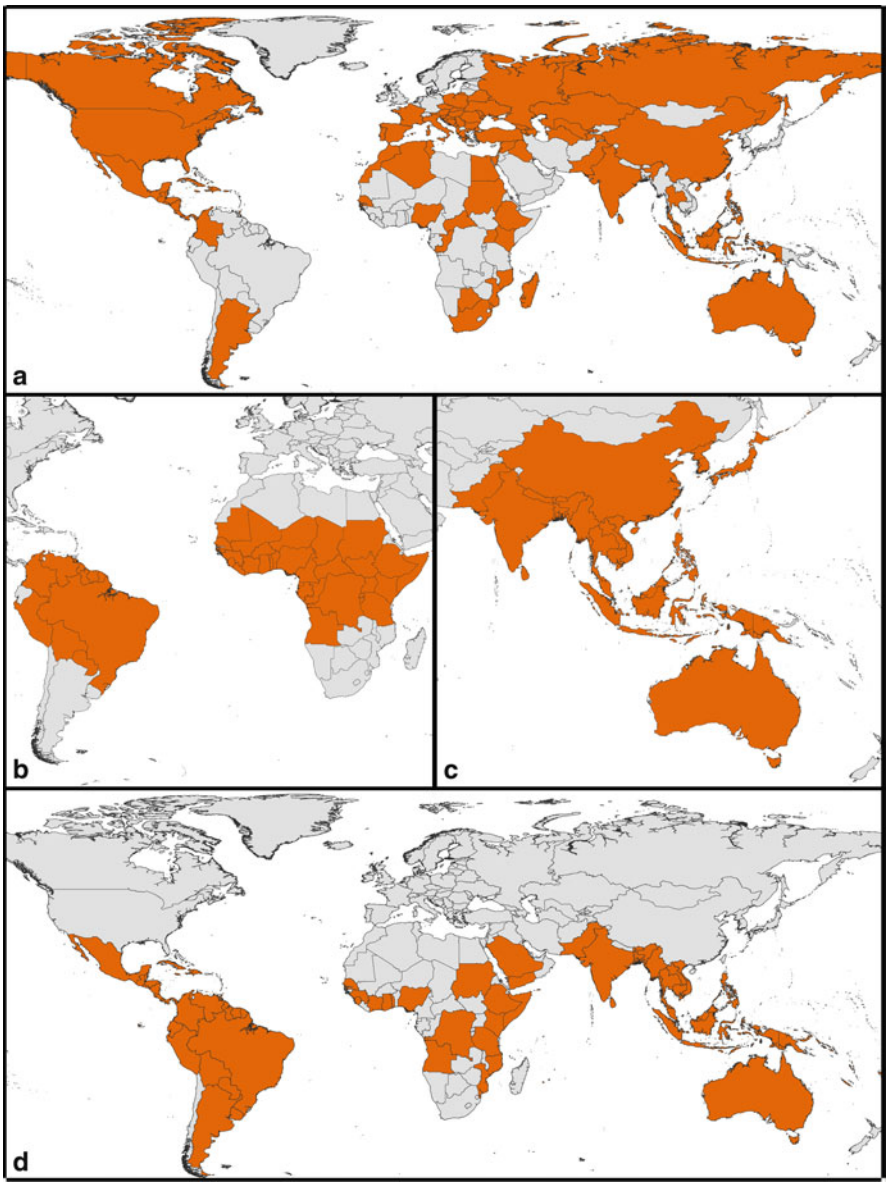

Fig. 3.2 Occurrence of viruses (**a**) West Nile virus: detected in human sera or antibodies in birds (Hubálek and Halouzka 1999; Gubler 2007); (**b**) Yellow fever: *dark orange* (do)—risk area (Travel approved 2010); (**c**) Japanese encephalitis virus (CDC 2012; Van der Hurk et al. 2009b); (**d**) Dengue fever: transmission risk areas (WHO 2009)

and Grose (1972) reviewed organisms, which act as vectors between bats, humans and domestic animals. They listed six references involving yellow fever records from two continents.

