



Review

Reptile vector-borne diseases of zoonotic concern

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ABSTRACT

Reptile vector-borne diseases (RVBDs) of zoonotic concern are caused by bacteria, protozoa and viruses transmitted by arthropod vectors, which belong to the subclass Acarina (mites and ticks) and the order Diptera (mosquitoes, sand flies and tsetse flies). The phyletic age of reptiles since their origin in the late Carboniferous, has favored vectors and pathogens to co-evolve through millions of years, bridging to the present host-vector-pathogen interactions. The origin of vector-borne diseases is dated to the early cretaceous with Trypanosomatidae species in extinct sand flies, ancestral of modern protozoan hemoparasites of zoonotic concern (e.g., *Leishmania* and *Trypanosoma*) associated to reptiles. Bacterial RVBDs are represented by microorganisms also affecting mammals of the genera *Aeromonas*, *Anaplasma*, *Borrelia*, *Coxiella*, *Ehrlichia* and *Rickettsia*, most of them having reptilian clades. Finally, reptiles may play an important role as reservoirs of arboviruses, given the low host specificity of anthropophilic mosquitoes and sand flies. In this review, vector-borne pathogens of zoonotic concern from reptiles are discussed, as well as the interactions between reptiles, arthropod vectors and the zoonotic pathogens they may transmit.

1. Introduction

Reptiles are among the most diverse and successful group of vertebrates, including more than 1200 genera and around 11,000 species (Roll et al., 2017). This class is divided in four orders: Squamata (i.e., 10, 417 species of lizards, snakes, and amphisbaenians), Testudines (i.e., 351 species of turtles and tortoises), Crocodylia (i.e., 24 species of crocodiles, alligators, caimans and gavials), and Rhynchocephalia, the latter represented by a single species of living fossils named tuataras (Pincheira-Donoso et al., 2013). Since the appearance of reptiles, 310–320 million years ago in the late Carboniferous, this class of animals has scarcely changed as per their morphology, biology and ecology (Tucker and Benton, 1982; Lepetz et al., 2009). Along with them, vectors and pathogens have co-evolved through millions of years, possibly bridging to the present host-vector-pathogen interactions. Under the above circumstances, the interactions amongst reptiles, arthropod vectors and transmitted pathogens could be considered a model for unravelling the intimate relationship within the vector-borne diseases (VBDs). An example is represented by the origin of pathogenic malaria parasites, which is believed to had diverged in the half of the Eocene epoch from reptilian ancestors (Hayakawa et al., 2008). Moreover,

many zoonotic diseases could have originated or are associated to a reptilian host. For example, some studies initially hypothesized that the origin of the SARS-COV-2, causative agent of the COVID-19 pandemic, were snakes (Tiwari et al., 2020; Ji et al., 2020). This is also the case of the evolution of VBDs, where many pathogens have a clade or cluster of species associated to reptiles or ectothermic tetrapods, like the reptile-associated *Borrelia* group (Morales-Diaz et al., 2020), or the reptile clade of *Leishmania* (subgenus *Sauroleishmania*) (Tuon et al., 2008). Also, some parasitic arthropods became well adapted to their reptilian host producing minimum deleterious effects on them (Bertrand et al., 2002; Bower et al., 2019), such as in the case of *Amblyomma rotundatum* ticks infesting reptiles in South America (Polo et al., 2021; Mendoza-Roldan et al., 2020a), or *Ixodes ricinus* parasitizing wild lizards (*Lacerta agilis*) in Europe (Wieczorek et al., 2020). Conversely, other parasitic arthropods (e.g., *Ophionyssus natricis* mites in snakes) may have a pronounced deleterious effect on their hosts, when there is a high parasitic load (Fuantos-Gámez et al., 2020). However, the vector-host interaction becomes noticeably important when considering vector-borne agents (i.e., bacteria, parasites, viruses) of zoonotic concern. The success of microorganisms in infecting the hosts depends on different factors acting in synergy (Prakasan et al., 2020). For

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example, in endemic areas of visceral leishmaniasis in Northwest China, where typical canid hosts are scarce, lizards were found to be molecularly positive for *Leishmania turanica*, *Leishmania tropica* and *Leishmania donovani* complex (Zhang et al., 2019), and snakes of *L. turanica* and *L. donovani* (Chen et al., 2019). In addition, reptiles may be infected by various zoonotic VBDs (i.e., bacterial, protozoal, viral) being the primary source of bloodmeal for arthropod vectors (i.e., ticks, mites, sand flies and mosquitoes) (Fig. 1) that equally may feed on humans (Mendoza-Roldan et al., 2020a,b, 2021). In this review, we discuss vector-borne pathogens associated to reptiles, as well as the interactions between reptiles, arthropod vectors and the pathogens they may transmit with a focus on those of zoonotic concern.

2. Arthropods feeding on reptiles

Arthropod vectors may transmit pathogens in which they partially develop (biological vectors) or are merely transported until their transmission (mechanical vectors) to a susceptible host (Di Giovanni et al., 2021). While many studies have been carried out concerning host-parasite relationship of mammals and birds with Acarina (i.e., ticks and mites) and insects (i.e., sand flies and mosquitoes), the relationships between ectoparasites and reptiles have been much less investigated (Mendoza-Roldan et al., 2020b, 2021a). In particular, knowledge on ectoparasites of reptiles mainly derive from ecological and biological studies (Mihalca, 2015), resulting in a consistent lack of information on their role as vectors of pathogens for reptiles and for mammalian species, as well as on their biological interactions and transmission modalities. Nonetheless, data on arthropod vectors of pathogens and host-arthropod association are of key importance to better understand the origin of zoonotic diseases. The relationship established by arthropods and reptiles dates back to dinosaurs when these arthropod parasites firstly appeared (Peñalver et al., 2017). For example, it is hypothesized that ticks originated in the Paleozoic Era (in the Devonian, Carboniferous or Permian periods) feeding on the ancestors of reptiles and amphibians (Dobson and Barker, 1999; Jeyaprakash and Hoy, 2009; Mans et al., 2016). While some authors indicated that ticks originated in the Mesozoic Era, between the Triassic and Jurassic periods (Balashov, 1994; Beati and Klompen, 2019), fossil data suggest that ixodid and argasid ticks already had diverged since the Cretaceous period (Poinar and Brown, 2003; Klompen and Grimaldi, 2001; Chitimia-Dobler et al., 2017; Estrada-Peña and de la Fuente, 2018).

