



## Relationships of South American marsupials (Didelphimorphia, Microbiotheria and Paucituberculata) and hard ticks (Acari: Ixodidae) with distribution of four species of *Ixodes*

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### Abstract

Historical information shows that South American marsupials are irrelevant hosts for South American hard ticks (Ixodidae Murray) of the genera *Haemaphysalis* Koch, *Rhipicephalus* Koch and *Dermacentor* Koch. Twenty two *Amblyomma* Koch species were occasionally found on Didelphimorphia Gill, but some records are doubtful (i.e., *A. dissimile* Koch, 1844) and only *A. fuscum* Neumann, 1907 appears to be a relevant parasite of this type of host. Twelve species of *Ixodes* Latreille were determined on these hosts, although one of them, *I. longiscutatus* Boero, 1944, is probably misidentified. Four species, *I. amarali* Fonseca, 1935b, *I. loricatus* Neumann, 1899, *I. luciae* Sènevet, 1940 and *I. venezuelensis* Kohls, 1953 are usual parasites of Didelphimorphia. These species (*I. venezuelensis* excluded) have adult ticks feeding mostly on Didelphidae Gray, and sub-adult ticks feeding mostly on Didelphidae and several species of sigmodontine rodents. All parasitic stages of *I. venezuelensis* were recorded from Didelphimorphia although rodents are also of importance for its life cycle. Records from marsupials and non-marsupial hosts show that *I. amarali* is established in eastern Brazil, and *I. venezuelensis* in Venezuela, Colombia, Panama and Costa Rica. The alleged southernmost record of *I. luciae* in Central Argentina was found to be erroneous and its southern limit is located in northwestern Argentina and its way northwards includes Bolivia, Peru, western Brazil, French Guiana, Surinam, Trinidad & Tobago, Panama, Guatemala, Belize and southern Mexico with unconfirmed but probably valid records for Ecuador, Colombia, Costa Rica, Nicaragua and Honduras. The distribution of *I. loricatus* has been historically considered to range from southern Argentina to southern Mexico but southernmost and northernmost records are now considered doubtful along with Venezuelan populations for this tick, while the only records for Panama and Colombia were based on wrong tick identifications. *Bona fide* populations of *I. loricatus* range from central-eastern Argentina and southern Uruguay to Paraguay up to north-eastern Brazil. *Dromiciops gliroides* Thomas, the only member of Microbiotheria Ameghino is the exclusive host of *Ixodes neuquenensis* Ringuet, 1947. There is only one record of tick infestation (*Ixodes jonesae* Kohls, Sonenshine & Clifford, 1969) of Paucituberculata Ameghino, indicating that these marsupials are of no apparent importance for maintenance of South American hard ticks. We speculate that the species of *Ixodes* feeding on Didelphimorphia and Sigmodontinae Wagner are a clade derived from ancestors feeding exclusively on Didelphidae that radiated after the invasion of South America by Sigmodontinae or their ancestors. *Ixodes neuquenensis* (established in south-western South America) is considered a relatively new species that radiated from *Ixodes* parasites of Sigmodontinae invaders in southern South America.

**Key words:** South American marsupials, hosts, ticks, Ixodidae, Metastrata, Prostrata, distribution, life history

### Introduction

Marsupials are currently divided into seven extant orders (Wilson & Reeder 2005; Voss & Jansa 2009), of which three are present in South America. Microbiotheria Ameghino and Paucituberculata Ameghino are exclusively Neotropical, while a third order, Didelphimorphia Gill, is distributed throughout the Neotropics and southern Nearctic. The first two orders are considered relictual because their current distribution and number of species has diminished in relation to the past and now comprises a total of seven species. Didelphimorphia are more ancient than

the other two orders but are still radiating with 18 genera and 95 extant species currently recognized (Gardner 2007; Voss & Jansa 2009); although it may not be a natural group (Goin 2003). Some authors consider the Paucituberculata and Didelphimorphia as the cohort Ameridelphia, and Microbiotheria and the four Australian orders in Australidelphia (Szalay 1982; Aplin & Archer 1987; Marshall *et al.* 1990; Amrine-Madsen *et al.* 2003; Cardillo *et al.* 2004); this question of ordinal relationship has important implications in order to understand the biogeographic history of living marsupials. The earliest undoubted metatherian (marsupial mammals and their nearest relative fossils) were found in the Early Cretaceous Period in Asia (Cifelli & Davis 2003; Luo *et al.* 2003) they then crossed from Siberia to Alaska, making their first appearance in the fossil record in the western part of North America (Johnson 2006). Some experts believe that metatherians arose in North America and moved southward into South America in the Cretaceous, and during the Cenozoic the southern continents seem to have served as major centers of metatherian diversification (Vaughan *et al.* 2010).

Ixodidae Murray (species of ticks with all postembryonic stages with the dorsum partially or totally covered by a chitinous scutum) contains 702 species in two groups: Prostriata represented by the 242 species of the genus *Ixodes* Latreille and Metastriata that contains 459 species in 11 extant and two extinct genera (Guglielmone *et al.* 2010b) plus *Ixodes fynbosensis* Apanaskevich, Horak, Matthee and Matthee 2010. However, French workers divide *Ixodes* into several genera (Camicas & Morel 1977; Camicas *et al.* 1998).

Prostriata appears to have evolved earlier than Metastriata (Black & Roehrdanz 1998; Jeyaprakash & Hoy 2009). Fossil evidence places the earliest emergence of Metastriata at 100 mya (Cretaceous) (Grimaldi *et al.* 2002) while molecular clock data placed its origin in the late Jurassic-early Cretaceous Periods (156-112 mya) (Jeyaprakash & Hoy 2009). There are no fossil records of that age or earlier for Prostriata but molecular clock data indicates that they preceded Metastriata by evolving between the late Jurassic Period (169 mya) and the upper Triassic Period (223 mya).

The genera *Amblyomma* Koch, *Dermacentor* Koch, *Haemaphysalis* Koch, *Ixodes* and *Rhipicephalus* Koch are currently present in South America, but *Dermacentor* and *Rhipicephalus* have no species exclusively South American, while the genus *Haemaphysalis* has one of 166 species exclusively South American, *Haemaphysalis cinnabarina* Koch, 1844. This species is known from two female ticks collected more than 170 years ago and Keirans and Restifo (1973) considered this species a synonym of the Palearctic *Haemaphysalis punctata* Canestrini and Fanzago, 1878, implying that the South American origin may be a consequence of mislabeling. However, Hoogstraal (1973) and Barros-Battesti *et al.* (2008) defend the validity of *H. cinnabarina*.

The only genera well represented in South America are *Ixodes* (Prostriata) with 24 species exclusively South American and *Amblyomma* (Metastriata) with 27 species only found in South America. This appears to be a clear indication that both *Amblyomma* and *Ixodes* were established in South America before its period of isolation from the late Cretaceous to the Pliocene (Benton 2009), and the remaining extant Metastriata evolved elsewhere in the late Cretaceous or later, or alternatively, evolution occurred in areas too remote to reach South America before it become separated from other land masses. This last scenario is probably true for *Haemaphysalis* ticks, with an alleged Oriental origin, but not for other genera that are considered of more recent origin. Balashov (1994, 2004) agrees in general terms with the statement above but considers the most probable origin of *Haemaphysalis* was Southeast Asia (Oriental Region) during the Paleocene Period when South America was still isolated. However, this theory still needs confirmation and we do not rule out an earlier origin of *Haemaphysalis*.

Members of alleged old lineages of Ixodidae (*Ixodes*, *Amblyomma*) and South American marsupial have shared territories for tens of millions of years but we are unaware of any analyses of their relationships. Therefore, a review was performed with the aim to obtain information for a better understanding of their relationships and its importance for hard tick life history in South America.

## Material and methods

Literature information of ixodid ticks feeding on marsupials in South America was compiled, but non-South American Neotropical records are also included, while Nearctic records on *Didelphis virginiana* Kerr (the only marsupial established in the Nearctic Region) are excluded. Ticks species are listed in alphabetical order with notes on distribution and hosts, according to the order of marsupials. Classification of marsupials follows Voss and Jansa (2009). The names of marsupials and names of other types of hosts are maintained according to the author from

whom the information was obtained, but whenever known the actual name is included between brackets. To this aim we followed Wilson and Reeder (2005), Gardner (2007) and Voss and Jansa (2009), plus Weksler *et al.* (2006) for oryzomyine rodents and synonyms for the genus *Necomys* Ameghino in D'Elía *et al.* (2008). Additionally, references are made when localities for valid species of hosts are out of the usual distribution with notes for the most relevant records. This is especially important for the genera *Didelphis* and *Philander*, because there are several records where the original hosts are questioned; all these proposals are derived from the study of Cerqueira and Tribe (2007) and Patton and Silva (2007).

Data for each species of tick include comments, country (in bold letters), main administrative division, locality and its coordinates, tick stages, hosts, references and further comments if appropriate. Especially relevant records are further commented upon under a note for the corresponding species of tick. Repeated records for same host, tick stages and locality were considered as one even if they have different dates. Literature information where hosts for ticks were broadly defined (Marsupialia, marsupials, opossums) and references that exclude tick stages found on marsupials were not considered for this study, but some of them, as well as other records, are included for the corresponding tick species when relevant (i.e., only record on South American marsupials for a given species or country). The following abbreviations are applied for tick stages: A (adult tick with no sex identification), M (male), F (female), N (nymph), L (larva), while LU= locality unknown.

The distribution of the four species of *Ixodes* found usually found on marsupials was analyzed. To this aim records on non-marsupial or undetermined hosts in countries or localities where these species of ticks have not been found on marsupials are included after the data on marsupial hosts under the heading "Additional geographical information from parasitism on non-marsupial or undetermined hosts". For this part of the study we emphasized localities where these tick species have been collected and the information on non-marsupial hosts is not exhaustive. Additionally, specimens from the southernmost record of *Ixodes luciae* Sénevet, 1940 in Argentina were revised and reclassified. Information on the only alleged record of *Ixodes loricatus* Neumann, 1899 in Panama obtained by Valeria C. Onofrio is also included in the study as well as a reevaluation of an unpublished alleged record of *I. loricatus* for Colombia. Results on this topic are included in notes for the corresponding species of ticks and country.

Records for the two species of *Ixodes* ticks most frequently found on South American marsupials were tabulated according to tribes and species of marsupial hosts to present a general picture of host usage. No attempts were made for statistical analysis of host distribution because data are relatively scanty and there exists lack of information on host and tick densities as well as trapping bias that may render a distorted picture beyond any statistically significant figures. Chi-square distribution was used for comparison of proportions of records of marsupials in relation to the total Neotropical records for tick genera. The information for this part of the work has been obtained from a compilation performed by one of the authors (AAG) that is available upon request; all references on number of records thereafter exclude date repetitions for the same locality and host. The information for records on marsupials and non-marsupial hosts of ticks whose stages on hosts are known were used to depict the distribution of the four species (all *Ixodes*) that were found to be relevant parasites of Didelphimorphia.

## Results

### Didelphimorphia: Didelphidae Gray (only family for this order)

1) *Amblyomma aureolatum* (Pallas, 1772) is a South American tick whose adults are mostly found on Carnivora Bowdich, while most records for subadult ticks are from birds (Guglielmone *et al.* 2003c).

**Unknown South American country**, M on *Didelphis* sp. (Guglielmone *et al.* 2003c).

**Brazil**, Río Grande do Sul, Pelotas (31°46'S 52°20'W), M on *Didelphis albiventris* Lund (Muller *et al.* 2005).

Santa Catarina, Area de Proteção Ambiental do Anhatomirim (27°25'S 48°34'W), MF on *Didelphis aurita* Wied-Neuweid; Ilha de Ratonas Grande (27°29'S 48° 34'W), MF on *D. aurita*; Ilha de Santa Catarina (27°43'S 48°31'W), MF on *D. aurita* (Salvador *et al.* 2007).

2) *Amblyomma auricularium* (Conil, 1878) is a Neotropical and Nearctic tick species prone to feed on Cingulata Illiger (Guglielmone *et al.* 2003a).

**Brazil.** There is a Brazilian record for *A. auricularium* on *Lutreolina crassicaudata* Desmarest but tick stages found on hosts were not determined (Linardi *et al.* 1991).

**Panama,** LU, MF on *Didelphis marsupialis* Linnaeus; LU, MFNL on *Philander opossum* (Linnaeus) (Fairchild *et al.* 1966).

3) *Amblyomma cajennense* (Fabricius, 1787) is a Neotropical and Nearctic tick species with an ample tetrapod host range and locality records (1435 records for the whole Neotropical Region) but the name is considered to represent a tick species group (Lorenza Beati personal communication).

**Argentina,** Chaco, Riacho El Correntino (26°41'S 59°14'W), N on *D. albiventris*.

Formosa, El Colorado INTA (26°19'S 59°21'W), N on *L. crassicaudata* (Ivancovich & Luciani 1992).

