Review

Reptile vector-borne diseases of zoonotic concern

Jairo Alfonso Mendoza-Roldan a, Miguel Angel Mendoza-Roldan b, Domenico Otranto a,c,*

a Department of Veterinary Medicine, University of Bari, Valenzano, Italy
b Independent Veterinarian, Mar y tierra, Agost, Alicante, Spain
c Department of Pathobiology, Faculty of Veterinary Science, Bu-Ali Sina University, Hamedan, Iran

ARTICLE INFO

Keywords:
Reptiles
Vectors
Mites
Ticks
Mosquitoes
Sand flies
Bacteria
Leishmania
Trypanosoma
Arboviruses
Evolution

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 phylogenic 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 tuatars (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 (Wieczerzk et al., 2020). Conversely, other parasitic arthropods (e.g., Ophionyxus naticis mites in snakes) may have a pronounced deleterious effect on their hosts, when there is a high parasitic load (Fuentes-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 (Prakash et al., 2020). For
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., 2020h, 2021a). In particular, knowledge on ectoparasites of reptiles mainly derive from ecological and biological studies (Mihala, 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 reptiles 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 (Peitalver 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 et al., 2008; Mendoza-Roldan et al., 2019a). In particular, knowledge on ectoparasites of reptiles already had diverged since the Cretaceous period (Poinar et al., 2008; Mendoza-Roldan et al., 2019a) and spotted fever group *Rickettsia* spp. (Fig. 2a) (Mendoza-Roldan et al., 2021b). This is the case of *I. ricinus* ticks feeding on lizards and associated to *Borrelia burgdorferi* sensu lato (Fig. 1a) (Majlathová 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 large parasites (Ixodida and Macronyssidae) choosing areas that are

![Fig. 1. Arthropod vectors associated to reptiles represented by a Podarcis siculus lizard and Tarantula mauritanica gecko and zoonotic pathogens they may transmit. a) *Ixodes ricinus* tick larva, b) *Ophionyssus natricis* mite, c) *Serpentomyia 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 negligible 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.)](https://example.com/fig1)

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; Munoz-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* (*Microargus*) *transversus* (Argasidae) from *Chelonia* *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 (Fielen 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 Facetti, 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, dysecdyosis), 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) (Majlathová 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
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 Trombidiiformes (Acariformes) and Mesostigmata. With seven families and more than 30 genera infesting reptiles and amphibians (Zhang et al., 2011; Rezende et al., 2012), the Trombidiiformes 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 Trombidiiformes 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 Trombidiiformes order (Trombiculidae and Pterygosomatidae) (Mendoza-Roldan et al., 2020b). Examples of mite vectors of pathogens are represented in both the Trombidiiformes and Mesostigmata orders (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-Ailla 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 Neartic region, and I. ricinus in the Palearctic region (Mendoza-Roldan et al., 2019). Conversely, B. burgdorferi sensu lato in the Neotropic 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 (Păuştiu et al., 2012).