2.1. Ticks and mites

On the whole, more than 500 species of mites and ticks (subclass

Acarina) parasitize ectothermic tetrapods (amphibians and reptiles) worldwide (Mendoza-Roldan et al., 2020a). They belong to the orders Trombidiformes (superorder Acariformes), Mesostigmata and Ixodida (superorder Parasitiformes). In particular, the order Trombidiformes encompasses around seven families and more than 30 genera infesting reptiles and amphibians, while Mesostigmata includes five families and 18 genera developing on ectothermic tetrapod fauna (Fain, 1962).

Within Ixodida, species parasitizing reptiles and amphibians are about 100 and they belong to 8 genera within the family Ixodidae and a few Argasidae (Barros-Battesti et al., 2006, 2015; Dantas-Torres et al., 2008; Muñoz-Leal et al., 2017). Very often larval and nymphal stages feed on reptiles but may also infest mammals and birds developing in rare cases exclusively on reptiles as principal hosts (e.g., species of the genus *Amblyomma*). This is the case of *Amblyomma humerale* whose larvae and nymphs feed on mammals and reptiles, whereas adults preferentially feed on turtles and tortoises (Martins et al., 2020). The high specialization exclusively on one reptile species (monoxenous parasitism) is rare, such as in the case of *Argas (Microargas) transversus* (Argasidae) from *Chelonoidis nigra* (Hoogstraal and Kohls, 1966). The long-lasting evolution of ticks with reptiles and amphibians is also suggested by the capacity some tick species have developed to survive underwater for certain periods (Fielden et al., 2011; Giannelli et al., 2012; Bidder et al., 2019). This strategy may also be advantageous for ticks to thrive in environments that experience seasonal floods or even for those parasitizing hosts which live in close contact with the water (Luz and Faccini, 2013; Dantas-Torres et al., 2019; Kwak et al., 2021). This is the case of *A. rotundatum* parasitizing reptiles and amphibians in South America (Luz et al., 2013; Dantas-Torres et al., 2019) and of the sea snake tick *Amblyomma nitidum* that parasitizes snakes of the genus *Laticauda*, being one of the few tick species regarded as semi-marine (Kwak et al., 2021).

While the direct negative-effect of mites and ticks on the fitness and health status of the infested animals is overall negligible (e.g., anemia, dehydration, emaciation, dysecdysis), they may be of major importance as vectors of pathogens to other animal species including humans (Mendoza-Roldan et al., 2019, 2021b). This is the case of *I. ricinus* ticks feeding on lizards and associated to *Borrelia burgdorferi* sensu lato (Fig. 1a) (Majláthová et al., 2008; Mendoza-Roldan et al., 2019) and spotted fever group *Rickettsia* spp. (Fig. 2a) (Mendoza-Roldan et al., 2021b) (Table 1). Permanent and temporary mites and ticks may colonize different areas of the host's body with varying degrees of clinical signs. For example, most ectoparasites attach on/or inside the connective tissue underneath the scales (Mendoza-Roldan et al., 2017). Overall, preferred niches depend on the ability and size of the mite or tick, with large parasites (Ixodida and Macronyssidae) choosing areas that are

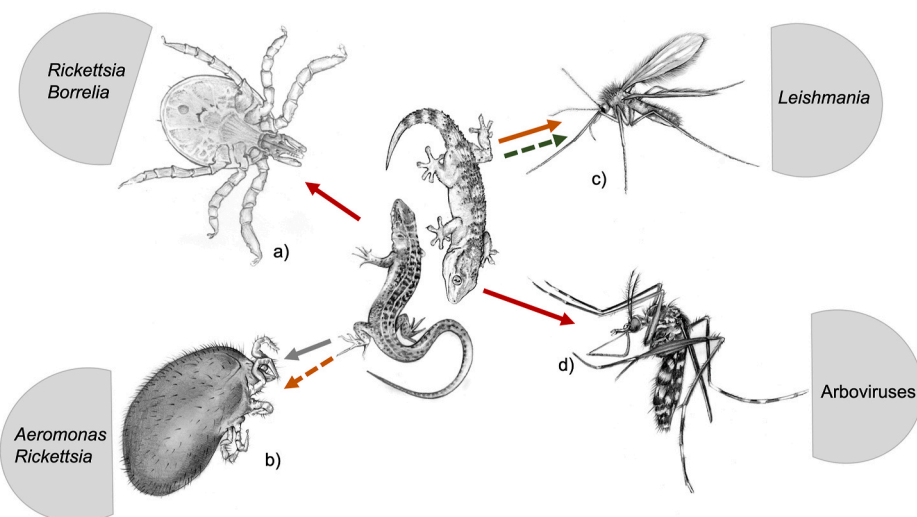


Fig. 1. Arthropod vectors associated to reptiles represented by a *Podarcis siculus* lizard and *Tarentola mauritanica* gecko and zoonotic pathogens they may transmit. a) *Ixodes ricinus* tick larva, b) *Ophionyssus natricis* mite, c) *Sergentomyia minuta* sand fly, d) *Aedes albopictus* mosquito. Red lines represent high importance role of transmission, orange line represents medium importance role of transmission, gray line represents mechanical vector and green line represents transmission of non-pathogenic zoonotic microorganisms. Dashed lines represent neglectable knowledge on actual role of vector. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

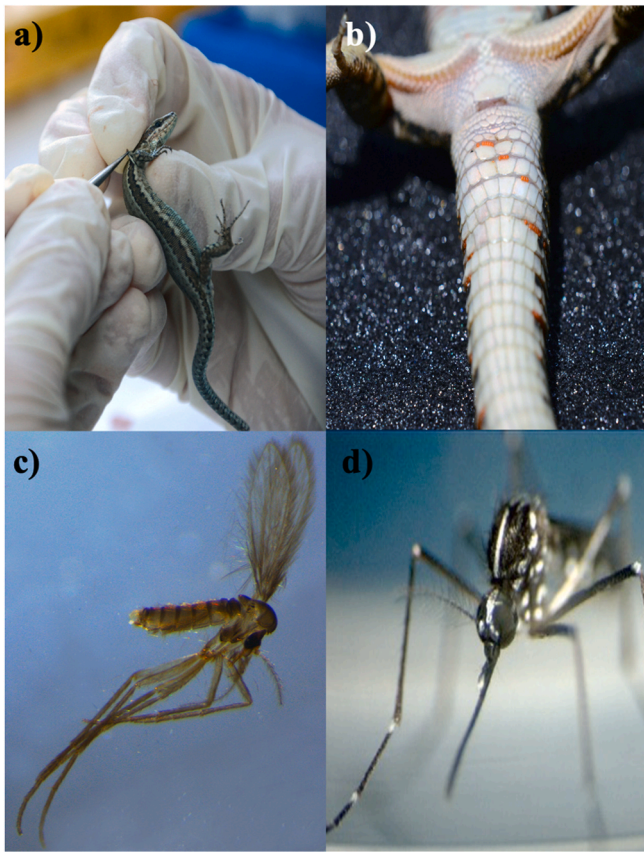


Fig. 2. Arthropod vectors that may feed on reptiles. a) *Ixodes ricinus* larva on *Podarcis siculus* lizard being collected with tweezers, b) *Neotrombicula autumnalis* larvae mites on *Podarcis siculus* lizard, c) female *Sergentomyia minuta* phlebotomine sand fly, d) *Aedes albopictus* mosquito.

