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Original article

Rickettsia species in ticks that parasitize amphibians and reptiles: Novel report from Mexico and review of the worldwide record

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ABSTRACT

Ticks are obligate haematophagous ectoparasites that are associated with a wide range of vertebrate hosts, among them also reptiles and amphibians. They have dynamic ecological interactions with multiple microorganisms, ranging from endosymbionts to pathogens, such as the members of the genus *Rickettsia*. The aim of this work was to detect *Rickettsia* in ticks from amphibians and reptiles from southern Mexico by the amplification, sequencing and phylogenetic reconstruction of the *gltA* and *ompA* genes, and also to compile all the published records worldwide of *Rickettsia* associated with ticks attached to reptiles and amphibians, in order to elucidate the host-parasite relationships, and to identify the geographical distribution of each bacterial species.

We record for the first time the presence of *Rickettsia* sp. strain Colombianensi and *Rickettsia amblyommatis* in ticks from several reptiles and amphibians collected in three new localities from the states of Guerrero and Veracruz, Mexico. Additionally, we here report 23 *Rickettsia* taxa associated with 18 tick species attached to 42 host taxa of amphibians and reptiles in 36 countries. Our findings increase the inventory of rickettsia reported in Mexico and summarizes the knowledge of these bacteria associated with ticks of this particular group of vertebrate host worldwide.

1. Introduction

Ticks are obligate haematophagous ectoparasites that are associated with a wide range of vertebrate hosts. More than 900 species are recognized worldwide (210 soft ticks, 707 hard ticks), with a significant increase in recent years of the species described from amphibians and reptiles (Guglielmone et al., 2014; Barros-Battesti et al., 2015; Muñoz-Leal et al., 2016a, 2017). Some tick species have established very close relationships with these vertebrate groups, with a marked preference for amphibians and reptiles, such as *Amblyomma rotundatum* in the Neotropical region or *Bothriocroton hydrosauri* in the Australian region (Smyth, 1973; Guglielmone and Nava, 2010). There are other tick species that are considered parasites of mammals or birds, yet they can also parasitize exceptionally reptiles or amphibians when their natural hosts are not available (e.g. *Amblyomma mixtum* or *Amblyomma maculatum*). In this case however, it is not known whether the change of the host also benefits these species (Estrada-Peña et al., 2005; Nava et al., 2014; Guglielmonne et al. 2014).

Ticks also have dynamic ecological interactions with multiple microorganisms, ranging from endosymbionts to pathogens. A well-studied group of microorganisms associated with ticks are the members of the genus *Rickettsia*. These taxa encompass 30 obligate intracellular

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Table 1
Sampling sites of specimens collected in this study.

State	Locality	Geographic reference	Collection date
Guerrero	Barra de Potosi (BP)	17.537400°-101.442137°	04-09 July, 2015 22 December, 2015
Tabasco	La Florida (LF)	17.462759°-92.770590°	18 November, 2015
	Villahermosa (VI)	18.006182°-92.931791°	31 July, 2016
Veracruz	Cotaxtla (CO)	18.833333°-96.383333°	05 February, 2018
Veracruz	Sontecomapan (SO)	18.490689°-95.064364°	18 May, 2018
Veracruz	Veracruz (VE)	19.171486°-96.210503°	03 November, 2018

coccobacilli, with 15 pathogenic species that can cause acute diseases such as Rocky Mountain spotted fever and *Rickettsia parkeri* rickettsiosis (Shpynov et al., 2018).

In Mexico, eight tick species (two soft ticks [*Ornithodoros talaje*, *Ornithodoros turicata*] and six hard ticks [*Amblyomma dissimile*, *A. mixtum*, *A. rotundatum*, *Amblyomma sabanerae*, *Amblyomma scutatum* and *Robertsicus elaphense*]) were found to be associated naturally with one amphibian species (a toad) and 19 reptiles (seven lizard, six turtle, three snake and three crocodylians species) (Paredes-León et al., 2008; Guzmán-Cornejo et al., 2011; Charruau et al., 2016). Despite the above, the presence and diversity of *Rickettsia* associated with ticks of both vertebrate groups, particularly those species of wide distribution and close to human settlements, have not been studied in Mexico. Furthermore, since the literature related to *Rickettsia* in ticks of amphibians and reptiles is very recent, and most of the studies have been conducted in South America (Muñoz-Leal et al., 2016b; Luz et al., 2018; Santodomingo et al., 2018), the aim of this work was to detect *Rickettsia* in ticks from amphibians and reptiles from southern Mexico, and to compile all the published records worldwide, in order to elucidate the host-parasite relationships, and to identify the geographical distribution of each *Rickettsia* species.