2.2. Sand flies

Similar to other arthropod vectors mentioned above, sand flies (Diptera: Psychodidae) 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 (Helcocyrtomyia) 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 trypanosomatid 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 spp. to humans (Ready, 2013). The protozoan Leishmania has highjacked 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 (Kilkenny-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 (Shahbosseini 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**        | *Eutrombicula alfredugesi* | Snakes | Brazil | *Rickettsia* sp. | Mendoza-Roldan et al. (2021a) |
| *Geohelioptes harrisi* | Lizards | Brazil | *Rickettsia* sp. | Mendoza-Roldan et al. (2021a) |
| *Ophiogypalia rotundata* | Snakes | Brazil | *Rickettsia* sp. | Mendoza-Roldan et al. (2021a) |
| *Neotrombicula autumnalis* | Snakes | United States | *Aeromonas* hydrophila | Mendoza-Roldan et al. (2021b) |
| *Oribatidae* | Lizards | Brazil | *Rickettsia* sp. | Mendoza-Roldan et al. (2021a) |
| *Amblyomma chabaudi* | Tortoises | Madagascar | *Rickettsia africana* | Sanchez et al. (2019) |
| *Amblyomma clypeolatum* | Tortoises | Japan | *Rickettsia* sp. | Andoh et al. (2015) |
| *Amblyomma dissimile* | Freshwater turtles | Colombia | *Rickettsia* sp. | Santodomingo et al. (2018) |
| *Amblyomma exornatum* | Snakes | Mexico | *Rickettsia* sp. | Sanchez et al. (2019) |
| *Amblyomma flavescens* | Lizards | Japan | *Borelia* sp. | Tsakan et al. (2010) |
| *Amblyomma georgii* | Tortoises | Honduras | *Rickettsia* sp. strain Colombiansensi | Novakova et al. (2015) |
| *Amblyomma helvomus* | Monitor lizards | Guinea Bissau | Castella burnettii | Arthur (1962) |
| *Amblyomma latum* | Snakes | Japan | *Ehrlichia* sp. | Mihalca (2015) |
| *Amblyomma milleri* | Lizards | United Kingdom | *Ehrlichia* sp. | Andoh et al. (2015) |
| *Amblyomma nutalli* | Snakes | Ghana | *Rickettsia* tamurae | Sanchez et al. (2019) |
| *Amblyomma parvum* | Lizards | Chile | *Anaplasma* phagocytophilum | Mihalca (2015) |
| *Amblyomma rotundatus* | Snakes | Brazil | *Rickettsia* aeschlimannii-like | Qiu et al. (2021) |
| *Amblyomma saharianae* | Freshwater turtles | United States | *Ehrlichia* sp. | Sanchez et al. (2019) |
| *Amblyomma spumigena* | Tortoises | Zambia | *Ehrlichia chaffeensis* | Andoh et al. (2015) |
| *Amblyomma transversale* | Snakes | Ghana | *Rickettsia* hoogstraalii | Sanchez et al. (2019) |
| *Amblyomma trivittatum* | Snakes | Japan | *Ehrlichia* sp. | Qiu et al. (2021) |
| *Amblyomma varanensis* | Monitor lizards | Indonesia | *Rickettsia* ehrlichiae | Takano et al. (2019) |
| *Amblyomma variegatum* | Reptiles | Congo | *C. burnetii* | Giroud (1951) |
| *Bohrnocrotalus hydrosaurus* | Lizards | Australia | *Rickettsia honei* | Whiley et al. (2016) |
| *Bohrnocrotalus undulatus* | Snakes | Snakes | *Rickettsia amblyomma* | Mendoza-Roldan et al. (2021a) |
| *Haemaphysalis maculata* | Lizards | Australia | *Rickettsia helvetica* | Sanchez et al. (2019) |
| *Hyalomma aegyptium* | Tortoises | Middle East | *Rickettsia* aeschlimannii | Sanchez et al. (2019) |
| *Ixodes ricinus* | Lizards | Turkey | *C. burnetii* | Sirolky et al. (2010) |
| *Ixodes pacificus* | Lizards | United States | *A. phagocytophilum* | Paegtiu et al., 2012 |
| *Ornithodoros moubata* | Tortoises | North America | *Rickettsia* africana | Estrada-Pena and Jongejan (1999) |
| *Ornithodoros turicata* | Tortoises | Africa | *Borrelia burgdorferi* (sensu lato) | Kuo et al. (2000) |
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). However, macronyssid mites *O. natricis* (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 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., 2011; Ebani et al., 2017; Mendoza-Roldan et al., 2020b). 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. natricis* mites infesting humans (Schultz, 1975; Amanatfard et al., 2010).

### Table 2

| Mosquito species | Host | Country | Zoonotic pathogen | Reference |
|-----------------|------|---------|-------------------|-----------|
| *Aedes albopictus* | Squamata reptiles | Cuba | Zika virus | Gutiérrez-Bugallo et al. (2019) |
| *Aedes aegypti* | Snakes | USA | Eastern equine encephalitis virus (EEEV) | Graham et al. (2012) |
| *Aedes notoscriptus* | Snakes | USA | Chikungunya virus | Bosco-Lauth et al. (2018) |
| *Aedes vexans* | Snakes | USA | Chikungunya virus | Bosco-Lauth et al. (2018) |
| *Culex tarsalis* | Snakes | USA | Western equine encephalitis (WEE) | Thomas and Eklund (1962) |
| *Culex quinquefasciatus* | Snakes | USA | West Nile Virus | Steinman et al. (2003) |
| *Culex peccator* | Snakes | USA | Rift Valley fever phlebovirus (RVFV) | Rissmann et al. (2019) |