unreachable after producing pruritus (e.g., head, nasal area, axillae, joints, toes and cloaca) (Chilton et al., 1992b; Bannert et al., 2000), and smaller mites (e.g., Trombiculidae, Pterygosomatidae) attaching evenly on the host body (Bertrand, 2002) or in the respiratory system of their hosts (e.g., Entonyssidae in snakes) (Fain et al., 1983). Mites parasitizing reptiles belong to the orders Trombidiformes (Acariformes) and Mesostigmata. With seven families and more than 30 genera infesting reptiles and amphibians (Zhang et al., 2011; Rezende et al., 2012), the Trombidiformes is the most represented order of mites parasitizing herpetofauna, whereas Mesostigmata includes five families and 18 genera (Lizaso, 1979, 1982). The role of mites as vectors of zoonotic pathogens has not been fully investigated although data suggest their implication as vectors for some of them, such as *Rickettsia* spp. (Fig. 2b) (Mendoza-Roldan et al., 2021a, 2021b). In spite of the paucity of information about mites, in areas where specific studies have been carried out in reptiles (e.g., in Brazil) many species have been described, as belonging to eight genera and 11 species of Trombidiformes and Mesostigmata (Mendoza-Roldan et al., 2017; Jacinavicius et al., 2018). In a comprehensive study of reptiles and amphibians in Brazil ($n = 4515$ specimens examined) the majority of infested animals ($n = 170$) were lizards ($n = 72$; 42.3%), infested mainly by Trombidiformes order (Trombiculidae and Pterygosomatidae) (Mendoza-Roldan et al., 2020b). Examples of mite vectors of pathogens are represented in both the Trombidiformes and Mesostigmata orders (Fig. 1b) (Table 1).

Moreover, in some studies in other geographical areas (e.g., the Palearctic, Nearctic and Ethiopic regions), a high parasitic load of ticks was observed on lizards, also with no apparent negative effect on the host health (Prendeville and Hanley, 2000; Soualah-Alila et al., 2015; Dudek et al., 2016; Mendoza-Roldan et al., 2019). Indeed, lizards have

been found infested by larvae and nymphs of *Ixodes pacificus* in the Nearctic region, and *I. ricinus* in the Palearctic region (Mendoza-Roldan et al., 2019). Conversely, *B. burgdorferi* sensu lato in the Neotropical region probably is maintained by birds and small mammals, rather than lizards (Barbieri et al., 2013; Ogrzewalska et al., 2016; De Oliveira et al., 2018). Furthermore, another paradigmatic example of the participation of ticks, associated to a certain level to reptiles, in the eco-epidemiology of zoonotic pathogens, is represented by *Hyalomma aegyptium*. This species of tick feeds mainly on *Testudo* tortoises in the Palearctic region, but may also feed on mammals. Given the high molecular prevalence of important zoonotic pathogens, normally associated to warm-blooded animals (i.e., *Anaplasma*, *Ehrlichia*, *Coxiella burnetii*) detected on this tick species in Romania, a possible host-switching behavior may have occurred, further increasing the zoonotic pathogens transmission implications of *H. aegyptium* (Paștiu et al., 2012).

2.2. Sand flies

Similar to other arthropod vectors mentioned above, sand flies (Diptera: Phlebotomidae) most likely evolved during the lower Cretaceous (105–100 mya) as they were found engorged in Burmese amber containing stages of a leishmanial trypanosomatid in their proboscis and abdominal midgut along with reptilian erythroid cells (Poinar and Poinar, 2004b). Incidentally, the fossil sand fly morphologically resembled those of the genus *Sergentomyia*, which includes species feeding on ectothermic animals (Fig. 1c) (Alkan et al., 2013). Based on these results, authors hypothesized that the extinction of dinosaurs could have been caused by epidemics of *Leishmania* spp. (Desowitz, 1991). The evolutionary history of Phlebotominae sand flies is directly linked to hemoparasites rather than to their definitive hosts. Indeed, sand fly species are distributed worldwide (Torres-Guerrero et al., 2017), mainly in the tropical and neotropical regions (Lozano-Sardaneta et al., 2018), and feed on diverse species of vertebrates. Consequently, sand flies are opportunistic blood feeders, depending on host availability rather than specific attractiveness (Pérez-Cutillas et al., 2020; Cotteaux-Lautard et al., 2016). For example, *Lutzomyia* (*Helicocyrtomyia*) *apache*, considered as an exclusive feeder of warm-blood vertebrates, may also feed on the western fence lizards (*Sceloporus occidentalis*; Reeves, 2009). The same occurred for *Sergentomyia minuta* (Fig. 2c), which may feed on lizards as well as on mammals (Bravo-Barriga et al., 2015; González et al., 2020). Therefore, the role of Squamata reptile populations and the ubiquitous distribution of sand fly species is of critical importance to understand the epidemiology of trypanosomid flagellates in endemic regions. Phlebotomine sand flies are the single natural vector of *Leishmania* spp. and may also be involved in the transmission of Arboviruses (Phlebovirus) and *Bartonella* sp. to humans (Ready, 2013). The protozoan *Leishmania* has hijacked the predatory mechanisms of the sand fly, enabling it to feed on potential hosts as it remains insatiate (Akhoundi et al., 2016). *Leishmania* spp. ancestors were divided in *Sauroleishmania* and current *Leishmania* genus (Killick-Kendrick et al., 1986). Nevertheless, the establishment of the sustained cycle between vector and vertebrate species, probably occurred during the Paleocene, after the appearance of placental mammals (Bates, 2007) (Table 2).

2.3. Mosquitoes

Mosquitoes (Diptera, Culicidae) are well known vectors of zoonotic pathogens (Fig. 1d), such as viruses causing diseases (e.g., Dengue fever, Yellow fever, West Nile Virus, Equine Encephalitis, Zika) or protozoa causing malaria (Table 3) (Chiang and Reeves, 1962; Benelli and Mehlhorn, 2016). The feeding patterns and host preferences may be considered diverse and overlapped, therefore, intraspecific and interspecific (e.g., mammalian, avian, reptilian hosts) transmission of pathogens is likely in some regions, depending on the availability or selection of the definitive host (Shahhosseini et al., 2018). The role of reptiles in the maintenance of mosquito-borne diseases is due to the noteworthy

Table 1
Species of mites and ticks, their reptile hosts and associated zoonotic pathogens.