Oelofsen and van der Ryst (1999) stated that bats can be infected orally by ingesting a single mosquito and that experiments with bats and yellow fever virus produced positive results. The virus was recovered from several organs of the bats (Oelofsen and van der Ryst 1999). Furthermore, serological prevalence of bats for yellow fever virus had been demonstrated in Uganda, Kenya and Sudan and in previous publications the laboratory capacity had been tested in the genera *Eidolon* and *Rousettus* (Ellis and Barrett 2008). The **Japanese encephalitis virus** (JEV) is eponymous for the JEV antigenic complex. Other members of this group are the West Nile virus, Murray Valley encephalitis virus, St. Louis encephalitis virus and Kunjin virus (Bengis et al. 2004; Campbell et al. 2002). It is the leading cause of viral encephalitis in rural regions of eastern, southeastern and southern Asia (Fig. 3.2c). The central nervous system may be affected, leading to severe complications and even death (Agarwal 2006; Mackenzie et al. 2006). Up to 50,000 cases of JEV are estimated to occur annually worldwide (Ravanini et al. 2012; Van der Hurk et al. 2009a). According to the sequence of its genomic RNA, JEV is classified into five genotypes (Nabeshima et al. 2009; Solomon et al. 2003). The majority of infections are subclinical, but the fatality rate is nearly 25 % (Ravanini et al. 2012; Van der Hurk et al. 2009b). Over the last 60 years, it has been estimated that the virus has been responsible in humans for more than ten million infections, three million deaths and four million cases of long-term disability. It is also calculated that today nearly two billion people live in JEV-prone areas. Historically, epidemics had been recorded in Japan since 1871 (Mackenzie et al. 2006; Van der Hurk et al. 2009a), but the first isolation of JEV in Japan was not until 1935 in Japan (Tiawsisirsup et al. 2012). A sequence closely related to JEV strains from Japan was isolated for the first time in Europe from the mosquito *Culex pipiens* (Ravanini et al. 2012). Birds and mosquitoes play the major role in the life cycle of JEV, but the virus can also infect a wide range of other vertebrates such as humans, domestic animals, bats, snakes or frogs (Agarwal 2006; Ravanini et al. 2012; Tiawsisirsup et al. 2012). The main vectors seem to be species of *Culex* mosquitoes such as *Cx. pipiens* (Korea), *Cx. annulirostris* (Australia) or *Cx. tritaeniorhynchus* (Nabeshima et al. 2009; Van der Hurk et al. 2009b), but JEV has also isolated from *Cx. gelidus*, *Cx. vishnui*, *Cx. fucocephala*, *Cx. pseudovishnui*, *Mansonia uniformis*, *Anopheles subpictus* and *Ochlerotatus japonicus* (Mackenzie et al. 2006; Van der Hurk et al. 2009a). Sulkin et al. (1970) isolated the virus in Japan from the bats *Miniopterus schreibersii* and *Rhinolophus cornutus*. Other bats, which have yielded antibodies or JEV, were *Myotis mystacinus*, *Pipistrellus abramus*, *Plecotus auritus*, *Vespertilio superans*, *Myotis macrodactylus* and *M. nattereri bombinus* (Banerjee et al. 1984). In China, JEV has been isolated from *Rousettus lechenaultii* and *Murina aurata* (Wang et al. 2009). **West Nile virus**, the disease causing agent of the West Nile fever, was first discovered in the blood of a native woman of the West Nile district of Uganda in 1937 (Garmendia et al. 2001; George et al. 1984). In South Africa, one of the biggest outbreaks, with