2. Material and methods

As a part of two ongoing projects aimed to identify the diversity of bacterial pathogens and ectoparasites in amphibians and reptiles, 23 hosts parasitized by ticks were enrolled in this study. They belonged to the following species: *Boa constrictor* (common boa), *Iguana iguana* (green iguana), and *Rhinella marina* (cane toad), and were captured in three coastal states of Mexico (Table 1). Animals were physically restrained, identified morphologically at species level using the taxonomic keys of Stebbins (2003), visually inspected for ticks, and finally released in situ. Procedures were carried out under authorization of the Secretaría del Medio Ambiente y Recursos Naturales (SEMARNAT), permit reference FAUT-0250.

Ticks were fixed in absolute ethanol, and identified using the taxonomic keys of Keirans and Durden (1998), and Martins et al. (2014) for nymphs and Guzmán-Cornejo et al. (2011); Nava et al. (2014) and Nava et al. (2017) for adults. Larvae were identified using molecular techniques; for that reason we realized pools of five specimens and amplified a fragment of 400 bp of the 16S-rRNA gene for each cluster (Norris et al., 1996). In order to detect the presence of *Rickettsia*-DNA from ticks, we extracted individually, amplified and sequenced two gene fragments [800 bp of the citrate synthase gene (*gltA*) and 542 bp of the outer membrane protein A gene (*ompA*)] (Regnery et al., 1991; De Sousa et al., 2006), using primers and conditions described elsewhere. We used DNA of *Rickettsia lusitaniae* as positive control, and free nuclease water as negative control (Sánchez-Montes et al., 2016a). The sequences were compared with those deposited in GenBank using the BLAST tool. We determine the identity of the rickettsias detected in this study based on the criteria of Fournier et al. (2003) and Fournier and Raoult (2009) which are based on the degree of nucleotide identity of the genes *gltA* (≥99.9%) and *ompA* (≥98.8) with the most homologous validated species.

In addition, we performed a phylogenetic reconstruction. For this reason, we performed global alignments using the Clustal W algorithm. Subsequently, the best substitution model was selected, based on the lowest value of the Bayesian Information Criterion (BIC). For *Rickettsia* identification, we conducted a phylogenetic reconstruction using the Maximum Likelihood method (ML) with 10,000 bootstrap replications using the close neighbor interchange method in the software Mega 7.0. Gaps were excluded from the analysis.

Additionally, an extensive review of *Rickettsia* identified in ticks from reptiles and amphibians was made in specialized databases (BioOne, Google Scholar, Highwire, Medline, Pubmed, Scielo, Scopus, and Zoological Records), using several combinations of keywords: “tick”, “tick borne-pathogen”, “tick borne-diseases”, “reptiles”, “amphibians” and “*Rickettsia*”.

3. Results

3.1. New records in Mexico

One hundred and sixty-five hard ticks were collected (163 *A. dissimile*, and 2 *A. mixtum*) and screened for *Rickettsia*. All the larvae pools produced a single sequence of the 16S-rRNA gene, which exhibits an identity of 100% with *A. dissimile* sequences deposited in GenBank under accession KY389390.1. Twenty-two hosts of the three inspected species were infested with *A. dissimile,* and a single *I. iguana* exhibited a coinfestation of *A. dissimile* together with *A. mixtum*. Amplicons of the *gltA* gene corresponding to the expected size were detected in 14 ticks, of which one was a female *A. mixtum* and 13 were *A. dissimile* (1 male, 2 females, 5 nymphs, and 5 larvae) from six individual hosts of the three species, where each tick was positive for a single *Rickettsia* species. The Blast analysis of the fragment of 760 bp fragment of the *gltA* gene of *Amblyomma dissimile* yielded an identity of 99.45% with *Rickettsia monacensis* strain IrR/Munich (LN794217.1) from Germany (Table 2). However, the fragment of *ompA* gene was 100% identical to *Rickettsia* sp. strain Colombianensi (KF691752.1, MG563769.1) reported in South America. On the other hand, a single female of *A. mixtum* was positive for *Rickettsia*-DNA. Sequences recovered exhibited an identity of 100% and 99.79% respectively, with the sequences of *gltA* and *ompA* genes of *Rickettsia amblyommatis* strain Ac37 (CP012420.1) from Brazil (Table 2). The phylogenetic analyses cluster our sequence of *gltA* recovered from *A. dissimile* with those of *R. monacensis* and *R. tamurae* in a cluster with a support value of 93, however our sequence is placed on a unique branch that differentiates it from both validated species (Fig. 1). On the other hand, the analysis of the fragment of the *ompA* gene places our sequence in a monophyletic group with a support value of 99 with the isolates of *Rickettsia* sp. strain Colombianensi from Colombia, Brazil and Honduras (Fig. 2). Finally, the phylogenetic analyzes of the sequences of the *gltA* and *ompA* genes obtained from *A. mixtum* reveals a

