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

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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, Parana 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

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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 ypsilophorum* 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. ypsilophorum* 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; Estaçao 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 Amapa 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	*Hydrochoerus hydrochaeris*	F	Ivancovich and Luciani (1992)
	Colonia Benítez	27°19′S 58°57′W	*H. hydrochaeris*	MF	*Ibid.*
	Estancia La Amalia	27°31′S 59°08′W	*H. hydrochaeris*	MN	*Ibid.*
	Estancia Legua 40	27°02′S 59°17′W	*H. hydrochaeris*	MFN	*Ibid.*
	Ruta 90 km 1099	26°41′S 59°14′W	*H. hydrochaeris*	MFN	*Ibid.*
Corrientes	Arroyo Ayuí	28°16′S 56°18′W	*H. hydrochaeris*	MF	FAVE
	30 km to SW of Colonia Pellegrini	28°40′S 57°26′W	*H. hydrochaeris*	MFNL**	INTA
	Estancia Ayuí	28°37′S 57°32′W	*H. hydrochaeris*	MFN	Ivancovich and Luciani (1992)
	Estancia Curupí Caí	29°23′S 57°47′W	*H. hydrochaeris*	MFN	*Ibid.*
	Estancia El Aguacerito	29°11′S 57°55′W	*H. hydrochaeris*	MFN	*Ibid.*
	Estancia El tigre	29°02′S 58°12′W	*H. hydrochaeris*	MFN	*Ibid.*
	Estancia Juan Angel	28°41′S 57°08′W	*H. hydrochaeris*	MFN	*Ibid.*
	Estancia La Armonía	28°48′S 58°41′W	*H. hydrochaeris*	MFN	*Ibid.*
	Estancia Palmita	28°46′S 57°48′W	*H. hydrochaeris*	MFN	*Ibid.*
	Estancia Yuquerí	29°08′S 57°46′W	*H. hydrochaeris*	MFN	*Ibid.*
	Goya	29°08′S 59°16′W	Cattle	N	INTA
	Laguna del Iberá	28°32′S 57°10′W	*H. hydrochaeris*	MFN	Ivancovich and Luciani (1992)
	Mercedes	29°07′S 58°07′W	*H. hydrochaeris*	MNL	INTA
	Monte Caseros N	31°12′S 57°39′W	Cattle	N	Guglielmone 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	Oscherov et al. (2006)
	Rincon del Socorro	28°35′S 56°51′W	*Sus scrofa*	MF	FAVE
	Santo Tomé	28°33′S 56°02′W	*H. hydrochaeris*	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	*H. hydrochaeris*	MFN	FAVE
	Concordia	31°24′S 58°01′W	*H. hydrochaeris*	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	*Lagostomus maximus*	N	FAVE
	Parque Nacional El Palmar II	31°55′S 58°11′W	*H. hydrochaeris*	MN	*Ibid.*
	Villaguay	31°52′S 59°01′W	*H. hydrochaeris*	X	Boero (1945)
Formosa	Colonia El Alba	26°20′S 59°18′W	*H. hydrochaeris*	MF	Ivancovich and Luciani (1992)
	El Colorado INTA	26°24′S 59°22′W	*H. hydrochaeris*	MFNL	*Ibid.*
	Estancia Bañadero	25°57′S 59°10′S	*Tapirus terrestris*	F	*Ibid.*
	Isla Payaguá	26°45′S 58°15′W	*H. hydrochaeris*	F	*Ibid.*
Misiones	Colonia Andresito	25°40′S 54°01′W	*H. hydrochaeris*	MFNL	Mastropaolo et al. (2004)
Santa Fe	Romang	29°30′S 59°46′W	*H. hydrochaeris*	X	Guglielmone and Viñabal (1994)
	Saladero Cabral	30°53′S 60°02′W	*H. hydrochaeris*	MF	FAVE
Brazil					
Espírito Santo	Aracruz	19°49′S 40°16′W	*H. hydrochaeris*	MF	Almeida et al. (2001)
	Colatina	19°32′S 40°38′W	Free	F	CNC
	Nova Venécia	18°43′S 40°24′W	Free	MF	Oliveira et al. (2008)
	Pancas	19°13′S 40°51′W	Free	MF	CNC
Goias	Anapolis	16°18′S 48°59′W	*	X	Aragão (1936)
Mato Grosso	Margens Río Cuyabá	15°35′S 56°06′W	*	X	*Ibid.*
	Margens Río Guaporé	13°59′S 60°25′W	*	X	Aragão (1911)
Mato Grosso do Sul	Bonito Region	21°07′S 56°28′W	*H. hydrochaeris*	F	Amorim et al. (2003)
	Porto Primavera Area	21°24′S 52°31′W	*H. hydrochaeris*	MFN**	Labruna et al. (2002)