nearly 18,000 human infections, was reported in 1974 (Dauphin et al. 2004). Molecular epidemiological survey indicates that WNV spread from Africa to the Mediterranean and southern European regions and then to India as well as Central and South Asia (Fig. 3.2a) (Buckley et al. 2003; Hayes 2006). In 1999, the virus was inadvertently introduced into North America (Pilipski et al. 2004). Up to now, over 12,000 human cases of meningitis or encephalitis and 1,100 deaths caused by WNV have been documented in the USA (Murray et al. 2010). Phylogenetic studies have identified several genetic lineages of the virus in different geographical locations (Campbell et al. 2002; Rappole et al. 2000). West Nile virus is transmitted in natural cycles between birds and mosquitoes (Mackenzie et al. 2004). So far, the virus has been isolated from at least 300 bird and 43 mosquito species from 11 genera. The major vectors for Africa and the Middle East are *Culex univittatus, Cx. poicilipes, Cx. neavei* or *Aedes albocephalus*. For Asia, it is *Cx. quinquefasciatus, Cx. tritaeniorhynchus* and *Cx. vishnui*. In Europe, *Cx. pipiens, Cx. modestus* as well as *Coquillettidia richardii* may act as important vectors. A huge number of infections (nearly 80 % symptomless) occur during summer, early fall and during the rainy season in the tropics (Campbell et al. 2002). The symptoms reach from fever, headache, tiredness or swollen lymph glands to neck stiffness, disorientation, coma and paralysis (Mackenzie et al. 2004; WHO 2011; Zeller and Schuffenecker 2004). The first identification of WNV in Chiroptera was in *Rousettus aegyptiacus* (fruit bat) in Uganda and Israel. Nearly 8 % of the surveyed *R. aegyptiacus* in Israel tested positive for WNV antibodies (Bunde et al. 2006). In India, the virus was isolated from *Rousettus leschenaultia* (Davis et al. 2005; Paul et al. 1970) and in 2,000 antibodies were isolated again from live *Eptesicus fuscus* (big brown bat) as well as from *Myotis lucifugus* (little brown bat) in New York City (Bunde et al. 2006). Pilipski et al. (2004) found antibodies again in *M. lucifugus* and in *M. septentrionalis*, whereas Davis et al. (2005) determined neutralizing antibodies for WNV from *Tadarida brasiliensis*. The **St. Louis encephalitis** virus is the etiological agent of St. Louis encephalitis and is a member of the Japanese encephalitis antigenic complex. It was first detected in 1933 during an outbreak of human encephalitis in St. Louis in the US State Missouri (Auguste et al. 2009; Flores et al. 2010; Rodrigues et al. 2010). Today, the virus is found all over the USA and Canada as well as Central and South America (Diaz et al. 2006; Pires and Gleiser 2010). The largest outbreak of SLEV among humans so far was in 2005 in Argentina (Diaz et al. 2006). The first detection of SLEV in Argentina was in 1957 (Flores et al. 2010). Studies have indicated *Cx. tarsalis*, *Cx. nigripalpus* and *Cx. quinquefasciatus* to be the major vectors in the USA (Reisen 2003). Diaz et al. (2012) isolated the virus from eight different mosquito species: *Cx. quinquefasciatus*, *Cx. interfor*, *Cx. apicinus*, *Ae. scapularis*, *Ae. aegypti*, *Ae. albifasciatus*, *An. albitarsis* and *Ps. ferox*. The primary transmission cycle is between mosquitoes and birds, but serological evidence of infection has also been found in horses, cattle and goats (Calisher 1994; Spinsanti et al. 2003). In a survey by Bunde et al. (2006), the bats *Eptesicus fuscus* (big brown bat) and *Myotis lucifugus* (little brown bat) were tested positive for SLEV antibodies. An infection with SLEV can cause a slight illness with fever and headache or serious illness with