**Brazil,** Mato Grosso do Sul, Campo Grande (20°27'S 54°36'W), A on *D. albiventris* (Costa *et al.* 2002).

Rio de Janeiro, Seropédica (22°44'S 43°42'W), N on *D. aurita* (Santos Abel *et al.* 2000).

Santa Catarina, Ilha de Ratoes Grande (27°29'S 48° 34'W), MFN on *D. aurita* (Salvador *et al.* 2007).

Sao Paulo, Caçapava (23°06'S 45°42'W), N on *Didelphis* sp.; Campinas (22°54'S 47°04'W), N on *Didelphis* sp. (Souza *et al.* 2006), A on *D. albiventris* (Souza & Souza, 2008); Jaguarina (22°40'S 46°59'W), N on *Didelphis* sp.; Monte Alegre do Sul (22°39'S 46°40'W), AN on *Didelphis* sp. (Souza *et al.* 2006); Pedreira (22°44'S 46°57'W), AN on *D. marsupialis* (Lemos *et al.* 1997, but the host is probably *D. aurita*); Piracicaba (22°43'S 47°38'W), NL on *D. albiventris* (Pérez *et al.* 2008); Porto Martin (22°39'S 48°22'W), N on *D. aurita* (Aragão 1918).

**Colombia** is included in the list of *A. cajennense* feeding on marsupials, but no tick stages found on hosts are provided by Wells *et al.* (1981).

**Mexico,** Tabasco, Frontera (18°32'N 92°38'W), N on *Didelphis* sp. (Keirans 1982).

**Panama,** LU, A on *Didelphis* sp. (Fairchild *et al.* 1966) but the host should be *D. marsupialis* because it is the only species of this genus found in Panama (Wilson & Reeder 2005).

4) *Amblyomma coelebs* Neumann, 1899 is basically a Neotropical tick species with a few records in the southern Nearctic. Adult ticks are prone to feed on Perissodactyla Owen (Guglielmone *et al.* 2003b).

**Brazil,** LU, N on *D. albiventris* (Labruna *et al.* 2005a).

5) *Amblyomma dissimile* Koch, 1844 is a Nearctic and Neotropical species usually feeding on Amphibia Linnaeus and Squamata Oppel with sporadic findings on Mammalia Linnaeus (Guglielmone & Nava 2010b).

**Brazil,** Pernambuco, Reserva Biológica (08°39'S 38°01'W), N on *Monodelphis domestica* Wagner, N on *D. albiventris* (Botelho *et al.* 2002), but these records were found unconvincing by Guglielmone and Nava (2010b) because the amphibian-squamatan *A. dissimile* was the only tick found on rodents and marsupials after two months of work and capture of 83 mammals recognized as hosts for several species of ticks.

6) *Amblyomma dubitatum* Neumann, 1899 is an exclusive South American species. The usual host for all tick stages is the caviid rodent *Hydrochoerus hydrochaeris* (Linnaeus) (Nava *et al.* 2010).

**Brazil,** São Paulo, Mogi das Cruzes (23°31'S 46°12'W), N on *D. albiventris* and-or *D. aurita* (Horta *et al.* 2007); Piracicaba (22°43'S 47°38'W), NL on *D. albiventris* (Pérez *et al.* 2008).

7) *Amblyomma fuscum* Neumann, 1907 is an exclusive South American species whose adults feed on a variety of hosts while immature stages have been found on rodents and marsupials (Barros-Battesti *et al.* 2005; Martins *et al.* 2010).

**Brazil,** Pernambuco, Paudalho (07°53'S 35°10'W), N on *D. aurita* and *D. albiventris*; São Lourenço da Mata (08°00'S 35°01'W), N on *D. albiventris*; Tamandaré (08°45'S 35°06'W), N on *D. albiventris* (Martins *et al.* 2010).

São Paulo, Guarujá (23°59'S 46°16'W), NL on *D. aurita* (Martins *et al.* 2010); Iguapé (24°42'S 47°33'W), N on *D. aurita* (Barros-Battesti *et al.* 2005); Serra do Mar State Park (23°52'S 46°26'W), N on *D. aurita* (Sabatini *et al.* 2010).

8) *Amblyomma geayi* Neumann, 1899 is a Neotropical species non-exclusively South American known mainly from adult ticks feeding on Pilosa Flower: Bradypodidae Gray and Rodentia Bowdich: Erethizontidae Bonaparte (Guglielmone *et al.* 2003b).



**Panama**, LU, MF on *D. marsupialis*, N on *Caluromys derbianus* (Waterhouse) (Fairchild *et al.* 1966).

9) *Amblyomma humerale* Koch, 1844 is a species found only in South America because records for Central America and Nearctic Region are considered misidentifications as discussed in Labruna *et al.* (2002a), who also state that the usual hosts for adult ticks are Testudines Linnaeus: Testudinidae Gray, while subadult ticks show a more ample host range than adult ticks. Differential diagnoses with *Amblyomma crassum* Robinson, 1926 and *Amblyomma sabanerae* Stoll, 1894 is difficult (Guglielmone *et al.* 2003b).

**Brazil**, Rondônia, Jamari River (10°17'S 63°14'W), N on *D. marsupialis* (Labruna *et al.* 2002a).

10) *Amblyomma incisum* Neumann, 1906 is an exclusive South American tick whose adults are usually found on Perissodactyla: Tapiridae Gray, redescribed convincingly by Labruna *et al.* (2005b)

**Brazil**. There are records of *A. incisum* on South American marsupials for this country in Barros-Battesti (2008) but tick stages found on hosts are not provided.

11) *Amblyomma maculatum* Koch, 1844 is a Neotropical-Nearctic tick species very close morphologically to *Amblyomma triste* Koch, 1844, that parasitizes an ample range of hosts (Barker *et al.* 2004; Estrada-Peña *et al.* 2005).

**Venezuela** is included in the range of *A. maculatum* by Díaz-Ungría (1957) who mentions its presence on Didelphimorphia in Venezuela, but the tick stages found on them were not provided.

12) *Amblyomma oblongoguttatum* Koch, 1844 feeds on different types of hosts from the southern Neartic into the Neotropical Region reaching Bolivia and Brazil (Guglielmone *et al.* 2003b).

**Panama**, LU, A on *Chironectes minimus* (Zimmermann) (Fairchild *et al.* 1966).

13) *Amblyomma ovale* Koch, 1844 is a Nearctic and Neotropical species whose adult ticks are usually found on Carnivora Bowdich (Canidae Fischer and Felidae Fischer de Waldheim), and to a lesser extent on Perissodactyla: Tapiridae apart from several findings on a variety of hosts (Guglielmone *et al.* 2003c).

**Central or South America country**, LU, NL on *Didelphis* sp., N on *D. albiventris* and *Marmosa robinsoni* Bangs (Guglielmone *et al.* 2003c).

**Brazil**. Barros-Battesti (2008) registers the presence of marsupials infested with *A. ovale*, but the tick stages found on hosts are not provided.

**Colombia**. There is a vague record of *A. ovale* on “marsupials” by López and Parra (1985).

14) *Amblyomma pacae* Aragão, 1911 is a Neotropical species distributed beyond South America whose usual hosts for adult ticks are Rodentia: Cuniculidae Miller and Gildney, although records on other types of hosts are not unusual (Guzmán Cornejo *et al.* 2006a).

**Brazil**, Rondônia, LU, N on *D. marsupialis* (Labruna *et al.* 2005a).

15) *Amblyomma parvum* Aragão, 1908a is a Neotropical species. Adult ticks have an ample host range, but Rodentia: Caviidae Fischer de Waldheim are the usual hosts for their larvae and nymphs (Nava *et al.* 2008).

**Argentina**, Formosa, El Colorado INTA (26°19'S 59°21'W), NL on *D. albiventris* (Ivancovich & Luciani 1992).

16) *Amblyomma pseudoconcolor* Aragão, 1908b is a South American species whose usual hosts are Cingulata: Dasypodidae Gray (Guglielmone *et al.* 2003a).

**South America**, Guglielmone *et al.* (2003a) register the parasitism of males of *A. pseudoconcolor* on *Philander* sp. without any additional data.

**Argentina**, Formosa, El Colorado (26°18'S 59°23'W), N on *D. albiventris* (Ivancovich 1973).

17) *Amblyomma romitii* Tonelli-Rondelli, 1939 had been considered a junior synonym of *A. extraoculatum* Neumann, 1899, but was definitively resurrected by Barros-Battesti *et al.* (2007). Santos Dias (1955) treat as erroneous the labeling of Singapore for the only known specimen of *A. extraoculatum* because he regarded *A. romitii* as a

junior synonym of the former, but *A. romitii* is now considered an exclusive South American tick whereas *A. extraoculatum* is considered an Oriental species. Most records are from Rodentia: Caviidae.

**Venezuela**, Bolívar, South-East of Ciudad Bolívar (06°52'N 63°29'W), M on *D. marsupialis* (Jones *et al.* 1972, who originally named this tick as *A. extraoculatum*).

18) *Amblyomma sabanerae* Stoll, 1894 is basically a parasite of Testudines with few records on other types of hosts with a Neotropical range from southern Mexico to Colombia. This species is very close morphologically to *A. cras-sum* and *A. humerale* (Fairchild *et al.* 1966; Guglielmo *et al.* 2003b).

**Panama**, Panamá, LU, M on *M. robinsoni* (Fairchild *et al.* 1966).

19) *Amblyomma scutatatum* Neumann, 1899 is a Neotropical species non-exclusively South American that usually feeds on reptiles (Guglielmo *et al.* 2003b).

**Brazil**, LU, N on *Didelphys* (sic) *pusilla* Desmarest (= *Thylamys pusillus* (Desmarest) (Neumann 1899)). The host in Neumann (1899) is probably wrong because Brazil is out of the range of *T. pusillus* (Wilson & Reeder 2005). Most probably the host is *Thylamys karimii* (Petter) (Giarla *et al.* 2010).

20) *Amblyomma tigrinum* Koch, 1844 is a Neotropical species with adults feeding mostly on Carnivora: Canidae, nymphs on Rodentia: Caviidae and larvae with a more ample range of hosts (Nava *et al.* 2006).

**Paraguay**, Massi Pallarés and Benítez Usher (1982) report infestation of “marsupials” with sub-adults of *A. tigrinum*. We consider these records doubtful because they were done long before the description of these stages by Estrada-Peña *et al.* (1993), who stress the difficulties to separate morphologically the larva and nymph of *A. tigrinum* from the same stages of related species (Estrada-Peña *et al.* 1993, 2005).

21) *Amblyomma triste* Koch, 1844, a Neotropical and Nearctic tick species (Guzmán-Cornejo *et al.* 2006b) whose larvae and nymphs are mainly collected from Cricetidae Fischer: Sigmodontinae Wagner and Caviidae, but to a much lesser extent on birds (Nava *et al.* 2011).

**Brazil**, São Paulo, Pedreira (22°44'S 46°57'W), A on *D. marsupialis* (Lemos *et al.* 1997, but the host is probably *D. aurita*).

**Uruguay**, LU, NL on *Monodelphis dimidiata* (Wagner) (Venzal *et al.* 2008a).

22) *Amblyomma varium* Koch, 1844 is a Neotropical species non-exclusively South American that usually feeds on Pilosa: Bradypodidae-Megalonychidae Ameghino (Onofrio *et al.* 2008).

**Panama**, Panamá, Canal Zone nearby Panamá City (08°57'N 79°32'W), F on *D. marsupialis* (Fairchild *et al.* 1966).

23) *Haemaphysalis leporispalustris* (Packard, 1869) is established in the Nearctic and Neotropical Regions, parasitizing usually Lagomorpha Brandt: Leporidae Fischer, although it was also found on an ample range of hosts.

**Colombia**, Bolívar, Socorro (09°14'N 74°25'W), N on *Metachirus nudicaudatus* (Geoffroy) (Kohls 1960).

**Costa Rica**. Campbell *et al.* (1979) register the presence of *H. leporispalustris* infesting Didelphimorphia in this country but tick stages found on hosts are not stated.

24) *Ixodes affinis* Neumann, 1899 is a Nearctic and Neotropical tick species, but there is confusion about the presence (and hosts) of *I. affinis* in the southern range of its distribution because they may represent *Ixodes aragaoi* Fonseca, 1935a or *Ixodes pararicinus* Keirans and Clifford, 1985 as discussed in Guglielmo *et al.* (2003b). Therefore, data below should be considered tentative. See also *I. aragaoi* for unjustified synonym with *I. affinis*.