### Table 3

| Mosquito species | Host | Country | Disease | Reference |
|-----------------|------|---------|---------|-----------|
| *Phlebotomus chinensis* | Lizards | China | Leishmania tropica | Zhang et al. (2019) |
| *Phlebotomus longicidatus* | Lizards | China | Leishmania tropica | Zhang et al. (2019) |
| *Phlebotomus wui* | Lizards | China | Leishmania tropica | Zhang et al. (2019) |
| *Phlebotomus alexandri* | Lizards | China | Leishmania tropica | Zhang et al. (2019) |
| *Phlebotomus dubei* | Lizards | Kenya | Leishmania tropica | Zhang et al. (2019) |
| *Phlebotomus kuzaren* | Lizards | Pakistan | Leishmania tropica | Zhang et al. (2019) |
| *Phlebotomus perniciosus* | Humans | Italy | Leishmania tropica | Zhang et al. (2019) |
| *Sergentomyia minuta* | Humans | France | Leishmania tropica | Zhang et al. (2019) |
| *Sergentomyia (Sergentomyia) dentata* | Lizards | Iran | L. adleri | Maleki-Ravasan et al. (2008) |
| *Sergentomyia sp.* | Lizards | Worldwide | Sauroleishmania spp. | Lozano-Sardana et al. (2018) |
causing gastrointestinal symptoms, such as diarrhea, emesis and abdominal pain (Lupescu and Baraitareanu, 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 (Croisy 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 Paleartic) 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 (i.e., *I. ricinus* in central and western Europe and *H. aegyptium* in eastern Europe; Václav et al., 2011; Tijjse-Klaasen et al., 2010; Pašti 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 varonense* (the Asian monitor lizard tick from Indonesia) were also detected positive for *Anaplasma* spp. (Novak et al., 2010; Takano et al., 2019). These *Anaplasma* spp. were genetically similar to species affecting cattle (e.g., *Anaplasma marginale* and *Anaplaspa 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 Anaplaspa* testudinas detected in *Gopherus polyphemus* tortoises in Florida, United States (Croisy et al., 2021). In addition, *Candidatus Cryptplasma* sp. REP was described from *Lacerta viridis* lizards and *I. ricinus* ticks in Slovakia (Kociková 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 Anaplaspa* testudinas 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 (Qi et al., 2021a). Other ehrlichial agents were detected from *H. aegyptium* ticks from Paleartic tortoises in Romania, *I. ricinus* ticks from lizards of Italy and *Amblyomma* spp. from snakes of Malaysia (Pašti 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*, monotype 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 borrelicidal 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 zoo prophylactic effect or reducing the vectors that can feed on competent hosts (Tijjse-Klaasen 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., *Bathrocroron* spp., *H. aegyptium*) (Günler et al., 2003; Takano et al., 2010; Panetta et al., 2017; Morales-Díaz et al., 2020; Colunga-Salas et al., 2020). This group of borreliais, 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; Siroky et al., 2010). Reptiles and their ticks can act as reservoirs, as for example *H. aegyptium* tick which parasitizes Mediterranean cheloniens (Siroky et al., 2010; Pašti et al., 2012). Other ehrlichial ticks have been recorded as vectors of *C. burnetii*, such as *Amblyomma exsorum* 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; Spitalka 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 the ancestral group, commonly associated to ticks of ectothermic tetrapods in the Americas, is *Rickettsia bellii* (Barbieri et al., 2011; Andoh et al., 2015; Ogzewalska 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 sousi* from lizards and snakes (Stenos et al., 2003; Whiteley 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 africana* and transmitted by *A. variegatum* (Parola et al., 1999). This rickettsial disease has been detected in ticks infesting reptiles imported into North America (Burridge 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., 2021a). Other rickettsial species reported in ticks, and in some cases mice, from reptiles are *Rickettsia aeschlimanni*, *Rickettsia amblyommatis*, *Rickettsia hoogstraali*, *Rickettsia massiliae*, *Rickettsia raoultii*, *Rickettsia rhizophilah*, *Rickettsia tamarae* and *Rickettsia typhi* (Sánchez-Montes et al., 2019). Genera of ticks that have been found infected with *Rickettsia* spp. are *Amblyomma*, *Boothicrotroton*, *Dermacentor*, *Haemaphysalis*, *Hyalomma*, and *Ixodes*. On the other hand, mite species recorded positive to *Rickettsia* spp. belong to the families *Ixodoryhynchidae*, *Macroonyssidae*, *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 *Lucerta* (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. (Burridge 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 their isolation and the ancestral features of ectothermic tetrapods are given by the international reptile trade, where reptiles are imported from lizards and snakes (Stenos et al., 2003; Whiley et al., 2016). Other species of *SFG* *Plasmodium* have been identified in ticks infesting reptiles imported into North America (Burridge and Simmons, 2003). This protozoa is the causative agent of Trypanosoma cruzi and transmitted by *A. variegatum* (Parola et al., 1999). Importantly, *Trypanosoma cruzi*, the causative agent of sleeping sickness, was detected in monitor lizards from Kenya (Njagu et al., 2003). Incidentally, this group of lizards has been pointed out as wild hosts for the tsetse fly (Chagas et al., 1999). On the other hand, *ectoparasites* need 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. major* 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 encephalitis, 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 trans-mission 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 (Siriý 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 ecotrophic 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, Coxella, 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 creataceous 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 anthropophilic 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 habitat expansion of some “cryptic” species with humans. Changes in the use of land by humans (e.g., fishing, hunting or logging) that lead to habitat expansion (e.g., forests and lakes) have triggered the appearance of new zoonoses. This has relevance for the risk of zoonotic zoonoses emerging from wildlife and the role of reptiles in the marine environment. The evolution of the hematophagous behavior of these invertebrates is strictly linked to ecotrophic tetrapods where 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, Coxella, 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 creataceous 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 anthropophilic 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 habitat expansion of some “cryptic” species with humans. Changes in the use of land by humans (e.g., fishing, hunting or logging) that lead to habitat expansion (e.g., forests and lakes) have triggered the appearance of new zoonoses. This has relevance for the risk of zoonotic zoonoses emerging from wildlife and the role of reptiles in the marine environment.

