



Rodents of the subfamily Sigmodontinae (Myomorpha: Cricetidae) as hosts for South American hard ticks (Acari: Ixodidae) with hypotheses on life history

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Abstract

Historical information shows that Sigmodontinae are irrelevant hosts for South American ticks of the genera *Haemaphysalis* Koch, *Rhipicephalus* Koch and *Dermacentor* Koch. Nine *Amblyomma* Koch species were found on Sigmodontinae but only *Amblyomma triste* Koch, 1844 appears strongly related to them. Eighteen species of *Ixodes* Latreille were determined on these hosts. Four species sporadically infest Sigmodontinae; eight are found mostly on Sigmodontinae but the records are too few for any inference. Six: *I. amarali* Fonseca, 1935, *I. longiscutatus* Boero, 1944, *I. loricatus* Neumann, 1899, *I. luciae* Sénevet, 1940, *Ixodes sigelos* Keirans, Clifford and Corwin, 1976 and *I. venezuelensis* Kohls, 1953 are usual parasites of Sigmodontinae. It is proposed that the *Ixodes*-Sigmodontinae relationship evolved from a South American tick ancestor parasite of Didelphidae. Their descendants are two extant clades, one formed by *I. loricatus*-*I. luciae* defined by analysis of 16S rDNA sequences further including *I. amarali* and *I. schulzei* by morphological affinities. These species (*I. schulzei* excluded) have adult ticks feeding on Didelphidae and sub-adult ticks feeding on Didelphidae and several species from five sigmodontin tribes. The second clade is formed by *I. abrocomae* Lahille, 1916 (known from few specimens, mostly collected from Sigmodontinae), *I. sigelos* (mainly a parasite of Sigmodontinae), *I. stilesi* Neumann, 1911 (parasite of deer), and possibly *I. taglei* Kohls, 1969 (parasite of deer) by morphological affinity. This clade is related to *I. neuquenensis* Ringuelet, 1947, an exclusive parasite of *Dromiciops gliroides* Thomas (Microbiotheriidae Ameghino).

Key words: Sigmodontinae, hosts, ticks, Ixodidae, Prostriata, Metastricata, life history

Introduction

Rodentia Bowdich originated in the ancient continent of Laurasia around the Cretaceous-Tertiary extinction event (65 mya) and is now represented by more than 40 % of extant species of mammals worldwide. It is speculated that caviomorph rodents rafted from Africa into isolated post-Gondwanian South America *circa* 30 mya with a rapid radiation thereafter (Benton, 2009). However, the most numerous species of rodents in South America belong to the Cricetidae Fischer, a family of probable Eocene origin in Asia (Gomes Rodrigues *et al.* 2010) that contains several hundred extant species with a wide distribution that encompasses the Nearctic, Neotropical, Oriental, and Palearctic Zoogeographic Regions (Musser and Carleton, 2005); therefore, Cricetidae has an origin independent of rodent ancestors introduced into South America from Africa. According to Musser and Carleton (2005) Cricetidae contains six subfamilies, but Sigmodontinae Wagner, is the predominant South American (Neotropical) subfamily. It contains more than 80 genera and *circa* 400 extant species, divided into several tribes. It is postulated that sigmodontins entered into northern South America not later than about 5 mya (Pliocene) because the first Sigmodontinae fossil is near this historical time in Argentina (Pardiñas *et al.* 2010). Many sources indicate that the radiation of Sigmodontinae was strong and diverse, with extant species occupying habitats at sea level, including riparian and arboreal species, up to high altitude deserts, taking advantage of different types of food resources throughout the Neotropics and southern Nearctic, but most species are South American (Pardiñas *et al.* 2002)

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 Metastricata that contains 458 species in 11 extant genera (Guglielmone *et al.* 2010b). However, French workers divide *Ixodes* into several genera (Camicas and Morel, 1977; Camicas *et al.* 1998). Prostriata

appears to have evolved earlier than *Metastricata* (Black and Roehrdanz, 1998; Jeyaprakash and Hoy, 2009). Fossil evidence shows the earliest emergence of *Metastricata* 100 mya (Cretaceous) (Grimaldi *et al.* 2002) while a molecular clock placed its origin in the late Jurassic-early Cretaceous Periods (156–112 mya) (Jeyaprakash and Hoy, 2009). There are no fossil records of that age or earlier for *Prostricata* but the molecular clock indicated the most recent period of its evolution in the late Jurassic Period (169 mya) and the latest in the upper Triassic Period (223 mya).

The genera *Amblyomma* Koch, *Dermacentor* Koch, *Haemaphysalis* Koch, *Ixodes* and *Rhipicephalus* Koch occur in South America, but *Dermacentor* and *Rhipicephalus* have no exclusively South American species, while the genus *Haemaphysalis* has just one species in the sub-continent, *Haemaphysalis cinnabarina* Koch, 1844. This species is known from two female ticks collected more than 170 years ago although authors such as Keirans and Restifo (1973) consider 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* (*Prostricata*) with 24 exclusively South American species and *Amblyomma* (*Metastricata*) with 27 species found only in the sub-continent. This appears to be a clear indication that *Amblyomma* and *Ixodes* were established in South America before its period of isolation from the late Cretaceous to the Pliocene, and the other extant *Metastricata* evolved elsewhere in the late Cretaceous or later, or alternatively, evolution occurred in areas too remote to reach South America before it 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 already isolated. However, this theory is still waiting confirmation and we do not rule out an earlier origin of *Haemaphysalis*.

Members of alleged old lineages of Ixodidae (*Ixodes*, *Amblyomma*) share South America with a relatively new group of potential placental mammal hosts. Therefore a revision of the relationship between Sigmodontinae and Ixodidae is presented herein. Additionally, with the fragmentary information on this topic we present conceptual frameworks for the evolutionary history of this host-parasite relationship not because we have a sound answer to this topic but rather to trigger a discussion about evolution of Neotropical ticks and their hosts, an issue that to the best of our knowledge has not been treated before.

Material and methods

Literature on ticks feeding on Sigmodontinae in South America was organized by listing the species of ticks in alphabetical order with notes on distribution and hosts. Nomenclature of Sigmodontinae follows Musser and Carleton (2005), except for oryzomyne rodents, where we have relied on the review of Weksler *et al.* (2006); synonyms presented by Francés and D'Elía (2006) and D'Elía *et al.* (2008) were also considered for this study. Non-South American records on Sigmodontinae for those species of ticks that are not exclusively South American are also included. Data are presented according to country, main administrative division, locality and its coordinates, tick stage, host, reference and comments if appropriate. Repeated records from the same host, tick stages and locality were considered as one record even if they have different dates. References that exclude tick stages found on Sigmodontinae were not considered for this study. The following abbreviations are applied for tick stages: A (adult tick with no sex identification), M (male), F (female), N (nymph), L (larva), LU (locality unknown).

Records for those species of ticks most frequently found on Sigmodontinae were tabulated according to tribes and species of hosts to present a general picture of host usage. No attempts were made for statistical analysis of the distribution of hosts because data are relatively scanty. Furthermore, lack of information on host and tick densities may render a distorted picture beyond any statistically significant figures. Alternatively, host profiles for the species most frequently infesting Sigmodontinae are presented. Chi-square distribution was used for records of Sigmodontinae 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.

Several references are made on tick records on Didelphidae in the results and discussion sections. The classification of Voss and Jansa (2009) was followed for the Didelphidae.

GenBank information on 16S rDNA mitochondrial gene sequences of the species of *Ixodes* named below was used to understand their relationship. The alignment of the sequences was carried out using BioEdit Sequence Alignment Editor (Hall 1999) with the program Clustal W (Thompson *et al.* 1994). Phylogenetic relationships were analyzed using neighbor-joining distance (NJ) method. The tree was generated from the Tamura-Nei model with the program Mega version 4.0 (Tamura *et al.* 2007), gaps were excluded in the pairwise comparison, and support for the NJ topology was tested by bootstrapping over 1,000 replications. Sequences of the argasid ticks *Ornithodoros moubata* and *Otobius megnini* were considered as outgroups. This technique was applied to all species of *Ixodes* established in the Neotropical Region (exclusively or not) whose 16S rDNA sequences are deposited in the GenBank and the Nearctic *Ixodes muris* Bishopp and Smith, 1937 that parasitizes mostly Cricetidae different to Sigmodontinae was also included to elaborate a NJ tree (a sequence of the Nearctic *I. woodi* Bishopp, 1911 which also feed mostly on Cricetidae different to Sigmodontinae, is available in the GenBank but we were unable to align it). In brief, the tree contains sequences of 15 species of *Ixodes*, six of them with several records from Sigmodontinae and three species that feed frequently on non-sigmodontine Cricetidae as follows: the Nearctic-Neotropical *Ixodes minor* Neumann, 1902 and *Ixodes spinipalpis* Hadwen and Nuttall, 1916 (in Nuttall 1916), and the Nearctic *I. muris*.

