

Hosts, distribution and genetic divergence (16S rDNA) of *Amblyomma dubitatum* (Acari: Ixodidae)

Santiago Nava · José M. Venzel · Marcelo B. Labruna ·
Mariano Mastropaoilo · Enrique M. González · Atilio J. Mangold ·
Alberto A. Guglielmone

Received: 31 August 2009 / Accepted: 14 December 2009
© Springer Science+Business Media B.V. 2010

Abstract We supply information about hosts and distribution of *Amblyomma dubitatum*. In addition, we carry out an analysis of genetic divergence among specimens of *A. dubitatum* from different localities and with respect to other Neotropical *Amblyomma* species, using sequences of 16S rDNA gene. Although specimens of *A. dubitatum* were collected on several mammal species as cattle, horse, *Tapirus terrestris*, *Mazama gouazoubira*, *Tayassu pecari*, *Sus scrofa*, *Cerdocyon thous*, *Myocastor coypus*, *Allouata caraya*, *Glossophaga soricina* and man, most records of immature and adult stages of *A. dubitatum* were made on *Hydrochoerus hydrochaeris*, making this rodent the principal host for all parasitic stages of this ticks. Cricetidae rodents (*Lundomys molitor*, *Scapteromys tumidus*), opossums (*Didelphis albiventris*) and vizcacha (*Lagostomus maximus*) also were recorded as hosts for immature stages. All findings of *A. dubitatum* correspond to localities of Argentina, Brazil, Paraguay and Uruguay, and they were concentrated in the Biogeographical provinces of Pampa, Chaco, Cerrado, Brazilian Atlantic Forest, Paraná Forest and *Araucaria angustifolia* Forest. The distribution of *A. dubitatum* is narrower than that of its principal host, therefore environmental variables rather than hosts determine the distributional ranges of this tick. The intraspecific genetic

S. Nava · M. Mastropaoilo · A. J. Mangold · A. A. Guglielmone
Instituto Nacional de Tecnología Agropecuaria, Estación Experimental Agropecuaria Rafaela,
CC 22, CP 2300 Rafaela, Santa Fe, Argentina

S. Nava (✉) · M. Mastropaoilo · A. J. Mangold · A. A. Guglielmone
Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Buenos Aires, Argentina
e-mail: snav@rafaela.inta.gov.ar

J. M. Venzel
Departamento de Parasitología Veterinaria, Facultad de Veterinaria, Universidad de la República,
Regional Norte, Sede Salto, Rivera 1350, CP 50000 Salto, Uruguay

M. B. Labruna
Faculdade de Medicina Veterinária e Zootecnia, Universidade de São Paulo, Av. Prof. Orlando M. de Paiva 87, 05508-900 São Paulo, Brazil

E. M. González
Museo Nacional de Historia Natural, Casilla de Correo 399, Montevideo 11000, Uruguay

divergence among 16S rDNA sequences of *A. dubitatum* ticks collected in different localities from Argentina, Brazil and Uruguay was in all cases lower than 0.8%, whereas the differences with the remaining *Amblyomma* species included in the analysis were always bigger than 6.8%. Thus, the taxonomic status of *A. dubitatum* along its distribution appears to be certain at the specific level.

Keywords *Amblyomma dubitatum* · Distribution · Biogeography · Hosts · Genetic divergence · 16S rDNA sequences

Introduction

Amblyomma dubitatum Neumann, 1899 is a South American tick species (Guglielmone et al. 2003a) extensively named as *Amblyomma cooperi* Nuttall and Warburton, 1908 and, in a lesser extent as *Amblyomma lutzi* Aragão, 1908, a name considered to have priority to *A. cooperi* according to Santos Dias (1958). *Amblyomma ypsiloniphorum* Schulze, 1941 was found to be a synonym of *A. cooperi* by Fonseca and Aragão (1952). However, Camicas et al. (1998) stated that *A. dubitatum* has priority to all previous names, which was confirmed by the study of Estrada Peña et al. (2002). Thus, it is accepted currently that *A. cooperi*, *A. lutzi* and *A. ypsiloniphorum* are synonymous of *A. dubitatum*.

Immature and adult stages of *A. dubitatum* were recorded feeding on *Hydrochoerus hydrochaeris* and, in a much lesser extent, have been mentioned as parasites of other large mammals as *Tapirus terrestris* and cattle (Barros-Battesti et al. 2006; Guglielmone and Nava 2006). Also, there are some records of *A. dubitatum* biting humans in Brazil and Uruguay (Guglielmone et al. 2006), although the role of *A. dubitatum* as vector of humans diseases is undetermined. In fact, *Rickettsia belli* and *Rickettsia parkeri* (strain COOPERI) have been detected in *A. dubitatum* ticks in Brazil (Labruna et al. 2004a), but the pathogenicity to humans of these agents is actually unknown.

With the aim of supply information on ecological preferences and natural hosts for both immature and adults stages of *A. dubitatum*, in this work we present and analyze data on host-range and distribution in relation to the biogeography of *A. dubitatum*. Also, because sequences of 16S rDNA mitochondrial gene are useful molecular markers to supplement and confirm the conventional determination of ticks based on morphological characters (Nava et al. 2009a), we carry out an analysis of divergence in partial sequences of 16S rDNA gene belonging to specimens of *A. dubitatum* collected in different localities and to other Neotropical *Amblyomma* species, in order to demonstrate that *A. dubitatum* ticks from different areas can be placed in the same specific taxon.

Materials and methods

The data on distribution and hosts of *A. dubitatum* used in this study were obtained on a appraisal of the scientific literature, and from unpublished records of ticks deposited in the following tick collections: Argentina: Instituto Nacional de Tecnología Agropecuaria, Estación Experimental Agropecuaria Rafaela, Santa Fe (INTA), and Facultad de Ciencias Veterinarias, Universidad Nacional del Litoral, Santa Fe (FAVE); Brazil: Coleção Nacional de Carrapatos da Faculdade de Medicina Veterinária e Zootecnia, Universidade de São Paulo, São Paulo (CNC); Uruguay: Departamento de Parasitología Veterinaria, Facultad de Veterinaria, Montevideo (DPVURU). The collections localities were plotted and

analyzed according to the biogeographic provinces described by Morrone (2006). The adults ticks identification was carried out by using the taxonomic keys of Guglielmone and Viñabal (1994) and Barros-Battesti et al. (2006), and the larvae and nymphs were identified following the descriptions of Joan (1930) and Estrada Peña et al. (2002), respectively. In a few cases stated below, species identification of immature ticks was carried out by rearing the collected larvae or nymphs to the adult stage in the laboratory, and then taxonomic identification of the resultant adults was performed.

Specimens of *A. dubitatum* from Argentina (Arroyo Ayuí, Corrientes: 28°16'S 56°18'W; Reserva Horco Molle, Tucumán: 26°48'S 65°19'W), Brazil (São Paulo, São Paulo: 23°35'S 46°39'W; Estação Ecológica Taim, Rio Grande do Sul: 33°26'S 53°16'W) and Uruguay (Rincón da Vassoura, Tacuarembó: 31°15'S 56°03'W; Río San José, Flores: 33°57'S 56°50'W) were used for DNA extraction and polymerase chain reaction (PCR) amplification as described by Mangold et al. (1998). The amplified DNA was purified using Wizard SV Gel and PCR Clean-Up (Promega®) according to the manufacturer's protocol, and the purified PCR products were employed to carry out the sequences of circa 420-bp fragment of the mitochondrial 16S rDNA gene. The sequences were edited and aligned using the BioEdit Sequence Alignment Editor (Hall 1999) with the CLUSTAL W program (Thompson et al. 1994), and they were compared to each other and with those of *Amblyomma* deposited in the GenBank. A pairwise estimate of percent sequence divergence was determined using Mega version 4.0 (Tamura et al. 2007).