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.

Acknowledgements

Authors thank Viviana Domenica Tarallo (Dipartimento di Medicina Veterinaria, Università degli Studi di Bari, Italy) for drawings used for figure, and Riccardo Paolo Lia (Dipartimento di Medicina Veterinaria, Università degli Studi di Bari, Italy) for photographing and providing images for Fig. 2. Jairo Mendoza Roldan thanks Research For Innovation – REFIN, Puglia, Italy, for partially funding this review with a grant (25904580).

References

Abbate, J.M., Maia, C., Pereira, A., Arfuso, F., Gago, G., Rizzon, M., Bianchi, E., 2020. Identification of trypanosomatids and blood feeding preferences of phlebotomine sand fly species common in Sicily. Southern Italy. PloS one 15 (3), e0229536.

Akhoundi, M., Kuhl, K., Keft, A., Votýpka, J., Marty, P., Delaunay, P., Serron, D., 2021. A histological and molecular approach for the classification, evolution, and dispersion of Leishmania parasites and sand flies. PloS Neglected Trop. Dis. 10 (3), e0004494.

Alkan, C., Bihuela, L., de Lambarlí, X., Aten, B., Gould, E.A., Charrel, R.N., 2013. Sand-fly borne phleboviruses of Eurasia and Africa: epidemiology, genetic diversity, geographic range, control measures. Antivir. Res. 100 (1), 54–74.

Amanatfard, E., Youssefi, M.R., Barimani, A., 2014. Human dermatitis caused by Amblyomma suberumae ticks in El Salvador. Pathog. Glob. Health 108 (3), 188–189.

Barbieri, A.M., Venzel, J.M., Marcili, A., Almeida, A.P., González, E.M., Labruna, M.B., 2013. Borelia burgdorferi sensu lato infecting ticks of the Ixodes ricinus complex in Uruguay: first report for the Southern Hemisphere. Vector Borne Zoonotic Dis. 13 (4), 147–153.