**Panama**, Colón, Piña (09°16'N 80°03'W), MF on *D. marsupialis* (Fairchild *et al.* 1966).

25) *Ixodes amarali* Fonseca, 1935b is a South American tick species whose adults are mostly found on Didelphimorphia and to a lesser extent on sigmodontin rodents, but most nymphs are found on Sigmodontinae (Barros-Bat-testi & Knysak 1999).

**Brazil**, LU in the northeastern area of the country, F on *Monodelphis domestica* (Wagner) (Barros-Battesti & Knysak 1999).

Ceará, São Benedito (04°02'S 40°45'W), F on *D. albiventris* (Barros-Battesti & Knysak 1999).

Paraíba, Princesa Isabel (07°44'S 37°59'W), F on *M. domestica* (Fonseca 1958).

Pernambuco, Pesqueira (08°21'S 36°43'W), F on *M. domestica* (Fonseca 1958); Triunfo (07°49'S 38°06'W), FNL on *M. domestica* (Barros-Battesti & Knysak 1999).

Rio de Janeiro, Seropedica (22°42'S 43°42'W), F on *Didelphis* sp. (Faccini *et al.* 1999, but the host is probably *D. aurita*).

#### Additional geographical information from parasitism on non-marsupial hosts

**Brazil**, Alagoas, Anadias (09°41'S 36°18'W), N on Rodentia; Palmeira dos Índios (09°24'S 36°37'W), N on Rodentia (Barros-Battesti & Knysak 1999).

Ceará, Viçosa (04°27'S 37°47'W), N on Rodentia (Barros-Battesti & Knysak 1999).

Minas Gerais, Belo Horizonte (19°55'S 43°56'W), F on *Bolomys lasiurus* (Lund) (= *Necromys lasiurus* (Lund)), F on *Oryzomys subflavus* (Wagner) (= *Cerradomys subflavus* (Wagner)) (Botelho and Linardi 1996); Guaraciaba (20°33'S 43°00'W), N on Rodentia (Barros-Battesti & Knysak 1999); Ouro Preto (20°23'S 43°30'W), N on *Oligoryzomys microtis* (Allen) (Barros-Battesti & Knysak 1999). The last host is mainly established in the Amazonian (Wilson & Reeder 2005; Oliveira & Bonvicino 2006) and the actual host is most probably different to *O. microtis*.

Pernambuco, Bom Conselho (09°09'S 36°41'W), N on *O. subflavus* (Wagner) (= *C. subflavus* (Wagner)); Garanhuns (08°53'S 36°29'W), FNL on *O. subflavus* (= *C. subflavus*) (Barros-Battesti & Knysak 1999).

26) *Ixodes aragaoi* Fonseca, 1935a, is a South American species very close to *Ixodes pararicinus* that is found on a variety of hosts (Guglielmone *et al.* 2003b). Durden and Keirans (1996) and Guzmán-Cornejo and Robbins (2010), among others, consider *I. aragaoi* to be a synonym of *I. affinis* but this is unjustified as discussed in Onofrio *et al.* (2009).

**Brazil**. Pinter *et al.* (2005) register the presence of *I. aragaoi* sub-adults on “marsupials”.

27) *Ixodes boliviensis* Neumann, 1904 is very close to *Ixodes diversifossus* Neumann, 1899 (Nearctic distribution); this last name will prevail if they are demonstrated to be synonyms. Under the current conditions *I. boliviensis* is a Neotropical species found on a vast array of hosts but more often on carnivores from southern Mexico to Bolivia (Guglielmone *et al.* 2003b).

**Panama**, Chiriqui, LU, F on *D. marsupialis* (Fairchild *et al.* 1966).

**Colombia**, Boyacá, Muzo (05°32'N 74°06'W), N on *D. marsupialis* (Osorno Mesa 1942, who states that the tick found is near to *I. boliviensis*).

28) *Ixodes fuscipes* Koch, 1844 is a South America species found usually on rodents (Guglielmone *et al.* 2003b).

**Brazil**, Santa Catarina, Florianópolis (27°36'S 48°33'W), N on *L. crassicaudata* (Arzuza *et al.* 2005).

29) *Ixodes lasallei* Méndez Arocha and Ortiz, 1958 is a South American tick species prone to feed on rodents (Guglielmone *et al.* 2003b).

**Venezuela**, Amazonas, Cerro La Neblina (00°48'N 66°00'W), MFNL on *Marmosa demerarae* Thomas (Guerrero 1996); Río Cunucunuma at North-North West of La Esmeralda (03°39'N 65°21'W), N on *P. opossum* (Jones *et al.* 1972). The last host is probably *Philander mondolfi* Lew, Pérez-Hernández and Ventura, and surely is not *P. opossum* because there are no Venezuelan populations of this species (Patton & Silva 2007).

30) *Ixodes longiscutatus* Boero, 1944 is a species found only in South American whose ecology need of further studies, but Sigmodontinae appears to be the most relevant host for its larvae and nymphs (Venzal *et al.* 2008b).

**Argentina**, Misiones, Ruta 14 and Río Victoria (26°57'S 54°27'W), F on *P. opossum* (= *Philander frenatus* (Olfers) (Ivancovich & Luciani 1992), but this record is considered doubtful by Venzal *et al.* (2008b).

31) *Ixodes loricatus* Neumann, 1899 is a Neotropical species with adult ticks usually found on South American didelphimorphs. Relevant hosts for larvae and nymphs are marsupials and sigmodontin rodents. All tick stages of *I. loricatus* were considered to be highly specific to Didelphidae (Hoogstraal & Aeschlimann 1982), but Nava *et al.*

(2004) clearly show that rodents are important for its life cycle. This study revealed that in the southern range of the distribution of *I. loricatus* adults were only found on Didelphidae and larvae and nymphs on Sigmodontinae.

**Argentina**, LU, MF on *Didelphis paraguayensis* Allen (= *D. albiventris*) (Aragão 1935).

Buenos Aires, LU, AN on *Didelphis azarae* Temminck (= *D. albiventris*) and *L. crassicaudata* (Mauri & Navone 1988), F on *Didelphis* (sic) *azarai* (sic) Temminck (= *D. albiventris*) (Neumann 1910, who previously classified this tick as *I. angustus* Neumann, 1889, and this error has been repeated until recently by several authors but *I. angustus* is a Nearctic-Palaearctic species); Delta del Paraná (33°43'S 59°15'W), MF on *L. crassicaudata* (Keirans 1982); Delta del Paraná INTA (34°25'S 58°35'W), MFN on *D. albiventris*, MFN on *L. crassicaudata* (Ivancovich & Luciani 1992), which is a controversial record for ticks classified first as *Ixodes brunneus* Koch, 1844, and then as *I. luciae* as discussed in the note below; La Balandra (34°56'S 57°42'W), F on *L. crassicaudata* (Nava *et al.* 2004).

Chaco, Campo Bermejo (26°38'S 59°03'W), F on *L. crassicaudata*; Campo Winter (26°44'S 59°17'W), MF on *D. albiventris* (Ivancovich & Luciani 1992), MFN on *L. crassicaudata* (Ivancovich 1973); Colonia Benítez INTA (27°19'S 58°56'W), ML on *D. albiventris*; Estancia La Aurora (26°44'S 58°59'W), F on *D. albiventris* (Ivancovich & Luciani 1992); Ruta 90 and Río de Oro (26°25'S 59°23'W), MFN on *D. albiventris* (Ivancovich 1973); General José de San Martín (26°32'S 59°21'W), F on *L. crassicaudata* (Ivancovich & Luciani 1992).

Córdoba, Morteros (30°42'S 62°00'W), MF on *D. albiventris* (Guglielmone *et al.* 2007a).

Corrientes, Corrientes (27°28'S 58°50'W), FL on *D. albiventris* (Gómez *et al.* 2000).

Formosa, Colonia El Colorado (26°18'S 59°24'W), MF on *L. crassicaudata*; Colonia Villafañe (26°12'S 59°03'W), M on *D. albiventris*; El Colorado (26°19'S 59°23'W), F on *D. albiventris*; El Colorado INTA (26°19'S 59°21'W), MF on *D. albiventris*, MFNL on *L. crassicaudata*, F on *P. opossum* (= *P. frenatus*); Laguna Blanca (25°08'S 58°15'W), F on *P. opossum* (= *P. frenatus*) (Ivancovich & Luciani 1992).

Misiones, Cuartel Victoria (26°44'S 54°20'W), F on *D. albiventris* (Ivancovich & Luciani 1992).

Salta, LU, M on *D. paraguayensis* (= *D. albiventris*) (Aragão 1935).

**Note:** the record in Aragón (1935) is considered doubtful for the reason explained for *I. loricatus* in Brazil under the heading “**Additional information from parasitism on non-marsupial hosts**”.

Santa Fe, Funes (32°55'S 60°48'W), M on *D. albiventris* (Nava *et al.* 2004); Malabrigo (29°20'S 59°59'W), MF on *D. paraguayensis* (= *D. albiventris*), F on *L. crassicaudata* (Aragão 1935); Santa Clara de Saguier (31°20'S 61°49'W), F on *D. albiventris* (Nava *et al.* 2004); Sauce Viejo (31°46'S 60°49'W), F on *D. albiventris*; Sauce Viejo Aeropuerto (31°43'S 60°48'W), F on *L. crassicaudata*; North of Sauce Viejo (31° 42'S 60°48'W) (Faccioli 2011).

**Note:** Ivancovich and Luciani (1992) present records of *I. luciae* from man, *D. albiventris* and *L. crassicaudata* in Delta of Paraná River which corresponds to the southernmost record for this species of tick. The authors state that the ticks were classified as *I. brunneus* but this diagnosis was later changed to *I. luciae*. These specimens (all collected on December 20, 1976) were kept in three vials at the Estación Experimental Agropecuaria Colonia Benítez, Chaco, Argentina; vial numbered 451 with a label of *I. brunneus* contained one nymph (host non-stated), vial 452 with *I. brunneus* label contained seven males, two females and three nymphs (host non-stated) and a vial with repeated number 452 and with an *Ixodes* label contained one male and four females (from *L. crassicaudata*). However, the vial 451 contained a nymph of the *Ixodes auritulus* Neumann, 1904 tick group, and all the remaining 17 ticks were identified as *I. loricatus*. We are not absolutely certain that all ticks indicated in Ivancovich and Luciani (1992) were revised because in the article it is stated that they found one female of *I. luciae* on man, eight males, one female and four nymphs on *D. albiventris* and one male, one female and four nymphs on *L. crassicaudata*. However, what is certain is: 1) most of the alleged records of *I. luciae* are in fact *I. loricatus*, 2) *I. auritulus* were first confused with *I. brunneus* and later with *I. luciae*, 3) the alleged infestation of man with *I. luciae* is most probably the result of tick misidentification. Consequently, we regard records of *I. luciae* on *D. albiventris* and *L. crassicaudata* in Ivancovich and Luciani (1992) as *I. loricatus*.

**Brazil**, LU, MF on *Didelphis quica* Temminck (= *P. frenatus*) (Neumann 1899); ML on *D. albiventris* (Keirans 1982), F on *C. minimus*, ML on *D. marsupialis* (Keirans 1985).

Meridional Region, LU, N on *D. quica* (= *P. frenatus*) (Neumann 1899).

Northeast Region, LU, MF on *D. albiventris* (Barros-Battesti & Knysak 1999).

Alagoas, Palmeira dos Índios (09°24'S 36°37'W), F on *D. albiventris* (Barros-Battesti & Knysak 1999).

Ceará, Coité (07°25'S 38°43'W), F on *Didelphis* sp. (Barros-Battesti & Knysak 1999, the host is most probably *D. albiventris*).



Goiás, Anápolis (16°19'S 48°57'W), MF on *D. albiventris*, F on *Philander* sp. (Barros-Battesti & Knysak 1999), MF on *Didelphis* sp. (Cooley & Kohls 1945, the host is most probably *D. albiventris*), F on *Metachirus opossum* (Linnaeus) (= *P. opossum*) (Fonseca & Aragão 1952).

**Note:** the *Didelphis* sp. hosts above are considered to be *D. albiventris* because it is the only species for the genus established in that locality.

Mato Grosso do Sul, Parque Estadual do Prosa (20°26'S 54°38'W), MFNL on *D. albiventris* (Miziara *et al.* 2008).

Minas Gerais, Araxá (19°35'S 46°56'W), F on *Didelphis* sp. (most probably *D. albiventris*), M on *Marmosa* sp. (Barros-Battesti & Knysak 1999); Belo Horizonte (19°49'S 43°57'W), F on *D. albiventris* (Schumaker *et al.* 2000); Mar de Espanha (20°52'S 43°00'W), MF on *D. marsupialis* (Keirans 1982, but the host is surely *D. aurita* because *D. marsupialis* is not established in this locality).

Paraíba, João Eugenio (coordinates unknown), F on *Didelphis* sp. (Barros-Battesti & Knysak 1999).