meningoencephalitis and death. **Dengue** is a viral infection and characterized by symptoms like fever, severe headache, orbital pain and general indisposition and start 5–7 days after infection. Haemorrhages and an increase in vascular permeability are the consequences of the Dengue haemorrhagic fever, which frequently leads to death. There is good evidence that sequential infection with different serotypes increases the risk of developing this dangerous form of dengue fever (Aguilar-Setién et al. 2008; Becker et al. 2010; Kalayanarooj et al. 1997). Dengue infections increased worldwide during the last decades and about one-fifth of the world population lives in Dengue risk zones (Fig. 3.2d) (Thomas et al. 2011). Dengue virus has been detected worldwide in tropical and subtropical regions, especially not only in the Southeast and South Asia but also in Central and South America and with an ongoing transmission risk in Africa (e.g. Chen and Wilson 2005). The first reported cases occurred at the end of the eighteenth century in Asia, Africa and North America, while Dengue haemorrhagic fever first occurred in the 1950s in the Philippines and Thailand (Becker et al. 2010). In the first half of the twentieth century in Europe (Austria, Greece, Italy and Spain), the virus caused epidemics. Primary vectors are species of the mosquito genus *Aedes* (*Aedes aegypti* and *Ae. albopictus*). Hypothetically, insectivore bats might become infected by ingestion of virus-infected mosquitoes, while fructivore species have to be infected by a mosquito bite (Aguilar-Setién et al. 2008). Wong et al. (2007) categorized the risk of bat to human transmission for the families Pteropodidae and Phyllostomidae as low because of low prevalence of pathogens in bats or inefficient vectorial capacity. However, de Thoisy et al. (2009) detected dengue viral RNA in 4 % of Chiroptera samples (*Carollia perspicillata*) from French Guiana. Platt et al. (2000) detected antibodies against Dengue virus in 22.6 % of examined bats from Costa Rica ($n = 53$) and 30 % of those from Ecuador ($n = 10$), mainly not only in bats of the genera *Artibeus* and *Uroderma* but also in four species of *Molossus*. In laboratory experiments, *Ae. aegypti* from Costa Rica fed on bats (Platt et al. 2000), but Scott (2001) doubted that this feeding is consistent with bat involvement in Dengue transmission and considered that there is no proof of interactions in natural conditions. In Mexico, Dengue virus is transmitted between humans by mosquitoes of the genus *Aedes*. Bat samples ($n = 162$) from five families (Emballonuridae, Mormoopidae, Phyllostomidae, Natalidae and Vespertilionidae) contained nine individuals of four species that were seropositive according to ELISA (*Artibeus jamaicensis, Myotis nigricans, Pteronotus parnellii* and *Natalus stramineus*). This is the first definite evidence of Dengue virus in *Myotis* species. These results support the contention that Dengue virus is present in bats from the Pacific and gulf coasts of Mexico (Aguilar-Setién et al. 2008). The first isolation of **Ilheus virus** (ILHV) was from mosquitoes of the genera *Ochlerotatus* and *Psorophora* from Brazil, especially *Psorophora ferox*, which is considered its main vector (da Silva Azevedo et al. 2010; Laemmert and Hughes 1947). Later it was isolated also from the genera *Culex, Haemagogus, Sabethes* and *Trichoprospon* (Venegas et al. 2012). In Brazil, it has been isolated also from birds, sentinel monkeys and horses (Iversson et al. 1993). Only a few reports of isolation from humans are available (Johnson et al. 2007; Spence et al. 1962; Srihongse and Johnson 1967;