Results

Most records of immature and adult stages of *A. dubitatum* were made on *H. hydrochaeris*, while other mammals belonging to different orders as cattle, horse, *T. terrestris*, *Mazama gouazoubira*, *Tayassu pecari*, *Sus scrofa*, *Cerdocyon thous*, *Myocastor coypus*, *Allouata caraya*, *Glossophaga soricina* and man appear to be occasional hosts for this tick (Table 1). Larvae and nymphs of *A. dubitatum* were also collected on *Didelphis albiventris*, *Didelphis aurita*, *Lagostomus maximus* and Cricetidae rodents (*Lundomys molitor*, *Scapteromys tumidus*), and there is a report of a nymph on the flightless ratite bird *Rhea americana* in Brazil (Table 1).

All findings of *A. dubitatum* were restricted to localities of Argentina, Brazil, Paraguay and Uruguay (Table 1), and they were concentrated in the Biogeographical provinces of Pampa, Chaco, Cerrado, Brazilian Atlantic Forest, Parana Forest and *Araucaria angustifolia* Forest, with the only exception of the records of Ilha de Marajó (Pará, Brazil) and Margens Río Guaporé (Mato Grosso, Brazil), which correspond to Amapá and Pantanal provinces, respectively (Fig. 1). The localities and hosts corresponding to a record of *A. dubitatum* in Bolivia (Squire 1972; Keirans and Brewster 1981) were not specified by the authors, and Vogelsang and Cordero (1940) also mentioned the presence of *A. dubitatum* in Venezuela, although this record should be considered carefully because Jones et al. (1972) could not confirm the presence of this tick species in spite of revising many samples from *H. hydrochaeris* in this country. Consequently, we do not include Bolivia and Venezuela in the distribution of *A. dubitatum*.

The intraspecific genetic divergence among 16S rDNA sequences of *A. dubitatum* ticks collected in different localities had a maximum difference of 0.8% and a minimum difference of 0.0%, whereas the differences with the remaining *Amblyomma* species including in the analysis were always bigger than 6.8% (Table 2). The nucleotide divergence between the 16S rDNA sequence of the nymph from Uruguay collected on *Scapteromys*

Table 1 Localities and hosts of *Amblyomma dubitatum* in the neotropical region

Province/state/department	Locality	Coordinates	Host	Stage	References
Argentina					
Chaco	Basail	27°52'S 59°18'W	<i>Hydrochoerus hydrochaeris</i>	F	Ivancovich and Luciani (1992)
	Colonia Benítez	27°19'S 58°57'W	<i>H. hydrochaeris</i>	MF	<i>Ibid.</i>
	Estancia La Analia	27°31'S 59°08'W	<i>H. hydrochaeris</i>	MN	<i>Ibid.</i>
	Estancia Legua 40	27°02'S 59°17'W	<i>H. hydrochaeris</i>	MFN	<i>Ibid.</i>
	Ruta 90 km 1099	26°41'S 59°14'W	<i>H. hydrochaeris</i>	MFN	<i>Ibid.</i>
	Arroyo Ayuí	28°16'S 56°18'W	<i>H. hydrochaeris</i>	MF	FAVE
	30 km to SW of Colonia Pelegriñi	28°40'S 57°26'W	<i>H. hydrochaeris</i>	MFNL**	INTA
	Estancia Ayuí	28°37'S 57°32'W	<i>H. hydrochaeris</i>	MFN	Ivancovich and Luciani (1992)
	Estancia Curupí Caí	29°23'S 57°47'W	<i>H. hydrochaeris</i>	MFN	<i>Ibid.</i>
	Estancia El Aguacerito	29°11'S 57°55'W	<i>H. hydrochaeris</i>	MFN	<i>Ibid.</i>
	Estancia El tigre	29°02'S 58°12'W	<i>H. hydrochaeris</i>	MFN	<i>Ibid.</i>
	Estancia Juan Angel	28°41'S 57°08'W	<i>H. hydrochaeris</i>	MFN	<i>Ibid.</i>
	Estancia La Armonía	28°48'S 58°41'W	<i>H. hydrochaeris</i>	MFN	<i>Ibid.</i>
	Estancia Palmita	28°46'S 57°48'W	<i>H. hydrochaeris</i>	MFN	<i>Ibid.</i>
	Estancia Yuquerí	29°08'S 57°46'W	<i>H. hydrochaeris</i>	MFN	<i>Ibid.</i>
	Goya	29°08'S 59°16'W	Cattle	N	INTA
	Laguna del Iberá	28°32'S 57°10'W	<i>H. hydrochaeris</i>	MFN	Ivancovich and Luciani (1992)
	Mercedes	29°07'S 58°07'W	<i>H. hydrochaeris</i>	MNL	INTA
	Monte Caseros N	31°12'S 57°39'W	Cattle	N	Guglielmino et al. (2002)
	Reserva Provincial Iberá I	28°31'S 58°10'W	Free	NL	INTA
	Reserva Provincial Iberá II	28°30'S 58°00'W	Man	MNL	Osherov et al. (2006)
	Rincón del Socorro	28°35'S 56°51'W	<i>Sus scrofa</i>	MF	FAVE
	Santo Tomé	28°33'S 56°02'W	<i>H. hydrochaeris</i>	X	Sarmiento et al. (2006)

Table 1 continued

Province/state/department	Locality	Coordinates	Host	Stage	References
Entre Ríos	Colonia Crespo	31°40'S 60°13'W	<i>H. hydrochaeris</i>	MEN	FAVE
	Concordia	31°24'S 58°01'W	<i>H. hydrochaeris</i>	X	Boero (1945)
	La Paz	30°44'S 59°38'W	Free	F	INTA
	Parque Nacional El Palmar I	31°53'S 58°12'W	<i>Lagostomus maximus</i>	N	FAVE
	Parque Nacional El Palmar II	31°55'S 58°11'W	<i>H. hydrochaeris</i>	MN	<i>Ibid.</i>
	Villaguay	31°52'S 59°01'W	<i>H. hydrochaeris</i>	X	Boero (1945)
	Colonia El Alba	26°20'S 59°18'W	<i>H. hydrochaeris</i>	MF	Ivancovich and Luciani (1992)
	El Colorado INTA	26°24'S 59°22'W	<i>H. hydrochaeris</i>	MFN	<i>Ibid.</i>
	Estancia Bañadero	25°57'S 59°10'S	<i>Tapirus terrestris</i>	F	<i>Ibid.</i>
	Isla Payaguá	26°45'S 58°15'W	<i>H. hydrochaeris</i>	F	<i>Ibid.</i>
Misiones	Colonia Andesito	25°40'S 54°01'W	<i>H. hydrochaeris</i>	MFN	Mastropaolo et al. (2004)
	Romang	29°30'S 59°46'W	<i>H. hydrochaeris</i>	X	Guglielmino and Viñabal (1994)
	Saladero Cabral	30°53'S 60°02'W	<i>H. hydrochaeris</i>	MF	FAVE
Brazil	Espirito Santo	19°49'S 40°16'W	<i>H. hydrochaeris</i>	MF	Almeida et al. (2001)
	Aracruz	19°32'S 40°38'W	Free	F	CNC
	Colatina	18°43'S 40°24'W	Free	MF	Oliveira et al. (2008)
	Nova Venécia	19°13'S 40°51'W	Free	MF	CNC
	Pancas	16°18'S 48°59'W	*	X	Aragão (1936)
	Anapolis	15°35'S 56°06'W	*	X	<i>Ibid.</i>
	Margens Rio Cuyabá	13°59'S 60°25'W	*	X	Aragão (1911)
	Margens Rio Guaporé	21°07'S 56°28'W	<i>H. hydrochaeris</i>	F	Amorim et al. (2003)
	Bonito Region	21°24'S 52°31'W	<i>H. hydrochaeris</i>	MFN***	Labruna et al. (2002)
	Porto Primavera Area				