The molecular information along with morphology, hosts and distribution data of species of *Ixodes* were used to propose several alternatives for the evolutionary history of the relationship of this genus and Sigmodontinae in South America.

Results

1) *Amblyomma auricularium* (Conil, 1878) is a Neotropical and Nearctic tick species usually feeding on Cingulata Illiger (Guglielmone *et al.* 2003a).

Panama, LU, N on *Sigmodon hispidus* Say and Ord (Fairchild *et al.* 1966).

2) *Amblyomma cajennense* (Fabricius, 1787) is a Neotropical and Nearctic tick species with an ample tetrapod host range and locality records (*circa* 1600 for the whole Neotropical Region) but the name is considered to represent a tick species group (L. Beati, personal communication).

Brazil, Paraná, Tijuca do Sul (25°55'S 45°24'W), NL on *Nectomys squamipes* (Brants) (Barros-Battesti *et al.* 1998, as *A. cajennense* or close to). São Paulo, Juréia-Itatins Ecological Station (24° 32'S 47° 15'W), NL on *N. squamipes*, L on *Oryzomys russatus* (Wagner) (= *Euryoryzomys russatus* (Wagner) (Bossi *et al.* 2002). However, current studies in the same locality where *A. cajennense* larvae and nymphs were detected by Bossi *et al.* (2002) failed to confirm this and instead they found *A. ovale* immature stages (Labruna, M.B., personal communication).

Venezuela, Carabobo, Montalbán (10°12'N 68°19'W), MF on *S. hispidus* (Jones *et al.* 1972).

3) *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 *Oryzomys subflavus* (Wagner) (= *Cerradomys subflavus* (Wagner)) (Botelho *et al.* 2002). This record was found unconvincing by Guglielmone and Nava (2010b) who wrongly cited L as the stage of *A. dissimile* recorded.

4) *Amblyomma dubitatum* Neumann, 1899 is a South American species. Usual hosts for all tick stages are *Hydrochoerus hydrochaeris* (Linnaeus) (Nava *et al.* 2010b).

Uruguay, Flores, Río San José (33°57'S 56°50'W), NL on *Lundomys molitor* (Wing) and *Scapteromys tumidus* (Waterhouse) (Nava *et al.* 2010b).

5) *Amblyomma longirostre* (Koch, 1844) is a Neotropical tick species with a distribution wider than South America. Adult ticks usually feed on Rodentia: Erethizontidae Bonaparte, and larvae and nymphs on passeriform birds (some of them migratory) but there are several records on other types of hosts (Nava *et al.* 2010a).

Trinidad and Tobago, Trinidad, Turure Forest (10°39'N 61°11'W) N on *Oryzomys capito* (Olfers) (= *Hylaeamys megacephalus* (Fischer)) (Everard & Tikansingh 1973).

6) *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 Owen: Tapiridae Gray apart from several records on a variety of hosts (Guglielmone *et al.* 2003c).

Brazil, LU, A on *Nectomys* sp. Peters (Aragão & Fonseca 1961). See also *A. cajennense* for a probable confusion of larvae and nymphs of this species with the larvae and nymphs of *A. ovale*.

Central or South America, LU, MN on *Zygodontomys brevicauda* (Allen and Chapman), M on *Oryzomys talamancae* Allen (= *Transandinomys talamancae* (Allen)) and *S. hispidus*, N on *H. megacephalus* and *Zygodontomys* sp. Allen (Guglielmone *et al.* 2003c).

Panama, LU, M on *Oryzomys* sp. Baird, N on *Zygodontomys microtinus* (Thomas) (= *Z. brevicauda*) (Fairchild *et al.* 1966).

Venezuela, Carabobo, Aguirre (10°10'N 68°18'W), N on *Holochilus brasiliensis* (Desmarest), but probably corresponds to *Holochilus sciureus* Wagner, because Venezuela is out of the range of *H. brasiliensis*. Miranda, south of Río Chico (10°14'N 65°59'W), NL on *Z. brevicauda*. Sucre, south-east of Carúpano (10°37'N 63°01'W), N on *Z. brevicauda*. Trujillo, west north-west of Valera (09°22'N 70°40'W), N on *Oryzomys concolor* (Wagner) (= *Oecomys concolor* (Wagner)) (Jones *et al.* 1972 that state findings of L on *Z. brevicauda* and N on *O. concolor* are provisional).

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

Argentina, Córdoba, Campo Los Socavones (30°12'S 64°34'W), L on *Graomys centralis* (Thomas) (Guglielmone *et al.* 2007b); Quilino (30°12'S 64°32'W), L on *Graomys* sp. Thomas (Nava *et al.* 2008).

Panama, Panama, Balboa (08°57'N 79°34'W), NL on *S. hispidus* (Dunn, 1923), MFN on *S. hispidus* (Keirans 1985).

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

Argentina, Buenos Aires, 25 de Mayo (37°37'S 68°24'W), NL on *Graomys* sp., L on *Calomys musculinus* (Thomas) (Nava *et al.* 2005). Córdoba, Campo INTA (30°22'S 64°18'W), NL on *Akodon dolores* Thomas, L on *Calomys venustus* (Thomas), L on *Graomys* sp. (Nava *et al.* 2005) and *G. centralis* (Guglielmone *et al.* 2007b); Campo La Esperanza (30°12'S 64°31'W), L on *A. dolores*, *C. venustus* and *G. centralis*; Campo La Luisiana (30°22'S 64°23'W), NL on *Calomys* sp. Waterhouse, NL on *G. centralis* and *Necromys benefactus* (Thomas), N on *Calomys laucha* (Fischer), L on *C. venustus* and *Oligoryzomys* sp. Bangs; Campo Los Socavones (*op. cit.*), N on *G. centralis*, L on *A. dolores* (Nava *et al.* 2005). La Pampa, Lihuel Calel (38°02'S 65°33'W), NL on *Akodon oenos* Braun, Mares and Ojeda, N on *Akodon molinae* Contreras. Mendoza, La Pega (32°48'S 68°40'W), NL on *A. oenos*, N on *C. musculinus*; Ñacunán (34°02'S 67°58'W), L on *A. oenos* and *Graomys* sp.; Saladillo (33°12'S 65°51'W), L on *Phyllotis xanthopygus* (Waterhouse) (Nava *et al.* 2005).

Venezuela, Bolívar, south-east of Ciudad Bolívar (06°51'N 63°28'W), MFN on *Oryzomys fulvescens* (probably meaning *Oligoryzomys fulvescens* (Saussure) (Jones *et al.* 1972).

9) *Amblyomma triste* Koch 1844, a Neotropical and Nearctic tick species (Guzmán-Cornejo *et al.* 2007) whose larvae and nymphs are mainly collected from Sigmodontinae and Caviidae, and to a lesser extent on birds (Nava *et al.* 2010c).

Argentina, Buenos Aires, INTA Delta del Paraná (34°11'S 58°50'W), NL on *Akodon azarae* (Fischer), *Oligoryzomys flavescens* (Waterhouse), *Oxymycterus rufus* (Fischer) and *Scapteromys aquaticus* Thomas, L on *Oligoryzomys nigripes* (Olfers) (Nava *et al.* 2010c). Corrientes, Loreto (27°46'S 57°16'W), NL on *A. azarae*, *Calomys callosus* (Rengger) and *O. rufus*, N on *O. nigripes* (Nava *et al.* 2010c). Formosa, Reserva El Bagual (26°10'S 58°56'W), NL on *A. azarae* and *Necromys lasiurus* (Lund) (Nava *et al.* 2010c).

Uruguay, LU, NL on *O. flavescens* (Venzal *et al.* 2003), NL on *Oxymycterus nasutus* (Waterhouse), NL on *Scapteromys tumidus* (Waterhouse), N on *Necromys obscurus* (Waterhouse) (Venzal *et al.* 2008a).

10) *Dermacentor nitens* Neumann, 1897 is a Nearctic and Neotropical species with most records on Perissodactyla: Equidae Gray and, to a lesser extent, on Artiodactyla Owen: Bovidae Gray, and a few records on other types of hosts.