Table 2
Results of analysis of *Rickettsia* sequences recovered from ticks in Mexico to *Rickettsia* sequences from GenBank. NA. Not amplified. BP = Barra de Potosi, LF = La Florida, VI = Villahermosa, CO = Cotaxtla, SO = Sontecomapan, VE = Veracruz.

Locality	Host species	Tick species	Stage	Prevalence	Comparison strain (GenBank accession no. and sequence identity)	
					gltA	***ompA***
CO	*Boa constrictor* (2)	*Amblyomma dissimile*	Nymphs (16)	6.3%(1/16)	*Rickettsia monacensis* (AF140706.1) 99% = 748/751	NA
			Female (8)	0% (0/8)	(-)	(-)
			Male (6)	0% (0/6)	(-)	(-)
VE	*B. constrictor* (2)	*A. dissimile*	Larvae (15)	0% (0/15)	(-)	(-)
			Nymphs (16)	19.7%(3/16)	*Rickettsia monacensis* (AF140706.1) 99% = 760/764	*Rickettsia* sp. strain Colombianensi (JF905458.1) 100% = 492/492
			Female (8)	12.5% (1/8)	*Rickettsia monacensis* (AF140706.1) 99% = 760/764	*Rickettsia* sp. strain Colombianensi (JF905458.1) 100% = 492/492
			Male (6)	16.6% (1/6)	*Rickettsia monacensis* (AF140706.1)99% = 760/764	*Rickettsia* sp. strain Colombianensi (JF905458.1) 100% = 492/492
SO	*Iguana iguana* (1)	*A. dissimile*	Female (5)	20% (1/5)	*Rickettsia monacensis* (AF140706.1)99% = 760/764	*Rickettsia* sp. strain Colombianensi (JF905458.1)100% = 492/492
			Male (4)	0% (0/4)	(-)	(-)
		Amblyomma mixtum	Female (2)	50% (1/2)	*Rickettsia amblyommatis* (CP015012.1)99% = 755/757	*Rickettsia amblyommatis* (MF188914.1)99% = 489/493
BP	*Rhinella marina* (15)	*A. dissimile*	Larvae (15)	13.3% (2/15)	*Rickettsia monacensis* (AF140706.1) 99 = 748/751	*Rickettsia* sp. strain Colombianensi (JF905458.1) 99% = 490/492
			Nymphs (16)	6.3%(1/16)	*Rickettsia monacensis* (AF140706.1) 99% = 748/75	*Rickettsia* sp. strain Colombianensi (JF905458.1) 99% = 490/492
			Female (8)	0% (0/8)	(-)	(-)
			Male (6)		(-)	(-)
LF	*R. marina* (2)	*A. dissimile*	Larvae (25)	12% (3/25)	*Rickettsia monacensis* (AF140706.1)99% = 760/764	*Rickettsia* sp. strain Colombianensi (JF905458.1) 100% = 492/492
VI	*R. marina* (1)	*A. dissimile*	Larvae (10)	0.0% (0/10)	(-)	(-)

monophyletic cluster of the *R. amblyommatis* isolates deposited in GenBank and our sequences, with branch support values ranging from 61 to 97 in both topologies (Figs. 1,2). Sequences recovered in this study were deposited in GenBank under accession number: MH521291-MH521294.

3.2. Review of the literature

As shown in Table 3, the first record of a *Rickettsia* associated with amphibian and reptile ticks was that of *Rickettsia honei*, the etiological agent of the Spotted Fever of Flinders Island, detected in several *B. hydrosauri* specimens collected from one lizard (*Tiliqua nigrolutea*) and two species of snakes (*Austrelaps superbus*, *Notechis scutatus*) in Australia in 2003 (Stenos et al., 2003). Since then, the inventory of *Rickettsia* species identified in ticks from amphibian and reptiles has increased 10 times. The records include one species from the Ancestral Group (*Rickettsia bellii*), nine from the Spotted Fever Group (e.g. *Rickettsia africae*, *R. honei*), and an atypical record of a Typhus Group member (*Rickettsi typhi*). Additionally, three species are in the process of validation (two as *Candidatus* and one as a strain), together with 10 lineages related to *Rickettsia massiliae*, *R. monacensis*, *Rickettsia raoultii*, and *R. tamurae*. The species with the highest number of records are *Rickettsia helvetica* and *R. bellii*, with five registers each. In contrast, *Rickettsia aeschlimannii* and *R. typhi* have only been detected once.