Table 1 continued

Province/state/department	Locality	Coordinates	Host	Stage	References
Minas Gerais	Benjamín Constant	21°57′S 42°53′W	*	X	Rohr (1909)
	Coronel Pacheco	21°35′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)
	Piráuba	21°17′S 43°02′W	*H. hydrochaeris*	MF	Aragão (1908)
	San Joao del Rey	21°08′S 44°15′W	*	X	Rohr (1909)
	Santa Barbara	19°58′S 43°25′W	*	X	Aragão (1936)
Pará	Ilha de Marajó	01°02′S 49°56′W	*	X	*Ibid.*
Paraná	Curitiba	25°24′S 49°19′W	*H. hydrochaeris*	MFL	Arzua et al. (2005)
	Guarapuava	25°23′S 51°27′W	*Tayassu pecari*	F	CNC
	Regiao de Foz de Iguaçu	25°30′S 54°09′W	*H. hydrochaeris*	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	*Ibid.*
	Iguassú	22°38′S 43°26′W	*	X	*Ibid.*
	Volta Redonda	22°31′S 44°07′W	*	X	Rohr (1909)
Rio Grande do Sul	Arroio Grande	32°12′S 53°05′W	*H. hydrochaeris*	MFN	Evans et al. (2000)
	Estaçao Ecológica Taim	33°26′S 53°16′W	*H. hydrochaeris*	MF	Sinkoc et al. (1997)
	Rio Grande	32°02′S 52°06′W	*H. hydrochaeris*	X	Evans et al. (2000)