Barreto, P.B., Mesquita, J.R., Lima, C., Cardoso, L., Albo, A.M., Ferreira, P., Gartner, F., 2020. Pathogenic Rickettsia in ticks of spurge-thighted tortoise (Testudo graeca) sold in a Qatari live animal market. Transbound Emerg Dis 67 (1), 461–465.

Barros-Battesi, D.M., Arzua, M., Bicha, G.H., 2009. Carrapatos de importación neotropical: un guía ilustrado para identificación de especies. In: Carrapatos de importación médico-veterinaria de la región neotropical: un guía ilustrado para identificación de especies. xiv–xxiii.

Benelli, G., Mehlhorn, H., 2016. Declining malaria, rising of dengue and Zika virus: insights for mosquito vector control. Parasitol. Res. 115 (5), 1747–1754, 2016.

Bertrand, M., 2002. Morphologic Adaptations to Parasitism on Reptiles: Pterygosomatidae (Prostigmata: Raphignathina). Acar. Phylogeny and Evolution: Adaptation in Mites and Ticks, pp. 233–240.

Besson-Jato, M.A., Mendoza-Roldan, J.A., Thompson, R., Dantas-Torres, F., Otranto, D., 2021a. Illegal wildlife trade: a gateway to zoonotic infectious diseases. Trends Parasitol. 37 (3), 181–184.

Bessa-et-Santos, M.A., Mendoza-Roldan, J.A., Thompson, R., Dantas-Torres, F., Otranto, D., 2021b. Reptile vector-borne diseases and the origin of zoonoses” declare to have no any competing interests.

Bessen-Jato, M.A., Mendoza-Roldan, J.A., Thompson, R., Dantas-Torres, F., Otranto, D., 2021a. Illegal wildlife trade: a gateway to zoonotic infectious diseases. Trends Parasitol. 37 (3), 181–184.

Bessa-et-Santos, M.A., Mendoza-Roldan, J.A., Thompson, R., Dantas-Torres, F., Otranto, D., 2021b. Legal versus illegal wildlife trade: zoonotic disease risks. Trends Parasitol. 26, S1471–S4922 (2021)0003-1.

Bidder, L.A., Amsussen, K.M., Campbell, S.E., Goffigan, K.A., Gaff, H.D., 2019. Assessing the Chironomus populations of two species, Chironomus plumosus. Trends Parasitol. 37 (10), 1097–1100.

Bosco-Lauth, A.M., Hartwig, A.E., Bowen, R.A., 2018. Reptiles and amphibians as potential reservoir hosts of Chikungunya virus. Am. J. Trop. Med. Hyg. 98 (3), 841–844.

Bower, D.S., Brannelly, L.A., McDonald, C.A., Webb, R.J., Greenpan, S.E., Vickers, M., Gardner, M.G., Greenlee, M.J., 2019. A review of the role of parasites in the ecology of reptiles and amphibians. Austral Ecol. 44 (3), 433–448.

Bueno, M.G., Martinez, N., Abdalla, L., Duarte dos Santos, C.N., Chame, M., 2016. Animals in the Zika virus life cycle: what to expect from megadiverse Latin American countries. PloS Neglected Trop. Dis. 10 (12), e0005073.

Burton, A.N., McIntosh, J., Rempel, J.G., 1966. Western equine encephalitis virus in Soviet Union, 1944: a tick-borne neurotropic agent. Nature 179 (4584), 97–99.

Charrel, R.N., Izri, A., Labruna, M.B., 2018. Ticks in the Americas: an intergeneric and species taxonomic review. Trends Parasitol. 34 (10), 841–844.

Chilton, N.B., Bull, C.M., Andrews, R.H., 1992. Differences in attachment site of the tick Amblyomma cajennense (Acari: Ixodidae) on two host species. J. Parasitol. 78 (4), 676–680.

Chow, H., Li, J., Zhang, J., Liu, M., Chen, Y., 2019. Multi-locus characterization and phylogenetic inference of Leishmania spp. in ticks from China. Ticks Tick Borne Dis 10 (1), 18–22.

Cochenour, C., Dittmann, D., Otranto, D., 2006. Pathogenic Rickettsia bellii, Rickettsia bellii, Rickettsia bellii, Rickettsia bellii, Rickettsia bellii and Rickettsia bellii infecting ticks of spur-thighed tortoise (Testudo saberi). J. Vet. Med. B. 53 (7), 388–391.