Of the 11 valid *Rickettsia* species, eight are responsible for various human diseases, e.g. tick-borne lymphadenopathy by *R. raoultii*. The pathogenicity of the species under validation is unknown, including the 10 lineages whose identity could not be clarified.

The 23 *Rickettsia* taxa that have been reported to be associated with 18 tick species belong to six genera (*Amblyomma*, *Bothriocroton*, *Dermacentor*, *Haemaphysalis*, *Hyalomma*, and *Ixodes*) of the family Ixodidae (hard ticks). *Ixodes ricinus* was the tick species that has been recorded infected by the highest number of *Rickettsia* species (*R. helvetica*, *R. hoogstraalii*, *R. monacensis* and *R. typhi*), most of which can cause diseases in humans. Although reptiles and some amphibian species are parasitized by ticks of the Argasidae family (soft ticks), there are no records of *Rickettsia* infecting Argasidae ticks in these two vertebrate groups.

The aforementioned 18 Ixodidae species were associated with 42 host taxa of amphibians and reptiles (18 species of lizards, 14 species of snakes, eight of turtles and two of anurans). Lizards and snakes concentrated most of the *Rickettsia* records in 32 species (18 of lizards and 14 of snakes) of 20 genera of reptiles. The host species with the highest number of ticks positive for *Rickettsia* was *Python molurus* with four, followed by three species of lizards (*Lacerta agilis*, *Lacerta viridis*, *Podarcis muralis*) with three reports each. None of the hosts parasitized by ticks infected with *Rickettsia* showed evidence of pathogenic processes. Although intentional search for *Rickettsia* has been carried out on several host tissue samples (e.g. blood, spleen), only two species of lizards (*L. agilis*, *L. viridis*) tested positive in blood and/or tissue for *R. monacensis* and *R. helvetica* in Europe.

Most of the hosts carrying ticks infected with *Rickettsia* were detected at airport customs offices (in Israel or Japan), or came from specimens that were kept in captivity (USA), but all animal-hosts positive for *Rickettsia* were exotic from those countries. The places of origin for the animals were 36 countries of the six zoogeographic regions, most of them from of the Neotropical/Neartic (19.4%), and the Oriental (16.7%) regions. The country with the highest number of records was Thailand (14%), followed by Australia (11.6%), Slovakia, Italy and the Netherlands with 7% each. In contrast, 14 countries have a single record (2.3%), e.g. Algeria, Brazil, Jordan. The most widely distributed *Rickettsia* species were *R. bellii* in four American countries (Brazil, El Salvador, the United States and Panama), *R. helvetica* in four European countries (Slovakia, Italy, the Netherlands and Portugal), and *R. monacensis* registered also in three European countries (Slovakia, Italy, Portugal). On the other hand, the species that were recorded in