Type of Acarina	Species of vector	Reptile host	Country	Zoonotic pathogen	Reference
Mite	<i>Eutrombicula alfreddugesi</i>	Snakes	Brazil	<i>Rickettsia</i> sp. <i>Rickettsia bellii</i> -like	Mendoza-Roldan et al. (2021a)
	<i>Geckobiella harrisi</i>	Lizards	Brazil	<i>Rickettsia</i> sp.	Mendoza-Roldan et al. (2021a)
	<i>Ophiogonylus rotundus</i>	Snakes	Brazil	<i>Rickettsia</i> sp.	Mendoza-Roldan et al. (2021a)
	<i>Neotrombicula autumnalis</i>	Lizards	Italy	<i>Rickettsia</i> sp.	Mendoza-Roldan et al. (2021b)
	<i>Ophionyssus natricis</i>	Snakes	United states	<i>Aeromonas hydrophila</i>	Camin (1984)
Tick	<i>Amblyomma chabaudi</i>	Lizards	Brazil	<i>Rickettsia</i> sp.	Mendoza-Roldan et al. (2021a)
	<i>Amblyomma clypeolatum</i>	Tortoises	Madagascar	<i>Rickettsia africana</i>	Sanchez et al. (2019)
	<i>Amblyomma dissimile</i>	Freshwater turtles	Colombia	<i>Rickettsia</i> sp.	Andoh et al. (2015)
		Snakes			Santodomingo et al. (2018)
		Lizards			
		Snakes	Mexico	<i>Rickettsia</i> sp.	Sanchez et al. (2019)
		Lizards	Japan	<i>Borrelia</i> sp.	Takano et al. (2010)
			Honduras	<i>Rickettsia</i> sp. strain Colombianensi	Novakova et al. (2015)
	<i>Amblyomma exornatum</i>	Monitor Lizards	Guinea Bissau	<i>Coxiella burnetii</i>	Arthur (1962)
			United Kingdom	<i>Ehrlichia</i> sp.	Mihalca (2015)
			Japan		Andoh et al. (2015)
	<i>Amblyomma fimbriatum</i>		Australia	<i>Rickettsia tamurae</i>	Sanchez et al. (2019)
	<i>Amblyomma flavomaculatum</i>		Poland	<i>Anaplasma phagocytophilum</i>	Mihalca (2015)
			Ghana	<i>Anaplasma</i> sp.	Nowak et al. (2010)
	<i>Amblyomma geoemydae</i>	Box turtles	Japan	<i>Rickettsia aeschlimannii</i> -like	Qiu et al. (2021)
	<i>Amblyomma helvolum</i>	Snakes	Malaysia	<i>Candidatus Ehrlichia occidentalis</i> <i>Ehrlichia</i> sp.	Kho et al. (2015)
				<i>Candidatus Rickettsia johorensis</i> <i>A. phagocytophilum</i>	
	<i>Amblyomma latum</i>	Snakes	Japan	<i>Rickettsia</i> sp.	Andoh et al. (2015)
		Lizards		<i>Ehrlichia</i> sp.	
	<i>Amblyomma nitidum</i>	Marine snakes		<i>Rickettsia</i> sp.	Qiu et al. (2021)
				<i>Candidatus Ehrlichia occidentalis</i>	
	<i>Amblyomma nuttalli</i>	Snakes	Ghana	<i>C. burnetii</i>	Kim et al. (1978)
	<i>Amblyomma parvitarsum</i>	Lizards	Chile	<i>Rickettsia parkeri</i> strain Parvitarsum	Sanchez et al. (2019)
	<i>Amblyomma rotundatum</i>	Snakes	Brazil	<i>Rickettsia bellii</i>	Mendoza-Roldan et al. (2021a)
				<i>Rickettsia amblyommatis</i>	
	<i>Amblyomma sabanerae</i>	Freshwater turtles	United states	<i>Rickettsia helvetica</i>	Sanchez et al. (2019)
			El salvador		
	<i>Amblyomma sparsum</i>	Tortoises	Zambia	<i>Ehrlichia chaffeensis</i> <i>Candidatus Neoehrlichia mikurensis</i> <i>Ehrlichia ruminantium</i> <i>R. bellii</i>	Andoh et al. (2015)
				<i>Rickettsia raoultii</i>	Peter et al. (2002)
			Japan	<i>Rickettsia</i> sp.	Sanchez et al. (2019)
				<i>Ehrlichia</i> sp.	Andoh et al. (2015)
	<i>Amblyomma transversale</i>	Snakes			
		Ghana	<i>Rickettsia hoogstraalii</i>	Sanchez et al. (2019)	
<i>Amblyomma trimaculatum</i>	Snakes	Japan	<i>Rickettsia</i> sp.	Andoh et al. (2015)	
<i>Amblyomma varanense</i>	Monitor lizards	Indonesia	<i>Anaplasma</i> sp.	Takano et al. (2019)	
<i>Amblyomma variegatum</i>	Reptiles	Congo	<i>C. burnetii</i>	Giroud (1951)	
<i>Bothriocroton hydrosauri</i>	Lizards	Australia	<i>Rickettsia honei</i>	Whiley et al. (2016)	
	Snakes				
<i>Bothriocroton undatum</i>	Monitor lizards	Australia	<i>Borrelia</i> sp.	Paneta et al. (2017)	
<i>Haemaphysalis sulcata</i>	Lizards	Italy	<i>R. hoogstraalii</i>	Sanchez et al. (2019)	
<i>Hyalomma aegyptium</i>	Tortoises	Algeria	<i>Rickettsia aeschlimannii</i>	Sanchez et al. (2019)	
		Middle East	<i>C. burnetii</i>	Široký et al. (2010)	
		Romania	<i>A. phagocytophilum</i> <i>Ehrlichia canis</i> <i>C. burnetii</i>	Paștiu et al., 2012	
		Turkey	Crimean-Congo hemorrhagic fever	Kar et al. (2020)	
<i>Ixodes ricinus</i>	Lizards	Netherlands	<i>Rickettsia helvetica</i>	Sanchez et al. (2019)	
	Snakes		<i>Rickettsia typhi</i>		
	Lizards	Italy	<i>R. helvetica</i> <i>Rickettsia monacensis</i>	Mendoza-Roldan et al. (2021a)	
		Europe	<i>Borrelia lusitaniae</i> <i>A. phagocytophilum</i>	Mendoza-Roldan et al. (2019)	
		Italy	<i>Ehrlichia</i> sp.	Nieto et al. (2009)	
<i>Ixodes pacificus</i>	Lizards	United states	<i>A. phagocytophilum</i> <i>Borrelia burgdorferi</i> (sensu lato)	Mendoza-Roldan et al. (2019)	
			<i>Borrelia turicatae</i> <i>Borrelia duttoni</i>	Nieto et al. (2009)	
<i>Ornithodoros moubata</i>	Tortoises	North America		Kuo et al. (2000)	
<i>Ornithodoros turicata</i>	Tortoises	Africa		Estrada-Peña and Jongejan (1999)	
	Snakes				

Table 2
Sand fly species, their reptilian blood meal source and associated zoonotic pathogens.