Table 1 continued

Province/state/department	Locality	Coordinates	Host	Stage	References
Minas Gerais	Benjamin Constant	21°57'S 42°53'W	*	X	Rohr (1909)
	Coronel Pacheco	21°15'S 43°15'W	Free	MF	Guedes et al. (2005)
	Itabira	19°37'S 43°14'W	*	X	Rohr (1909)
	Juiz de Fora	21°44'S 43°21'W	Free	MF	Monteiro et al. (2004)
Lassance		17°54'S 44°34'W	Horse	MF	Aragão (1918)
Livramento		21°05'S 44°03'W	*	X	Aragão (1936)
Piau		21°31'S 43°19'W	*	X	Rohr (1909)
Pirapora		17°20'S 44°56'W	*	X	Aragão (1936)
Pitáubia		21°17'S 43°02'W	<i>H. hydrochaeris</i>	MF	Aragão (1908)
San Joao del Rey		21°08'S 44°15'W	*	X	Rohr (1909)
Santa Barbara		19°38'S 43°25'W	*	X	Aragão (1936)
Pará	Illa de Marajó	01°02'S 49°56'W	*	X	<i>Ibid.</i>
Paraná	Curitiba	25°24'S 49°19'W	<i>H. hydrochaeris</i>	MFL	Arzua et al. (2005)
	Guarapuava	25°23'S 51°27'W	<i>Tayassu pecari</i>	F	CNC
	Regiao de Foz de Iguaçu	25°20'S 54°09'W	<i>H. hydrochaeris</i>	MFN	Sinkoc et al. (1998)
Rio de Janeiro	Angra dos Reis	23°00'S 44°19'W	*	X	Aragão (1936)
	Barra Mansa	22°18'S 43°06'W	*	X	<i>Ibid.</i>
Iguassú		22°38'S 43°26'W	*	X	<i>Ibid.</i>
	Volta Redonda	22°31'S 44°07'W	*	X	Rohr (1909)
Rio Grande do Sul	Arroio Grande	32°12'S 53°05'W	<i>H. hydrochaeris</i>	MFN	Evans et al. (2000)
	Estação Ecológica Taim	33°26'S 53°16'W	<i>H. hydrochaeris</i>	MF	Sinkoc et al. (1997)
	Rio Grande	32°02'S 52°06'W	<i>H. hydrochaeris</i>	X	Evans et al. (2000)

Table 1 continued

Province/state/department	Locality	Coordinates	Host	Stage	References
São Paulo	Santana do Livramento	30°53'S 55°32'W	<i>H. hydrochaeris</i>	MFNL	<i>Ibid.</i>
	Santa Vitória do Palmar	33°31'S 53°22'W	<i>H. hydrochaeris</i>	F	Evans et al. (2000)
	Uruguaiana	29°45'S 57°05'W	<i>H. hydrochaeris</i>	X	Freire (1972)
	Aracariguama	23°26'S 47°04'W	Free	MF	Labruna and Souza (1999)
	Barao Geraldo	22°48'S 47°05'W	<i>H. hydrochaeris</i>	MF	de Souza et al. (2004)
	Botucatu	22°33'S 48°26'W	<i>H. hydrochaeris</i>	MF	CNC
	Bragança Paulista	22°57'S 46°32'W	<i>H. hydrochaeris</i>	MF	<i>Ibid.</i>
	Bonfim Paulista	21°09'S 47°49'W	<i>H. hydrochaeris</i>	MF	Pacheco et al. (2007)
	Campinas	22°52'S 47°03'W	<i>H. hydrochaeris</i> , Free	MN	Estrada et al. (2006)
	Cordeirópolis	22°28'S 47°27'W	<i>H. hydrochaeris</i>	MF	Pacheco et al. (2007)
Cosmorama	Cosmorama	20°28'S 49°46'W	<i>H. hydrochaeris</i>	MF	CNC
	Cosmorama	20°28'S 49°46'W	<i>Rhea americana</i>	N	<i>Ibid.</i>
	Franca	20°32'S 47°24'W	<i>H. hydrochaeris</i>	F	<i>Ibid.</i>
	Ibitinga	21°46'S 48°48'W	<i>H. hydrochaeris</i>	X	van der Heijden et al. (2003)
	Ilu	23°15'S 47°22'W	<i>H. hydrochaeris</i> ; <i>Man</i>	MFNL	Pacheco et al. (2004), Labruna et al. (2007)
	Jaguaríúna	22°44'S 46°57'W	Free	MF	De Souza et al. (2006)
	Jordanésia	23°21'S 46°52'W	<i>Cerdyon thous</i>	X	Labruna et al. (2005)
	Jundiai	23°11'S 46°52'W	<i>H. hydrochaeris</i>	MFN	Labruna et al. (2004a)
	Jundiai	23°11'S 46°52'W	<i>Mazama gonzalezibra</i> ; <i>Myocastor coypus</i> ; <i>Allouata caraya</i>	N	<i>Ibid.</i>
	Lorena	22°44'S 45°07'W	*	X	Aragão (1936)
Paulicéia	Mogi das Cruzes	23°38'S 46°11'W	<i>Didelphis aurita</i>	N	Horta et al. (2007)
	Monte Alegre do Sul	22°39'S 46°40'W	<i>H. hydrochaeris</i>	MF	Souza et al. (2004)
	São Bernardo do Campo	23°42'S 46°33'W	<i>H. hydrochaeris</i>	MF	Estrada Peña et al. (2002)
	Paulicéia	21°06'S 51°46'W	Free	MFNL	Szabó et al. (2007)