Brazil, Rio de Janeiro, Paracambi (22°36'S 43°42'W), MFN on *N. squamipes* (Amorim *et al.* 2002).

11) *Haemaphysalis juxtakochi* Cooley, 1946 is established in the Nearctic and Neotropical Regions. Adult ticks are a common parasite of artiodactyl hosts while larvae and nymphs present a vast array of hosts, including Sigmodontinae.

Argentina, Buenos Aires, INTA Delta del Paraná (*op. cit.*), L on *A. azarae* and *O. rufus* (Nava *et al.* 2010c).

12) *Ixodes abrocomae* Lahille, 1916 is an exclusively South American species known from six specimens from Chile, one found on Rodentia: Abrocomidae Miller and Gidley, and the rest on Sigmodontinae as shown below.

Chile, Region III, Parque Nacional Fray Jorge (30°40'S 71°39'W), M on *Abrothrix longipilis* (Waterhouse), Río Los Molles (30°45'S 70°25'W), M on *Abrothrix olivaceus* (Waterhouse), F on *P. xanthopygus* (Guglielmone *et al.* 2010a).

13) *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 aragaoui* Fonseca, 1935 or *Ixodes pararicinus* Keirans and Clifford, 1985 as discussed in Guglielmone *et al.* (2003b). Therefore, data below should be considered tentative.

Peru, Arequipa, El Sauce (04°25'S 80°26'W), NL on *Oryzomys xanthocolus* surely meaning *Oryzomys xantheolus* Thomas (= *Aegialomys xantheolus* (Thomas)), FN on *Sigmodon peruanus* Allen (Fonseca, 1960).

USA, Georgia, Bullock County, LU, N on *S. hispidus* (Oliver *et al.* 1987); St. Catherine Island, (31°45'N 81°03'W), NL on *Oryzomys palustris* (Harlan) (Durden & Oliver 1999).

14) *Ixodes amarali* Fonseca, 1935 is a tick species found only in South American whose adults are mostly found on didelphimorphs of the family Didelphidae Gray, but most nymphs are found on Sigmodontinae (Barros-Battesti & Knysak 1999).

Brazil, LU in northeastern area of the country, N on *C. subflavus*. Ceará, São Benedito (04°02'S 40°45'W), N on *Oligoryzomys eliurus* (Wagner) (= *O. nigripes*), N on *C. subflavus* (Barros-Battesti & Knysak 1999). Minas Gerais, Belo Horizonte (19°55'S 43°56'W), FN on *Zygodontomys lasiurus* (= *N. lasiurus*), F on *C. subflavus* (Linardi *et al.* 1984); Ouro Preto (20°23'S 43°30'W), N on *Oryzomys mattogrossae* (Allen) (= *Oligoryzomys microtis* (Allen)), L on *C. subflavus* (Fonseca & Trindade 1957). Pernambuco, LU, F on *C. subflavus* (Fonseca 1958); Bom Conselho (09°09'S 36°41'W), N on *C. subflavus*; Caruarú (08°16'S 35°58'W), L on *Rhipidomys mastacalis* (Lund); Garanhuns (08°53'S 36°29'W), FNL on *C. subflavus*, N on *Akodon arviculoides* (Wagner) (= *N. lasiurus*), N on *Holochilus* sp. Brandt, N on *O. nigripes* (Barros-Battesti & Knysak 1999).

15) *Ixodes andinus* Kohls, 1956 is an exclusively South American species known from the specimens used to describe the species, all of which were found on sigmodontin rodents.

Peru, Ancash, Huaraz (09°32'S 77°31'W), FNL on *Phyllotis darwini* (Waterhouse), NL *Hesperomys sorella* (Thomas) (= *Calomys sorellus* (Thomas)) (Kohls 1956).

16) *Ixodes auritulus* Neumann, 1904 is a name considered to represent a cosmopolitan tick species group that parasitizes Aves (González-Acuña *et al.* 2009) excepting a few records on Mammalia, including some of them on Sigmodontinae.

Venezuela, Mérida, southeast of Tabay (08°36'N 71°01'W), L on *Oryzomys minutus* (Tomes) (= *Microrozomys minutus* (Tomes)). Trujillo, east of Trujillo (09°22'N 70°18'W), L on *Oryzomys albigularis* (Tomes) (= *Nephelelomis albigularis* (Thomes)), L on *Thomasomys lugens* (Thomas) (= *Aepeomys lugens* (Thomas)) (Jones *et al.* 1972, who considered that these records of *I. auritulus* need verification).

17) *Ixodes galapagoensis* Clifford and Hoogstraal, 1980 is an exclusively South American tick species known from the type specimens found on Sigmodontinae.

Ecuador, Islas Galápagos, Burrington Island (00°49'N 90°04'W), MFN on *Oryzomys bauri* Allen (= *Aegialomys galapagoensis* (Waterhouse)) (Clifford & Hoogstraal 1980).

18) *Ixodes jonesae* Kohls, Sonenshine and Clifford, 1969 is an exclusively South American species known from several specimens collected from Sigmodontinae and several larvae from Paucituberculata Ameghino: Caenolastidae Trouessart.

Venezuela, Mérida, southeast of Tabay (*op. cit.*), MFNL on *Thomasomys laniger* (Thomas), FL on *M. minutus*, west of Timotes (08°59'N 70°45'W), N on *T. laniger* (Kohls *et al.* 1969).

19) *Ixodes lasallei* Méndez Arocha and Ortiz, 1958 is a Neotropical tick species with all parasitic stages feeding usually on Rodentia: Cuniculidae Miller and Gidley, and Dasyproctidae Bonaparte, with an uncertain record on Sigmodontinae.

Venezuela, Araguá, Rancho Grande Biological Station (10°21'N 67°36'W), M on *N. albigularis* Jones *et al.* (1972, who consider this specimen probably *I. lasallei*).

20) *Ixodes longiscutatus* Boero, 1944 is an exclusively South American species whose ecology needs further studies, but Sigmodontinae appears to be the most relevant host for its larvae and nymphs (Venzal *et al.* 2008b). There is a record of nymphs of *I. longiscutatus* on *A. azarae* in Ivancovich and Luciani (1992); however, we consider this record doubtful because it was done long before the peculiar nymph of this tick was recognized by Venzal *et al.* (2001).

Argentina, Salta, Parque Nacional El Rey (24°41'S 64°40'W), L on *Akodon lutescens* Allen (Venzal *et al.* 2008b).

Uruguay, Cerro Largo, southeast of Melo (32°31'S 54°03'W), L on *Oryzomys flavescens* (Waterhouse) (= *Oligoryzomys flavescens* (Waterhouse)) (Kohls & Clifford 1967). Maldonado, Barra del Arroyo Maldonado (34°54'S 54°52'W), NL on *O. nasutus* and *S. tumidus* (Kohls and Clifford, 1967; Venzal *et al.* 2008b), L on *Akodon obscurus* (Waterhouse) (= *Necromys obscurus* (Waterhouse)) (Kohls & Clifford 1967); Piriápolis (34°52'S 55°16'W), N on *S. tumidus*, L on *O. nasutus*. Rocha, Castillos (34°10'S 53°50'W), L on *O. nasutus*; La Coronilla (33°53'S 53°30'W), NL on *O. nasutus*, N on *S. tumidus* (Venzal *et al.* 2008b). San José, Balneario Kiyú (34°41'S 56°45'W), NL on *S. tumidus* (Venzal *et al.* 2008b). Soriano, east of Cardona (33°52'S 57°20'W), NL on *S. tumidus* (Kohls & Clifford 1967; these authors use the name *Ixodes uruguayensis* Kohls and Clifford, 1967 that later become a synonym of *I. longiscutatus*).

21) *Ixodes loricatus* Neumann, 1899 is a Neotropical species with adult ticks usually found on Didelphimorphia Gill: Didelphidae. Relevant hosts for larvae and nymphs are Didelphidae and Sigmodontinae. 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 sigmodontin rodents are important for its life cycle. This study revealed that in the southern range of the distribution of *I. loricatus* adults were found only on Didelphidae and larvae and nymphs on Sigmodontinae.