Phlebotomine species	Host species	Country	Zoonotic pathogen	Reference
<i>Phlebotomus chinensis</i> <i>Phlebotomus longiductus</i> <i>Phlebotomus wui</i> <i>Phlebotomus alexandri</i> <i>Phlebotomus clydei</i> <i>Phlebotomus kazerun</i> <i>Phlebotomus perniciosus</i> <i>Sergentomyia minuta</i>	Lizards	China		Zhang et al. (2019)
	Lizards	Kenya	<i>Leishmania tropica</i> <i>Leishmania donovani</i> <i>Leishmania adleri</i>	Heisch (1958)
	Lizards	Pakistan	<i>Trypanosoma</i> sp.	Kato et al. (2010)
		France	Toscana Virus	Cotteaux-Lautard et al. (2016)
		Spain	<i>Leishmania</i> sp.	Gonzalez et al. (2019)
		Spain	<i>Leishmania tarentolae</i>	Bravo-Barriga et al. (2015)
	Humans	Italy	<i>Leishmania donovani</i> complex <i>L. tarentolae</i>	Abbate et al. (2020)
		France	Toscana Virus	Charrel et al. (2006)
<i>Sergentomyia (Sergentomyia) dentata</i> <i>Sergentomyia</i> sp.	Lizards	Iran	<i>L. adleri</i>	Maleki-Ravasan et al. (2008)
	Lizards	Worldwide	<i>Sauroleishmania</i> spp.	Lozano-Sardaneta et al. (2018)

Table 3
Mosquito species, their reptilian blood meal source and associated zoonotic viral disease.

Mosquito species	Host	Country	Disease	Reference
<i>Aedes albopictus</i> <i>Aedes aegypti</i> <i>Aedes notoscriptus</i> <i>Aedes vexans</i> <i>Ae. Vittatus</i> <i>Ae. luteocephalus</i> <i>Aedes (Och.) camptorhynchus</i> <i>Culiseta melanura</i>	Squamata reptiles	Cuba	Zika virus	Gutiérrez-Bugallo et al. (2019)
	Lizards Snakes Turtles	USA	Eastern equine encephalitis virus (EEEV)	Graham et al. (2012)
Inoculation (lab conditions)	Crocodiles Lizards Snakes Turtles	USA	Chikungunya virus	Bosco-Lauth et al. (2018)
<i>Culex tarsalis</i> <i>Culex</i> sp.	Snakes Alligators Monitor lizards Crocodiles	USA Israel	Western equine encephalitis (WEE) West Nile Virus	Thomas and Eklund (1962) Steinman et al. (2003)
In vitro	Lizards	Germany	Rift Valley fever phlebovirus (RVFV)	Rissmann et al. (2020)

fragment of Chordata biomass they constitute in the terrestrial biosphere and to their potential role as reservoirs of zoonotic diseases. For example, *Culex* spp. feed on reptilian populations in Southern United States of America, both as generalist or specialized feeders, and they may harbor arboviruses (Burkett-Cadena et al., 2008). Similarly, anophelines are indiscriminate blood feeders of mammals, birds, reptiles and humans, a behavior that is determined by the potential host abundance, their anthropophilic attitude (Bashar et al., 2012), searching patterns, access to hosts and environmental characteristics (Silva-Santos et al., 2019). For instance, host richness and habitat have a bold effect on the distribution and abundance of *Culex peccator* and *Culex territans* mosquitoes, which are blood feeders of reptiles and amphibians (Burkett-Cadena et al., 2013). Reports of mosquito-borne pathogens in reptile populations around the world raise concern on the potential role as reservoirs or overwintering hosts in both endemic and exotic regions (Table 3).

3. Zoonotic vector-borne pathogens associated to reptiles

Reptiles may harbor a myriad of organisms, such as parasites, bacteria, fungi, protozoa and viruses, many being innocuous to them. Hence, reptiles may act as hosts of zoonotic pathogens associated to Acarina subclass (i.e., mites and ticks) or Diptera (i.e., mosquitoes and sand flies) (Václav et al., 2011; Ebani, 2017; Mendoza-Roldan et al., 2020b). Those microorganisms that cause RVBDs can be separated accordingly, being bacteria mainly associated to Acarina, viruses to Diptera and protozoa to both groups of vectors (Mendoza-Roldan et al., 2021a).

3.1. Bacteria

Within the vector-borne bacteria that are, in certain way, associated to reptiles, those of zoonotic importance belong to the genera *Aeromonas*, *Anaplasma*, *Borrelia*, *Coxiella*, *Ehrlichia* and *Rickettsia* (Table 1). In addition, there is a single report of *Bartonella henselae* or a species genetically related to *Bartonella vinsonii* subsp. *berkhoffii* in marine turtles (Valentine et al., 2007).

3.1.1. *Aeromonas*

This genus of bacteria is an important pathogen for reptiles and transmission to humans is mainly water-borne (i.e., through contact of wounds and/or ingestion with contaminated water or reptile meat, and wounds produced by reptiles in contact or living in contaminated water) (Lupescu and Baraitareanu, 2015; Ebani et al., 2008; Miranda et al., 2017). However, macronyssid mites *O. natrixis* (Fig. 1b) can be mechanical vectors of *Aeromonas hydrophila*, mainly in snakes (Camin, 1984; Jacobson et al., 2007; Lupescu and Baraitareanu, 2015). Reptiles develop systemic disease due to *Aeromonas* spp., therefore they are not effective reservoirs for these bacteria. Generally, infection occurs after mechanic transmission events such as, trauma, secondary infection of abscesses, mite infestation or stress due to suboptimal environmental conditions (Lupescu and Baraitareanu, 2015; Thomas et al., 2020). Infection in reptiles may induce systemic disease (i.e., stomatitis, sepsis, pneumonia) or be asymptomatic, acting *A. hydrophila* as an opportunistic pathogen (Jacobson et al., 2007). Zoonotic vector-borne risk of infection of *A. hydrophila* from reptiles is given from previous reports of *O. natrixis* mites infesting humans (Schultz, 1975; Amanatfard et al.,

2014), causing gastrointestinal symptoms, such as diarrhea, emesis and abdominal pain (Lupescu and Baraitreanu, 2015).