Table 1 continued

Province/state/department	Locality	Coordinates	Host	Stage	References
Pedreira	Pedreira	22°44'S 46°54'W	<i>Glossophaga soricina</i> ; <i>H. hydrochaeris</i> ; Man	MF	Famadas et al. (1997), Lemos et al. (1997), Barros et al. (1998)
Pedreira	Pedreira	22°44'S 46°55'W	Free	MF	Labruna et al. (2004b)
Pedreira	Pedreira	22°47'S 46°54'W	Free	MF	<i>Ibid</i>
Pedreira	Pedreira	22°41'S 46°53'W	Free	MF	Pacheco et al. (2004), Horta et al. (2007)
Pracicaba		22°43'S 47°38'W	<i>Didelphis albiventris</i>	LN	
Ribeirao Grande		24°16'S 48°25'W	<i>H. hydrochaeris</i>	MFN	
Rio Piracicaba		22°43'S 47°37'W	Man	M	Labruna et al. (2007)
Santa Cruz do Rio Pardo		22°23'S 40°38'W	*	X	Aragão (1936)
Sao Luis de Pirahytinga		23°15'S 45°18'W	Free	MF	CNC
Sao Paulo		23°32'S 46°37'W	<i>H. hydrochaeris</i>	MFN	Pacheco et al. (2007); CNC
São Paulo		23°06'S 47°43'W	<i>H. hydrochaeris</i>	MFN	Pacheco et al. (2004)
São Paulo, Parque Ecológico Tieté		23°07'S 47°43'W	<i>H. hydrochaeris</i>	MFN	<i>Ibid</i>
Sorocaba		23°30'S 47°26'W	<i>H. hydrochaeris</i>	MF	CNC
Teodoro Sampaio		22°32'S 52°10'W	<i>H. hydrochaeris</i>	MF	<i>Ibid</i>
Paraguay					
Concepción	Puerto Cooper	23°03'S 57°43'W	<i>H. hydrochaeris</i>	MF	Nava et al. (2007)
Misiones	San Juan Bautista	26°40'S 57°09'W	<i>H. hydrochaeris</i>	X	<i>Ibid</i>
Uruguay					
Canelones	INIA Las Brujas	34°40'S 56°20'W	<i>H. hydrochaeris</i>	MF	DPVURU
Durazno	La Paloma	32°43'S 55°36'W	<i>H. hydrochaeris</i>	M	DPVURU
Flores	Rio San José	33°57'S 56°50'W	<i>Lundomys molitor</i> ; <i>Scapteromys tumidus</i>	NL	

Table 1 continued

Province/state/department	Locality	Coordinates	Host	Stage	References
Rocha Tacuarembó	Prox. Santa Teresa	34°00'S 53°35'W	<i>H. hydrochaeris</i>	MFN	<i>Ibid.</i>
	Rincón da Vassoura	31°15'S 56°03'W	Man; Free	N	Guglielmino et al. (2006)

* Rohr (1909) and Aragão (1911, 1936) mention that *A. dubitatum* is quasi-exclusively associated to the capybaras (*H. hydrochaeris*), with occasional records on tapirs (*T. terrestris*). X: Tick stage was not specified

** Larvae and nymphs were identified to species after rearing the ticks to the adult stage in the laboratory

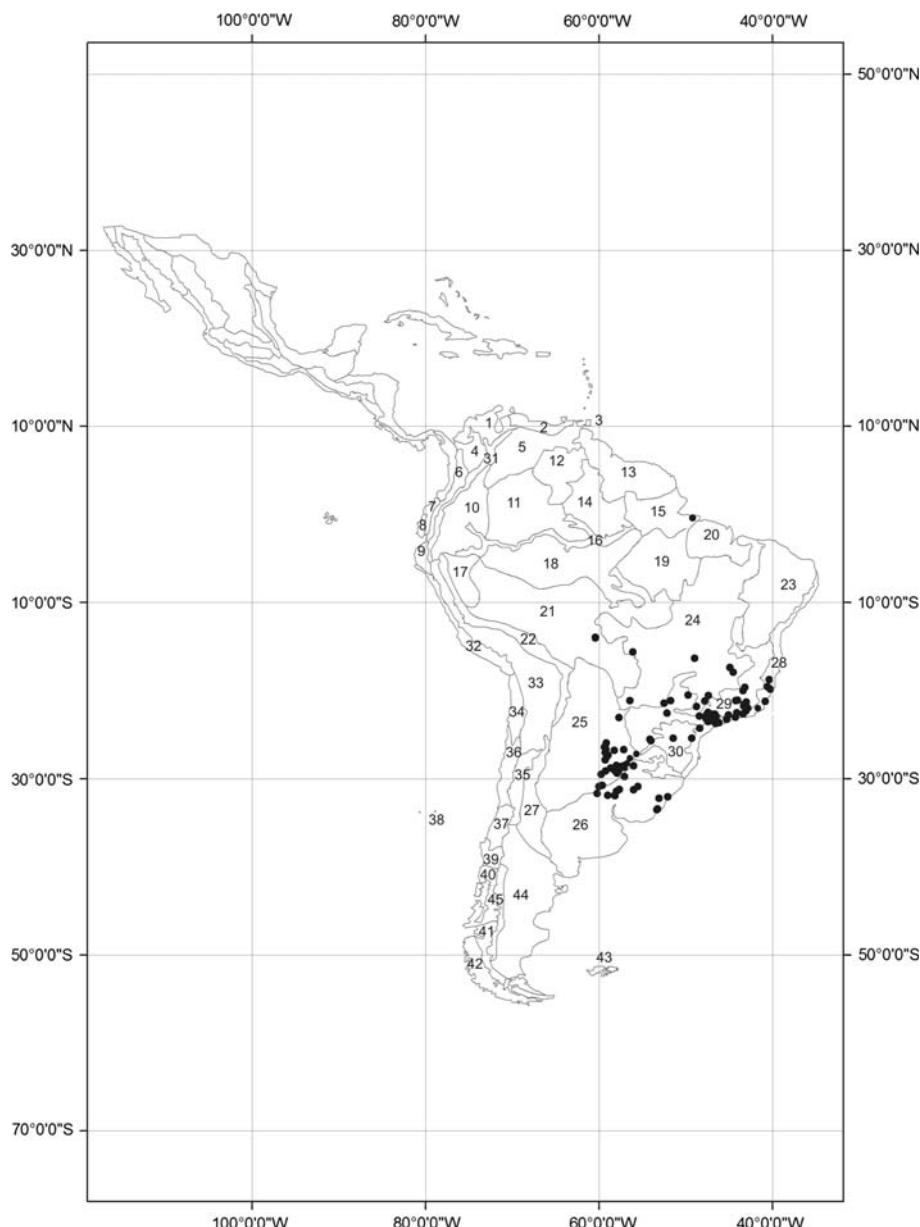


Fig. 1 The known distribution of *Amblyomma dubitatum* (closed circle) across the Biogeographic provinces of South America outlined by Morrone (2006). (1) Maracaibo; (2) Venezuelan Coast; (3) Trinidad & Tobago; (4) Magdalena; (5) Venezuelan Llanos; (6) Cauca; (7) Western Ecuador; (8) Arid Ecuador; (9) Tumbes-Piura; (10) Napo; (11) Imeri; (12) Guyana; (13) Humid Guyana; (14) Roraima; (15) Amapa; (16) Varzea; (17) Ucayali; (18) Madeira; (19) Tapajos-Xingu; (20) Para; (21) Pantanal; (22) Yungas; (23) Caatinga; (24) Cerrado; (25) Chaco; (26) Pampa; (27) Monte; (28) Brazilian Atlantic Forest; (29) Parana Forest; (30) Araucaria angustifolia Forest; (31) North Andean Paramo; (32) Coastal Peruvian Desert; (33) Puna; (34) Atacama; (35) Prepuna; (36) Coquimbo; (37) Santiago; (38) Juan Fernandez Islands; (39) Maule; (40) Valdivian Forest; (41) Magellanic Forest; (42) Magellanic Paramo; (43) Malvinas Islands; (44) Central Patagonia; (45) Subandean Patagonia