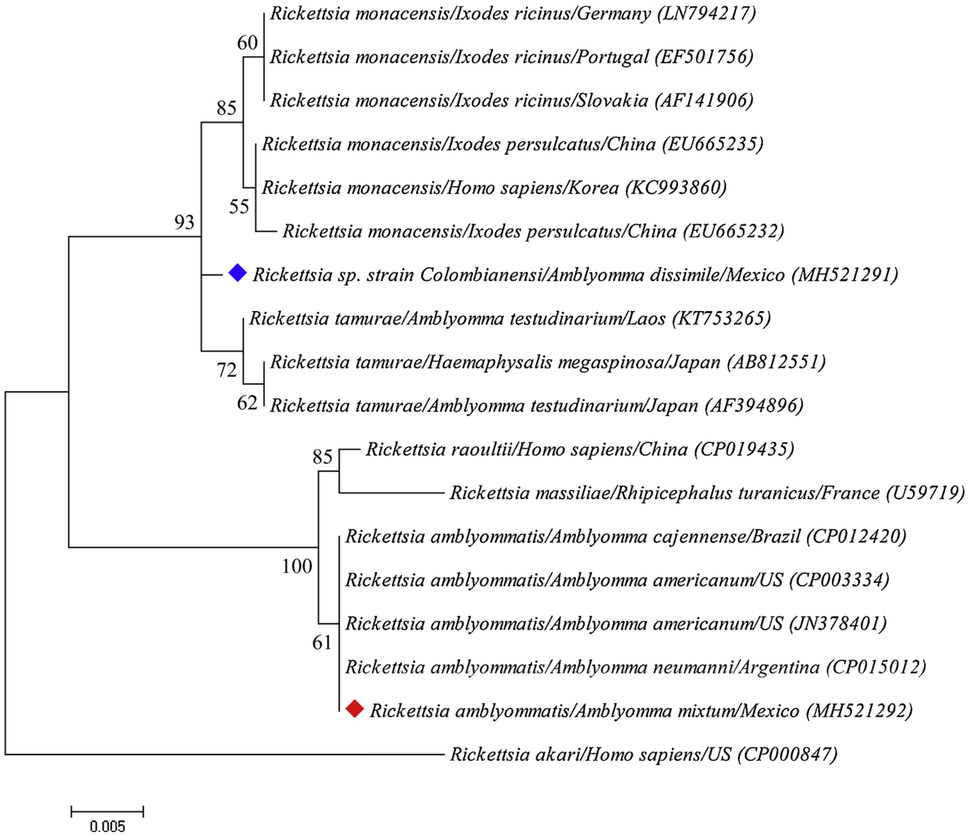

Fig. 1. Maximum-likelihood phylogenetic tree generated using the Tamura three parameter model (T93) with invariable sites for a total of 760 bp of the *gltA* gene from a few members of *Rickettsia* of the Spotted fever group. Diamond indicates sequences generated in Mexico. Bootstrap values $> 50\%$ are indicated at the nodes ($-\ln = -1273.56$). Numbers in parentheses are GenBank accession numbers.

more than one zoogeographic region were *Rickettsia hooogtralii* (in the Afrotropical and Paleartic regions) and *R. raoultii* (in the Afrotropical and Oriental regions). In contrast, the species with the most restricted geographical distribution were *R. aeschlimannii* and *R. africae*, recorded in three African countries (Algeria, Madagascar and the Republic of Zambia), followed by *R. honei* and *R. tamurae*, detected only in Australia (Table 3).

4. Discussion

This is the first study on the presence and characterization of *Rickettsia* associated with ticks of reptiles and amphibians in Mexico, which also increases the number of *Rickettsia* species recorded in this country to 10 species, with the recent record of *Rickettsia parkeri* strain Black Gap, *Rickettsia parkeri* strain Maculatum 20 and *Candidatus* Rickettsia andenae, which demonstrates the imperative need to continue working with the detection of these microorganisms in order to complete the list of species that circulate in the country (Sánchez-Montes et al., 2018; Delgado de la Mora et al., 2019).

Rickettsia sp. strain Colombianensi was isolated and described from *A. dissimile* in Colombia, although, it has also recently been detected in Colombia, Honduras and Brazil (Miranda et al., 2012; Novakova et al., 2015; Luz et al., 2018; Santodomingo et al., 2018). These new findings of the *Rickettsia* sp. strain Colombianensi in Mexico correspond to the most northern record of its known distribution. It has been postulated that this species is an endosymbiont of *A. dissimile*, which is distributed from the North of Mexico to the Southern Cone of America (Guglielmone and Nava, 2010). *Rickettsia amblyommatis*, a member of the spotted fever group, was previously detected in *A. mixtum* from two Mexican states (Jalisco and Veracruz), however it was never reported in ticks associated with the reptile *I. iguana* in the country (Sanchez-Montes et al., 2016b). Due to the fact that this tick species is associated mainly with cattle and horses in the country, and that multiple studies in Central America have detected questing ticks and ticks attached to mammals positive to this *Rickettsia* species, it is possible to think that reptiles do not play a relevant role in the life cycle of this bacteria (Guzmán-Cornejo et al., 2011; Bermudez and Troyo, 2018). However, the relevance of this *Rickettsia* species in public health has increased, because it is suspected to cause a mild illness in humans, although its pathogenicity still needs to be evaluated in humans and other vertebrate species (Apperson et al., 2008).

Despite the fact that several members of the *Rickettsia* genus represent a serious emerging and re-emerging health problem, the surveillance of these pathogens in ticks from wildlife has focused mainly on mammals and birds, whereas reptiles and amphibians remain as unattended hosts groups. The studies focused on the detection of *Rickettsia* in ticks of amphibians and reptiles are scarce and have been carried out very recently. Less than 1% of amphibian (0.02% = 2/7799) and reptile (0.33% = 32/9546) species worldwide have been analyzed for ticks infected with *Rickettsia*, so the inventory of these bacteria species associated with both vertebrate groups is far from complete (Pincheira-Donoso et al., 2013; Frost, 2018). One of the 30 *Rickettsia* species (*R. honei*) was isolated from ticks associated with reptiles (Stenos et al., 2003), and three new species in validation (*Rickettsia* sp. strain Colombianensi, *Candidatus* "Rickettsia johorensis", and *Candidatus* "Rickettsia sepangensis") were detected in ticks of these animals (Table 3), so it is feasible to assume that there are still many undescribed species.