Argentina, Buenos Aires, Hudson (34°45'S 58°06'W), NL on *A. azarae*, N on *O. nigripes*, L on *O. flavescens* (Nava *et al.* 2004); INTA Delta del Paraná (*op. cit.*), NL on *A. azarae*, *O. flavescens* and *S. aquaticus*, L on *O. rufus* (Nava *et al.* 2010c); La Balandra (34°56'S 57°42'W), NL on *A. azarae*, N on *O. rufus*; Punta Lara (34°47'S 58°01'W), NL on *O. flavescens*, *O. rufus* and *S. aquaticus*, L on *A. azarae*; Ramallo (33°32'S 59°52'W), N on *O. flavescens*; San Nicolás (33°20'S 60°13'W), NL on *A. azarae* (Nava *et al.* 2004). Salta, Parque Nacional El Rey (*op. cit.*), NL on *Calomys* sp., N on *Akodon* sp. Meyen. Santa Fe, Funes (32°55'S 60°48'W), NL on *A. azarae* and *O. flavescens*; Santa Clara de Saguier (31°20'S 61°49'W), NL on *Akodon* sp. (Nava *et al.* 2004).

Brazil, northeastern Brazil, LU, A on *C. subflavus* and *Zygodontomys pixuna* (Moojen) (= *N. lasiurus*) (Fonseca 1958). Alagoas, Palmeira dos Índios (09°24'S 36°37'W), F on *Zygodontomys* sp. Pernambuco, Garanhuns (*op. cit.*), A on *C. subflavus*. São Paulo, São Paulo (23°31'S 46°37'W), NL on *Oryzomys* sp. (Barros-Battesti & Knysak 1999).

Uruguay, Canelones, Solymar Norte (34°47'S 55°56'W), N on *O. flavescens*. Maldonado, Barra del Arroyo Maldonado (*op. cit.*), L on *O. nasutus* (Nava *et al.* 2004).

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

Argentina, Salta, southwest of Pulares (25°05'S 65°37'W), N on *C. callosus* (Autino *et al.* 2006).

Brazil, Rondônia, close to Monte Negro (10°15'S 63°19'W), A on *Oecomys* sp. Thomas, N on *Oligoryzomys* sp. and *Oryzomys* sp. (Labruna *et al.* 2005).

Panama, Darién, Cerro Pirre (07°45'N 77°50'W), N on *Oryzomys* sp. Baird; Tacarcuna Station (08°05'N 77°17'W), N on *Zygodontomys microtinus* (Thomas) (= *Z. brevicauda*) (Fairchild *et al.* 1966).

Peru, Loreto, El Dorado (03°58'S 73°23'W), N on *Hylaeamys perenensis* (Allen); Fundo San Martín (03°58'S 73°24'W), N on *H. perenensis*, L on *Oecomys bicolor* (Tomes); Moralillo (03°54'S 73°21'W), N on *H. perenensis*, *Hylaeamys yunganus* (Thomas) and *O. microtis*; Ninarumi (03°51'S 73°22'W), N on *H. yunganus*; San Juan (03°59'S 73°25'W), N on *H. perenensis*; San Lucas (04°06'S 73°22'W), N on *H. perenensis*; Varillal (03°52'S 73°22'W), N on *H. perenensis* (Díaz *et al.* 2007).

Trinidad and Tobago, Trinidad, Bush Forest (10°24'N 61°00'W), *Oryzomys laticeps* (Lund) (= *Hylaeamys laticeps* (Lund)), *O. bicolor* and *Zygodontomys* sp. infested with larvae and/or nymphs of *I. luciae* identified as "immature stages" by Aitken *et al.* (1968).

Venezuela, Amazonas, Tamatana (03°09'N 65°50'W), N on *O. concolor* (Jones *et al.* 1972). Araguá, Rancho Grande (10°21'S 67°36'W), F on *Ichthyomys pittieri* Handley and Mondolfi (Guerrero, 1996). Carabobo, Montalbán (10°12'N 68°19'W), NL on *S. hispidus*. Miranda, east of Caracas (10°29'S 66°44'W), L on *O. concolor* (Jones *et al.* 1972). The following Venezuelan records are from Jones *et al.* (1972) who considered the specimens as probable *I. luciae* without further comments. Amazonas, Boca Mavaca (02°31'N 65°16'W), L on *O. concolor*. Araguá, Rancho Grande Biological Station (*op. cit.*), L on *N. albigularis*. Distrito Federal, southwest of Caracas (10°27'N 67°20'W), L on *H. megacephalus*. Miranda, east of Caracas (*op. cit.*), L on *O. fulvescens*. Yaracuy, Aroa (10°26'N 68°53'W), L on *H. megacephalus*.

23) *Ixodes nectomys* Kohls, 1956 known only from the type specimen.

Peru, Cusco, Marcapata (13°30'S 70°53'W), M on *N. squamipes* (Kohls, 1956).

24) *Ixodes pararicinus* Keirans and Clifford, 1985, is an exclusively South American species with several hosts for all parasitic stages. Sigmodontinae have been found infested with larvae and nymphs of this tick but these stages have been found on birds and marsupials also (Venzal *et al.* 2005; Autino *et al.* 2006).

Argentina, Salta, Finca Barba Yaco (25°58'S 64°55'W), L on *Oligoryzomys destructor* (Tschudi); Parque Nacional El Rey (*op. cit.*), NL on *Calomys fecundus* (Thomas) (= *Calomys boliviae* Thomas) (Venzal *et al.* 2005); southwest of Pulares (*op. cit.*), N on *C. callosus* (Autino *et al.* 2006).

Uruguay, LU, N on *A. azarae*. Maldonado, Posada La Laguna (30°17'S 54°40'W), N on *O. nigripes* (Venzal *et al.* 2003).

25) *Ixodes schulzei* Aragão and Fonseca, 1951 is a poorly-known exclusively South American species, collected in the wild only from Sigmodontinae.

Brazil, Minas Gerais, Juiz de Fora (21°45'S 43°21'W), F on *N. squamipes* (Labruna *et al.* 2003). Rio de Janeiro, Tinguá (22°35'S 42°26'W), F on *N. squamipes* (Aragão & Fonseca 1951). São Paulo, Santa Branca (23°23'S 45°52'W), F on *N. squamipes* (Labruna *et al.* 2003).

26) *Ixodes sigelos* Keirans, Clifford and Corwin, 1976 is an exclusively South American tick but this name may represent a species group complex (Sánchez *et al.* 2010b). All stages are parasites of Rodentia, especially Sigmodontinae.

Argentina, Catamarca, Las Máscaras cave (27°01'S 66°45'W), L on *Eligmodontia* sp. Cuvier found in an owl pellet from late Holocene (Sánchez *et al.* 2010a). Chubut, Estancia El Maitén (42°03'S 71°09'W), NL on *A. longipilis*, N on *Loxodontomys micropus* (Waterhouse); Estancia La Madrugada (43°37'S 68°57'W), L on *C. musculinus*; Estancia Laleque (42°19'S 70°59'W), NL on *A. longipilis* and *P. xanthopygus*, L on *A. olivaceus* and *Euneomys chinchilloides* (Waterhouse); Estancia Quichuara (43°42'S 70°20'W), F on *Reithrodon auritus* (Fischer); Gorro Frigio (43°02'S 69°19'W), L on *Eligmodontia morgani* Allen; east of Lago Blanco (45°55'S 71°14'W), FNL on *P. xanthopygus*, N on *A. longipilis*; Campamento PNG Somuncura (41°27'S 66°53'W), L on *A. longipilis* and *P. xanthopygus*; Laguna Blanca-Cerro Corona (41°25'S 66°57'W), NL on *P. xanthopygus* (Sánchez *et al.* 2010b). Tucumán, southwest of Hualinchay (26°20'S 65°39'W), N on *Akodon spegazzinii* Thomas (Guglielmone *et al.* 2005). Río Negro, Bahía Túnel-Lago Viedma, NL on *A. olivaceus* and *P. xanthopygus*; Cerro Ventana (48°59'S

70°15'W), N on *P. xanthopygus* and *R. auritus*, L on *A. olivaceus* and *E. morgani*; Estancia Alta Vista (50°27'S 72°36'W), L on *A. longipilis* and *A. olivaceus*; Estancia Pali Aike (51°56'S 69°36'W), FN on *A. olivaceus*; west of Punta Quilla-Puerto Santa Cruz (50°06'S 68°27'W), FNL on *A. olivaceus* (Sánchez *et al.* 2010b).