Paraná, Antonina (25°26'S 48°42'W), F on *P. opossum* (= *P. frenatus*) (Arzua *et al.* 2005); Caiobá (25°50'S 48°33'W), M on *M. opossum* (= *P. frenatus*) (Guimaraes 1945); Campo Largo (25°28'S 49°32'W), F on *Didelphis* sp.; Castro (24°39'S 50°04'W), F on *D. albiventris*; Curitiba (25°25'S 49°17'W), M on *D. albiventris*, F on *D. marsupialis* but most probably *D. aurita*; Pinhao (25°42'S 51°40'W), MN on *D. albiventris*; MN on *P. opossum* (= *P. frenatus*) (Arzua *et al.* 2005); Matinhos (25°49'S 48°33'W), FNL on *P. opossum* (= *P. frenatus*) (Barros & Baggio 1992; Arzua *et al.* 2005); Ponta Grossa (25°06'S 50°10'W), MFN on *D. albiventris*, MFN on *D. marsupialis* but most probably *D. aurita*, MFN on *L. crassicaudata* (Barros & Baggio 1992); Ponta Grossa "Parque Estadual Vila Velha" (25°12'S 50°05'W), MF on *D. albiventris*, MFL on *D. marsupialis* but most probably *D. aurita*, FN on *L. crassicaudata*; Quatro Barras "Morro do Anhangava" (25°23'S 48°59'W), MF on *P. opossum* (= *P. frenatus*); Ríó Ivaí (coordinates unknown), MF on *Didelphis* sp., MF on *P. opossum* (= *P. frenatus*); Tunas do Paraná "Parque Estadual de Campinhos" (25°02'S 49°03'W), F on *P. opossum* (= *P. frenatus*) (Arzua *et al.* 2005).

Pernambuco, Caruarú (08°16'S 35°58'W), F on *D. albiventris*; Garanhuns (08°52'S 36°29'W), MF on *D. albiventris* (Barros-Battesti & Knysak 1999); Reserva Ecológica de Gurjaú (08°14'S 35°00'W), A on *Didelphis* sp., A on *D. albiventris*, A on *D. marsupialis* but most probably *D. aurita*, N on *Monodelphis americana* (Müller), N on *Marmosa* sp.; N on *Marmosa murina* (Linnaeus) (Botelho *et al.* 2004).

Rio de Janeiro, Gavea (22°58'S 43°14'W), F on *Didelphis* sp. (Cooley & Kohls 1945); Teresópolis (22°24'S 42°57'W), F on *Didelphis* sp. (Labruna *et al.* 2002b); Tijuca (22°56'S 43°15'W), F on *Didelphis* sp. (Cooley & Kohls 1945). The hosts are most probably *D. aurita*.

Rio Grande do Sul, LU, NL on *Microdelphys sorex* (Hensel) (= *Monodelphis sorex* (Hensel) (Neumann 1899); Eldorado do Sul (30°05'S 51°25'W), M on *D. marsupialis*; Guaíba (30°04'S 51°44'W), M on *D. marsupialis* (Evans *et al.* 2000); Pelotas (31°46'S 52°20'W), MFNL on *D. albiventris*, FN on *D. marsupialis*, F on *L. crassicaudata* (Barros-Battesti & Knysak 1999; Brum *et al.* 2003; Muller *et al.* 2005). Most probably the hosts identified as *D. marsupialis* in Rio Grande do Sul are in fact *D. aurita*. If this is confirmed the southern distribution of *D. aurita* in Cerqueira and Tribe (2008) will increase about 240 km.

Santa Catarina, Ilha de Ratoes Grande (27°29'S 48° 34'W), MF on *D. aurita* (Salvador *et al.* 2007); Joinville (26°18'S 48°50'W), F on *D. marsupialis* (Keirans 1985, the host is most probably *D. aurita*).

São Paulo, Caçapava (23°06'S 45°42'W), A on *D. aurita* (Souza *et al.* 2006); Cotia (23°36'S 46°55'W), F on *D. marsupialis* (Labruna *et al.* 2002b, but the host is most probably *D. aurita*); Francisco Morato (23°15'S 46°45'W), F on *Didelphis* sp. (Barros-Battesti & Knysak 1999); Fundação Parque Zoológico São Paulo (23°38'S 43°38'W), A on *D. aurita* (Labruna *et al.* 2004); Ipiranga (21°48'S 47°42'W), F on *D. aurita* (Aragão 1918); Itapevi (23°33'S 46°56'W), F on *D. aurita* (Barros-Battesti *et al.* 2000, several adult ticks were named as *Ixodes didelphidis* Fonseca and Aragão, 1952); Mogi das Cruzes (23°38'S 46°11'W), F on *D. aurita* (Horta *et al.* 2006), A on *D. albiventris* and-or *D. aurita* (Horta *et al.* 2007); Mogi das Cruzes-Serra de Itapety (23°26'S 46°09'W), F on *D. marsupialis* but most probably *D. aurita*, N on *Marmosa* sp., MF on *P. opossum* (= *P. frenatus*) (Labruna *et al.* 1997); Monte Alegre do Sul (22°39'S 46°41'W), A on *D. albiventris* (Souza *et al.* 2006); Pirassununga (21°59'S 47°25'W), F on *Didelphis* sp. (Labruna *et al.* 2002b), A on *D. albiventris* and-or *D. aurita* (Horta *et al.* 2007); Ribeirão Pires (23°43'S 46°24'W), F on *Marmosa* sp. (Barros-Battesti & Knysak 1999); Sampaio Moreira (coordinates unknown), F on *Marmosa* sp. (Barros-Battesti & Knysak 1999); São Paulo (23°31'S 46°37'W), F on *Didelphis* sp., F on *D. albiventris*, MF on *D. marsupialis* but most probably *D. aurita*, M on *Marmosa* sp. (Barros-

Battesti & Knysak 1999), A on *D. albiventris* and-or *D. aurita* (Horta *et al.* 2007); Serra do Mar State Park (23°52'S 46°26'W), A on *D. aurita* (Sabatini *et al.* 2010).

**Colombia.** In the tick collection of the Instituto Nacional de Tecnología Agropecuaria, Estación Experimental Agropecuaria Rafaela (INTA), Rafaela, Argentina there is a female labeled as *Ixodes loricatus*, from *Metachirus nudicaudatus*, 25 noviembre 1970, La Tirana (06°50'N 75°34'W), Antioquia, gift from the United States National Tick Collection (USNTC), Statesboro, U.S.A. It is part of a lot of eight female ticks maintained in the USNTC under accession number RML57488. We compared this specimen with *bona fide I. loricatus* females from Argentina and Brazil and with the descriptions contained in Marques *et al.* (2004) and Onofrio *et al.* (2009) because the types of *I. loricatus* are not available (Guglielmone *et al.* 2003b). The results are in the note below.

**Note:** the Colombian specimen, almost unfed, resembles at first sight under low magnification *I. loricatus* although it is pale brown and the coxae not as dark as in Argentinian and Brazilian specimens. However, this situation changed drastically when morphological details were compared under high stereoscopy magnification. The Colombian specimen differs from the Argentinian and Brazilian ticks as follows: pronounced ridges lateral to each porose area surpassing the posterior border of the basis capituli giving the impression of sharp cornua, a feature absent in *I. loricatus*; scutum obviously longer than wide (ratio 1.5) while it is just longer than wide (ratio 1.2) in *I. loricatus*; coxae I with two acute spurs with the external longer than the internal, while the spurs are less acute in *I. loricatus*; hypostome pointed, while it is blunt in *I. loricatus*; presence of a dark elevated borders on the ventral basis capituli which is absent from the Argentinian and Brazilian *I. loricatus*. We conclude that the alleged specimen of *I. loricatus* from Colombia is not a representative of this species. Lorenza Beati examined the specimens in RML57488 (USNTC) and found that they are not *I. loricatus* and their morphologies are similar to the specimen deposited in INTA. Additional studies are needed to determine if these specimens belong to a known species or represent a still undescribed taxon.

**Guatemala.** Monroy Lefebvre and Cejas González (1988) state that *I. loricatus* is established in this country, but locality, hosts and tick stages found on them are not provided. This is a controversial record that will be further discussed below.

**Panama, Note:** Fairchild *et al.* (1966) allegedly found a *bona fide* female of *I. loricatus* in Darién, Tacarcuna Station (08°05'N 77°17'W) on *Metachirus nudicaudatus* on September 1, 1958. This specimen is kept in the United States Tick Collection under accession number RML37477 where it was examined by Valeria C. Onofrio, who concluded that it is not *I. loricatus* and species identification is under way. Therefore, Panama is excluded from the range of this species.

**Paraguay, LU, A** on *D. albiventris* (Whitaker & Abrell 1987).

Cordillera, probably from Sapucay (25°19'S 56° 55'W), MF on *Didelphis* sp. (Keirans 1982), but we were unable to locate this place with the coordinates provided by the author.

Presidente Hayes, Fortín Juan de Zalazar (23°06'S 59°18'W), MF on *D. albiventris* (Valeria C. Onofrio, personal communication). These ticks are deposited in the Gorgas Memorial Laboratory Tick Collection, and the locality is named "Juan de Zalazar" and allegedly located in the Boquerón Department. However, there is no Paraguayan locality named "Juan Zalazar" but "Fortín Juan de Zalazar" often named as "Fortín Zalazar" is located in the Department Presidente Hayes, close to the borderline with the Department Boquerón.

**Uruguay, LU, MFN** on *D. albiventris*, NL on *M. dimidiata* (Venzal *et al.* 2003).

Maldonado, Barra del Arroyo Maldonado (34°58'S 54°56'W), F on *D. albiventris* (Nava *et al.* 2004).

Montevideo, Paso de la Arena (34°53'S 56°09'W), MF on *L. crassicaudata* (Wolffhugel 1933).

**Venezuela,** Araguá, Rancho Grande Biological Station (10°21'N 67°36'W), NL on *Monodelphis brevicaudata* (Erxleben) (Jones *et al.* 1972). See the note about *M. brevicaudata* in *I. luciae*.

Miranda, east of Caracas (10°29'N 66°44'W), L on *M. robinsoni* (Jones *et al.* 1972).

**Note:** Jones *et al.* (1972) consider the precedent diagnosis of *I. loricatus* as tentative. There are other records from Venezuelan marsupials in Vogelsang and Cordero (1940) but the tick stages found on hosts and morphological support for the identification are not provided, bringing uncertainty about the presence of this tick in the country.

#### **Additional geographical information from parasitism on non-marsupial or undetermined hosts**

**Argentina,** Buenos Aires, Hudson (34°45'S 58°06'W), LN on *Akodon azarae* (Fischer); Punta Lara (34°47'S 58°01'W), L on *A. azarae*, Ramallo (33°32'S 59°52'W), N on *Oligoryzomys flavescens* (Waterhouse); San Nicolás (33°20'S 60°13'W), NL on *A. azarae* (Nava *et al.* 2004).

Salta, Parque Nacional El Rey (24°41'S 64°40'W), NL on *Calomys* sp. (Nava *et al.* 2004).

Santa Fe, Reserva Natural de la Universidad Nacional del Litoral (31°23'S 60°55'W), L in nests of sigmodontine rodents (Manzoli *et al.*, 2006); Santa Clara de Saguier (31°20'S 61°49'W), NL on *Akodon* sp. (Nava *et al.* 2004).

Tierra del Fuego, LU, F from an unknown hosts (Neumann 1901). This is a controversial record that will be further discussed below.

**Brazil**, Minas Gerais, Pacau (15°14'S 43°41'W), F on *Agouti paca* (Linnaeus) (= *Cuniculus paca* (Linnaeus)) (Aragão 1918).

São Paulo, Araraquara (21°47'S 48°10'W), F on undetermined host; Barueri (23°29'S 46°51'W), M on undetermined host; Biritiba Mirim (23°34'S 46°01'W), F on undetermined host; Bragança Paulista (22°57'S 46°32'W), M on undetermined host; Taubaté (23°02'S 45°33'W) (Marques *et al.* 2004).

**Note:** Aragón (1936) has a record of *I. loricatus* on an undetermined host at Curralinho (01°43'S 49°43'W) in the state of Pará that represents the northernmost record of this species in Brazil. However, it should be noted that this diagnosis was made before the description of *I. luciae* in 1940. The armature of coxae (crucial for differential diagnosis between these species) was not considered in the key used by this author bringing some uncertainty about the identification. We can not say that this diagnosis is erroneous but being cautious it is considered that it at least requires confirmation.

**Mexico**, Tabasco, Frontera (18°32'N 92°38'W), MF on *Ateles geoffroyi* Kuhl (Keirans 1982, 1985).

**Note:** this Mexican record of *I. loricatus* is controversial. This tick species has not been found yet on Mexican marsupials or rodents but only once on this unusual monkey host for *I. loricatus*. We doubt about the origin of the specimens (see also the discussion section).