Venegas et al. 2012). Results of infection are widely variable, ranging from asymptomatic to encephalitis, but most of the cases are accompanied by fever, headache, chills, photophobia, arthralgia, myalgia and asthenia (da Silva Azevedo et al. 2010). Price (1978) found sera in bats from Trinidad that protect against Ilheus. According to da Silva Azevedo et al. (2010), it has been isolated also from bats, but unfortunately no details of which species were involved were mentioned by the authors. **Zika virus** is known from Africa and Southeast Asia (Dick et al. 1952; Duffy et al. 2009; Hayes 2009). It is related to West Nile, Dengue and Yellow fever viruses (Duffy et al 2009). The first isolation of Zika virus was in 1947 from a rhesus monkey (Simpson 1964) in 1948 was the first isolation from a mosquito (*Aedes africanus*) and in 1968 from humans in Nigeria (Hayes 2009). Other serological studies showed human Zika virus infection in Africa also e.g. in Senegal, Uganda, Central African Republic and Egypt and for Asia e.g. in India, Malaysia, Vietnam or Indonesia (Duffy et al. 2009; Hayes 2009). Zika virus has been isolated from *Ae. aegypti, Ae. africanus, Ae. furcifer, Ae. luteocephalus* and *Ae. vittifer* (Dick 1952; Haddow et al. 1964; Hayes 2009; Lee and Moore 1972; Marchette et al. 1969). So far, no natural infections of bats with Zika virus have been documented, but in the laboratory the cave bat *Myotis lucifugus* was infected successfully when the virus was injected intraperitoneal, intradermal, intracerebral and intrarectal. But the bats were not susceptible to the virus after intranasal exposure (Reagan et al. 1955). **Tacaribe virus** (TCRV) belongs to the Arenaviridae (genus *Arenavirus*) (Bowen et al. 1996; Rossi et al. 1996). Diseases caused by the Tacaribe virus complex of the new world are Argentine haemorrhagic fever, Brazilian haemorrhagic fever, Venezuelan haemorrhagic fever and another yet unnamed haemorrhagic fever, induced by Junín, Sabiá, Guanarito, Machupo and Chapare viruses (Carballal et al. 1987; Cogswell-Hawkinson et al. 2012; Tesh et al. 1994). In contrast to the other arenaviruses, which have all been isolated from rodents, Tacaribe virus was originally isolated from two bat species: great fruit-eating bats (*Artibeus lituratus*) and Jamaican fruit bats (*A. jamaicensis*) (Downs et al. 1963; Price 1978). Furthermore, Price (1978) was able to detect antibodies against TCRV in the little yellow-shouldered bat (*Sturnira lilium*), Heller's broad-nosed bat (*Platyrrhinus helleri*) and in the vampire bat (*Desmodus rotundus*). Nevertheless, the study of Cogswell-Hawkinson et al. (2012) does not support the hypothesis that *A. jamaicensis* is a natural reservoir host for TCRV, because the injection of high doses resulted in significant and fatal disease including pneumonia, pathological changes in liver and spleen and brain lesions. One study (Downs et al. 1963) however revealed close correspondence between a strain isolated from a mosquito pool and one isolated from a bat. Unfortunately, the pool consisted of 18 mosquito species, so that no precise information about the possible vector can be given.

Besides viruses, some parasites are known, which occur in bats and humans, and can be transmitted through haemorrhagic insects. The first one is the **Chagas disease** an infection with the flagellate *Trypanosoma cruzi* (Zeledón and Rabinovich 1981). The disease occurs in Central and South America and is transmitted by the intestinal content of triatomine kissing bugs (Mehlhorn 2001). It is the

leading cause of heart disease in South America with the major vector species *Triatoma infestans*, *T. dimidiata* and *Rhodnius prolixus* (Reduviidae) (Dorn et al. 2003). Flagellates of the genus *Trypanosoma* are parasitic in nearly all mammalian species. In more than 100 species of bats more than 30 trypanosome species are recorded, while the subgenus *Schizotrypanum* comprises species restricted to bats as well as *T. cruzi* (Cavazzana et al. 2010). Kissing bugs live for example in caves, burrows, nests of wild animals on which they feed during the night. During the blood meal infected faeces is set free and after the bite scratched by the victim in the itching wound. During the life cycle in man or other reservoir hosts, amastigotes reproduce in the cytoplasm of different host cell types, which appear as "pseudocysts" when they are completely filled with parasites. The most important lesions are in the heart and a myocardial failure results to death years after the infection (Mehlhorn 2001). The symptoms range from fever to inflammation of heart, muscles and brain (CDC 2010).

Beneath the usual triatomine vector, several wild animals are associated with the Chagas disease. Among others Marsupialia, Rodentia, Edentata, Primates and Chiroptera had been positive investigated for *T. cruzi* (Coura et al. 2002). Common species of neotropical bats, including those of the genera *Artibeus*, *Noctilio*, *Mormoops*, *Nautilus*, *Pteronotus*, *Myotis*, *Carollia*, *Desmodus*, *Glossophaga*, *Phyllostomus* and *Molossus*, have been reported to be susceptible to *T. cruzi* infection under natural as well as under experimental conditions (Añez et al. 2009). Bats can get infected by the blood meal of the kissing bugs or through the ingestion of infected arthropods. So it is not astonishing that most infected bats are insectivorous. The prevalence in South American bats varied widely. In Colombia and in the Amazonia of Brazil, it is approximately 9.0 %, respectively 2.4–4.6 % (García et al. 2012).