3.1.2. *Anaplasma* and *Ehrlichia*

The genus *Anaplasma* comprises species of pathogenic bacteria mainly transmitted by ticks. These Gram-negative bacteria replicate in vertebrate and invertebrate hosts, and can cause severe symptoms and even death in animals, including humans (Crosby et al., 2021). Among these potentially fatal bacteria, the most important is *Anaplasma phagocytophilum*, the causative agent of granulocytic anaplasmosis (GA) (Nieto et al., 2009). Although main vectors of this pathogen (i.e., *I. pacificus* in the Nearctic and *I. ricinus* in the Palearctic) occasionally feed on reptiles, especially in their immature stages (i.e., larvae and nymphs), studies have shown that reptiles (i.e., lizards and snakes) play a minor role as reservoirs of GA (Nieto et al., 2009). In addition, *Anaplasma* spp. have been molecularly identified in tick species associated to reptiles to a certain level (e.g., *I. ricinus* in central and western Europe and *H. aegyptium* in eastern Europe; Václav et al., 2011; Tjisse-Klasen et al., 2010; Paştiu et al., 2012). Other tick species strictly associated with reptiles such as *Amblyomma flavomaculatum* (known as yellow-spotted monitor lizard tick from Ghana) and *Amblyomma varanense* (the Asian monitor lizard tick from Indonesia) were also detected positive for *Anaplasma* spp. (Nowak et al., 2010; Takano et al., 2019). These *Anaplasma* spp. were genetically similar to species affecting cattle (e.g., *Anaplasma marginale* and *Anaplasma bovis*), or *A. phagocytophilum*. Considering that reptiles are widely traded in the international pet market, it is pivotal to monitor imported animals to avoid the spreading of these pathogens and their vectors (Mihalca, 2015; Bezerra-Santos et al., 2021a, 2021b).

Recently, other groups of *Anaplasmataceae* have been detected from reptiles or their ectoparasites, such as *Candidatus Anaplasma testudines* detected in *Gopherus polyphemus* tortoises in Florida, United States (Crosby et al., 2021). In addition, *Candidatus Cryptoplasma* sp. REP was described from *Lacerta viridis* lizards and *I. ricinus* ticks in Slovakia (Kočíková et al., 2018), and *Podarcis* spp. and *I. ricinus* ticks from Italy (Mendoza-Roldan et al., 2021b). Both of these species of bacteria have an unknown pathogenicity, yet *Candidatus Anaplasma testudines* seems to be pathogenic to its natural reservoir. In addition, *Ehrlichia* spp. have been detected in different Acarina ectoparasites of reptiles worldwide. *Ehrlichia ruminantium*, the causative agent of heartwater disease, common to ruminants and that can occasionally infect humans, has been reported in *Amblyomma sparsum* from leopard tortoises imported into the United States from Zambia (Peter et al., 2002; Omondi et al., 2017), *Ehrlichia chaffeensis* and *Candidatus Neoehrlichia mikurensis* were detected in *Amblyomma* spp. from reptiles imported to Japan (Andoh et al., 2015). Possible new species of *Ehrlichia* were detected in *Amblyomma* spp. from sea snakes and tortoises also from Japan, closely related to *Candidatus Ehrlichia occidentalis*. Recent studies highlighted that the diversity of ehrlichial agents might be underestimated and the pathogenicity remains still unknown (Qiu et al., 2021). Other ehrlichial agents were detected from *H. aegyptium* ticks from Palearctic tortoises in Romania, *I. ricinus* ticks from lizards of Italy and *Amblyomma* spp. from snakes of Malaysia (Paştiu et al., 2012; Kho et al., 2015; Mendoza-Roldan et al., 2021b), which further indicates that the diversity of ehrlichial microorganisms infecting reptiles is presently underestimated in their pathogenicity, distribution and evolution.

3.1.3. *Borrelia*

Borrelia are spirochete bacteria divided in the relapsing fever, the reptilian *Borrelia*, monotreme associated *Borrelia*, and the Lyme borreliosis groups. This latter group englobes around 20 species within the *B. burgdorferi* sensu lato complex, nine of which can be pathogenic to animals and humans (Majláthová et al., 2008; Mendoza-Roldan et al., 2019). Lyme disease and other borrelioses include species such as *Borrelia lusitaniae*, a species pathogenic to humans, that has reptiles as natural reservoirs. Ticks of the genus *Ixodes* (e.g., *I. ricinus*, *I. pacificus*,

Ixodes persulcatus and *Ixodes scapularis*) are vectors of these bacteria (Kuo et al., 2000; Szekeres et al., 2016; MacDonald et al., 2017; Mendoza-Roldan et al., 2019). Moreover, Lyme disease species are likely associated to lacertid lizards, being natural reservoirs (Majláthová et al., 2006, 2008; Mendoza-Roldan et al., 2019), or refractory to the infection (e.g., species of lizards in the United States) by means of complement-mediated killing effect (Kuo et al., 2000). Similarly, some species of lacertid lizards seem to be incompetent hosts for many pathogenic *Borrelia* spp. in Europe (i.e., *Lacerta* spp.), due to borrellicidal effect of blood components that can reduce the bacterial load in infected ticks. Thus, some species of lizards, in specific epidemiological contexts, might reduce the prevalence of borrelial bacteria resulting in a zooprophylactic effect or reducing the vectors that can feed on competent hosts (Tjisse-Klasen et al., 2010). Additionally, a separate clade of reptile-associated *Borrelia*, with no demonstrated pathogenicity, has been detected in Turkey, Mexico, Japan, and Australia from reptiles (i.e., varanid lizards, snakes and tortoises) and ticks (i.e., *Amblyomma* spp., *Bothriocroton* spp., *H. aegyptium*) (Güner et al., 2003; Takano et al., 2010; Panetta et al., 2017; Morales-Diaz et al., 2020; Colunga-Salas et al., 2020). This group of borrelial agents, and also those from the relapsing fever group, have been detected in imported reptiles to non-endemic areas together with their ticks, highlighting the need of quarantine and control measures (Takano et al., 2010; Colunga-Salas et al., 2020). The origin of these distinct groups of *Borrelia* is still not clear, though phylogenetic analyses showed that the reptilian *Borrelia* spp. diverged from a common ancestor of relapsing fever *Borrelia* (Takano et al., 2010). Conversely, main clades of *Borrelia* (i.e., Lyme disease and relapsing fever) are thought to have co-evolved when Ixodidae and Argasidae ticks diverged. Given that reptile-*Borrelia* group is associated with ixodid ticks, current hypothesis suggest that a switching event could have occurred, either by host or vector switching (Charleston and Perkins, 2003). In addition, since ticks from both families may occur in sympatry on the same species of reptile host, it is likely that co-feeding and vector-switching events could have happened in the past, thus originating this reptile-associated monophyletic group.