**Uruguay**, Canelones, Solymar Norte (34°47'S 55°56'W), L on *O. flavescens* (Nava *et al.* 2004).

32) *Ixodes luciae* Sénevet, 1940 is a Neotropical species close morphologically and in host usage to the precedent species, *I. loricatus*. The only study on the ecology of *I. luciae* shows the relevance of sigmodontin rodents as hosts for larvae and nymphs of this tick (Díaz *et al.* 2007, 2009) because all specimens but two were found on them. However, other authors present several records of sub-adults ticks on Didelphidae (see below).

**Argentina**, LU, M on *D. paraguayensis* (= *D. albiventris*) (Cooley & Kohls 1945).

Salta, road to Isla de las Cañas (22°57'S 64°33'W), N on *Micoureus constantiae* (Thomas) (= *Marmosa constantiae* Thomas), N on *Thylamys* sp., N on *Thylamys venustus* (Thomas), F on *L. crassicaudata* (Autino *et al.* 2006).

Tucumán, El Siambón (26°40'S 65°24'W), N on *Thylamys cinderella* Thomas (Autino *et al.* 2006).

**Note:** the Argentinian record for *I. luciae* in Buenos Aires province, Delta del Paraná INTA (34°25'S 58°35'W) on *D. albiventris* and *L. crassicaudata* in Ivancovich and Luciani (1992) was changed to *I. loricatus* after examining the specimens as stated in the note of *I. loricatus* in Argentina (see details in the note under *I. loricatus* in Argentina).

**Belize**, Middlesex (17°01'N 88°30'W), MF on *Didelphis mesamericana* Allen (= *D. marsupialis*) (Cooley & Kohls 1945).

**Bolivia**, Santa Cruz, Buen Retiro (17°16'S 63°42'W), MFNL on *D. paraguayensis* (= *D. albiventris*) (Fonseca 1959).

**Brazil**, Acre, Assis (10°56'S 69°34'W), A on *D. marsupialis* (Marcelo B. Labruna, personal communication).

Pará, Igarapé Açú (01°07'S 47°37'W), MF on *P. opossum* (Barros-Battesti & Knysak 1999).

Rondônia, LU, MF on *Monodelphis* sp. (Labruna *et al.* 2005a, most probably the host is *Monodelphis glirina* (Wagner); Jamari River headwaters (10°18'S 63°14'W), F on *D. marsupialis* (Labruna *et al.* 2009).

**Colombia**. There are records of *I. luciae* in Wells *et al.* (1981) and Osorno-Mesa (1942 as *I. loricatus spinosus* Nuttall, 1910, a preoccupied name replaced by *I. loricatus vogelsangi* Santos Dias, 1954) on South American marsupials, but there is no information about tick stages found on hosts.

**Costa Rica**. Guglielmone *et al.* (2003b) state that *I. luciae* is present in the country but no host and tick stages are provided.

**Ecuador**. Guglielmone *et al.* (2003b) state that *I. luciae* is found in the country, but no host and tick stages are provided.

**French Guiana**, Cayena, Cayenne, (04°56'N 52°19'W), F on *D. marsupialis* (Floch & Fauran 1958).



**Guatemala**, Izabal, Bobos (15°21'N 88°48'W), MF on *D. mesamericana* (= *D. marsupialis*); Escobas (15°41'N 88°38'W), F on *D. mesamericana* (= *D. marsupialis*) (Cooley & Kohls 1945).

**Honduras**. Onofrio *et al.* (2002) state that *I. luciae* is established in this country, but hosts and tick stages found on them are not provided.

**Mexico**, Chiapas, Finca Germania (15°04'N 92°31'W), MF on *Didelphis* sp. (Vázquez 1946 as *Ixodes scuti-crenatus* Vázquez, 1946).

Colima, La Barragana (19°20'N 103°45'W), MF on *D. marsupialis* (Guzmán-Cornejo *et al.* 2007).

Tabasco, Frontera (18°32'N 92°38'W), F on *Didelphis* sp. (Keirans 1982).

Veracruz, North-East of las Minas (19°41'N 97°09'W), M on *Didelphis* sp. (Guzmán-Cornejo *et al.* 2007).

**Nicaragua**. Jones *et al.* (1972) state that *I. luciae* is established in this country, but hosts and tick stages found on them are not provided.

**Panama**, Bocas del Toro, Almirante (09°18'N 82°24'W), N on *M. robinsoni* (Fairchild *et al.* 1966).

Colón, Alhajueta (09°11'N 79°38'W), MF *D. mesamericana* (= *D. marsupialis*) (Cooley & Kohls 1945), M on *D. marsupialis* (Fairchild 1943); Camp Piña (09°16'N 80°03'W), MF on *D. marsupialis*, F on *P. opossum*; Fort Gulick (currently named Fuerte Espinar) (09°18'N 79°53'W), F on *P. opossum* (Fairchild *et al.* 1966).

Comarca de Kuna Yala (previously known as Comarca San Blas), Río Mandinga (09°29'N 79°05'W), M on *D. marsupialis* (Fairchild *et al.* 1966).

Darién, Tacarcuna Station (08°10'N 77°18'W), A on *D. marsupialis* (Fairchild *et al.* 1966).

Panama, Cerro Azul (09°12'N 79°21'W), A on *D. marsupialis*, F on *P. opossum*; Cerro Campana (08°41'N 79°56'W), A on *D. marsupialis* (Fairchild *et al.* 1966); Panamá City (08°58'N 79°32'W), F on *D. marsupialis* (Bermúdez *et al.* 2010).

**Peru**, Loreto, 13 de Febrero (04°02'S 73°26'W), F on *P. opossum*; Belén (03°50'S 73°13'W), F on *Caluromys lanatus* (Olfers); Ex Petroleros (04°05'S 73°27'W), F on *P. opossum*; Fundo San Martín (03°58'S 73°24'W), F on *P. opossum*; Los Delfines (03°51'S 73°21'W), F on *P. opossum*; Moralillo (03°54'S 73°21'W), F on *P. opossum*, F on *Marmosops* sp., now identified as *Marmosops impavidus* Tschudi by one of the authors (MMD) Palo Seco (04°00'S 73°26'W), F on *M. nudicaudatus*, L on *Micoureus* Lesson (= *Marmosa*) sp. (most probably *Micoureus regina* (Thomas), F on *Philander andersoni* Pine; Paujil (04°04'S 73°27'W), F on *D. marsupialis*, F on *P. opossum*; Peña Negra (03°52'S 73°20'W), MF on *P. opossum*; San Juan (03°59'S 73°25'W), F on *P. opossum*, F on *P. andersoni*; San Lucas (04°06'S 73°22'W), F on *P. andersoni* (Díaz *et al.* 2007).

**Surinam**, LU, F on *Didelphis* sp. (Keirans 1985).

**Trinidad and Tobago**, Trinidad, Bush Bush Forest (10°24'N 61°00'W), A on *D. marsupialis*, A on *Marmosa* sp. (Aitken *et al.* 1968).

**Venezuela**, Amazonas, Boca Mavaca (02°31'N 65°16'W), F on *P. opossum*; Capibara (02°36'N 66°20'W), F on *P. opossum* (Jones *et al.* 1972); Cerro Tamacuari (01°41'N 64°26'W), MF on *P. opossum* (Guerrero 1996); Tamatama (03°09'N 65°50'W), FN on *M. robinsoni*, F on *P. opossum* (Jones *et al.* 1972); however these localities are out of the distribution range of *P. opossum* as stated by (Patton & Silva 2007) and the hosts should be either *P. mondolfii* or *P. andersoni*.

Araguá, Rancho Grande Biological Station (10°21'N 67°36'W), NL on *M. brevicaudata* (Jones *et al.* 1972).

Barinas, Altamira (08°49'N 70°30'W), M on *D. marsupialis*, N on *M. brevicaudata*; south-west of Altamira (08°47'N 70°31'W), NL on *M. brevicaudata* (Jones *et al.* 1972).

Carabobo, Aguirre (10°11'N 68°19'W), NL on *M. brevicaudata*; Montalbán (10°12'N 68°19'W), N on *M. robinsoni*, NL on *M. brevicaudata*; south-east of Montalbán (10°10'N 68°20'W), F on *D. marsupialis*, L on *M. robinsoni* (Jones *et al.* 1972).

Distrito Federal, south-west of Caracas (10°27'N 67°09'W), M on *D. marsupialis* (Jones *et al.* 1972).

Falcón, La Pastora (11°12'N 68°35'W), MF *D. marsupialis*, NL on *M. brevicaudata* (Jones *et al.* 1972); San Esteban (11°28'N 69°22'W), M on *D. marsupialis* (Keirans 1982).

Guárico, south-east of Caracas (09°56'N 66°32'W), MF on *D. marsupialis* (Jones *et al.* 1972).

Miranda, near Turgua (10°21'N 66°44'W), N on *Marmosa cinerea* (Temminck) (= *Marmosa demerarae* (Thomas), because the name *cinerea* was preoccupied); Naiguatá (10°29'N 66°44'W), MF on *Didelphis* sp. (Méndez Arocha & Ortiz, 1958, the host is most probably *D. marsupialis*); South of Río Chico (10°15'N 65°59'W), N on *M. brevicaudata* (Jones *et al.* 1972, but the host is doubtful because there is no evidence of its presence in Miranda).



Yaracuy, Aroa (10°25'N 68°53'W), MF *D. marsupialis*; north-west of Urama (10°34'N 68°26'W), M on *D. marsupialis*, N on *M. cinerea* (= *M. demerarae*) (Jones *et al.* 1972).

Zulia, south-west of Machiques (09°58'N 72°42'W), N on *M. brevicaudata* (Jones *et al.* 1972), but the host is most probably *Monodelphis palliolata* (Osgood).

**Note:** the following Venezuelan records are from Jones *et al.* (1972) who considered the specimens as probable *I. luciae* without further comments. In the light of the many records of *I. luciae* in Venezuela we treat these records as provisionally valid.

Amazonas, Río Cunucunuma at North-North West of La Esmeralda (03°39'N 65°21'W), L on *Caluromys philander* (Linnaeus), L on *M. murina*.

Distrito Federal, South-West of Caracas (10°27'N 67°20'W), L on *M. brevicaudata*.

Falcón, North-West of La Pastora (11°12'N 68°36'W), NL on *M. brevicaudata*; Mirimire (11°09'N 68°53'W), M on *D. marsupialis*.

Guárico, South-East of Caracas (09°58'N 66°33'W), L on *M. brevicaudata*, but the host is most probably *M. palliolata* or a related species instead of *M. brevicaudata*.

Miranda, South of Caracas (10°25'N 66°55'W), L on *M. robinsoni*.

Trujillo, West-North West of Valera (09°23'N 70°40'W), L on *M. robinsoni*.

**Note:** all records of *M. brevicaudata* have to be considered cautiously because considerable controversy exists about it and related species (Pine & Handley 2007).

#### **Additional geographical information from parasitism on non-marsupial or undetermined hosts**

**Argentina**, Salta, West South West of Pulares (25°05'S 65°37'W), N on *Calomys callosus* (probably) from Autino *et al.* (2006), but host and locality position reevaluated.

**Brazil**, Amazonas, Santa Isabel do Río Negro (02°23'S 65°04'W), F on undetermined host (Onofrio *et al.* 2010).

Mato Grosso do Sul, Dos Irmãos do Buriti (20°41'S 55°17'W), F on undetermined host (Onofrio *et al.* 2010).

Pará, Belém (01° 26' S 48° 29' W), MF on undetermined host; Mirabá (05°20'S 49°07'W), F on undetermined host; São João de Pirabas (00°46'S 47°10'W), F on undetermined host; Tucuruí (03°40'S 49°42'W), M on undetermined host (Onofrio *et al.* 2010).

Rondônia, Amorim Farm (10°38'S 63°31'W), N on undetermined host (Labruna *et al.* 2005a); Campo Novo de Rondônia (10°36'S 63°37'W), MF on undetermined host (Onofrio *et al.* 2010); Line C (10°26'S 63°21'W), N on undetermined host (Labruna *et al.* 2005a); Monte Negro (10°02'S 63°08'W), NL on undetermined host; Porto Velho (08°45'S 63°54'W), MF on undetermined host (Onofrio *et al.* 2010).

**Panamá**, Darién, Cerro Pirre (07°51'N 77°44'W), N on *Oryzomys* sp. (Fairchild *et al.* 1966).

**Perú**, Loreto, Ninarumi (03°51'S 73°22'W), N on *Hylaeamys perenensis* (Allen); Varillal (03°53'S 73°22'W), N on *H. perenensis* (Díaz *et al.* 2007).