Table 1 continued

Province/state/department	Locality	Coordinates	Host	Stage	References
	Santana do Livramento	30°53′S 55°32′W	*H. hydrochaeris*	MFNL	*Ibid.*
	Santa Vitoria do Palmar	33°31′S 53°22′W	*H. hydrochaeris*	F	Evans et al. (2000)
	Uruguaiana	29°45′S 57°05′W	*H. hydrochaeris*	X	Freire (1972)
São Paulo	Aracariguama	23°26′S 47°04′W	Free	MF	Labruna and Souza (1999)
	Barao Geraldo	22°48′S 47°05′W	*H. hydrochaeris*	MF	de Souza et al. (2004)
	Botucatu	22°53′S 48°26′W	*H. hydrochaeris*	MF	CNC
	Bragança Paulista	22°57′S 46°32′W	*H. hydrochaeris*	MF	*Ibid.*
	Bonfim Paulista	21°09′S 47°49′W	*H. hydrochaeris*	MF	Pacheco et al. (2007)
	Campinas	22°52′S 47°03′W	*H. hydrochaeris*, Free	MN	Estrada et al. (2006)
	Cordeirópolis	22°28′S 47°27′W	*H. hydrochaeris*	MF	Pacheco et al. (2007)
	Cosmorama	20°28′S 49°46′W	*H. hydrochaeris*	MF	CNC
	Cosmorama	20°28′S 49°46′W	*Rhea americana*	N	*Ibid*
	Franca	20°32′S 47°24′W	*H. hydrochaeris*	F	*Ibid.*
	Ibitinga	21°46′S 48°48′W	*H. hydrochaeris*	X	van der Heijden et al. (2003)
	Itu	23°15′S 47°22′W	*H. hydrochaeris*; Man	MFNL	Pacheco et al. (2004), Labruna et al. (2007)
	Jaguariúna	22°44′S 46°57′W	Free	MF	De Souza et al. (2006)
	Jordanésia	23°21′S 46°52′W	*Cerdocyon thous*	X	Labruna et al. (2005)
	Jundiai	23°11′S 46°52′W	*H. hydrochaeris*	MFN	Labruna et al. (2004a)
	Jundiai	23°11′S 46°52′W	*Mazama gouazoubira*; *Myocastor coypus*; *Allouata caraya*	N	*Ibid*
	Lorena	22°44′S 45°07′W	*	X	Aragão (1936)
	Mogi das Cruzes	23°38′S 46°11′W	*Didelphis aurita*	N	Horta et al. (2007)
	Monte Alegre do Sul	22°39′S 46°40′W	*H. hydrochaeris*	MF	Souza et al. (2004)
	São Bernardo do Campo	23°42′S 46°33′W	*H. hydrochaeris*	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	22°44′S 46°54′W	*Glossophaga soricina; H. hydrochaeris*; Man	MF	Famadas et al. (1997), Lemos et al. (1997), Barros et al. (1998)
	Pedreira	22°44′S 46°55′W	Free	MF	Labruna et al. (2004b)
	Pedreira	22°47′S 46°54′W	Free	MF	*Ibid*
	Pedreira	22°41′S 46°53′W	Free	MF	*Ibid*
	Piracicaba	22°43′S 47°38′W	*Didelphis albiventris* *H. hydrochaeris*	LN MFN	Pacheco et al. (2004), Horta et al. (2007)
	Ribeirao Grande	24°16′S 48°25′W	Man	M	Labruna et al. (2007)
	Río Piracicaba	22°43′S 47°37′W	*	X	Aragão (1936)
	Santa Cruz do Rio Pardo	22°23′S 40°38′W	Free	MF	CNC
	Sao Luis de Pirahytinga	23°15′S 45°18′W	*	X	Rohr (1909)
	Sao Paulo	23°32′S 46°37′W	*H. hydrochaeris*	MFN	Pacheco et al. (2007); CNC
	São Paulo	23°06′S 47°43′W	*H. hydrochaeris*	MFN	Pacheco et al. (2004)
	São Paulo, Parque Ecológico Tieté	23°07′S 47°43′W	*H. hydrochaeris*	MFN	*Ibid*
	Sorocaba	23°30′S 47°26′W	*H. hydrochaeris*	MF	CNC
	Teodoro Sampaio	22°32′S 52°10′W	*H. hydrochaeris*	MF	*Ibid.*
Paraguay					
Concepción	Puerto Cooper	23°03′S 57°43′W	*H. hydrochaeris*	MF	Nava et al. (2007)
Misiones	San Juan Bautista	26°40′S 57°09′W	*H. hydrochaeris*	X	*Ibid.*
Uruguay					
Canelones	INIA Las Brujas	34°40′S 56°20′W	*H. hydrochaeris*	MF	DPVURU
Durazno	La Paloma	32°43′S 55°36′W	*H. hydrochaeris*	M	DPVURU
Flores	Río San José	33°57′S 56°50′W	*Lundomys molitor*; *Scapteromys tumidus*	NL	

Table 1 continued

Province/state/department	Locality	Coordinates	Host	Stage	References
Rocha	Prox. Santa Teresa	34°00′S 53°35′W	*H. hydrochaeris*	MFN	*Ibid*.
Tacuarembó	Rincón da Vassoura	31°15′S 56°03′W	Man; Free	N	Guglielmone 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