Añez et al. (2009) detected in *Molossus molossus* in western Venezuela a congenital transmission from pregnant female bats to their foetus. Trypomastigotes had been found in 100 % of all examined foetus. In their natural habitat, *M. molossus* is associated with *R. prolixus* kissing bugs. The insectivore *M. molossus* shows a high susceptibility for *T. cruzi*, due to the fact that 80 % of the examined bats are infected. These results emphasize the role of Chiroptera as host for Chagas disease in endemic areas and their impact for the sylvatic cycle of *T. cruzi* (Añez et al. 2009).

Recent examinations detected new genotypes of *T. cruzi* associated with bats, which indicate that the complexity of *T. cruzi* is larger than known and confirmed bats as important reservoir for infections to humans (e.g. Maeda et al. 2011; Marcili et al. 2009) and the strong association between bats and, for instance, *Schizotryphanum* suggests a long shared evolutionary development (García et al. 2012). Furthermore, the molecular examination of Chagas virus strains reveals the movement of bats, naturally or by human transport, between the Old and the New World (Hamilton et al. 2012b). Hamilton et al. (2012a) suggested that *T. cruzi* evolved from bat trypanosomes and have successful switched into other mammalian hosts.

Coccidia (Apicomplexa) are characterized by intracellular life cycles consisting of the three phases: schizogony, gamogony and sporogony. The coccidian genus ***Plasmodium*** is the pathogenic agent of malaria, a mosquito-borne infectious disease of humans and animals, which causes fever, headache and in severe cases death (Mehlhorn 2001). Worldwide 3.3 billion people live in risk areas (Africa, Southeast Asia region and the Eastern Mediterranean) of malaria transmission and each year at least one million people die after infection (Snow et al. 2005). The order Haemosporidia consists of the five genera: *Plasmodium, Hepatocystis, Polychromophilus, Nycteria and Rayella*. The vectors of the first three genera are respectively haematophagous Diptera of the families Culicidae (*Anopheles* spp.), Ceratopogonidae and Nycteribiidae (Witsenburg et al. 2012). With the exception of *Rayella*, all haemosporidia genera are known to infect insectivorous bats in temperate and tropical regions (Duval et al. 2012). Megali et al. (2011) investigated 237 bats of four species from Switzerland to obtain a better understanding of the complex co-evolutionary processes between hosts and parasites. A total of 34 % ($n = 70$) was infected with *Plasmodium murinus*. In detail, *Myotis daubentonii* was the most parasitized species (51 %), followed by *Eptesicus serotinus* (11 %), *Nyctalus noctula* (7 %) and *Myotis myotis* (4 %) (Megali et al. 2011). The prevalence (P) of *P. murinus* in *M. daubentonii* was twice as great as found by Gardner and Molyneux (1988) in England and Scotland. Duval et al. (2007) examined 530 bat individuals (Pteropodidae, Rhinolophidae, Hipposideridae, Megadermatidae, Emballonuridae, Vespertilionidae and Molossidae) from Madagascar and Cambodia. In Madagascar haemosporidian infections were found in Hipposideridae (*Triaenops furculus*, P 4 %) and Vespertilionidae (*Miniopterus gleni*, P 23 %; *Myotis goudoti*, P 24 % and *Miniopterus manavi*, P 38 %). In Cambodia, infections were found in the Hipposideridae (*Hipposideros larvatus*, P 8 %), Megadermatidae (*Megaderma spasma*, P 80 %) and Vespertilionidae (*Kerivoula hardwickii*, P 20 %) (Duval et al. 2007). In *Pteropus poliocephalus* from Australia (P 36 %), Landau et al. (1980) described *Hepatocystis levinei*, which under laboratory conditions, used *Culicoides nubecolusus* (Diptera and Ceratopogonidae) to complete its life cycle. Landau et al. (2012) listed bat hosts of six families in which different types of gametocytes were detected. The authors concluded that the Microchiroptera harbour mainly parasites of the *falciparum* and *malariae* groups, while Megachiroptera harbour parasites of the *vivax* group (Landau et al. 2012). Duval et al. (2012) sampled 164 bats from Gabon in Central Africa of which only *Miniopterus inflatus* was positively tested for haemosporidian parasites. The prevalences ranged from 17.6 % to 66.7 % (blood smear examinations), while the molecular prevalence ranged from 63.2 % to 88.9 %. The nycteribiid *Polychromophilus fulvida* was found infected with *Polychromatophilia* sp. in Faucon Cave in Gabon (Landau et al. 1980). *Miniopterus inflatus* and other bat species (e.g. *H. gigas, H. caffer* and *C. afra*) are potentially exposed to this blood parasite (Duval et al. 2012). The five host specific *Polychromophilus* species are restricted, regarding their vertebrate hosts, to insectivorous bats of the order Microchiroptera. Vectors are Nycteribiidae (Diptera, Hippoboscoidea) (Witsenburg et al. 2012).