**Venezuela**, Distrito Federal, Caracas (10°29'N 66°55'W), MF on dog (Méndez Arocha & Ortiz 1958).

33) *Ixodes pararicinus* Keirans and Clifford, 1985 in Keirans *et al.* (1985) is a South American species with several hosts for all parasitic stages (Venzal *et al.* 2005; Autino *et al.* 2006).

**Argentina**, Salta, Parque Nacional El Rey (24°15'S, 64°40'W), L on *T. venustus* (Beldoménico *et al.* 2003).

**Peru**, Loreto, Fundo San Martín (03°58'S 73°24'W), L on *Monodelphis adusta* (Thomas) (Díaz *et al.* 2007).

34) *Ixodes rubidus* Neumann, 1901 is a Nearctic-Neotropical species but it is not established in South America. Their usual hosts are carnivore mammals (Guglielmone *et al.* 2003b).

**Guatemala**, Chimaltenango, Yepocapa (14°29'N 90°56'W), F on *Didelphis* sp. (Fairchild *et al.* 1966).

35) *Ixodes venezuelensis* Kohls, 1953 is a Neotropical tick species feeding on Didelphimorphia and Rodentia with Sigmodontinae playing a relevant role as hosts for all parasitic stages (Durden & Keirans 1994).

**Costa Rica**, Heredia, LU (10°25'N 84°00'W), N on *Marmosa mexicana* Merriam, N on *P. opossum* (Durden & Keirans 1994).

**Panama**, Darién, LU, F on *M. adusta* (Durden & Keirans 1994).

**Venezuela**, northern region, LU, FN on *M. brevicaudata* (Durden & Keirans 1994).

Amazonas, LU, L on *Philander* sp. (Durden & Keirans 1994); Boca Mavaca (02°31'N 65°16'W), NL on *D.*

*marsupialis*; Casiquiare Canal Capibara (02°36'N 66°21'W), L on *P. opossum*; Río Cunucuma north-north west of La Esmeralda (03°39'N 65°21'W), NL on *P. opossum* (Jones *et al.* 1972). Most probably the species of *Philander* in Jones *et al.* (1972) are *P. andersoni* or *P. mondolfii*.

Araguá, Sierra Maestra (coordinates unknown), FN on *M. brevicaudata* (Kohls 1953).

Barinas, Altamira (08°49'N 70°30'W), NL on *M. brevicaudata* (Jones *et al.* 1972).

Falcón, LU, N on *M. brevicaudata* (Durden & Keirans 1994).

Táchira, LU, L on *Marmosa* sp. (Durden & Keirans 1994).

Trujillo, West-Northwest of Valera (09°23'N 70°40'W), FNL on *M. brevicaudata* (Jones *et al.* 1972); these last authors have a record considered "probable *I. venezuelensis*" for this state at east of Trujillo (09°22'N 70°17'W), L on *Marmosa dryas* (Thomas) (= *Gracilinanus dryas* (Thomas)).

See the note about *M. brevicaudata* in *I. luciae*.

#### Additional geographical information from parasitism on non-marsupial hosts

**Colombia**, Antioquía, Valdivia (07°11'N 75°27'W), F on *Melanomys caliginosus* (Tomes) (Kohls 1953).

**Costa Rica**, Alajuela, LU (10°30'N 84°30'W), F on *Heteromys desmarestianus* Gray (Durden & Keirans 1994).

**Venezuela**, Amazonas, South East of Boca Mavaca (02°22'N 65°08'W), N on *Myoprocta pratti* Pocock; North of Raya (05°25'N 67°36'W), N on *Proechimys guyannensis* (Geoffroy) (Jones *et al.* 1972).

Apure, North of Nula (07°18'N 71°54'W), N on *Proechimys semispinosus* (Tome) (Jones *et al.* 1972), but this host is not established in Venezuela and the species of *Proechimys* found in the state of Apure are uncertain (Gómez-Laverde *et al.* 2008).

Aragua, Rancho Grande (10°21'N 67°36'W), F on *Ichthyomys pittieri* Handley and Mondolfi (Guerrero 1996).

Bolívar, South East of El Dorado (06°13'N 61°28'W), N on *P. guyannensis*; North East of Icaburú (04°34'N 61°30'W), N on *P. guyannensis* (Jones *et al.* 1972).

Carabobo, Montalbán (10°12'N 68°20'W), NL on *Dasyprocta aguti* (Linnaeus) (= *Dasyprocta leporina* (Linnaeus)) (Jones *et al.* 1972); Bejuma (10°10'N 68°15'W), F on *I. pittieri* (Guerrero 1996).

Mérida, East of Tabay (08°38'N 71°02'W), *Oryzomys minutus* (Tomes) (= *Microrizomys minutus* (Tomes)) (Jones *et al.* 1972).

Miranda, South of Caracas (10°25'N 66°55'W), F on *Heteromys anomalus* (Thompson) (Jones *et al.* 1972).

Trujillo, East of Trujillo (09°22'N 70°18'W), NL on *O. minutus* (= *M. minutus*) (Jones *et al.* 1972).

36) *Rhipicephalus microplus* (Canestrini, 1888) is an extremely important tick species that affects the cattle industry in most tropical and sub-tropical areas of the world, and is found occasionally on mammalian hosts different to artiodactyls.

**Argentina**. Boero (1954) and Boero and Boehringer (1967) present vague information of infestation of *R. microplus* on South American marsupials.

37) *Rhipicephalus sanguineus* (Latreille, 1806) species complex has a world wide distribution feeding mainly on domestic dogs, but there are also records on a wide variety of hosts. The number of species that forms this complex is undetermined.

**Argentina and Peru**. Santa Cruz *et al.* (1998) and Need *et al.* (1991) present records of ticks of *R. sanguineus* complex on South American marsupials for Argentina and Peru, respectively, without stating tick stages found on hosts.

#### Microbiotheria: Microbiotheridae Ameghino (only family in the order)

1) *Ixodes neuquenensis* Ringuelet, 1947 is a South American tick known only from *bona fide* specimens collected on *Dromiciops gliroides* Thomas (see below).

**Argentina**, Neuquén, Isla Victoria (40°56'S 71°32'W), F on *Dromiciops australis* Philippi (= *D. gliroides*) (Ringuelet 1947, who received this tick that had been classified as *I. brunneus* by Boero 1945)

Río Negro, Llao Llao Reserve (41°02'S 71°32'W), FNL on *D. gliroides* (Guglielmone *et al.* 2004).

**Note:** Daciuk *et al.* (1981) allegedly found the male of *I. neuquenensis* on *Dusicyon griseus* (= *Lycalopex gri-*

*seus* (Gray) (Carnivora: Canidae) in Argentina, but the tick was in fact a male of *A. tigrinum*, and this sex of *I. neuquenensis* remains unknown (Guglielmone & Nava 2005).

**Chile**, Región X, Fundación Senda Darwin (41°52'S 73°40'W), FNL on *D. gliroides*; Fundo Los Cisnes (41°50'S 73°36'W), FNL on *D. gliroides* (Marín-Vial *et al.*, 2007).

### **Paucituberculata Ameghino: Caenolestidae Trouessar (only family in the order)**

1) *Ixodes jonesae* Kohls, Sonenshine and Clifford, 1969 is a South American species known from several specimens collected from Sigmodontinae and several larvae from Caenolestidae (Guglielmone *et al.* 2003b).

**Venezuela**, Táchira, South-West of San Cristóbal (07°28'N 72°27'W), L on *Caenolestes obscurus* (= *Caenolestes fuliginosus* (Tomes)) (Jones *et al.* 1972).

A total of 37 tick species were allegedly found on Didelphimorphia. Most tick species were occasionally found on these types of hosts, apart from some doubtful diagnoses such as those of *A. dissimile* on *Monodelphis* and *Didelphis* by Botelho *et al.* (2002), vague reports on marsupial infestation like that for *A. tigrinum* in Paraguay by Massi Pallarés and Benítez Usher (1982) or South American records of *A. pseudoconcolor* on *Philander* sp. in Guglielmone *et al.* (2003a).

Ticks found on Didelphimorphia are mostly *Ixodes* and to a lesser extent *Amblyomma*. Records from the Neotropical region with known tick stages found on South American marsupials total 239 for *Ixodes* versus 46 for *Amblyomma*. The difference in usage of Didelphimorphia as hosts for these genera is further enhanced because the total records for all species of *Amblyomma* for the whole Neotropical Region is 6947, while the corresponding number for all *Ixodes* is 1127. In other words, 21.2 % and 0.7 % of all records of *Ixodes* and *Amblyomma*, respectively, established in South America (exclusively or non-exclusively) are for infestation on Didelphimorphia and this difference is statistically significant ( $P < 0.001$ , chi-square distribution).

Several species of *Amblyomma* were detected on Didelphimorphia, but with one exception, none of them appear to be strongly bound to these hosts. A total of 15 records correspond to the Neotropical and Nearctic *A. cajennense*; however, this represents a minimum of the approximately 1435 Neotropical records for this species. The same applies for the five records of *A. aureolatum* (a tick with an ample South American distribution) because total records for this species are 237. The only exception may apply to *A. fuscum* because there are six records of sub-adult ticks of this species on *D. aurita* (Barros-Battesti *et al.* 2005; Martins *et al.* 2010; Sabatini *et al.* 2010).

The situation is quite different for *Ixodes*. A total of 12 species were determined on didelphimorph marsupials, but records of *I. affinis*, *I. aragaii*, *I. boliviensis*, *I. fuscipes*, *I. lasallei*, *I. pararicinus* and *I. rubidus* do not seem to have ecological relevance, while the alleged record of *I. longiscutatus* is probably the result of an erroneous identification. Nevertheless, Didelphimorphia are important hosts for *I. amarali*, *I. loricatus*, *I. luciae* and *I. venezuelensis*.

*Ixodes amarali* has been recorded on six occasions on Didelphidae belonging to Didelphinae; four of them were adult ticks collected (one record included larvae and nymphs of *I. amarali*) from *M. domestica* (Marmosini Hershkovitz), while the remaining records corresponded to adult ticks from *D. albiventris* and *D. cf. aurita* (Didelphini Gray). These few findings of *I. amarali* are considered of ecological relevance because they represent the majority of records for adult *I. amarali*. All records of *I. amarali*, including those records different to Didelphidae, are from Brazil, more specifically from eastern Brazil (Figure 1).

The situation of *I. venezuelensis* is similar to that described for *I. amarali* because the records on didelphimorphs are not abundant (14) but they are relevant for the total records for the species that is distributed in Colombia, Costa Rica, Panama and Venezuela (Figure 1). Nine records were from Marmosini as follows: two from *Marmosa* (all for subadult ticks), one for *Gracilinanus* (subadult ticks) and five for *Monodelphis* (two for subadult ticks, two for subadult and adult ticks and one for adult ticks), while the five records from Didelphini were for the genera *Philander* (four records of subadult ticks) and *Didelphis* (one record of adult ticks)

The records of *I. loricatus* and *I. luciae* on Didelphimorphia are numerous and they represent the majority of all records for both species. Hosts of the different tribes and species of Didelphidae for the different combination of parasitic stages of *I. loricatus* (including records from Argentina, Brazil, Paraguay and Uruguay) and *I. luciae* are

shown in Tables 1 and 2, respectively. *Caluromys* Allen has been found infested only twice with *I. luciae*; the contribution of Metachirini Hershkovitz was also minimal with just one record for *I. luciae*, while representatives of Thylamyini Hershkovitz have been found infested four times with *I. luciae*.

**TABLE 1.** Records of *Ixodes loricatus* and their parasitic stages found on Didelphimorphia of the family Didelphidae from *bona fide* records in Argentina, Brazil, Uruguay and Paraguay, L= larva, N= nymph, A= adult.

| Hosts                           | A  | AN | AL | ANL | N | L | NL | Total |
|---------------------------------|----|----|----|-----|---|---|----|-------|
| Didelphidae                     |    |    |    |     |   |   |    |       |
| Didelphinae                     |    |    |    |     |   |   |    |       |
| Didelphini                      |    |    |    |     |   |   |    |       |
| <i>Chironectes minimus</i>      | 1  | 0  | 0  | 0   | 0 | 0 | 0  | 1     |
| <i>Didelphis albiventris</i> *  | 31 | 6  | 3  | 2   | 0 | 0 | 0  | 42    |
| <i>D. aurita</i> **             | 19 | 2  | 1  | 0   | 0 | 0 | 0  | 22    |
| <i>D. marsupialis</i>           | 0  | 0  | 1  | 0   | 0 | 0 | 0  | 1     |
| <i>Didelphis</i> sp.***         | 24 | 1  | 1  | 0   | 0 | 0 | 0  | 26    |
| <i>Lutreolina crassicaudata</i> | 9  | 5  | 0  | 1   | 0 | 0 | 0  | 15    |
| <i>Philander frenatus</i>       | 9  | 1  | 0  | 1   | 1 | 0 | 0  | 12    |
| <i>P. opossum</i>               | 1  | 0  | 0  | 0   | 0 | 0 | 0  | 1     |
| <i>Philander</i> sp.            | 1  | 0  | 0  | 0   | 0 | 0 | 0  | 1     |
| Marmosini                       |    |    |    |     |   |   |    |       |
| <i>Marmosa murina</i>           | 0  | 0  | 0  | 0   | 1 | 0 | 0  | 1     |
| <i>Marmosa</i> sp.              | 4  | 0  | 0  | 0   | 2 | 0 | 0  | 6     |
| <i>Monodelphis americana</i>    | 0  | 0  | 0  | 0   | 1 | 0 | 0  | 1     |
| <i>M. dimidiata</i>             | 0  | 0  | 0  | 0   | 0 | 0 | 1  | 1     |
| <i>M. sorex</i>                 | 0  | 0  | 0  | 0   | 0 | 0 | 1  | 1     |
| Total                           | 99 | 15 | 6  | 4   | 5 | 0 | 2  | 131   |

\* Includes two records classified as probably *D. albiventris*; \*\*Includes 17 records classified as probably *D. aurita*; \*\*\*Includes three records classified as *D. albiventris* and/or *D. aurita*.