Chile, Región VII, Vilches Altos (35°35'S 71°04'W), F on *Phyllotis* sp. (Keirans *et al.* 1976). Región VIII, Chillán (36°36'S 72°06'W), L on *Oligoryzomys longicaudatus* (Bennett); Concepción (36°49'S 73°03'W), NL on *A. longipilis* and *A. olivaceus* but it is not absolutely certain that both tick stages were on these hosts (González-Acuña & Guglielmone 2005). Región XI, Lago General Carrera (46°26'S 72°00'W), N on *O. longicaudatus*; Puerto Aysen (45°23'S 72°41'W), N on *Akodon olivaceus* (Waterhouse) (= *Abrothrix olivaceus*); Puerto Ibañez (46°17'S 71°56'W), N on *Akodon xanthorhinus* (Waterhouse) (= *Abrothrix olivaceus*) (Guglielmone *et al.* 2005).

27) *Ixodes stilesi* Neumann, 1911 is an exclusively South American tick usually found on Artiodactyla: Cervidae Goldfuss (Guglielmone *et al.* 2007a).

Chile, Region XIV, San Martín (39°38'S 73°35'W), N on *O. longicaudatus* (Guglielmone *et al.* 2007a).

28) *Ixodes tropicalis* Kohls, 1956 is an exclusively South American parasite of Rodentia, especially Sigmodontinae.

Colombia, Antioquía, Valdivia (07°11'N 75°26'W), F on *Thomasomys aureus* (Tomes) (Kohls, 1956). Valle del Cauca, Pichinde Valley (03°25'N 76°35'W), NL on *N. albigularis* (Trapido & Sanmartín 1971).

29) *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).

Colombia, Antioquía, Valdivia (*op. cit.*), F on *Melanomys caliginosus* (Tomes) and *Sigmodontomys alfari* Allen (Kohls 1953).

Costa Rica, Heredia, LU, F on *M. caliginosus* (Durden & Keirans 1994).

Panama, Darién, LU, F on *Oryzomys* sp. and *Z. brevicaudata* (Durden & Keirans 1994); Tacarcuna Station (*op. cit.*), F on *Z. brevicauda* (Fairchild *et al.* 1966). Panama, LU, F on *T. talamancae* (Durden & Keirans 1994); Cerro Azul (09°09'N 79°45'W), F on *Oryzomys* sp. (Fairchild *et al.* 1966).

Venezuela, Araguá, Rancho Grande (*op. cit.*), F on *I. pittieri* (Guerrero, 1996), Rancho Grande Biological Station (*op. cit.*), L on *N. albigularis* (Jones *et al.* 1972, that indicate that the diagnosis of tick species is tentative). Carabobo, Bejuma (10°10'N 68°15'W), F on *I. pittieri* (Guerrero, 1996). Distrito Federal (10°28'N 66°58'W), F on *N. albigularis* (Durden & Keirans 1994), north northeast of Caracas (10°31'N 66°53'W), F on *N. albigularis* (Jones *et al.* 1972). Mérida, LU, NL on *M. minutus* (Durden & Keirans 1994); east of Tabay (08°38'N 71°02'W), L on *M. minutus* (Jones *et al.* 1972). Táchira, LU, NL on *M. minutus*, L on *Oryzomys* sp., *Rhipidomys fulviventer* Thomas and *Thomasomys hylophilus* Osgood. Trujillo, east of Trujillo (09°22'N 70°18'W), NL on *M. minutus*, L on *N. albigularis* (Jones *et al.* 1972).

As shown above, ticks found on Sigmodontinae are mostly *Ixodes* and to a lesser extent *Amblyomma*, with two records from *Haemaphysalis* and one for *Dermacentor*. The total number of records for *Ixodes* is 166 (164 for the Neotropical Region and two for the Nearctic Region) versus 65 records for *Amblyomma* (all Neotropical). The difference in usage of Sigmodontinae as hosts for these genera is further enhanced because the compilation of records for all species of *Amblyomma* for the whole Neotropical Region is circa 8,900, while the corresponding number for all *Ixodes* is circa 1,700. In other words, 9.8 % and 0.7 % of all records of *Ixodes* and *Amblyomma*, respectively, from South America (exclusively or non-exclusively) are infestations on Sigmodontinae, a statistically significant difference ($P < 0.001$, chi-square distribution).

Indeed, most records for the nine species of *Amblyomma* infesting Sigmodontinae appear to be exceptional, while the opposite is true for several of the 18 species of *Ixodes* infesting this type of rodent (see discussion below)

A summary of the situation is presented in Table 1 with total records for the different species and tribes of Sigmodontinae found infested with *Amblyomma* and *Ixodes* ticks. Additionally, the four species with most records on Sigmodontinae: *I. loricatus* (27 records), *I. luciae* (28), *I. sigelos* (33) and *I. venezuelensis* (21 records) are presented in Table 2 according to tribes and species of Sigmodontinae infested for each tick. Provisional valid diagnoses are included in the Tables. *Ixodes loricatus* were determined on several species of Oryzomyini and Akodontini, and one species of Phyllotini, while *I. luciae* were mostly found on several species of Oryzomyini and one species each of Ichtiomyini, Phyllotini and Sigmodontini. *Ixodes sigelos* was determined mostly from

specimens collected on Abrotrichini and Phyllotini with few collections on Akodontini and Oryzomyini, while *I. venezuelensis* were found mostly on Oryzomyini with few records from Ichthyomyini and Thomasomyini.

TABLE 1. Records of *Ixodes* or *Amblyomma* tick species on sigmodontin rodents for the whole Neotropical Region. Numbers underlined represent the total records for the corresponding tribe, numbers not underlined represent the total records for each species.

Species of rodents	<i>Amblyomma</i>	<i>Ixodes</i>
Abrotrichini	<u>0</u>	<u>17</u>
<i>Abrothrix longipilis</i>	0	7
<i>A. olivaceus</i>	0	10
Akodontini	<u>19</u>	<u>32</u>
<i>Akodon azarae</i>	3	8
<i>A. dolores</i>	3	0
<i>A. lutescens</i>	0	1
<i>A. molinae</i>	1	0
<i>A. oenos</i>	3	0
<i>A. spegazzinii</i>	0	1
<i>Akodon</i> sp.	0	2
<i>Necromys benefactus</i>	1	0
<i>N. lasiurus</i>	1	3
<i>N. obscurus</i>	1	1
<i>N. temchuki</i>	0	0
<i>Oxymycterus nasutus</i>	1	5
<i>O. rufus</i>	2	4
<i>Scapteromys aquaticus</i>	1	2
<i>S. tumidus</i>	2	5
Ichthyomyini	0	3
<i>Ichthyomys pittieri</i>	0	3
Oryzomyini	<u>23</u>	<u>82</u>
<i>Aegialomys galapagoensis</i>	0	1
<i>A. xantheolus</i>	0	1
<i>Cerradomys subflavus</i>	1	9
<i>Euryoryzomys russatus</i>	1	0
<i>Holochilus sciureus</i>	1	0
<i>Holochilus</i> sp.	0	1
<i>Hylaeamys laticeps</i>	0	1
<i>H. megacephalus</i>	2	2
<i>H. perenensis</i>	0	6
<i>H. yunganus</i>	0	2
<i>Lundomys molitor</i>	1	0
<i>Melanomys caliginosus</i>	0	2
<i>Microryzomys minutus</i>	0	6
<i>Nectomys squamipes</i>	2	4
<i>Nectomys</i> sp.	1	0
<i>Nephelomys albigularis</i>	0	8
<i>Oecomys bicolor</i>	0	2
<i>O. concolor</i>	1	3

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TABLE 1. (continued)

Species of rodents	<i>Amblyomma</i>	<i>Ixodes</i>
<i>Oecomys</i> sp.	0	1
<i>Oligoryzomys destructor</i>	0	1
<i>O. flavescens</i>	2	7
<i>O. fulvescens</i>	1	1
<i>O. longicaudatus</i>	0	2
<i>O. microtis</i>	0	3
<i>O. nigripes</i>	2	4
<i>Oligoryzomys</i> sp.	1	1
<i>Oryzomys palustris</i>	0	1*
<i>Oryzomys</i> sp.	1	6
<i>Sigmodontomys alfari</i>	0	1
<i>Transandinomys talamancae</i>	1	1
<i>Zygodontomys brevicauda</i>	4	3
<i>Zygodontomys</i> sp.	1	2
Phyllotini	<u>18</u>	<u>22</u>
<i>Calomys boliviae</i>	0	1
<i>C. callosus</i>	1	2
<i>C. laucha</i>	1	0
<i>C. musculus</i>	2	1
<i>C. sorellus</i>	0	1
<i>C. venustus</i>	3	0
<i>Calomys</i> sp.	1	1
<i>Eligmodontia morgani</i>	0	2
<i>Eligmodontia</i> sp.	0	1
<i>Euneomys chinchilloides</i>	0	1
<i>Graomys centralis</i>	5	0
<i>Graomys</i> sp.	4	0
<i>Loxodontomys micropus</i>	0	1
<i>Phyllotis darwini</i>	0	1
<i>P. xanthopygus</i>	1	7
<i>Phyllotis</i> sp.	0	1
<i>Reithrodon auritus</i>	0	2
Sigmodontini	<u>5</u>	<u>3</u>
<i>Sigmodon hispidus</i>	5	2*
<i>S. peruanus</i>	0	1
Thomasomyini	<u>0</u>	<u>7</u>
<i>Aepeomys lugens</i>	0	1
<i>Rhipidomys fulviventer</i>	0	1
<i>R. mastacalis</i>	0	1
<i>Thomasomys aureus</i>	0	1
<i>T. hylophilus</i>	0	1
<i>T. laniger</i>	0	2
	65	166

* The record from *Oryzomys palustris* and one record from *Sigmodon hispidus* correspond to *Ixodes affinis* from Nearctic localities.