Table 2 Matrix of sequence divergence (% nucleotide differences) on pairwise comparisons of the 16S mitochondrial rDNA sequences for *A. dubitatum* from different localities and for other Neotropical *Amblyomma* species

	<i>A. dubitatum</i> C. Arg.	<i>A. dubitatum</i> T. Arg.	<i>A. dubitatum</i> F. Uru.	<i>A. dubitatum</i> SP. Bra.	<i>A. dubitatum</i> T. Uru.	<i>A. dubitatum</i> RGS. Bra.
<i>A. dubitatum</i> C. Arg.	—					
<i>A. dubitatum</i> T. Arg.	0.5	—				
<i>A. dubitatum</i> F. Uru.	0.2	0.2	—			
<i>A. dubitatum</i> T. Uru.	0	0.5	0.2	—		
<i>A. dubitatum</i> SP. Bra.	0	0.5	0.2	0.0	—	
<i>A. dubitatum</i> RGS. Bra.	0.8	0.8	0.5	0.8	0.8	—
<i>A. boeroi</i>	11.5	11.2	11.2	11.5	11.5	11.8
<i>A. auricularium</i>	14.4	14.1	14.1	14.4	14.4	14.1
<i>A. pseudoparvum</i>	14.1	13.8	13.8	14.1	14.1	14.1
<i>A. parvum</i>	17.5	17.2	17.2	17.5	17.5	17.5
<i>A. triste</i>	11.8	11.5	11.5	11.8	11.8	11.5
<i>A. aureolatum</i>	12.3	12.0	12.0	12.3	12.3	12.3
<i>A. brasiliense</i>	9.0	8.7	8.7	9.0	9.0	9.0
<i>A. cajennense</i>	12.1	12.1	12.4	12.1	12.1	12.7
<i>A. calcaratum</i>	7.7	7.7	7.4	7.7	7.7	7.7
<i>A. coelebs</i>	7.1	6.8	6.8	7.1	7.1	7.1
<i>A. geayi</i>	14.1	13.8	13.8	14.1	14.1	14.1
<i>A. incisum</i>	7.2	6.9	6.9	7.2	7.2	7.5
<i>A. longirostre</i>	15.5	15.1	15.1	15.5	15.5	15.5
<i>A. maculatum</i>	12.7	12.4	12.4	12.7	12.7	12.4
<i>A. napense</i>	11.2	11.1	10.9	11.2	11.2	11.2
<i>A. neumannii</i>	11.5	11.2	11.2	11.5	11.5	11.2
<i>A. nodosum</i>	9.0	8.7	8.7	9.0	9.0	9.0
<i>A. oblongoguttatum</i>	12.5	12.2	12.2	12.5	12.5	12.5
<i>A. ovale</i>	12.0	11.7	12.0	12.0	12.0	12.0

Table 2 continued

	<i>A. dubitatum</i> C. Arg.	<i>A. dubitatum</i> T. Arg.	<i>A. dubitatum</i> F. Uru.	<i>A. dubitatum</i> T. Uru.	<i>A. dubitatum</i> SP. Bra.	<i>A. dubitatum</i> RGS. Bra.
<i>A. parkeri</i>	13.9	13.6	13.6	13.9	13.9	13.9
<i>A. parvitarsum</i>	10.9	10.6	10.6	10.9	10.9	10.6
<i>A. pseudoconcolor</i>	15.3	15.0	15.0	15.3	15.3	15.3
<i>A. tigrinum</i>	12.2	11.8	11.9	12.2	12.2	11.9

C.Arg: Corrientes, Argentina; T.Arg: Tucumán, Argentina; F.Uru: Flores, Uruguay; T.Uru: Tacuembó, Uruguay; SP.Bra: São Paulo, Brazil; RGS.Bra: Rio Grande do Sul, Brazil

GenBank accession numbers: *A. dubitatum* C. Arg. (GU301910); *A. dubitatum* T. Arg. (GU301911); *A. dubitatum* F. Uru. (GU301912); *A. dubitatum* T. Uru. (DQ858955); *A. dubitatum* SP.Bra. (GU301914); *A. dubitatum* RGS.Bra. (GU301913); *A. boeroi* (FJ464416); *A. auriculatum* (FJ627951); *A. parvum* (EU306136); *A. triste* (AY498563); *A. aureolatum* (AF541254); *A. brasiliense* (FJ424399); *A. cejiense* (L34317); *A. calcaratum* (FJ424400); *A. coelebs* (FJ424408); *A. geayi* (EU805567); *A. incisum* (FJ424405); *A. longirostre* (FJ424401); *A. maculatum* (AY498560); *A. nodosum* (FJ424402); *A. oblongoguttatum* (FJ424407); *A. ovale* (AF541255); *A. parkeri* (EU805568); *A. parvitarsum* (AY498561); *A. pseudocolor* (AY628137); *A. tigrinum* (DQ342290)

tumidus in Río San José (GenBank accession number: GU301912) and those of adults of *A. dubitatum* was in all cases lower than 0.5%, supporting the standard morphological identification.

Discussion

As was expected according to previous bibliographical information, the data obtained in this study showed that the principal host for all parasitic stages of *A. dubitatum* is the capybara *H. hydrochaeris*, while other large mammals such as cattle, horse, *T. terrestris*, *M. gouazoubira*, *S. scrofa* and *T. pecari* only have a minor role as feed resource for this tick species. In this way, *H. hydrochaeris* can sustain the complete cycle of *A. dubitatum*. Considering that opossums and small and medium sized-rodents are important hosts for the immature stages in the life cycle of Neotropical *Amblyomma* species as *Amblyomma ovale* (Guglielmone et al. 2003b), *Amblyomma maculatum* (Barker et al. 2004), *Amblyomma tigrinum* (Nava et al. 2006), *Amblyomma parvum* (Nava et al. 2008a), *Amblyomma triste* (Venzal et al. 2008) and *Amblyomma fuscum* (Martins et al. 2009), the findings of larvae and nymphs on opossums (*D. albiventris* and *D. aurita*), Cricetidae rodents (*L. moltor*; *S. tumidus*) and the Chinchillidae rodent *L. maximus*, indicate that these small and medium-sized mammals could be alternative hosts for the immature stages of *A. dubitatum*. However, it is necessary to carry out ecological studies to evaluate if the interrelationship between those mammals and the preimagos of *A. dubitatum* is occasional or has some degree of relevance for the life cycle of this tick.

The results of this study show that this tick is associated to a restricted South American area that includes the Biogeographical provinces of Pampa, Chaco, Cerrado, Brazilian Atlantic Forest, Parana Forest and *Araucaria angustifolia* Forest, with most records present in the north-east of Argentina, south-east of Brazil, east of Paraguay and north half of Uruguay. Taking into consideration that *H. hydrochaeris* is distributed from Venezuela and Colombia to Uruguay and northeast of Argentina (Woods and Kilpatrick 2005), the distribution area of *A. dubitatum* is lesser than that of its principal host, suggesting that environmental variables rather than hosts determine the distributional ranges of *A. dubitatum* in South America. A similar conclusion was reached for other Neotropical *Amblyomma* species that feed on large mammals as *Amblyomma cajennense* (Estrada-Peña et al. 2004), *Amblyomma parvum* (Nava et al. 2008b) and *Amblyomma neumannii* (Nava et al. 2009b). Moreover, it is accepted for several tick species that factors such as climate and vegetation are more determinant for their distribution than hosts (Klompen et al. 1996; Estrada Peña 2001; Cumming 2002). Future studies should be focused on the identification of the ecological factors that limit the distribution of *A. dubitatum* in South America.