Some species of ticks of the genera *Amblyomma*, *Bothriocroton* and *Hyalomma* present a marked tropism for parasitizing reptiles and amphibians, since they have established a close parasite-host relationship with these vertebrate groups (Guglielmone et al., 2010). Therefore it is

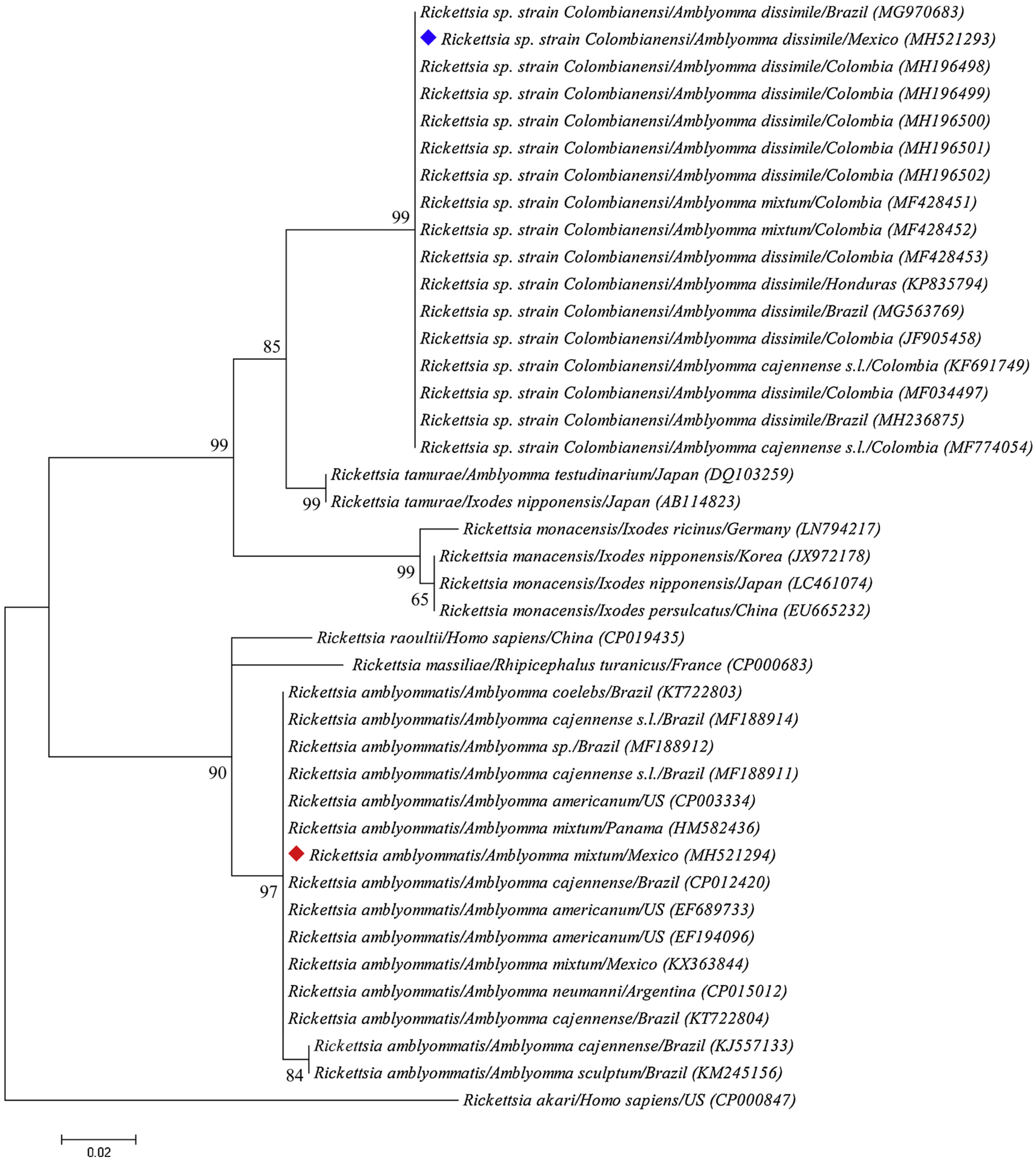

Fig. 2. Maximum-likelihood phylogenetic tree generated using the Tamura three parameter model (T93) with invariable sites for a total of 492 bp of the *ompA* gene from a few members of *Rickettsia* of the Spotted fever group. Diamond indicates sequences generated in Mexico. Bootstrap values > 50% are indicated at the nodes (−In = -923.91). Numbers in parentheses are GenBank accession numbers.