TABLE 2. Records of *Ixodes loricatus*, *I. luciae*, *I. sigelos* and *I. venezuelensis* and their parasitic stages found on sigmodontin rodents for the whole Neotropical Region. Numbers underlined represent the total for the corresponding tribe and numbers not underlined represent the total records for each species. L= larva, N= nymph, A= adult .

Hosts	<i>I. loricatus</i>	<i>I. luciae</i>	<i>I. sigelos</i>	<i>I. venezuelensis</i>
Abrotrichini	<u>0</u>	<u>0</u>	<u>15</u>	<u>0</u>
<i>Abrothrix longipilis</i>	0	0	6 (NL)	0
<i>A. olivaceus</i>	0	0	9 (ANL)	0
Akodontini	<u>14</u>	<u>0</u>	<u>1</u>	<u>0</u>
<i>Akodon azarae</i>	6 (NL)	0	0	0
<i>A. spegazzinii</i>	0	0	1 (N)	0
<i>Akodon</i> sp.	2 (NL)	0	0	0
<i>Necomys lasiurus</i>	1 (A)	0	0	0
<i>Oxymycterus nasutus</i>	1 (L)	0	0	0
<i>O. rufus</i>	2 (NL)	0	0	0
<i>Scapteromys aquaticus</i>	2 (NL)	0	0	0
Ichthyomyini	<u>0</u>	<u>1</u>	<u>0</u>	<u>2</u>
<i>Ichthyomys pittieri</i>	0	1 (A)	0	2 (A)
Oryzomyini	<u>12</u>	<u>25</u>	<u>2</u>	<u>27</u>
<i>Cerradomys subflavus</i>	3 (A)	0	0	0
<i>Hylaeamys laticeps</i>	0	1 *	0	0
<i>H. megacephalus</i>	0	2 (L)	0	0
<i>H. perenensis</i>	0	6 (N)	0	0
<i>H. yunganus</i>	0	2 (N)	0	0
<i>Melanomys caliginosus</i>	0	0	0	2 (A)
<i>Microryzomys minutus</i>	0	0	0	4 (NL)
<i>Nephelomys albigularis</i>	0	1 (L)	0	4 (ANL)
<i>Oecomys bicolor</i>	0	2 (L) *	0	0
<i>O. concolor</i>	0	3 (NL)	0	0
<i>Oecomys</i> sp.	0	1 (A)	0	0
<i>Oligoryzomys flavescens</i>	6 (NL)	0	0	0
<i>O. fulvescens</i>	0	1 (L)	0	0
<i>O. longicaudatus</i>	0	0	2 (NL)	0
<i>O. microtis</i>	0	1 (N)	0	0
<i>O. nigripes</i>	1 (N)	0	0	0
<i>Oligoryzomys</i> sp.	0	1 (N)	0	0
<i>Oryzomys</i> sp.	1 (NL)	2 (N)	0	3 (AL)
<i>Sigmodontomys alfari</i>	0	0	0	1 (A)
<i>Transandinomys talamancae</i>	0	0	0	1 (A)
<i>Zygodontomys brevicauda</i>	0	1 (N)	0	2 (A)
<i>Zygodontomys</i> sp.	1 (A)	1 *	0	0
Phyllotini	<u>1</u>	<u>1</u>	<u>15</u>	<u>0</u>
<i>Calomys callosus</i>	0	1 (N)	0	0
<i>C. musculinus</i>	0	0	1 (L)	0
<i>Calomys</i> sp.	1 (NL)	0	0	0
<i>Eligmodontia morgani</i>	0	0	2 (L)	0

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TABLE 2. (continued)

Hosts	<i>I. loricatus</i>	<i>I. luciae</i>	<i>I. sigelos</i>	<i>I. venezuelensis</i>
<i>Eligmodontia</i> sp.	0	0	1 (L)	0
<i>Euneomys chinchilloides</i>	0	0	1 (L)	0
<i>Loxodontomys micropus</i>	0	0	1 (N)	0
<i>Phyllotis darwini</i>	0	0	0	0
<i>P. xanthopygus</i>	0	0	6 (ANL)	0
<i>Phyllotis</i> sp.	0	0	1 (A)	0
<i>Reithrodon auritus</i>	0	0	2 (AN)	0
Sigmodontini	<u>0</u>	<u>1</u>	<u>0</u>	<u>0</u>
<i>Sigmodon hispidus</i>	0	1 (NL)	0	0
Thomasomyini	<u>0</u>	<u>0</u>	<u>0</u>	<u>2</u>
<i>Rhipidomys fulviventer</i>	0	0	0	1 (L)
<i>Thomasomys hylophilus</i>	0	0	0	1 (L)
	27	28	33	21

* One record for each species is for Suriname in Aitken *et al.* (1968) who determined “immature stages” on hosts without identifying if they were nymphs, larvae or both.

The total records for *I. sigelos* are 37. The importance of Sigmodontinae is shown by its 33 records (89.2 % of total records), representing larval, nymphal and adult ticks. The other records of *I. sigelos* are nymphs collected on Rodentia of the families Abrocomidae and Muridae Illiger, and larval, nymphal and adult ticks collected on Octodontidae Waterhouse.

The host profile of *I. venezuelensis* was obtained from 74 records; 21 (28.3 %) and 20 (27.0 %) were from larvae, nymphs and adult ticks from Sigmodontinae and Didelphidae, respectively, followed by 13 records (17.6 %) of larvae and nymphs collected from Echimyidae Gray. The remaining records correspond to hosts representing a vast array of orders of Rodentia for all parasitic stages of *I. venezuelensis*.

TABLE 3. Host profiles of *Ixodes loricatus* and *Ixodes luciae* constructed from a compilation of Neotropical tick records. In brackets the corresponding percentages for each tick stage.

	Adult ticks	Nymphs	Larvae
<i>I. loricatus</i>			
Didelphidae			
Didelphini	110 (84.6)	16 (34.8)	9 (26.5)
Marmosini	5 (3.8)	7 (15.2)	4 (11.8)
Metachirini	1 (0.8)	0 (0.0)	0
Sigmodontinae	5 (3.9)	21 (45.7)	21 (61.8)
Other hosts	9 (7.0)	2 (4.3)	0
Total	130	46	34
<i>I. luciae</i>			
Didelphidae			
Didelphini	52 (82.5)	3 (7.7)	1 (4.0)
Marmosini	4 (6.3)	19 (48.7)	14 (56.0)
Metachirini	1 (1.6)	0 (0.0)	0 (0.0)
<i>Caluromys</i>	1 (1.6)	0 (0.0)	0 (0.0)
Sigmodontinae	2 (3.2)	16 (41.0)	8 (32.0)
Other hosts	3 (4.8)	1 (2.6)	2 (8.0)
Total	63	39	25

Host profiles for the other main species feeding on Sigmodontinae, *I. loricatus* and *I. luciae* are presented in Table 3. These tick species show an apparently similar pattern of host usage with adult ticks feeding on Didelphidae Gray and larvae and nymphs feeding on Didelphidae and Sigmodontinae. However, there are differences about host usage of these species when genera of Didelphidae are divided into the subfamilies Didelphini Gray and Marmosini Hershkovitz. Didelphini are the usual hosts for adult ticks of both species of *Ixodes* but the percentage of records for larvae and nymphs is higher for Didelphini than for Marmosini in *I. loricatus*, while the opposite is true for *I. luciae*.