There is a finding of *A. dubitatum* on *T. terrestris* in Reserva Horco Molle, Tucumán Province, Argentina (Yungas Biogeographic province) (Zerpa et al. 2003). However, it is important to assert that there are not natural populations of *H. hydrochaeris* in this locality (Alvarez and Martinez 2006). Then, the records of females and nymphs of *A. dubitatum* on *T. terrestris* in Reserva Horco Molle probably is due to the fact that the infested specimen of *T. terrestris* cohabits under semi-captivity conditions with capybaras introduced artificially (Zerpa et al. 2003).

The genetic divergence among the 16S rDNA sequences of the ticks from Argentina, Brazil and Uruguay identified by means of morphological characters as *A. dubitatum*, was substantially low (0.0–0.8%). These levels of genetic variation in the sequences of 16S gene are usual at the intraspecific level for Neotropical species of the genus *Amblyomma*.

(Estrada-Peña et al. 2005; Venzal et al. 2005; Nava et al. 2006, 2008b, 2009b; Labruna et al. 2009). Therefore, the analysis of 16S rDNA sequences confirms the specific determination by means of morphological characters, and the taxonomic status of *A. dubitatum* along its distribution appears to be certain.

Taking into account that *H. hydrochaeris* has capacity to act as amplifier host of *Rickettsia rickettsii* (Souza et al. 2009), and that the co-infestation of *H. hydrochaeris* with *A. dubitatum* and the vector of *R. rickettsii* *A. cajennense* has usually been reported (Pacheco et al. 2007; Souza et al. 2009), it is important to study if *A. dubitatum* could be involved as an enzootic vector of this rickettsia species.

Acknowledgments We are grateful to INTA and Asociación Cooperadora INTA Rafaela for the financial support to SN, MM, AJM and AAG. We acknowledge the collaboration of P.M. Beldomenico and G. Aprile for sending tick samples.

References

- Almeida ATS, Daemon E, Faccini JLH (2001) Life cycle of female ticks of *Amblyomma cooperi* Nuttall & Warburton, 1908 (Acarı: Ixodidae) under laboratory conditions. Arq Bras Med Vet Zootec 53:316–320
- Alvarez MR, Martinez RA (2006) Familias Hydrochoeridae, Agoutidae, Dasyprotidae. In: Barquez RM, Díaz MM, Ojeda RA (eds) Mamíferos de Argentina: sistemática y distribución, Sociedad Argentina para el Estudio de los Mamíferos (SAREM), Tucumán (Argentina), pp. 210–212
- Amorim M, Pedro MVJ, Teixeira RHF, Gazeta GS, Serra Freire NM (2003) Ixodofauna de mamíferos na região de Bonito, Mato Grosso do Sul, Brasil. Res. 18º Congr. Bras. Parasitol., Rio de Janeiro, Brasil, p. 104
- Aragão HB (1908) Algumas novas espécies de carrapatos brasileiros. Braz Med 22:111–115
- Aragão HB (1911) Notas sobre ixodídas brasileiros. Mem Inst Oswaldo Cruz 3:145–195
- Aragão HB (1918) Notas ixodológicas. Rev Mus Paulista 10:375–417
- Aragão HB (1936) Ixodidas brasileiros e de alguns países limítrofes. Mem Inst Oswaldo Cruz 31: 759–843
- Arzua M, Onofrio VC, Barros-Battesti DM (2005) Catalogue of the tick collection (Acarı, Ixodidae) of the Museu de História Natural Capao da Imbuia, Curitiba, Paraná, Brazil. Rev Bras Zool 22:623–632
- Barker RW, Kocan AA, Ewing SA, Wettemann RP, Payton ME (2004) Occurrence of the gulf coast tick (Acarı: Ixodidae) on wild and domestic mammals in north-central Oklahoma. J Med Entomol 41:170–178
- Barros SLJ, Famadas KM, Lopes LMS, Serra Freire NM (1998) Revisão sobre parasitismo de Mammalia: Chiroptera por Acari: Ixodidae com registro de *Amblyomma cooperi* Nuttall & Warburton, 1907 em Phyllostomidae no Brasil. Entomol Vect 5:123–136
- Barros-Battesti DM, Arzua M, Bechara GH (2006) Carrapatos de importância médica-veterinária da região Neotropical: um guia ilustrado para identificação de espécies. Vox/ICTTD-3/Butantan, São Paulo
- Boero JJ (1945) Los ixodídeos de la República Argentina. Rev Med Vet (Buenos Aires) 26:1–10
- Camicas JL, Hervy JP, Adam F, Morel PC (1998) Les tiques du monde: nomenclature, stades décrits, hôtes, répartition (Acarida, Ixodida). ORSTOM, Paris
- Cumming GS (2002) Comparing climate and vegetation as limiting factors for species ranges of African ticks. Ecology 83:255–268
- da Fonseca F, Aragão H (1952) Notas de ixodologia. IV. Considerações sobre a nomenclatura do gênero *Amblyomma* do Brasil e países limítrofes. (Acarı: Ixodidae). Mem Inst Oswaldo Cruz 50:729–731
- de Souza CE, Calic SB, Camargo MC GO (2004) O papel de capivaras *Hydrochaeris hydrochaeris* na cadeia epidemiológica da febre maculosa brasileira. Rev Bras Parasitol Vet 13(1):203–205
- De Souza SSAL, de Souza CE, Rodrigues Neto EJ, do Prado AP (2006) Dinâmica sazonal de carrapatos (Acarı: Ixodidae) na mata ciliar de uma área endêmica para febre maculosa na região de Campinas, São Paulo, Brasil. Cienc Rur 36:887–891
- Estrada Peña A (2001) Forecasting habitat suitability for ticks and prevention of tick-borne diseases. Vet Parasitol 31:1–22
- Estrada Peña A, Venzal JM, Guglielmone AA (2002) *Amblyomma dubitatum* Neumann: description of nymph and redescription of adults, together with the description of the immature stages of *A. triste* Koch. Acarologia 42:323–333