possible to assume, that the *Rickettsia* detected in these species may not have an impact on human public health since these tick species do not naturally parasitize mammals, particularly humans. Yet the finding of new *Rickettsia* species has an implication in the resolution of the phylogeny of the group.

Of concern is the particular case of *I. ricinus*, a tick with more generalist habits, which can parasitize reptiles, birds and mammals (Guglielmone et al., 2014). This could explain the atypical record of *R. typhi* (a member of the Typhus group) in this tick species, which possibly acquired the pathogen during a previous feeding on a mammalian host in the Netherlands.

The role of amphibians and reptiles in the life cycle of *Rickettsia* is still a mystery. However, it is recognized that these vertebrates maintain the populations of ticks, because the larvae (*I. ricinus* on lizards), nymphs and adults (*B. hydrosauri* in snakes) feed on them. These ticks possibly maintain the cycle of these microorganisms by transovarial transmission (Stenos et al., 2003; Whitworth et al., 2003). However, the few studies currently available do not allow identifying the effect of *Rickettsia* on reptile and amphibian populations, but it is a concern that warrants further investigation.

Table 3
Records of species of the genus *Rickettsia* associated with ticks from amphibians and reptiles. *Records of exotic animals whose origin is unknown.

Disease	*Rickettsia* species	Tick species	Host	Country	Reference
Unnamed rickettsiosis	*Rickettsia aeschlimannii*	*Hyalomma aegyptium*	*Testudo graeca*	Algeria	(Bitam et al., 2009)
African tick bite fever	*Rickettsia africae*	*Amblyomma chabaudi*	*Astrochelys radiata*	Madagascar	(Ehlers et al., 2016)
			Pyxis arachnoides		
		Amblyomma sparsum	*Geochelone paradalis*	Zambia	(Andoh et al., 2015)
Unknown	*Rickettsia bellii*	*Amblyomma dissimile*	*Bothrops atrox*	Brazil	(Ogrzewalska et al., 2019)
		Amblyomma rotundatum	*Bothrops jaraca*		(Ogrzewalska et al., 2019)
			Crotalus dusissus		(Ogrzewalska et al., 2019)
			Bufo sp.		(Labruna et al., 2004)
			Rhinella jimi		(Horta et al., 2015)
			R. marina	Panama	(Andoh et al., 2015)
				Panama	(Ogrzewalska and Bermúdez, 2019)
			Chelonoidis carbonaria	US	(Erster et al., 2015)
		Amblyomma sabanerae	*Kinosternon* sp.	El Salvador	Barbieri et al., 2012
Unnamed rickettsiosis	*Rickettsia helvetica*	*Ixodes ricinus*	*Lacerta agilis*	Netherlands	(Tijsse-Klasen et al., 2010)
			Lacerta schreiberi	NR	(Kubelová et al., 2015)
			Lacerta viridis	Slovakia	(Václav et al., 2011)
			Podarcis muralis	Italy	(Tomassone et al., 2017)
			Teira dugesii	Portugal	(de Sousa et al., 2012)
Flinders Island spotted fever	*Rickettsia honei*	*Bothriocroton hydrosauri*	*Tiliqua nigrolutea*	Australia	(Stenos et al., 2003; Whitworth et al., 2003)
			Austrelaps superbus	Australia	(Stenos et al., 2003; Whitworth et al., 2003)
			Notechis scutatus	Australia	(Stenos et al., 2003)
Unknown	*Rickettsia hoogstraalii*	*Amblyomma transversale*	*Python regius*	Ghana	(Andoh et al., 2015)
		Haemaphysalis sulcata	*P. muralis*	Italy	(Tomassone et al., 2017)
		I. ricinus			
Unnamed rickettsiosis	*Rickettsia monacensis*	*I. ricinus*	*L. schreiberi*	NR	(Kubelová et al., 2015)
			L. viridis	Slovakia	(Václav et al., 2011)