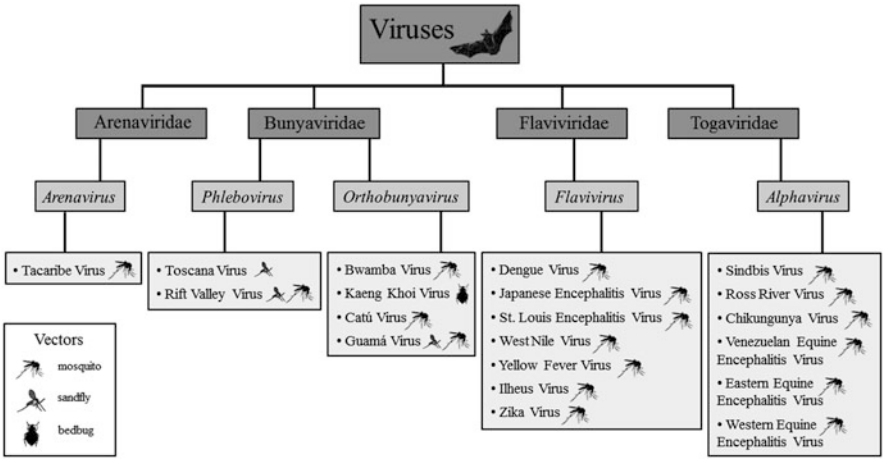

Fig. 3.3 Overview of the pathogens found in bats and human with their family, genera and vectors, which are discussed in this chapter

3.3 Conclusion

In the past, a high number of viruses and parasites has been detected in bats, which are important reservoir hosts. On the contrary, many haematophagous insects serve as vectors for numerous arboviruses and parasites, with mosquitoes (Culicidae) being the most important vectors worldwide. So the presence of certain viruses in both mosquitoes and bats is not really surprising and a transmission cycle between bats, mosquitoes and humans is thinkable. However, it is not possible to say whether the mosquitoes served as vector for the bats or the bats as reservoir both options must be taken into consideration.

In the present chapter, we describe 20 viruses from four different families as well as two parasitic pathogens, which have been detected in bats, in haematophagous insects and in humans (see also Table 3.1, Fig. 3.3). Therefore, for these pathogens is a probability to be transmitted from bats to humans via insects. However, because of the amount of publications in these fields and the quantity of described viruses it is difficult to give a definite number for the possible diseases and the chapter makes no claim to be complete. So far, this way of transmission between bats–mosquito–humans could not be proven for any of the diseases, but vectors being in relation with bat infections (e.g. *Cx. quinquefasciatus, Ae. vexans* or *Ae. aegypti* and *Ae. albopictus*) are also known to bite humans. Climate change as well as global trade could not only increase the risk for such way of transmission e.g. when potential hosts but also competent vectors expand their distribution. Apart from the listed viruses and parasites (see Table 3.1, Fig. 3.3) are some pathogens often described only in humans or bats but has been detected already also in mosquitoes or is, at least, suspected to be transmitted by arthropods, like Bimiti, Oriboca, Mayaro or Yokose virus. With climate change range swift of vectors and possible spontaneous

mutations, new hosts and/or vector competences can occur. For some diseases like WNV, Dengue or Yellow fever, the way of transmission is already well known, while this is not the case for others like Kaeng Khoi, Catu, Guama, Zika or Bwamba virus, but knowledge about these things is essential as epidemics cause high social as well as economic impact.

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