

REVIEW ARTICLE

Birds and hard ticks (Acari: Ixodidae), with discussions about hypotheses on tick evolution

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SUMMARY. The relationship between birds (Aves) and hard ticks (Ixodidae) was analyzed for the 386 of 725 tick extant species whose larva, nymph and adults are known as well as their natural hosts. A total of 136 (54 Prostriata= *Ixodes*, 82 Metastriata= all other genera) are frequently found on Aves, but only 32 species (1 associated with Palaeognathae, 31 with Neognathae) have all parasitic stages feeding on birds: 25 *Ixodes* (19% of the species analyzed for this genus), 6 *Haemaphysalis* (7%) and 1 species of *Amblyomma* (2%). The species of *Amblyomma* feeds on marine birds (MB), the six *Haemaphysalis* are parasites of non-marine birds (NMB), and 14 of the 25 *Ixodes* feed on NMB, one feeds on NMB and MB, and ten on MB. The Australasian *Ixodes + I. uriae* clade probably originated at an uncertain time from the late Triassic to the early Cretaceous. It is speculated that Prostriata first hosts were Gondwanan theropod dinosaurs in an undetermined place before Pangaea break up; alternatively, if ancestral monotremes were involved in its evolution an Australasian origin of Prostriata seems plausible. As for Prostriata the Motherland of Ixodida is probably Gondwana.

RESUMEN. Aves y garrapatas duras (Ixodidae), con discusión sobre hipótesis sobre evolución de las garrapatas. En esta revisión se analizó la relación entre aves y garrapatas duras (Ixodidae) para las 386 de 725 especies de garrapatas que utilizan aves como hospedadores para larvas, ninfas y adultos. Un total de 136 especies (54 Prostriata= *Ixodes*, 82 Metastriata= restantes géneros) son frecuentemente encontradas sobre aves, pero solo 32 especies (1 asociada con Palaeognathae, 31 con Neognathae) tienen ciclos donde todos los estadios se alimentan sobre aves: 25 *Ixodes* (19% de las especies analizadas para este género), 6 *Haemaphysalis* (7% del total) y 1 especie de *Amblyomma* (2% del total). Las especies de *Amblyomma* se alimentan sobre aves marinas (MB), las seis de *Haemaphysalis* son parásitas de aves no-marinas (NMB), y 14 de las 25 especies de *Ixodes* se alimentan sobre NMB, una sobre NMB y MB, y diez sobre MB. El clado de Australasia *Ixodes + I. uriae* probablemente se originó entre el fin del Triásico y comienzos del Cretácico. Se especula que los primeros hospedadores de Prostriata fueron dinosaurios terópodos con distribución Gondwánica; alternatively, si monotremas ancestrales estuvieron involucrados en su evolución, un origen de Prostriata en Australasia es plausible. Al igual que para Prostriata, el área de origen de Ixodida es probablemente Gondwana.

Key words: Aves, Ixodidae, Prostriata, Metastriata, evolution.

Palabras clave: Aves, Ixodidae, Prostriata, Metastriata, evolución.

Introducción

Birds (Class Aves) evolved from theropod dinosaurs in the Jurassic period (Mesozoic) with the first fossils dated 165-150 mya. They are the only clade of dinosaurs that survived the Cretaceous-Paleogene boundary (K-Pg boundary) with a strong radiation in the Tertiary along with Mammalia (Chiappe, 2009; Brusatte et al., 2015). The modern Aves (Neornithes) contains about 10,000 extant species covering all the ecosystems on earth (strictly aquatic environments excluded) which are further divided into two clades:

the Palaeognathae constituted by about 60 species of flightless birds distributed in the Afrotropical, Australasia and Neotropical Zoogeographic Regions, and the Neognathae formed by almost all extant birds with a worldwide distribution.

Ixodidae (ticks with all postembryonic stages with the dorsum partially or totally covered by a chitinous scutum) currently contains 725 species (Guglielmone and Nava, 2014; Hornok et al., 2016; Apanaskevich and Bermudez, 2017; Ash et al., 2017; Nava et al., 2017) This tick family is divided in two groups: Prostriata, containing the genus *Ixodes* although French workers divide it into several genera (Camicas and Morel, 1977; Camicas et al., 1998) and Metastriata that contains 11

extant and two fossil genera (Guglielmone et al., 2014). Hypotheses based on molecular data state that Prostriata probably evolved earlier than Metastriata (Black and Roehrdanz, 1998; Jeyaprakash and Hoy, 2009; Mans et al., 2012) and Australasian species such as *Ixodes tasmani* Neumann, 1899 and *Ixodes holocyclus* Neumann, 1899 plus the circumpolar avian-dependant *Ixodes uriae* White, 1852 are claimed to be basal to the rest of the group (Norris et al., 1999; Klompen, 1999; Klompen et al., 2000). The basal position of *I. uriae* has been long recognized, among others, by Zumpt (1952 as *Ceratixodes uriae*) who stated that this tick is peculiar by having primitive morphology, and Morel (1969 also as *C. uriae*) asserted that this species was associated to marine birds in the Cretaceous and the genus may have originated in the Jurassic feeding on reptiles.