- Estrada DA, Schumaker TTS, Souza CE, Neto EJR, Linhares AX (2006) Detecção de riquetsias em carapatos do gênero *Amblyomma* (Acarí: Ixodidae) coletados em parque urbano do município de Campinas, SP. Rev Soc Bras Med Trop 39:68–71
- Estrada-Peña A, Guglielmone AA, Mangold AJ (2004) The distribution and ecological “preferences” of the tick *Amblyomma cajennense* (Acarí: Ixodidae), an ectoparasite of humans and other mammals in the Americas. Ann Trop Med Parasitol 98:283–292
- Estrada-Peña A, Venzel JM, Mangold AJ, Cafrune MM, Guglielmone AA (2005) The *Amblyomma maculatum* Koch, 1844 (Acarí: Ixodidae: Amblyomminae) tick group: diagnostic characters, description of the larva of *A. parvitarsum* Neumann, 1901, 16S rDNA sequences, distribution and hosts. Syst Parasitol 60:99–112
- Evans DE, Martins JR, Guglielmone AA (2000) A review of the ticks (Acarí, Ixodida) of Brazil, their hosts and geographical distribution—1. The state of Rio Grande do Sul, southern Brazil. Mem Inst Oswaldo Cruz 95:453–470
- Famadas K, Lemos ERS, Coura JR, Machado RD, Serra Freire NM (1997) *Amblyomma cooperi* (Acarí: Ixodidae) parasitando humano em área de foco de febre maculosa, São Paulo—Brasil. Acta Parasitol Port 4:154
- Freire JJ (1972) Revisão das espécies da família Ixodidae. Rev Med Vet (Sao Paulo). 8:1–16
- Guedes E, Leite RC, Prata MCA, Pacheco RC, Walker DH, Labruna MB (2005) Detection of *Rickettsia rickettsii* in the tick *Amblyomma cajennense* in a new Brazilian spotted fever-endemic area in the state of Minas Gerais. Mem Inst Oswaldo Cruz 100:841–845
- Guglielmone AA, Nava S (2006) Las garrapatas argentinas del género *Amblyomma* (Acarí: Ixodidae): distribución y hospedadores. Rev Inv Agro (RIA) 35:135–155
- Guglielmone AA, Viñabal AE (1994) Claves morfológicas dicotómicas e información ecológica para la identificación de garrapatas del género *Amblyomma* Koch, 1844 de la Argentina. Rev Inv Agro (RIA) 25:39–67
- Guglielmone AA, Mangold AJ, Boero C, Piccinini A, Keirans JE (2002) Hallazgo de *Amblyomma cooperi* Nuttall & Warburton, 1907 en bovinos de Corrientes, Argentina. Vet Arg 19:124–125
- Guglielmone AA, Estrada Peña A, Keirans JE, Robbins RG (2003a) Ticks (Acarí: Ixodidae) of the neotropical zoogeographic region. Houten, Atalanta
- Guglielmone AA, Estrada-Peña A, Mangold AJ, Barros-Battesti DM, Labruna MB, Martins JR, Venzel JM, Arzua M, Keirans JE (2003b) *Amblyomma aureolatum* (Pallas, 1772) and *Amblyomma ovale* Koch, 1844 (Acarí: Ixodidae): DNA sequences, hosts and distribution. Vet Parasitol 113:273–288
- Guglielmone AA, Beati L, Barros-Battesti DM, Labruna MB, Nava S, Venzel JM, Mangold AJ, Szabó MJP, Martins JR, González Acuña D, Estrada-Peña A (2006) Ticks (Ixodidae) on humans in South America. Exp Appl Acarol 40:83–100
- Hall TA (1999) BioEdit: a user friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. Nucleic Acid Symp Ser 41:95–98
- Horta MC, Labruna MB, Pinter A, Linardi PM, Schumaker TTS (2007) *Rickettsia* infection in five areas of the state of São Paulo, Brazil. Mem Inst Oswaldo Cruz 102:793–801
- Ivanovich JC, Luciani CA (1992) Las garrapatas de Argentina. Asociación Argentina de Parasitología Veterinaria. Buenos Aires
- Joan T (1930) El amblyomma (sic) de Cooper y demás garrapatas de los carpinchos. 5^a Reun. Soc. Arg. Pat. Reg. Norte, octubre 1929, Jujuy, Argentina 2:1168–1179
- Jones EK, Clifford CM, Keirans JE, Kohls GM (1972) The ticks of Venezuela (Acarina: Ixodoidea) with a key to the species of *Amblyomma* in the Western Hemisphere. Brigh Young Univ Sci Bull Biol Ser 17:1–40
- Keirans JE, Brewster BE (1981) The Nuttall and British Museum (Natural History) tick collections: lectotype designations for ticks (Acarina: Ixodoidea) described by Nuttall, Warburton, Cooper and Robinson. Bull Br Mus Nat Hist 41:153–178
- Klompen JSH, WC BlackIV, Keirans JE, Oliver JH (1996) Evolution of ticks. Annu Rev Entomol 41: 141–161
- Labruna MB, Souza SIP (1999) Levantamento de fauna ixodológica através de armadilha de dióxido de carbono, em um parque ecológico no estado de São Paulo. An. XI Sem. Bras. Parasitol. Vet. Salvador, Bahia, Brasil, p. 87
- Labruna MB, de Paula CT, Lima TF, Sana DA (2002) Ticks (Acarí:Ixodidae) on wild animals from the porto-primavera hydroelectric power station area, Brazil. Mem Inst Oswaldo Cruz 97:1133–1136
- Labruna MB, Whitworth T, Horta MC, Bouyer DH, McBride J, Pinter A, Popov V, Gennari SM, Walker DH (2004a) *Rickettsia* species infecting *Amblyomma cooperi* ticks from an area in the state of São Paulo, Brazil, where Brazilian spotted fever is endemic. J Clin Microbiol 42:90–98