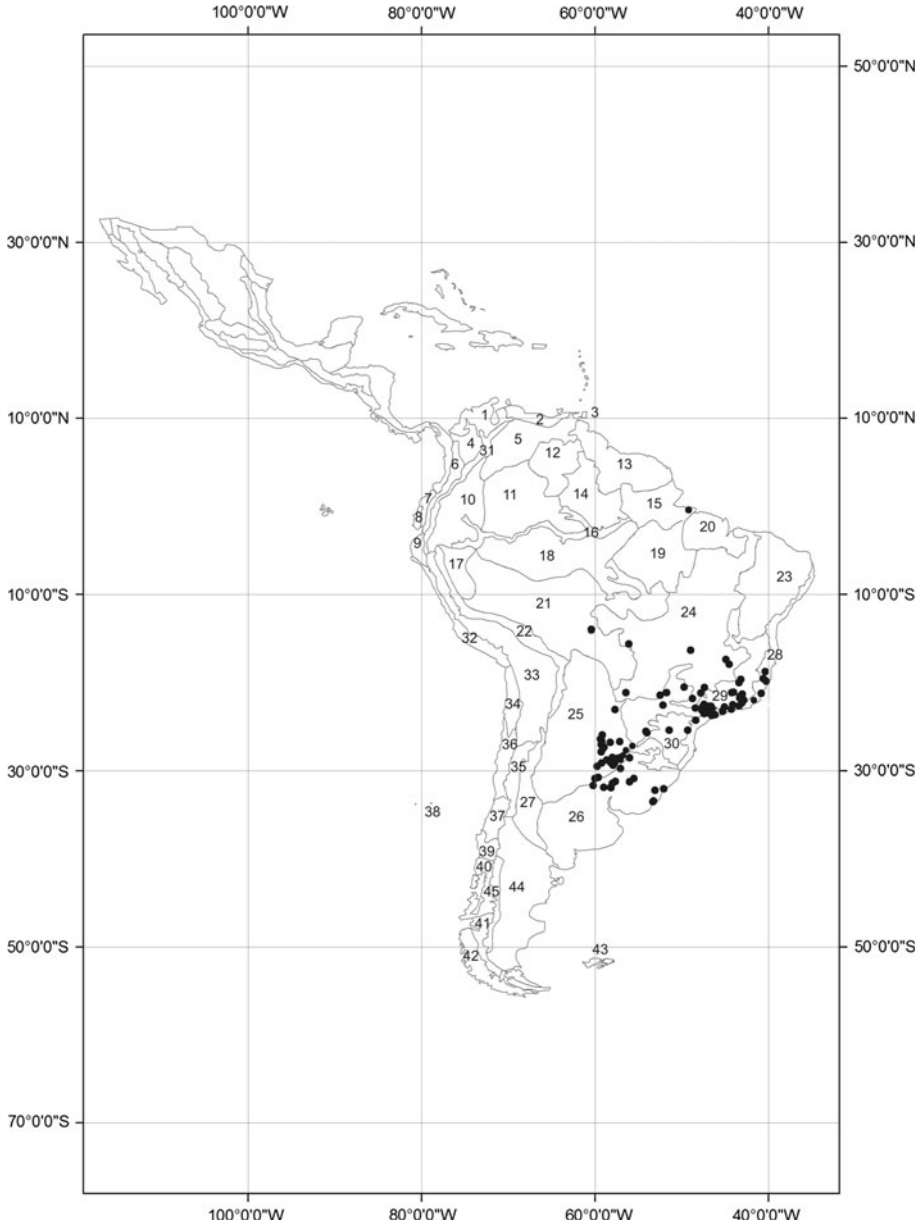

Fig. 1 The known distribution of *Amblyomma dubitatum* (*closed circle*) across the Biogeographic provinces of South America outlined by Morrone (2006). (1) Maracaibo; (2) Venezuelan Coast; (3) Trinidad & Tobago; (4) Magdalena; (5) Venezuelan Llanos; (6) Cauca; (7) Western Ecuador; (8) Arid Ecuador; (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

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

Table 2 continued

	A. dubitatum C. Arg.	*A. dubitatum* T. Arg.	*A. dubitatum* F. Uru.	*A. dubitatum* T. Uru.	*A. dubitatum* SP. Bra.	*A. dubitatum* RGS. Braz.
A. parkeri	13.9	13.6	13.6	13.9	13.9	13.9
A. parvitarsum	10.9	10.6	10.6	10.9	10.9	10.6
A. pseudoconcolor	15.3	15.0	15.0	15.3	15.3	15.3
A. tigrinum	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: Tacurembó, 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. auricularium* (FJ627951); *A. pseudoparvum* (FJ627952); *A. parvum* (EU306136); *A. triste* (AY498563); *A. aureolatum* (AF541254); *A. brasiliense* (FJ424399); *A. cajennense* (L34317); *A. calcaratum* (FJ424400); *A. coelebs* (FJ424408); *A. geayi* (EU805567); *A. incisum* (FJ424405); *A. longirostre* (FJ424401); *A. maculatum* (AY498599); *A. naponense* (FJ424406); *A. neumanni* (AY498560); *A. nodosum* (FJ424402); *A. oblongoguttatum* (FJ424407); *A. ovale* (AF541255); *A. parkeri* (EU805568); *A. parvitarsum* (AY498561); *A. pseudoconcolor* (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. molitor*; *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 neumanni* (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.

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