Therefore, most records were from species belonging to the tribes Didelphini and Marmosini. The great majority of *I. loricatus* and *I. luciae* adults were found on Didelphini, but the situation is different for subadult ticks. Table 1 shows that 30 records of *I. loricatus* on Didelphimorphia involved larval and/or nymphal ticks, of which 24 (80 %) were determined on Didelphini. Table 2 shows 27 records of subadult *I. luciae* on Didelphimorphia, 21 of which (78 %) were from Marmosini. It appears that species belonging to Didelphini are the most important hosts for all parasitic stages of *I. loricatus*, while *I. luciae* appears to depend on Didelphini for adult maintenance and Marmosini to feed subadult tick. However, this should be considered a general statement because records are few, no information was obtained about densities of hosts and ticks, and the probability of trapping bias which was not considered for the analysis.

Literature on *I. loricatus* infesting Didelphimorphia shows a wide distribution range that includes Argentina, Uruguay, Paraguay, Brazil, Venezuela, Panama, while the record from Colombia is first record for this species. This range is augmented considering the records in Guatemala on a "wild host" by Monroy Lefebvre and Cejas González (1988) and on *A. geoffroyi* in México by Keirans (1982, 1985). The southernmost record of *I. loricatus* is from an unknown host in Tierra del Fuego (Argentina) (Neumann 1901).

However, the only record each of *I. loricatus* from Panama and Colombia are known now to be the result of misidentification. Moreover, all records of this species from Venezuela have to be considered cautiously because Vogelsang and Cordero (1940) do not specify tick stages found on hosts and provide no clue how the diagnoses was obtained, while Jones *et al.* (1972) treat as tentative their records on Didelphidae, bringing doubts about the presence of *I. loricatus* in the country. The same condition applies to the record on "wild hosts" for Guatemala and conversely for the Mexican record on a monkey. Finally the record from Tierra del Fuego is also unconvincing



because *I. loricatus* has not been found again south of 35°S where Didelphimorphia is absent (see discussion section for further details). In brief, *bona fide* records of *I. loricatus* encompass Uruguay, Argentina, Paraguay and Brazil, most of them in eastern South America. The southernmost confirmed record for this tick is in La Balandra (34°56'S 57°42'W), province of Buenos Aires, Argentina (Nava *et al.*, 2004), while the northernmost record lies in the Reserva Ecológica de Gurjaú (08°14'S 35°00'W) in the State of Pernambuco, Brazil (Botelho *et al.* 2004) (see the note above in *I. loricatus* for not considering Currealinho (01°43'S 49°43'W) as the northernmost record of this species). Figure 2 shows the distribution of *I. loricatus* with indication of wrong and doubtful records.

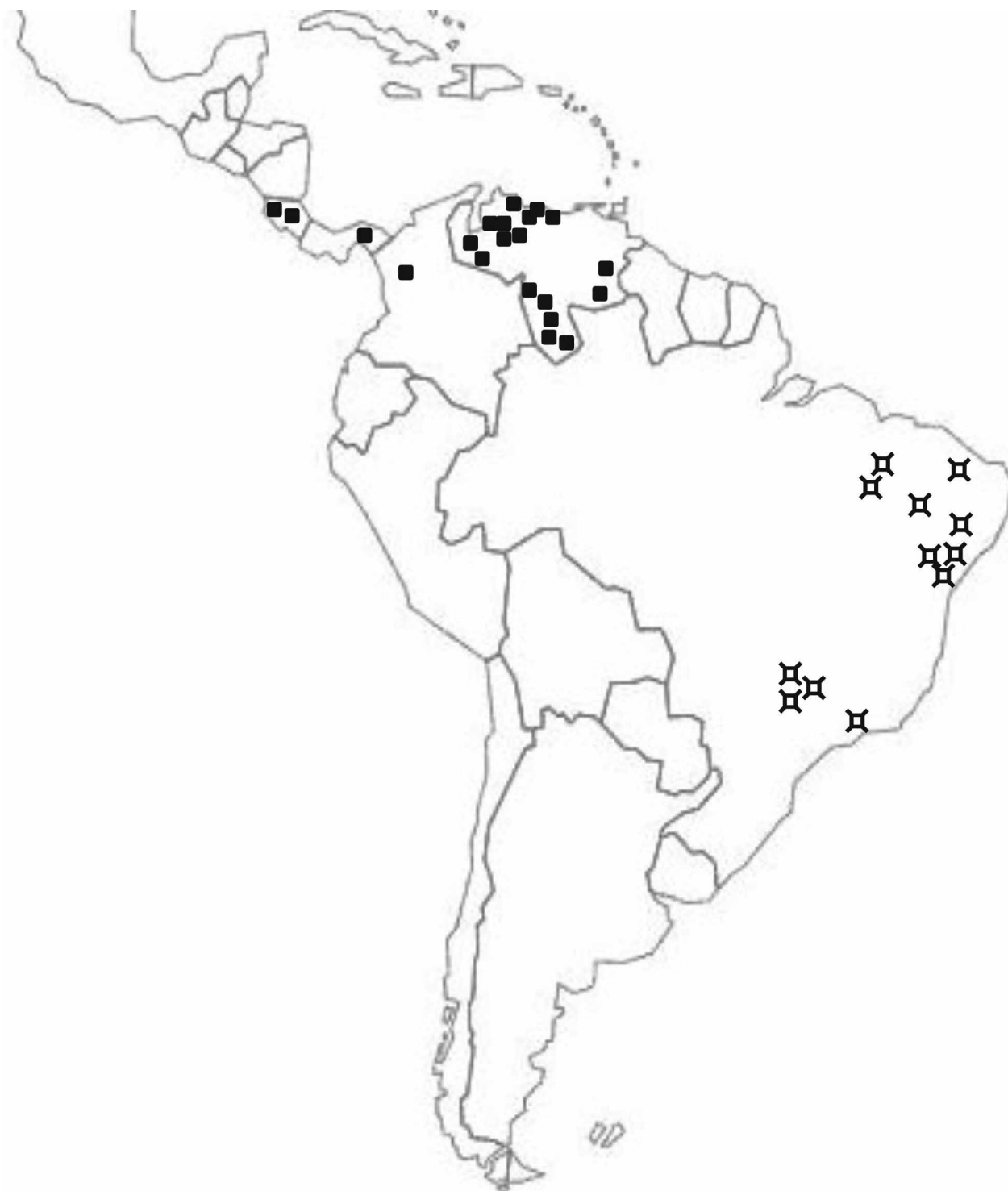
**TABLE 2.** Records of *Ixodes luciae* and their parasitic stages found on Didelphimorphia of the family Didelphidae from *bona fide* records in Argentina, Belize, Bolivia, Brazil, French Guiana, Guatemala, Panama, Peru, Surinam, Trinidad and Tobago, and Venezuela. L= larva, N= nymph, A= adult .

| Hosts                              | A  | AN | AL | ANL | N  | L | NL | Total |
|------------------------------------|----|----|----|-----|----|---|----|-------|
| Didelphidae                        |    |    |    |     |    |   |    |       |
| Caluromyinae                       |    |    |    |     |    |   |    |       |
| <i>Caluromys lanatus</i>           | 1  | 0  | 0  | 0   | 0  | 0 | 0  | 1     |
| <i>C. philander</i>                | 0  | 0  | 0  | 0   | 0  | 1 | 0  | 1     |
| Didelphinae                        |    |    |    |     |    |   |    |       |
| Didelphini                         |    |    |    |     |    |   |    |       |
| <i>Didelphis albiventris</i>       | 1  | 0  | 0  | 1   | 0  | 0 | 0  | 2     |
| <i>D. marsupialis</i>              | 26 | 0  | 0  | 0   | 0  | 0 | 0  | 26    |
| <i>Didelphis</i> sp.               | 4  | 0  | 0  | 0   | 0  | 0 | 0  | 4     |
| <i>Lutreolina crassicaudata</i>    | 1  | 0  | 0  | 0   | 0  | 0 | 0  | 1     |
| <i>Philander andersoni</i>         | 3  | 0  | 0  | 0   | 0  | 0 | 0  | 3     |
| <i>P. opossum</i>                  | 16 | 0  | 0  | 0   | 0  | 0 | 0  | 16    |
| Marmosini                          |    |    |    |     |    |   |    |       |
| <i>Marmosa constantiae</i>         | 0  | 0  | 0  | 0   | 1  | 0 | 0  | 1     |
| <i>M. murina</i>                   | 0  | 0  | 0  | 0   | 0  | 1 | 0  | 1     |
| <i>M. demererae</i>                | 0  | 0  | 0  | 0   | 2  | 0 | 0  | 2     |
| <i>M. robinsoni</i>                | 0  | 1  | 0  | 0   | 1  | 1 | 2  | 5     |
| <i>Marmosa</i> sp.                 | 1  | 0  | 0  | 0   | 0  | 1 | 0  | 2     |
| <i>Monodelphis breviceaudata</i> * | 0  | 0  | 0  | 0   | 2  | 1 | 6  | 9     |
| <i>Monodelphis</i> sp.             | 1  | 0  | 0  | 0   | 1  | 0 | 1  | 3     |
| Metachirini                        |    |    |    |     |    |   |    |       |
| <i>Metachirus nudicaudatus</i>     | 1  | 0  | 0  | 0   | 0  | 0 | 0  | 1     |
| Thylamyini                         |    |    |    |     |    |   |    |       |
| <i>Marmosops impavidus</i>         | 1  | 0  | 0  | 0   | 0  | 0 | 0  | 1     |
| <i>Thylamys cinderella</i>         | 0  | 0  | 0  | 0   | 1  | 0 | 0  | 1     |
| <i>T. venustus</i>                 | 0  | 0  | 0  | 0   | 1  | 0 | 0  | 1     |
| <i>Thylamys</i> sp.                | 0  | 0  | 0  | 0   | 1  | 0 | 0  | 1     |
| Total                              | 56 | 1  | 0  | 1   | 10 | 5 | 9  | 82    |

\* All references to *Monodelphis breviceaudata* have to be considered cautiously because considerable controversy exists about it and related species.

The distribution of *I. luciae* is also wide, including Argentina (north-west), Bolivia, Peru, Brazil, French Guiana, Surinam, Trinidad-Tobago, Venezuela, Panama, Guatemala, Belize and Mexico for records on Didelphimorphia. This distribution is augmented if Colombia (Wells *et al.* 1981), Costa Rica, Ecuador (Guglielmone *et al.* 2003b), Nicaragua (Jones *et al.* 1972) and Honduras (Onofrio 2002), all from undetermined hosts and unknown tick stages, are included in its range. However, the alleged southernmost record of *I. luciae* in Buenos Aires prov-

ince, Argentina, by Ivancovich and Luciani (1992) is in error (see the note above in *I. luciae* and the discussion section for details). Figure 3 shows the distribution of *I. luciae*.



**FIGURE 1.** Distribution of *Ixodes amarali* (♂) and *I. venezuelensis* (■).

The monotypic order Microbiotheridae is peculiar because *D. gliroides* is infested by *I. neuquenensis* in southwestern Argentina and southern Chile in coincidence with the range of the hosts. The records are not numerous but all of them were from this host. Therefore, *I. neuquenensis* is the only species exclusively found on a South American marsupial.

Finally, Paucituberculata does not appear to be important hosts for Ixodidae because there is just one record for *I. jonesae* for this type of host. Nevertheless, this may also be a consequence of inadequate tick searching.



**FIGURE 2.** Distribution of *Ixodes loricatus*. ✕ Symbol indicates unconfirmed or doubtful records.

## Discussion

The only *Dermacentor* species found in South America are the Nearctic and Neotropical *D. imitans* Warburton, 1933, and *D. nitens* Neumann, 1897 (Guglielmone *et al.* 2003b, who name this species as *Anocentor nitens* (Neumann, 1897)). No infestations of marsupials with any of these tick species were recorded.