			P. muralis	Italy	(Tomassone et al., 2017)
			T. dugesii	Portugal	(de Sousa et al., 2012)
Unknown	*Rickettsia parkeri* strain Parvitarsum	*Amblyomma parvitarsum*	*Liolaemus pleopholis*	Chile	(Muñoz-Leal et al., 2016b)
Tick-borne lymphadenopathy	*Rickettsia raoultii*	*Amblyomma sparsum*	*G. paradalis*	Zambia	(Andoh et al., 2015)
		Amblyomma trimaculatum	*Boiga forsteni*	Sri Lanka	
Unnamed rickettsiosis	*Rickettsia tamurae*	*Amblyomma fimbriatum*	*Varanus panoptes*	Australia	(Vilcins et al., 2009)
			Dendrelaphis punctulatus		
			Liasis fuscus		
Murine typhus	*Rickettsia typhi*	*I. ricinus*	*L. agilis*	Netherlands	(Tijsse-Klasen et al., 2010)
Unknown	*Candidatus* "Rickettsia johorensis"	*Amblyomma helvolum*	*Naja sumatrana*	Malasia	(Kho et al., 2015)
			Python molurus		
		Amblyomma varanensis	*P. molurus*		
Unknown	*Candidatus* "Rickettsia sepangensis"	*A. varanensis*	*P. molurus*	Malasia	(Kho et al., 2015)
Unknown	*Rickettsia* sp. strain Colombianensi	*Amblyomma dissimile*	*Ameiva bifrontata*	Colombia	(Santodomingo et al., 2018)
			Anolis auratus	Colombia	(Santodomingo et al., 2018)
			Basiliscus basiliscus	Colombia	(Santodomingo et al., 2018)
			Boa constrictor	Colombia	(Santodomingo et al., 2018)
			Botrox atrox	Brazil	(Ogrzewalska et al., 2019)
			Corallus ruschenbergerii	Colombia	(Santodomingo et al., 2018)
			Cnemidophorus gaigei	Colombia	(Santodomingo et al., 2018)
			Ctenosaura bakeri	Honduras	(Novakova et al., 2015)
			Iguana iguana	Colombia	(Miranda and Mattar, 2014; Santodomingo et al., 2018)
				Honduras	(Novakova et al., 2015)
			Porthidium lansbergii	Colombia	(Santodomingo et al., 2018)
			Rhinella horribilis	Colombia	(Cotes-Perdomo et al., 2018)
			Rhinella humboldti	Colombia	(Cotes-Perdomo et al., 2018)
			R. marina	Brazil	(Luz et al., 2018)
			Rhinoclemmys melanosterna	Colombia	(Santodomingo et al., 2018)
Unknown	*Rickettsia* sp. related with *R. africae*	*H. aegyptium*	*Testudo horsfieldii*	Russia	(Andoh et al., 2015)
				Uzbekistan	(Andoh et al., 2015)
Unknown	*Rickettsia* sp. related with *R. bellii*	*A. varanensis*	*Ophiophagus hannah*	Thailand	(Sumrandee et al., 2014)
Unknown	*Rickettsia* sp. related with *R. raoultii*	*A. helvolum*	*Varanus salvator*	Thailand	(Doornbos et al., 2013)
			P. molurus bivittatus	Thailand	(Sumrandee et al., 2014)
			Xenochrophis piscator	Thailand	(Sumrandee et al., 2014)
Unknown	*Rickettsia* related with *R. raoultii*/*R. massiliae*	*A. varanensis*	*O. hannah*	Thailand	(Sumrandee et al., 2014)
Unknown	*Rickettsia* sp. related with *R. tamurae*	*A. hydrosauri*	*Tiliqua rugosa*	Australia	(Whiley et al., 2016)

(*continued on next page*)

Table 3 (*continued*)

Disease	*Rickettsia* species	Tick species	Host	Country	Reference
Unknown	*Rickettsia* sp. related with *R. tamurae/ R. massiliae*	*A. helvolum*	*Ptyas korros*	Thailand	(Sumrandee et al., 2014)
Unknown	*Rickettsia* sp. related with *R. tamurae/ R. monacensis*	*Amblyomma exornatum*	*Varanus olivaceus**	US	(Reeves et al., 2006)
		Amblyomma latum	*Phelsuma dubia*	Madagascar	(Andoh et al., 2015)
		H. aegyptium	*T. graeca*	Jordan	(Andoh et al., 2015)
Unknown	*Rickettsia* sp.	*Dermacentor marginatus*	*L. viridis*	Slovakia	(Václav et al., 2011)
		I. ricinus	*L. agilis*	Netherlands	(Tijsse-Klasen et al., 2010)

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