3.1.4. *Coxiella*

Coxiella is a genus of obligatory intracellular Gram-negative bacteria, with only one species described (i.e., *Coxiella burnetii*), the causative agent of zoonotic Q fever (Johnson-Delaney, 1996; Siroký et al., 2010). Reptiles and their ticks can act as reservoirs, as for example *H. aegyptium* tick which parasitizes Mediterranean chelonians (Siroký et al., 2010; Paştiu et al., 2012). Other reptilian ticks have been recorded as vectors of *C. burnetii*, such as *Amblyomma exornatum* from Guinea Bissau (Arthur, 1962) and *Amblyomma variegatum* in Africa (Giroud, 1951). Importantly, an outbreak of Q fever was described in New York, USA in people that had contact with imported *Python regius* snakes parasitized with *Amblyomma nuttalli* from Ghana (Kim et al., 1978). Nonetheless, *Coxiella* has been found to be a common symbiont of ticks (Machado-Ferreira et al., 2016; Špitalská et al., 2018).

3.1.5. *Rickettsia*

Rickettsia are Gram-negative, aerobic and obligate intracellular bacteria which multiply by binary fission and are associated with invertebrate vectors (Parola et al., 2005). As mentioned before, reptiles participate directly in the epidemiology of some pathogens of both the Rickettsiales order and the Rickettsiaceae family (Andoh et al., 2015; Novakova et al., 2015). A representative species of *Rickettsia* of the ancestral group, commonly associated to ticks of ectothermic tetrapods in the Americas, is *Rickettsia bellii* (Barbieri et al., 2012; Andoh et al., 2015; Ogrzewalska et al., 2019; Mendoza-Roldan et al., 2021a). This basal clade, seems to have originated from herbivorous arthropods or non-blood feeding hosts, suggesting a horizontal transmission. Indeed, the *R. bellii* clade is currently linked to arthropod vectors (i.e., ticks) and rarely or unlikely infects vertebrate hosts, thus, demonstrating the cryptic position of this group, and that the vector capacity originated in

the transitional group of *Rickettsia* (e.g., *Rickettsia akari* and *Rickettsia australis*) (Weinert et al., 2009). While the pathogenicity of *R. bellii* to vertebrate hosts is still unknown, most of the *Rickettsia* species of zoonotic concern, associated to reptiles, are englobed in the Spotted Fever Group (SFG). For example, *Rickettsia honei*, the causative agent of Flinders Island spotted fever, was first described from *Bothriocroton hydrosauri* from lizards and snakes (Stenos et al., 2003; Whiley et al., 2016). Other eight species of SFG *Rickettsia* have been detected in ectoparasites and in reptiles, such as a rickettsial disease in humans, known as African Fever, caused by *Rickettsia africae* and transmitted by *A. variegatum* (Parola et al., 1999). This rickettsial disease has been detected in ticks infesting reptiles imported into North America (Burrige and Simmons, 2003). Moreover, a species similar to *Rickettsia anan* was detected in *A. exornatum* ticks in varanid lizards imported to the USA (Reeves, 2006). In Europe, SFG *Rickettsia* are represented in reptiles by species such as *Rickettsia helvetica* and *Rickettsia monacensis* detected in ticks, such as *I. ricinus* (Fig. 1a) and in blood and tail of lacertid lizards (Mendoza-Roldan et al., 2021b). Other rickettsial species reported in ticks, and in some cases mites, from reptiles are *Rickettsia aeschlimannii*, *Rickettsia amblyommatis*, *Rickettsia hoogstraalii*, *Rickettsia massiliae*, *Rickettsia raoultii*, *Rickettsia rhipicephali*, *Rickettsia tamurae* and *Rickettsia typhi* (Sánchez-Montes et al., 2019). Genera of ticks that have been found infected with *Rickettsia* spp. are *Amblyomma*, *Bothriocroton*, *Dermacentor*, *Haemaphysalis*, *Hyalomma*, and *Ixodes*. On the other hand, mite species recorded positive to *Rickettsia* spp. belong to the families Ixodidae, Macronyssidae, Pterygosomatidae and Trombiculidae (Sánchez-Montes et al., 2019; Mendoza-Roldan et al., 2021a). Molecular diagnosis of *Rickettsia* spp. in reptile tissues has been achieved only in Europe in lacertid lizards from the genus *Lacerta* (e.g., *L. agilis* and *L. viridis*) and *Podarcis* (e.g., *Podarcis muralis* and *Podarcis siculus*) (Sánchez-Montes et al., 2019; Mendoza-Roldan et al., 2021b). An important role of reptiles in the epidemiology of rickettsial agents is given by the international reptile trade, where reptiles are imported with their ectoparasites harboring *Rickettsia* spp. (Burrige and Simmons, 2003; Pietzsch et al., 2006; Mihalca, 2015; Barradas et al., 2020; Bezerra-Santos et al., 2021a, 2021b). In fact, given that some tick species that usually parasitize reptiles can also infest humans, the risk of emergence of rickettsial agents in non-endemic areas exists (Norval et al., 2020).

3.2. Protozoa

Vector-borne protozoa associated to reptiles are represented by hemoparasites (i.e., plasmodiids, hemogregarines, and trypanosomatid flagellates), which have a greater diversity than those of mammals and birds. The higher diversity in species associated to reptiles could be due to their isolation and the ancestral features of ectothermic tetrapods (Telford, 2009). Nonetheless, those of zoonotic concern associated to reptiles belong solely to the family Trypanosomatidae (Poinar and Poinar, 2004a). Importantly, *Trypanosoma brucei*, the causative agent of sleeping sickness, was detected in monitor lizards from Kenya (Njagu et al., 1999). Incidentally, this group of lizards has been pointed out as wild hosts for the tsetse fly (*Glossina fuscipes fuscipes*) in Uganda (Waiswa et al., 2003). Accordingly, experimental evidence suggests that reptiles could be potential reservoirs of this protozoa (Woo et al., 1969). Furthermore, reptile associated *Trypanosoma* spp., especially from snakes, may be vectored by sand flies (Viola et al., 2008). Also, studies indicate that vector-borne Trypanosomatidae represented in the genus *Paleoleishmania* originated in the early Cretaceous. This genus was found in sand flies from Cretaceous Burmese amber (Poinar and Poinar, 2004a). Other *Paleoleishmania* species were described from extinct species of sand flies (i.e., *Lutzomyia adiketis*) from Dominican amber (Poinar, 2008). In addition, *Palaeomyia burmitis* was also identified with different stages of a leishmanial trypanosomatid, which had nucleated blood cells of reptilian origin (Poinar and Poinar, 2004b). Despite evidence of *Leishmania* divergence in the Cretaceous, it is still not clear