Colunga-Salas, P., Sanchez-Montes, S., Ochoa-Ochoa, L.M., Grostietta, E., Becker, I., 2020. Molecular detection of the reptile-infecting tick group in Amblyomma dissimile, Mexico. Med. Vet. Entomol. https://doi.org/10.1111/ave.12478.
Fuantos-G, A., 1962. Les Acariens Mesostigmatiques parasites des serpents. Bull Royal Sci Nat
Güner, E.S., Hashimoto, N., Kadosaka, T., Imai, Y., Masuzawa, T., 2003. A novel, fast-
Estrada-Peña, A., Jongejan, F., 1999. Ticks feeding on humans: a review of records on
evolution of extant malaria parasites. Mol. Biol. Evol. 25 (10), 2233
Welbourn, C., Barros-Battesti, D.M., 2018. A checklist of chiggers from Brazil,
evolution of Zika virus. Nat. Ecol. Evol. 3 (4), 561
Kuo, M.M., Lane, R.S., Giclas, P.C., 2000. A comparative study of mammalian and
Kho, K.L., Koh, F.X., Tay, S.T., 2015. Molecular evidence of potential novel spotted fever
dog tick
molurus bivittatus
Yarto-Jaramillo, E., Heredia-Cardenas, R., Miranda-Contreras, L., 2020. Successful
human-biting Ixodoidea with special reference to pathogen transmission. Exp. Appl.
capone (Acari: Ixodidae). Exp. Appl. Acarol 46 (5), 351
Jacobson, E.R. (Ed.), 2007. Infectious Diseases and Pathology of Reptiles: Color Atlas and
Text. CRC Press.
Hui, C.K., Wang, W., Zhao, X., Zai, J., Li, X., 2020. Cross-species transmission of the newly
defined coronavirus 2019 (SARS-CoV-2). J. Med. Virol. 92, 1728–1735
Johnson-Delaney, C.A., 1996. Reptile Zoonoses and Threats to Public Health. reptile Medicine
and surgery, pp. 20–33,
Kar, S., Rodríguez-Sánchez, E., Alcázar, C., Cantoral, F., Dark, A., Hernández, H.,
Hashiguchi, Y., 2010. Natural infection of the sand fly Phlebotomus kuzenreni by
Trypanosoma species in Pakistan. Parasites Vectors 25 (3), 10,
Killick-Kendrick, R., Lainon, R., Rioux, J., Saranjovan, V.M., 1986. The taxonomy of Leishmania-like parasites of reptiles. Leishmaniose. Taxonomie et phylogénie. Applications éco-épidémiologiques 143–148.
Kim, S., Guising, S., Harris, D., Keelan, T., Mayer, M.Q., 1978. Q fever.—New York.—Center
for Disease Control MMWR 27, 321–323.
Koikova, B., Majlath, I., Vichova, B., Maliničová, L., Prfatis, P., Connors, V.A.,
Takano, A., Goka, K., Une, Y., Shimada, Y., Fujita, H., Shiino, T., Kawabata, H., 2010. Isolation and characterization of a novel *Borrelia* group of tick-borne borreliae from imported reptiles and their associated ticks. Environ. Microbiol. 12 (1), 134–146.

Takano, A., Kuwata, R., Shimoda, H., Hadi, U.K., Setiyono, A., Agungpriyono, S., Maeda, K., 2019. Detection and isolation of tick-borne bacteria (*Anaplasma* spp., *Rickettsia* spp., and *Borrelia* spp.) in *Amblyomma* varanense ticks on lizard (*Varanus salvator*). Microbiol. Immunol. 63 (8), 328–333.

Telford, S.R., 2009. Hemoparasites of the Reptilia. CRC Press.

Tijsse-Klasen, E., Fonville, M., Reimerink, J.H., Spitzen-van der Sluijs, A., Sprong, H., 2010. Role of sand lizards in the ecology of Lyme and other tick-borne diseases in The Netherlands. Parasites Vectors 3 (1), 1–11.

Tiwari, R., Dhamal, K., Sharun, K., Iqbal Yatoo, M., Malik, Y.S., Singh, R., Rodriguez-Morales, A.J., 2020. COVID-19: animals, veterinary and zoonotic links. Vet. Q. 40 (1), 169–182.