Discussion

The genus *Rhipicephalus* is represented in South America by an undetermined number of species of the *R. sanguineus* (Latreille, 1806) complex and *R. microplus* (Canestrini, 1888). No infestations of Sigmodontinae by either tick species were recorded.

The genus *Haemaphysalis* in South America contains, apart from *H. cinnabarina* (see introduction), the Nearctic and Neotropical *H. juxtakochi* Cooley, 1946 and *H. leporispalustris* (Packard, 1969) (Guglielmone *et al.* 2003b). Two records of larvae of *H. juxtakochi* were determined on Sigmodontinae indicating that they are not relevant hosts for this tick species.

The only *Dermacentor* species found in South America are the Nearctic and Neotropical *D. imitans* Warburton, 1933, and *D. nitens* (Guglielmone *et al.* 2003b). There is just one record of *D. nitens* on Sigmodontinae that if confirmed (the information was not presented in a formal scientific publication) will be the only one from *circa* 600 records of this tick species for all the Neotropical Region, stressing its exceptionality.

The genus *Amblyomma* has 50 species established in South America (27 of them found only there) and the 65 records on Sigmodontinae include nine species of ticks. However, most of them can be judged as unusual records of tick species that rely on other types of hosts for their nourishment. Nevertheless, there are several records for *A. ovale*, *A. tigrinum* and *A. triste*. Larvae and nymphs of *A. triste* are regularly found on Sigmodontinae and this type of host is of importance for its cycle (Nava *et al.* 2010c). Larvae of *A. tigrinum* are also frequently found on Sigmodontinae (Nava *et al.* 2006) but it is not certain that Sigmodontinae are crucial for its survival. It is possible that the role of Sigmodontinae is of relevance for *A. ovale* but ecological studies on the host-usage of larvae and nymphs are needed to confirm this.

We considered that the relationship of *Amblyomma* and Sigmodontinae is, in general, of opportunistic nature as a result of the introduction of sigmodontin rodents into South America and include tick species rather catholic in host parasitism. In other words, we consider that Sigmodontinae is of little importance for survival of *Amblyomma* species with the exception of *A. triste*, and, perhaps *A. tigrinum* and *A. ovale*.

The relationship between several species of *Ixodes* (Prostriata group) and Sigmodontinae contrasts with the corresponding relationship with ticks of the Metastriata group. Records of *I. affinis*, *I. auritulus*, *I. lasallei* and *I. stilesi* on these types of rodents appear to be unusual or, at least, of no obvious ecological significance. Sigmodontinae are of apparent importance for *I. abrocomae*, *I. andinus*, *I. galapagoensis*, *I. jonesae*, *I. nectomys*, *I. schulzei* and *I. tropicalis*; however, all these species are known only from a very limited number of specimens and few ecological inferences can be made with the data at hand. The same applies to *I. pararicinus* with five records of larvae and nymphs on Sigmodontinae but also with several records on birds and one on a marsupial (Venzal *et al.* 2005; Autino *et al.* 2006). In contrast *I. amarali*, *I. longiscutatus*, *I. loricatus*, *I. luciae*, *I. sigelos* and *I. venezuelensis* have life cycles characterized by frequent parasitism of Sigmodontinae.

Ixodes amarali, *I. loricatus*, *I. luciae* and *I. venezuelensis* have life cycles based on feeding on Sigmodontinae and Didelphidae. The first three species have immature stages feeding 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 hosts for this tick apart from Didelphidae. Larvae and nymphs of *I. longiscutatus* are common parasites of Sigmodontinae, but common hosts for adult ticks are still undetermined; however, marsupials were not recorded as *bona fide* hosts for any parasitic stage of this species of tick (Guglielmone & Nava 2010a). Finally, *I. sigelos* is unique in having all its live stages feeding mainly on Sigmodontinae. All these tick species are exclusively South American with the exception of *I. luciae* and *I. venezuelensis* that are Neotropical ticks also established out of South America (Guglielmone *et al.* 2003b). *Ixodes loricatus* was con-

sidered to be established from Mexico to Argentina (Guglielmone *et al.* 2003b), but a recent study indicates that non-South American records of *I. loricatus* are doubtful or erroneous (Guglielmone *et al.*, in preparation). In any situation, these host-parasite relationships are relatively new in respect to historical time considering the period of introduction of Sigmodontinae into South America. Nevertheless, *I. longiscutatus* (eventually *I. pararicinus*) with larvae and nymphs feeding on Sigmodontinae and adults ticks also parasitizing placental mammals (Guglielmone *et al.* 1992; Venzal *et al.* 2008b) appears to be a species that evolved even later than the species currently parasitizing primitive marsupial mammals and sigmodontin rodents.

As we stated before, *Ixodes* and *Amblyomma* are considered 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 (eventually Miocene Period). Indeed, *Ixodes* ticks radiated among Sigmodontinae occupying new South American habitats, a condition that *Amblyomma* ticks, also established in South America before isolation, did not achieve with the same degree of success.

There is not sufficient data for an assertive answer about the historical relationship of *Ixodes* and Sigmodontinae. However, we consider of evolutionary importance the species of Neotropical *Ixodes* (*loricatus*, *luciae*, *neuquenensis*, *stilesi*, *abrocomae* and *sigelos*) grouped in Figure 1. This assemblage of ticks is formed by the clade of *I. luciae* (Neotropical but not exclusively South American) plus *I. loricatus*, now considered a South American tick (Guglielmone *et al.*, in preparation), and the clade of exclusively South American species *I. stilesi*, *I. abrocomae* and *I. sigelos* plus *I. neuquenensis* bound to this clade. The first clade may be enlarged by the inclusion of the morphological related species *I. amarali* and *I. schulzei* (Barros-Battesti *et al.* 2007), while the second clade may include *I. taglei* Kohls, 1969 by morphological affinity (Guglielmone *et al.* 2004, 2006, 2010a).

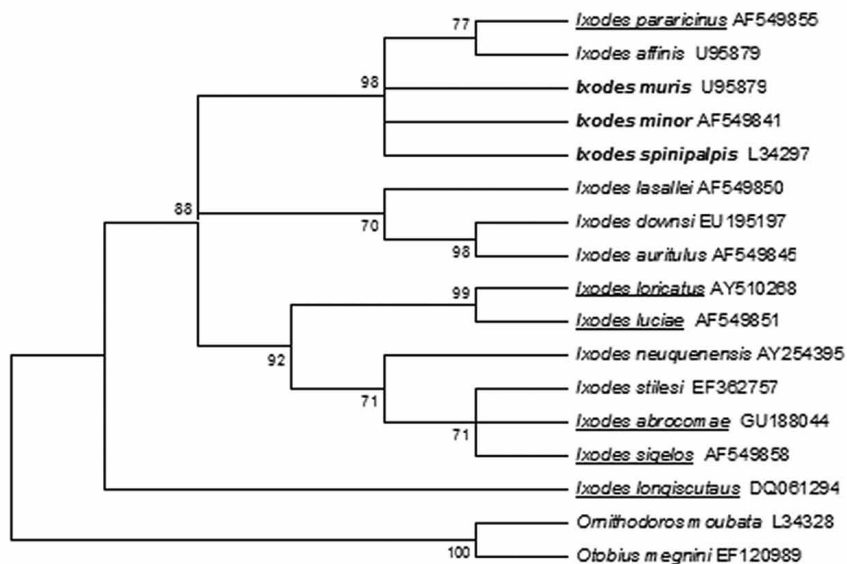


FIGURE 1. Neighbour-joining condensed tree using the Tamura-Nei model for 16S rDNA mitochondrial sequences of all Neotropical (exclusive and non-exclusive) species of *Ixodes* deposited in GenBank and for Nearctic species usually found on Cricetidae, with species of Argasidae (*Ornithodoros moubata* and *Otobius megnini*) as outgroups. Numbers on the branches represent bootstrap support (more than 70 %) generated from 1,000 replications. Codes following each species name correspond to GenBank accession numbers. Names in bold indicate ticks often found on Cricetidae different to Sigmodontinae in the Nearctics and Neotropics. Names underlined indicate ticks often found on Sigmodontinae.

The first clade is characterized by the presence of species of ticks with adult ticks feeding principally on Didelphidae and sub-adult stages predominant on Didelphidae and Sigmodontinae (*I. loricatus*, *I. luciae*, *I. amarali*) while the few specimens of *I. schulzei* collected on identified free-ranging hosts were female ticks from *N. squamipes*.