whether this genus originated from the New or Old World, yet, most likely trypanosomatids may have originated in different localities and at different time points over the past 100 million years (Poinar, 2008). More importantly, different hypothesis suggest that *Leishmania* spp. spread through the forming continents following the migration of vectors and their hosts. Also, it is hypothesized that definitive hosts of primitive *Leishmania* most likely were reptiles or primitive mammals (Tuon et al., 2008). The species of *Leishmania* that infect reptiles belong to the subclade *Sauroleishmania*, which is a sister group of the pathogenic species of mammalian *Leishmania*, with around 10 species infecting reptiles (Ovezmukammedov, 1991). Phylogenetic inference supports the origin of lizard *Leishmania* from parasites of mammals (Klatt et al., 2019). Thus, species of *Leishmania* typical of reptiles could transiently infect mammals and vice versa. For example, *Leishmania adleri* from lacertid lizards may produce cutaneous leishmaniasis in mammals (Manson-Bahr and Heisch, 1961; Coughlan et al., 2017). Also, *Leishmania tarentolae* from geckoes has been molecularly detected in human mummies from Brazil (Novo et al., 2015), and human blood from Italy (Pombi et al., 2020). Additionally, *S. minuta* (Fig. 1c), the putative vector of this *Leishmania* sp., has been recently detected feeding from humans, also in Italy (Table 2) (Abbate et al., 2020). The role of *L. tarentolae* infection in protecting mammals against other pathogenic *Leishmania* spp. needs to be further investigated also considering the promising results of preliminary heterologous vaccination attempts (Klatt et al., 2019). On the other hand, reptiles could also act as reservoirs of pathogenic *Leishmania* spp. in areas where primary hosts do not occur or where reptiles and typical hosts live in sympatry. Recent studies have detected pathogenic *Leishmania*, such as *L. tropica*, *L. donovani* and *L. turanica* in lizards and snakes in northwestern China (Zhang et al., 2019; Chen et al., 2019). Given all of the above, future studies should focus on the role reptiles could have in the epidemiology of leishmaniasis and trypanosomiasis.

3.3. Viruses

Reptiles and amphibians may have an important role as reservoirs or overwintering hosts for viruses, mainly arboviruses. Many species of mosquitoes may feed on reptiles, including medically important anthropophilic species such as *Aedes aegypti* and *Aedes albopictus* (Fig. 1d; 2d) (Bosco-Lauth et al., 2018). In addition, most groups of reptiles (i.e., Testudines, Squamata, Crocodylia) have been found serologically and molecularly positive for various arboviruses (Steinman et al., 2003). In fact, many reptile species are considered reservoirs for other arboviruses such as western and eastern equine encephalites, Venezuelan equine encephalitis, West Nile Virus, and most recently Chikungunya virus (Burton et al., 1966; Bingham et al., 2012; Bosco-Lauth et al., 2018). Moreover, given the convergent evolution of hematophagous Diptera and terrestrial vertebrates, blood meal identification has proven that arbovirus vectors may predominantly feed on reptiles (Cupp et al., 2004; Burkett-Cadena et al., 2008). Importantly, *Culex tarsalis* mosquitoes may feed on reptiles such as the garter snake, that can maintain the virus of the western equine encephalitis during winter, and then infect other hosts. Thus, snakes maintain the virus during brumation (overwintering). Other viruses that are related to reptiles are the Japanese encephalitis and Zika viruses (Thomas and Eklund, 1962; Oya et al., 1983; Bueno et al., 2016). Furthermore, reptiles could be involved to a lesser extent in the maintenance of Rift Valley fever phlebovirus (Rissmann et al., 2020). Other phleboviruses have been identified in the herpetophilic sand fly *S. minuta* in France, such as the Toscana virus (Table 3) (Charrel et al., 2006).

Finally, *Testudo* tortoises may serve as primary hosts of *H. aegyptium* ticks, that have been found as competent vectors of Crimean-Congo hemorrhagic fever (CCHF). This disease is caused by a zoonotic *Bunyavirales* that is distributed through Africa, the Balkans, the Middle East, and Western Asia (Kar et al., 2020). While the primary transmission cycle of CCHF is guaranteed by birds, mammals and associated

Hyalomma marginatum ticks in the western Palearctic, tortoises, along with *H. aegyptium* tick vectors, play a role in the cryptic transmission cycle (Široký et al., 2014; Kar et al., 2020).

4. Conclusions

Studying RVBDs of zoonotic concern may aid to elucidate the origins of modern VBDs (i.e., bacteria, protozoa, viruses). Arthropod vectors associated to reptiles belong to two groups, Acarina subclade (i.e., mites and ticks) and Diptera order (i.e., mosquitoes, sand flies and tsetse flies). The evolution of the hematophagous behavior of these invertebrates is strictly linked to ectothermic tetrapods whereas the origin of VBDs may be dated back to the early Cretaceous, at least for protozoan parasites. Bacterial RVBDs are represented by genera that commonly affect also mammals (e.g., *Aeromonas*, *Anaplasma*, *Borrelia*, *Coxiella*, *Ehrlichia* and *Rickettsia*), most of which have a clade associated to reptiles. Protozoan hemoparasites of reptiles of zoonotic concern belong to the family Trypanosomatidae and their origin is related to reptiles and other cretaceous creatures with nucleated erythrocytes. Although some zoonotic species of *Leishmania* and *Trypanosoma* may infect reptiles, their role as reservoirs and hosts has not been fully elucidated. On the other hand, reptiles may be of relevance as primary hosts of viruses, especially arboviruses, or for their maintenance (e.g., overwintering), given the low host specificity of anthrophilic mosquitoes and sand flies.

Moreover, the COVID-19 pandemic has highlighted the role that wildlife can have in the emergence of new zoonotic diseases given the anthropic pressure on forested populations of animals, including reptiles. Certainly, future studies on RVBDs are advocated to reveal the role of reptiles in different epidemiological contexts and geographical areas, thus reducing the risk of zoonotic transmission through proper control and preventative measures.

Declaration of interests

We undersigned Authors of the manuscript entitled “Reptile vector-borne diseases and the origin of zoonoses” declare to have no any competing interests.

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