Thomas, L.A., Eklund, C.M., 1962. Overwintering of western equine encephalomyelitis virus in garter snakes experimentally infected by *Culex tarsalis*. Proc Soc Exp Biol Med 109 (2), 421–424.

Thomas, S.G., Glover, M.A., Parthasarathy, A., Wong, N.H., Shipman, P.A., Hudson, A.O., 2020. Expression of a shiga-like toxin during plastic colonization by two multidrug-resistant bacteria, *Arromonas* hydrophila RIT668 and *Citrobacter freundii* RIT669, isolated from endangered turtles (*Clemmys guttata*). Microorganisms 8 (8), 1172.

Torres-Guerrero, E., Quintanilla-Cedillo, M.R., Ruiz-Esmenjaud, J., Arenas, R., 2017. Leishmaniasis: a review. F1000Research 6, 750.

Tucker, E., Benton, J., 1982. Triassic environments, climates and reptile evolution. Palaeogeogr. Palaeoclimatol. Palaeoecol. 40 (4), 361–379.

Tuon, F.F., Amato Neto, V., Sabbaga Amato, V., 2008. *Leishmania*: origin, evolution and future since the Precambrian. EMS Immuno Med Microbiol 54 (2), 158–166.

Václavík, R., Ficová, M., Prokop, P., Betáková, T., 2011. Associations between coinfected prevalence of *Borrelia lusitaniae*, *Anaplasma* sp., and *Rickettsia* sp. in hard ticks feeding on reptile hosts. Microb. Ecol. 61 (2), 245–253.

Valentine, K.H., Harms, C.A., Cadenas, M.B., Birkenheuer, A.J., Marr, H.S., Braun-McNeill, J., Breitschwerdt, E.B., 2007. Bartonella DNA in loggerhead sea turtles. Emerg. Infect. Dis. 13 (6), 949–950.

Viola, L.B., Campaner, M., Takata, C.S., Ferreira, R.C., Rodrigues, A.C., Freitas, R.A.D., Teixeira, M.M.G., 2008. Phylogeny of snake trypanosomes inferred by SSU rDNA sequences, their possible transmission by phlebotomines, and taxonomic appraisal by molecular, cross-infection and morphological analysis. Parasitology 135 (5), 595–605.

Waiswa, C., Picozzi, K., Olaho-Mukani, W., Katunguka-Rwakishaya, E., 2003. Monitor lizard (*Varanus niloticus*, Linnaeus, 1766) as a host for tsetse (*Glossina fusipes* fuscipes, Newstead, 1910) in the sleeping sickness endemic foci of Uganda. Afr. J. Ecol. 41 (4), 349–351.

Weinert, L.A., Werren, J.H., Aebi, A., Stone, G.N., Jiggins, F.M., 2009. Evolution and diversity of *Rickettsia* bacteria. BMC Biol. 7 (1), 1–15.

Whiley, H., Castance, G., Graves, S., Stenton, J., Taylor, M., Ross, K., Gardner, M.G., 2016. *Rickettsia* detected in the reptile tick *Bothriocroton hydroauri* from the lizard *Tiliqua rugosa* in South Australia. Pathogens 5 (2), 41.

Wieczorek, M., Rektor, R., Najbar, B., Morelli, F., 2020. Tick parasitism is associated with home range area in the sand lizard, *Lacerta agilis*. Amphibia-Reptilia 1 (aop), 1–10.

Woo, P., Soltys, M.A., 1969. The experimental infection of reptiles with *Trypanosoma brucei*. Ann. Trop. Med. Parasitol. 63 (1), 35–38.

Zhang, L., Zhang, Y., Adusumilli, S., Liu, L., Narasimhan, S., Dai, J., Zhao, Y.O., Fikrig, E., 2011. Molecular interactions that enable movement of the Lyme disease agent from the tick gut into the hemolymph. PLoS Pathog. 7 (6), e1002079.

Zhang, J.R., Guo, X.G., Chen, H., Liu, J.L., Gong, X., Chen, D.L., Chen, J.P., 2019. Pathogenic *Leishmania* spp. detected in lizards from Northwest China using molecular methods. BMC Vet. Res. 15 (1), 1–13.