Didelphidae represent the most ancient extant group of marsupials and its origin is South American (Horovitz *et al.* 2009) with an ample distribution that currently includes Neotropical areas north to the Isthmus of Panama and southern Nearctic where Didelphidae entered in the great American interchange. This clade of *Ixodes* species also

has geographic congruence and all of them are present in Brazil with two of these species, *I. amarali* and *I. schulzei*, found only there. The distribution of *I. loricatus* includes north-eastern, central and southern Brazil in Ceará, Paraíba, Pernambuco, Alagoas, Goiás, Mato Grosso do Sul, Minas Gerais, Rio de Janeiro, São Paulo, Paraná, Santa Catarina and Rio Grande do Sul (Aragão 1936; Keirans 1985; Barros-Battesti & Knysak 1999; Arzua *et al.* 2005; Miziara *et al.* 2008) while *I. luciae* is distributed west of the area of establishment of *I. loricatus* in the states of Acre, Amazonas, Mato Grosso do Sul, Pará and Rondônia (Labruna *et al.* 2005; Labruna MB, personal communication). *Ixodes amarali* is restricted to eastern Brazil in Ceará, Paraíba, Pernambuco, Alagoas, Minas Gerais and Rio de Janeiro (Fonseca 1958; Barros-Battesti & Knysak 1999; Faccini *et al.* 1999) in sympatry with the distribution of *I. loricatus*, while the ecologically poorly-known *I. schulzei* has been found in central and southern Brazil in the states of Rondônia (ticks collected from the environment), Minas Gerais, Rio de Janeiro, São Paulo, Paraná (ticks collected from the environment and “small mammals”) and Santa Catarina (host defined as “wild rat”) (Aragão & Fonseca 1951; Labruna *et al.* 2003; Arzua *et al.* 2005; Arzua & Barros-Battesti 2008) which matches the distribution of *I. loricatus* with the exception of Rondônia. These distributions may indicate that these *Ixodes* radiated from northern or central Brazil.

The second clade contains *I. sigelos* which is widespread from southern to northwestern Argentina and southern to northern Chile and is mainly a parasite of Sigmodontinae (Guglielmone *et al.* 2010a; Sánchez *et al.* 2010b), while *I. stilesi* is a parasite of *Pudu puda* (Molina) in central Chile with an odd record on Sigmodontinae (Guglielmone *et al.* 2007a), and *I. taglei* is known from a few specimens collected from *P. puda* in central Chile (Kohls 1969). The last member of this clade, *I. abrocomae*, is a poorly-known species collected on sigmodontin and abrocomid rodents in northern Chile along with *I. sigelos* (Guglielmone *et al.* 2010a). These species are also related to *I. neuquenensis*, the only tick species known to parasitize the microbiotherian *Dromiciops gliroides* Thomas (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 extend along the Pacific Rim in Argentina and Chile, home of an endemic and endangered flora and fauna (Armesto *et al.* 1998). These distributions suggest that these species of *Ixodes* radiated from a place in southwestern South America.

The scenario immediately above suggests that the common ancestor of the clades was a parasite of microbiotherian marsupials. From there *Ixodes* species diverged with one branch becoming parasites of Sigmodontinae and deer that irrupted into South America via the great American interchange, while the other branch evolved to *Ixodes* ticks whose adults feed on Didelphidae and sub-adult ticks parasitizing Didelphidae and Sigmodontinae. It can be hypothesized that Sigmodontinae sharing primeval habitats with marsupials at the edge of extinction and their *Ixodes* (probably close to *I. neuquenensis*) adjusted their life cycles to the intruders.

A second scenario may favor the view that South American *Ixodes* entered into this part of the world with their hosts (sigmodontins or its ancestor) to radiate along with Sigmodontinae diversification to form the group of Neotropical *Ixodes* shown in Figure 1. Under this condition, the Neotropical *I. luciae* distributed from southern Mexico to Argentina (Guglielmone *et al.* 2003b) and *I. loricatus* with *bona fide* records in Uruguay, Argentina, Paraguay and Brazil (Guglielmone *et al.*, in preparation) may represent the descendants of extinct species of *Ixodes* that entered into South America with sigmodontin or proto-sigmodontin rodents and adapted their life cycles to parasitize some Didelphidae and Microbiotheridae.

A third scenario involves South American *Ixodes* ancestors whose larvae, nymphs and adult ticks fed on marsupials. Under this hypothetical condition, the irruption of sigmodontin rodents led them to share the habitat with marsupial hosts for sub-adult ticks and new species like *I. loricatus* and *I. luciae* adapted to the new situation with considerable success to colonize vast areas of the Neotropical Region. The second branch evolved to feed on sigmodontins, other hosts introduced in the great American interchange, and *D. gliroides*.

We consider improbable a fourth scenario where sigmodontin rodents arrived at South America carrying the ancestor of the clade related to *I. neuquenensis* because the distribution of these tick species in southwestern South America appears remote considering the most probable locality of introduction of Sigmodontinae in South America. Even more improbable appears to be the radiation of both clades from different ancestors because current molecular data indicates that these clades share a common ancestor, which is independent of ancestors of *Ixodes* that currently parasitize Cricetidae different to Sigmodontinae in Nearctic (*I. muris*) and Nearctic and Neotropical (*I. minor* and *I. spinipalpis*) Regions (Figure 1)

We are uncertain about which of the likely scenarios explained above, if any, corresponds with the primeval scenario that derived into the current *Ixodes*-Sigmodontinae relationship. However, the second scenario (sigmo-

dontins or proto-sigmodontins entering into South America carrying *Ixodes* tick ancestors) does not appear convincing in our view, because all *Ixodes* species analyzed above most probably originated in South America (see below).

We consider more probable the conceptual scenario of a South American *Ixodes* ancestor whose larvae, nymphs and adult ticks fed on Didelphidae. This family is of South American origin and contains the oldest extant marsupial, giving them more chances to harbor ancestral *Ixodes* ticks than the microbiotherian *D. gliroides*. The wide Neotropical distribution of *I. luciae* and to a lesser extent *I. loricatus*, also indicates a more ancient origin than their relatives in the same group shown in Figure 1. Furthermore, adults of *I. loricatus* and *I. luciae* evolved to feed mostly on marsupials of the tribe Didelphini of the genera *Didelphis* Linnaeus. Thus 71 % of all marsupial records of *I. loricatus* adults are from *Didelphis*, 13 % from *Lutreolina* and 11 % for *Philander* Brisson (13 %), while infestation on *Didelphis*, *Philander* and *Lutreolina* represented 55, 34 and 2 %, respectively of *I. luciae* adults (Guglielmone *et al.*, in preparation).

On the other hand, sigmodontin hosts for larvae and nymphs are dispersed among four genera of Oryzomyini, five genera of Akodontini, and one genus of Phyllotini for *I. loricatus*, and six genera of Oryzomyini and one genus each for Ictiomyini, Phyllotini and Sigmodontini for *I. luciae*. Although Oryzomyini are the most important hosts for *I. luciae* (also for *I. venezuelensis*), and are important hosts for *I. loricatus*, this tribe has a wide distribution and contains the highest number of species among tribes of Sigmodontinae. Therefore, the tick life cycle appears to be governed by the presence of Didelphidae (especially Didelphini which are the main hosts for adult ticks), making the scenario of a South American origin for the current *Ixodes*-Sigmodontinae relationship more attractive than an alternative scenario of ancestor ticks introduced with this type of rodent.

Such a 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* on Sigmodontinae and Didelphini, and sub-adults of *I. luciae* feeding on Sigmodontinae and Marmosini. However, the role of Sigmodontinae as hosts 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 Peruvian Amazon (Díaz *et al.* 2009). Nevertheless, studies from other locations are needed to examine this relationship under different circumstances.

We also based our discussion on a hypothetical common ancestor of the group of Neotropical species of *Ixodes* discussed above. However, additional information on tick species of this group or new data on *I. venezuelensis*, *I. longiscutatus*, *I. pararicinus*, *I. schulzei* among other ticks plus morphological and molecular descriptions of new taxa would help to complete our knowledge for a better understanding of *Ixodes*-Sigmodontinae relationship.

No fossil ixodid ticks are available for the Neotropical Region and the alleged Nearctic *Ixodes tertiaris* Scudder is, in fact, a *nomen nudum* (Guglielmone *et al.* 2009). Evidently, more exhaustive taxonomy (alpha and beta) along with morphological, molecular and ecological studies of *Ixodes* as well as efforts to find Neotropical and Nearctic fossil of ticks of the Prostriata group are needed to understand the evolutionary history of the host-parasite relationship treated here, and to improve our current empirical conceptual proposal.

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