- Labruna MB, Pinter A, Teixeira RHF (2004b) Life cycle of *Amblyomma cooperi* (Acari: Ixodidae) using capybaras (*Hydrochaeris hydrochaeris*) as hosts. *Exp Appl Acarol* 32:79–88
- Labruna MB, Jorge RSP, Sana DA, Jácomo ATA, Kashivakura CK, Furtado MM, Ferro C, Perez SA, Silveira L, Santos TS, Marques SR, Morato RG, Nava A, Adania CH, Teixeira RHF, Gomes AAB, Conforti VA, Azevedo FCC, Prada CS, Silva JCR, Batista AF, Marvuló MFV, Morato RLG, Alho CJR, Pinter A, Ferreira PM, Ferreira F, Barros-Battesti DM (2005) Ticks (Acari: Ixodidae) on wild carnivores in Brazil. *Exp Appl Acarol* 36:149–163
- Labruna MB, Pacheco RC, Ataliba AC, Szabó MJP (2007) Human parasitism by the capibara tick, *Amblyomma dubitatum* (Acari: Ixodidae). *Entomol News* 118:77–80
- Labruna MB, Onofrio VC, Beati L, Arzua M, Bertola PB, Ribeiro AF, Barros-Battesti DM (2009) Redescription of the female, description of the male, and several new records of *Amblyomma parkeri* (Acari: Ixodidae), a South America tick species. *Exp Appl Acarol* 49:243–260
- Lemos ERS, Machado RD, Coura JR, Guimaraes MAA, Serra Freire NM, Amorim A, Gazeta GS (1997) Epidemiological aspects of the Brazilian spotted fever: seasonal activity of ticks collected in an endemic area in São Paulo, Brazil. *Rev Soc Bras Med Trop* 30:181–185
- Mangold AJ, Bargues MD, Mas-Coma S (1998) Mitochondrial 16S rRNA sequences and phylogenetic relationships of *Rhipicephalus* and other tick genera among Metastriata (Acari: Ixodidae). *Parasitol Res* 84:478–484
- Martins TF, Dantas-Torres F, Nieri-Bastos FA, Marcili A, de Siqueira DB, Aléssio F, da Silva JCR, Labruna MB (2009) Host records for the immature stages of *Amblyomma fuscum* (Acari: Ixodidae), a rare South American tick species. *Entomol News* (in press)
- Mastropaoletti M, Aprile G, Solis G, Beldomenico PM, Peralta JL, Guglielmone AA (2004) Primer registro de *Amblyomma dubitatum* Neumann 1899 (Acari: Ixodidae) en la provincia de Misiones (Argentina). *Revista FAVE* 3:67–70
- Monteiro CMO, Santos-Rosa L, Dabés L, Rodrigues AFSF (2004) Levantamento preliminar da ixodofauna da mata do Morro do Imperador Juiz de Fora-MG, Brasil. *Rev Bras Parasitol Vet* 13(1):315
- Morrone JJ (2006) Biogeographic areas and transition zones of Latin American and the Caribbean Islands based on the panbiogeographic and cladistic analyses of the entomofauna. *Annu Rev Entomol* 51: 467–494
- Nava S, Mangold AJ, Guglielmone AA (2006) The natural hosts of larvae and nymphs of *Amblyomma tigrinum* Koch, 1844 (Acari: Ixodidae). *Vet Parasitol* 140:124–132
- Nava S, Lareschi M, Rebollo C, Benítez Usher C, Beati L, Robbins RG, Durden LA, Mangold AJ, Guglielmone AA (2007) The ticks (Acari: Ixodida: Argasidae, Ixodidae) of Paraguay. *Ann Trop Med Parasitol* 101:255–270
- Nava S, Mangold AJ, Guglielmone AA (2008a) Aspects of the life cycle of *Amblyomma parvum* (Acari: Ixodidae) under natural conditions. *Vet Parasitol* 156:270–276
- Nava S, Szabó MPJ, Mangold AJ, Guglielmone AA (2008b) Distribution, hosts, 16S rDNA sequences and phylogenetic position of the Neotropical tick *Amblyomma parvum* (Acari: Ixodidae). *Ann Trop Med Parasitol* 102:409–425
- Nava S, Guglielmone AA, Mangold AJ (2009a) An overview of systematics and evolution of ticks. *Front Biosci* 14:2857–2877
- Nava S, Estrada-Peña A, Mangold AJ, Guglielmone AA (2009b) Ecology of *Amblyomma neumanni* (Acari: Ixodidae). *Act Trop* 111:226–236
- Oliveira KA, Oliveira LS CCA, Dias Silva A, Almeida MR, Almada G, Bouyer DH, Galvão MAM, Mafra CL (2008) Molecular identification of *Rickettsia felis* in ticks and fleas from an endemic area for Brazilian spotted fever. *Mem Inst Oswaldo Cruz* 103:191–194
- Oscherow EB, Bar ME, Milano AMF, Damborsky MP (2006) Presencia de garrapatas del género *Amblyomma* (Ixodidae) en áreas naturales protegidas. *Acta Bioquím Clín Latinoam* 3:185
- Pacheco RC, Pinter A, Ferreira PM, Ferreira M, Labruna MB (2004) Carrapatos infestando capivaras em cinco áreas do Estado de São Paulo. *Rev Bras Parasitol Vet* 13(1):315
- Pacheco RC, Horta MC, Moraes-Filho J, Ataliba AC, Pinter A, Labruna MB (2007) Rickettsial infection in capybaras (*Hydrochoerus hydrochaeris*) from São Paulo, Brazil: serological evidence for infection by *Rickettsia bellii* and *Rickettsia parkeri*. *Biomédica* 27:364–371
- Rohr CJ (1909) Estudos sobre ixódidas do Brasil. Gómes Irmao, Rio de Janeiro
- Santos Dias JAT (1958) Notes on various ticks (Acarina-Ixodoidea) in collection at some entomological institutes in Paris and London. *An Inst Med Trop* 15:459–563
- Sarmiento NF, Santa Cruz ACM, Comolli JA, Cayo D, Roux JP (2006) Aspectos morfológicos de *Amblyomma cooperi* Nuttal y Warburton 1908 (Arthropoda: Ixodidae) aislados de *Hydrochaeris hydrochaeris* en un criadero de Santo Tome (Corrientes). 1^a Jornada Nacional de Ectoparasitología Veterinaria. Corrientes, Argentina, p 38

- Sinkoc AL, Brum JGW, Muller G, Begrow A, Paulsen RMM (1997) Ocorrencia de Ixodidae parasitos de capivara (*Hydrochoerus hydrochaeris* Linnaeus, 1776) na Estação Ecológica do Taim, Rio Grande-RD, Brasil. Cienc Rur 27:119–122
- Sinkoc AL, Brum JGW, Moraes W, Crawshaw P (1998) Ixodidae parasitos de animais silvestres na regiao de Foz de Iguaçú, Brasil e Argentina. Arq Inst Biol 65:29–33
- Souza CE, Moraes-Filho J, Ogrezewalska M, Uchoa FC, Horta MC, Souza SSL, Borba RCM, Labruna MB (2009) Experimental infection of capybaras *Hydrochoerus hydrochaeris* by *Rickettsia rickettsii* and evaluation of the transmission of the infection to ticks *Amblyomma cajennense*. Vet Parasitol 161: 116–121
- Squire FA (1972) Entomological problems in Bolivia. PANS 18:249–268
- Szabó MPJ, Castro MB, Ramos HGC, Garcia MV, Castagnoli KC, Pinter A, Veronez VA, Magalhães GM, Duarte JMB, Labruna MB (2007) Species diversity and seasonality of free-living ticks (Acari: Ixodidae) in the natural habitat of wild marsh deer (*Blastocerus dichotomus*) in Southeastern Brazil. Vet Parasitol 143:147–154
- Tamura K, Dudley J, Nei M, Kumar S (2007) MEGA 4: molecular evolutionary genetics analysis (MEGA) software version 4.0. Mol Biol Evol 24:1596–1599
- Thompson JD, Higgins D, Gibson TJ (1994) CLUSTAL W: improving the sensitivity of progressive multiple sequence alignment through sequence weighting, position-specific gap penalties and weight matrix choice. Nucl Acids Res 22:4673–4680
- van der Heijden KM, Szabó MPJ, Matushima ER, Leite da Veiga M, Santos AA, Egami MI (2003) Valores hematológicos e identificação morfo-citoquímica de células sanguíneas de capivaras (*Hydrochoerus hydrochoeris*) parasitadas por carrapatos e capivaras livres de infestação. Acta Scientiarum. Anim Sci 25:43–150
- Venzal JM, Félix ML, Olmos A, Mangold AJ, Guglielmone AA (2005) A collection of ticks (Ixodidae) from wild birds in Uruguay. Exp Appl Acarol 36:325–331
- Venzal JM, Estrada-Peña A, Castro O, de Souza CG, Félix ML, Nava S, Guglielmone AA (2008) *Amblyomma triste* Koch, 1844 (Acari: Ixodidae): hosts and seasonality of the vector of *Rickettsia parkeri* in Uruguay. Vet Parasitol 155:104–109
- Vogelsang EG, Cordero EH (1940) Las garrapatas (Ixodidae) de Venezuela. Rev Med Vet Parasitol 2:71–76
- Woods CA, Kilpatrick CW (2005) Infraorder Hystricognathi Brandt, 1855. In: Wilson DE, Reeder DM (eds) Mammal species of the world: a taxonomic and geographic reference, 3rd edn. The Johns Hopkins University Press, Baltimore, pp 1538–1600
- Zerpa C, Venzal JM, López N, Mangold AJ, Guglielmone AA (2003) Garrapatas de Catamarca y Tucumán: estudio de una colección de hospedadores silvestres y domésticos. Revista FAVE 2:167–171