The genus *Rhipicephalus* is represented in South America by *R. microplus* and an undetermined number of species of the *R. sanguineus* complex (Moraes-Filho *et al.* 2011). There are some references about infestation of Didelphimorphia with *Rhipicephalus* ticks but the relevance of these hosts as a food source for *Rhipicephalus* appears to be almost irrelevant considering the 1925 and 610 Neotropical records for *R. microplus* and *R. sanguineus* complex, respectively.



**FIGURE 3.** Distribution of *Ixodes luciae*.

The genus *Haemaphysalis* contains, apart of *H. cinnabarina* (see introduction), the Nearctic and Neotropical *H. juxtakochi* Cooley, 1946 and *H. leporispalustris* (Packard, 1969) (Guglielmone *et al.* 2003b). Two records, one



for nymphs in South America and other for an undetermined tick stage in Central America were registered on marsupials, indicating that they are not relevant hosts for this tick species.

Therefore, the irrelevant relationship *Dermacentor-Haemaphysalis-Rhipicephalus* with Didelphimorphia is similar to the irrelevance of Caviinae Fischer de Waldheim and Sigmodontinae relationships for the same genera of ticks as shown in Guglielmone and Nava (2010a, 2011).

The genus *Amblyomma* has 50 species established in South America (27 of them found only in this part of the World) and the 44 records on Didelphimorphia include 22 species of ticks from this genus. Most of them can be judged as unusual records of tick species that rely on other types of hosts for their nourishment with the exception of *A. fuscum* that may depend on feeding on Didelphimorphia for the maintenance of larvae and nymphs. This situation is broadly similar to the relationship of *Amblyomma*-Sigmodontinae, although in this case, *Amblyomma triste* subadult ticks usually feed on this type of rodent, a condition that may include *A. tigrinum* and *A. ovale* (Guglielmone & Nava 2011). The relationships between *Amblyomma*-Didelphimorphia and *Amblyomma*-Sigmodontinae both differ from the association between *Amblyomma*-Caviinae because the records of Caviinae are substantially fewer than the records of *Amblyomma* on Didelphimorphia and Sigmodontinae; however, Caviinae are vital for the life cycle of *A. parvum*, *A. tigrinum* and probably for *A. triste* in Argentina (Guglielmone & Nava 2010a).

The relationship of several species of *Ixodes* (Prostriata group) and Didelphimorphia contrasts with the corresponding association with ticks of the Metastriata group shown above. Records of species different to *I. amarali*, *I. loricatus*, *I. luciae* and *I. venezuelensis* on these types of hosts appear to be unusual and some cases (i.e., *I. longiscutatus*) are probably a result of misidentification. In contrast the four species named above have life cycles characterized by a frequent parasitism of Didelphidae.

*Ixodes amarali*, *I. loricatus*, *I. luciae* and *I. venezuelensis* have life cycles based on feeding on Sigmodontinae and Didelphidae (Guglielmone & Nava 2011). The first three species have immature stages feeding mostly on sigmodontin rodents and marsupials, while adult ticks are commonest on Didelphidae. Data on *I. venezuelensis* indicates that all parasitic stages feed on Sigmodontinae although other types of rodents are also hosts for this tick apart from Didelphidae. *Ixodes amarali* is an exclusive South American tick species, while *I. venezuelensis* is also found in Costa Rica and Panamá and *I. loricatus* and *I. luciae* are Neotropical ticks considered established from southern Mexico to Argentina (Guglielmone *et al.* 2003b), although this statement may not be true for *I. loricatus*.

The distributions of *I. loricatus* and *I. luciae* merit some considerations. The two northernmost records for *I. loricatus* are from Guatemala (on "wild host") and Frontera, state of Tabasco in México on the monkey *A. geoffroyi*, representing the only record for this country. It is considered that the Guatemalan record needs confirmation. On the other hand, we have no doubt about the identification of Mexican specimens by Keirans (1982). These specimens (two males and two females) were collected on an unknown date but previous to 1910, because there is a remark following locality in the original label saying "Compared with Neumann's types at Toulouse, 1910; agrees fully but Nn's type larger" (sic) (Keirans 1982, 1985). Mislabeling, a common source for wrong locality identification, is probable because *Amblyomma quasicyprum* Robinson, 1926, a synonym of *Amblyomma breviscutatum* Neumann, 1899 (Santos Dias 1956), maintained in the same collection where the Mexican *I. loricatus* are deposited, was also collected from the monkey *A. geoffroyi* at Tabasco, Frontera, Mexico, but this tick is established exclusively in the Australian and Oriental Zoogeographic Regions, therefore, the host and collection data are considered wrong (Keirans 1982, 1985; Keirans & Hillyard 2001). The only other tick record on Didelphimorphia in Frontera, state of Tabasco in México, and other reports from this country in Chiapas, Colima and Veracruz correspond to *I. luciae* (Cooley & Kohls 1945; Keirans 1982; Guzmán-Cornejo *et al.* 2007; Guzmán-Cornejo & Robbins 2010). Obviously, it is possible that *I. loricatus* and *I. luciae* have areas of sympatry in Mexico and Guatemala, but the lack of new records of *I. loricatus* for more than a century in Mexico, the absence of records on marsupials and wrong labeling for other ticks allegedly collected at the same locality, indicates the need for a new search to confirm that Mexico (and Guatemala) are included in the distribution range of this species.

Furthermore, the alleged records of *I. loricatus* in Tacarcuna Station (08°05'N 77°17'W), Darién, Panama in Fairchild *et al.* (1966) and from La Tirana (06°50'N 75°34'W), Antioquía, Colombia (this article) are invalid, while all Venezuelan records of this tick species requires confirmation. The southernmost record of *I. loricatus* in Tierra del Fuego, Argentina in Neumann (1901) is also controversial. Apart of the consideration given in the result section, the southern limit for an extant South American marsupial is about 47° S for the genus *Lestodelphys* Tate (Voss & Jansa 2009), which is quite further north from Tierra del Fuego bringing additional doubts about this locality for *I. loricatus*.

Therefore, it is emphasized that *bona fide* populations of *I. loricatus* range from north-eastern Brazil to north-eastern Argentina and southern Uruguay (Fig. 2). This distribution based on *bona fide* records may be an artifact due to poor sampling and additional efforts are needed to confirm the presence of *I. loricatus* in the vast territory from northeastern Brazil to Mexico. In the meantime there is no reason to consider *I. loricatus* as a tick species ranging from southern Mexico to Argentina as presented in Guglielmone *et al.* (2003b) but rather a South American tick with an allopatric distribution in relation to *I. luciae*.

The alleged southernmost record of *I. luciae* corresponds to Delta del Paraná INTA (34°25'S 58°35'W), province of Buenos Aires, Argentina where it was determined on Didelphimorphia and humans by Ivancovich and Luciani (1992). However, this and adjacent localities with the same ecological conditions were subject of numerous searches for ticks on sigmodontine rodents and to a lesser extent, on Didelphimorphia. The only *Ixodes* tick found on this type of host was *I. loricatus* (Keirans 1982; Lareschi 1996, 2000; Lareschi & Sánchez López 2000; Liljestrom & Lareschi 2002; Lareschi *et al.* 2003; Nava *et al.* 2003, 2004; Beldoménico *et al.* 2005; Nava *et al.* 2011). This has been further confirmed after the revision of the alleged *I. luciae* collected in Buenos Aires because, apart from a nymph of the *I. auritulus* tick group, all the specimens were in fact *I. loricatus*. Therefore, the southernmost *bona fide* record for this tick species is located in El Siambón (26°40'S 65°24'W), province of Tucumán, Argentina, on *T. cinderella* (Autino *et al.* 2006). This situation is depicted in Fig. 1, where the distribution of *I. luciae* ranges from northwestern Argentina to southern Mexico in a rather continuous distribution that will be even more homogeneous if record for this tick in Ecuador, Colombia, Costa Rica and Nicaragua are confirmed.

In brief, the current study shows that the related species *I. loricatus* and *I. luciae* share hosts but not territories in the Neotropical Zoogeographic Region, with *I. luciae* colonizing central-western regions in South America reaching southern Mexico via Central America, while *I. loricatus* colonize mostly eastern South America.

Didelphidae, which originated in South America, is thought to be the most ancient extant group of marsupials (Horovitz *et al.* 2009). However, the host-parasite relationships of the four species of *Ixodes* found frequently on Didelphidae are relatively new measured in historical time because all of them usually feed on Sigmodontinae, which are relatively new invaders of South American mainland (Pardiñas *et al.* 2010)

As stated before, *Ixodes* and *Amblyomma* were likely to be established in South America long before its isolation as a consequence of the break up of Gondwana, while Sigmodontinae or its ancestor entered South America in the Pliocene Period or, eventually during the Miocene Period (Pardiñas *et al.* 2010). Indeed, *Ixodes* ticks had (and have) the ability to radiate along Didelphimorphia occupying Neotropical South American and extra-South American habitats, a condition that *Amblyomma* ticks, also established in South American land before isolation, did not achieve with the same degree of success. Guglielmone and Nava (2011) present a hypothesis that the clade formed by *I. loricatus* and *I. luciae* (geographical, morphological and molecularly associated) plus the morphological-geographically associated *I. amarali* and *I. schulzei* Aragão and Fonseca, 1951 (known for a few ticks feeding on Sigmodontinae, Labruna *et al.* 2003) derived from *Ixodes* ancestors feeding on Didelphidae, but new species like *I. loricatus* and *I. luciae* were formed when Sigmodontinae irrupted in South America where this speciation hypothetically occurred. This scenario is based on Sigmodontinae sharing ancestral South American habitats with marsupials. This phenomenon appears to be supported by the current parasitism of nymphs and larvae of *I. loricatus* mostly on Sigmodontinae and Didelphini, and sub-adults of *I. luciae* feeding mostly on Sigmodontinae and Marmosini. However, the role of Sigmodontinae as host for immature tick stages of these species of ticks is crucial for the life cycle of *I. loricatus* in the southern range of its distribution (Nava *et al.* 2004) and for *I. luciae* in the Peruvian Amazon (Díaz *et al.* 2009). Nevertheless, studies on other locations are needed to confirm if this relationship is maintained under different circumstances. Therefore, new information (ecological, morphological and molecular) about Neotropical *Ixodes*, including more exhaustive alpha and beta taxonomy and discovery of fossil ticks are needed to understand the evolution of Ixodidae. In any condition, *I. venezuelensis* is not morphologically related to the other species of *Ixodes* usually feeding on Didelphidae and most probably its relation with South American marsupials evolved in a different way.

The only species of tick exclusively found on a South American marsupial is *I. neuquenensis*, the only tick known to parasitize the microbiotherian *D. gliroides* (Guglielmone *et al.* 2004), a strictly arboreal mammal strongly related to Australian marsupials. It is endemic to the northern temperate forests of southern South America that extends along the Pacific rim in Argentina and Chile, home of an endemic and endangered flora and fauna (Armesto *et al.* 1998). *Ixodes neuquenensis* is morphological and molecularly related to the clade formed by *I. abrocomae* Lahille, 1916, a parasite known for a few specimens collected from sigmodontin and abrocomid

rodents; *I. sigelos* Keirans Clifford and Corwin, 1976, mainly a parasite of Sigmodontinae; *I. stilesi* Neumann, 1911 and *I. taglei* Kohls, 1969 both known from specimens collected mostly from Artiodactyla Owen: Cervidae Goldfuss, all found in south-western South America (Guglielmone *et al.* 2004, 2005, 2006, 2007b, 2010a; Sánchez *et al.* 2010a, b). This South American clade is, according to the conceptual framework of Guglielmone and Nava (2011), derived from the *I. loricatus* clade and radiated along with the invasion of Sigmodontinae of southern South America. Under this condition *I. neuquenensis*, a parasite of an ancestral host should be a relatively new parasite that invaded the ecological niche of *D. gliroides* while Sigmodontinae colonized the region.

In synthesis, Didelphimorphia are important hosts for at least four species of *Ixodes*; Microbiotheria is fundamental for the life cycle of one species of *Ixodes*, while Paucituberculata appears to be of no importance to sustain any South American tick species. The species of *Ixodes* that feed usually on Didelphimorphia also feed frequently on Sigmodontinae. These groups of hosts are of importance only for *Ixodes*, being of minor importance for *Amblyomma* and irrelevant for species of other tick genera currently established in South American lands. This host-parasite relationship is relatively new measured in historical times bringing no evidence of the evolutionary path of South American ticks during the long period of South America isolation, rather it brings some evidence of a host-parasite relationship at the time around the great American interchange (about 2.5 mya) when Central America collided with northern South America.

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