Fossil evidence shows the earliest emergence of Metastriata including the extant genus *Amblyomma* 100 mya (Cretaceous) (Grimaldi et al., 2002) while molecular clock placed its origin in the late Jurassic-early Cretaceous Periods (156-112 mya) (Jeyaprakash and Hoy, 2009) and from mid Jurassic-early Cretaceous (166-101 mya) by Mans et al. (2012). There is no Prostriata fossil as old as Metastriata fossil record, but molecular clock indicates the earliest period of its evolution in late Triassic Period (223 mya) and the latest in mid Jurassic Period (169 mya) according to Jeyaprakash and Hoy (2009) and from 266 (Permian) to mid Jurassic (171 mya) in Mans et al. (2012). The origin of Ixodida and their primeval host are also controversial with several competing theories proposed in Jeyaprakash and Hoy (2009), Mans et al. (2011, 2012, 2014, 2016) and Barker et al. (2014), among others, a topic that will be further treated in the discussion about hypotheses of tick evolution.

The evolutionary histories of Aves and Ixodidae may indicate an ancient relationship as hypothesized by Morel (1969), Stothard and Fuerst (1995), Kolonin (2008), Dietrich et al. (2014) and de la Fuente et al. (2015). There are works about Aves as hosts for particular species of ticks, but few give an ample scope on this tick-host relationship. Kolonin (2008) shows the broad relationship as Aves as hosts for adult ixodid ticks, Arthur (1958, 1960) and Dietrich et al. (2011) summarized the distribution of ticks from marine birds, Zumpt (1952) presented data about Ixodidae and sea birds in the Antarctic, while Guglielmone et al. (2014) analyzed the role of Aves for all species of Ixodidae. Here we analyze Aves as hosts for Ixodidae focusing on species whose post embryonic stages (larva, nymph, adult) are strictly related to Aves considering that this information is relevant to understand part of tick life history. Related to this

topic we take the opportunity to discuss some aspects of tick evolution from alleged ancient Prostriata ticks feeding on marine birds as well as hypotheses of the origin of ticks.

Materials and methods

Basic information for this study was obtained from Guglielmone et al. (2014), who analyzed host profiles of 378 species of Ixodidae whose adults, nymphs and larvae are known as well as their natural hosts plus new information for a total of 386 species (133 Prostriata, 253 Metastriata). The genera with new information on this topic are *Amblyomma* after the studies of Apanaskevich et al. (2016) with *Amblyomma integrum* Karsch, 1879 and Muñoz-Leal et al. (2016) with *Amblyomma parvitarsum* Neumann, 1901, and *Dermacentor* based on the studies of Apanaskevich (2013), Apanaskevich and Bermúdez (2013), Apanaskevich et al. (2014) and Apanaskevich and Apanaskevich (2015, 2016). Many of these species have been found on Aves, 68 species of *Ixodes* (67 in Guglielmone et al., 2014 plus *Ixodes asanumai* Kitaoka, 1973 in Takano et al., 2014), and 152 of Metastriata (147 in Guglielmone et al., 2014 plus *Amblyomma auricularium* (Conil, 1878) in Lugarini et al., 2015, *A. integrum* in Apanaskevich et al. 2016, *Amblyomma rotundatum* Koch, 1844 in Scott and Durden, 2015, *Amblyomma varium* Koch, 1884 in Lugarini et al. (2015) and *Dermacentor bellulus* (Schulze, 1935) in Apanaskevich and Apanaskevich, 2015). These numbers diminished to 54 for Prostriata and 82 for Metastriata, when exceptional avian host records are excluded from the analysis. Finally, those numbers are further reduced to 32 (Prostriata + Metastriata) when considered only the species with all parasitic stages bound to Aves.

The 32 species strictly dependent on birds for the maintenance of all parasitic stages are considered relevant for life history of Ixodidae and treated in detail below. The remainder 108 species (Prostriata + Metastriata) are found on Aves and Mammalia (88 species), and the rest on Aves and other types of hosts (data not shown). Some species (i.e. *Amblyomma longirostre* (Koch, 1844), *Amblyomma nodosum* Neumann, 1899) use Aves as source of nourishment for larvae and nymphs (Guglielmone et al., 2014; Lugarini et al., 2015; Maturano et al., 2015; Ramos et al., 2015), while larvae and nymphs of species as *Ixodes scapularis* Say, 1821 are frequently found on Passeriformes but most commonly on small mammals (Keirans et al., 1996) being uncertain if Aves are crucial for its life cycle. It is quite probable that Aves are vital for the cycle of many of the more than 100 species cited above, but the host parasite relationships of tick-Aves + Mammalia or other types of hosts are treated as a Cenozoic event alongside the radiation of Aves

and Mammalia after the K-Pg boundary and will not be further discussed.

We focused on the 32 species of Ixodidae that use Aves as a vital source for the nourishment of all parasitic stages according to Guglielmone et al. (2014) plus the addition of *Haemaphysalis wellingtoni* Nuttall and Warburton, 1908 following Hoogstraal et al. (1972) and Rajagopalan (1972). For each of these species the orders and families of hosts and zoogeographical tick distribution are listed. Orders of avian hosts parasitized by these species were additionally classified as marine (MB) and non-marine birds (NMB). Some of these avian orders have MB and NMB species but the categorization follows the habits of parasitized species (data not shown). Orders and families of birds followed mainly Clements et al. (2012) and are similar but not identical to orders and families used in Guglielmone et al. (2014).

Tick distribution in the Afrotropical (=Ethiopian, African), Australasian, Nearctic, Neotropical, Oriental (= Indomalaya) and Palearctic Zoogeographic Regions were obtained following Cox and Moore (2005) as detailed in Guglielmone et al. (2014). Some species are established in Islands difficult to be associated to any of the regions above mentioned (these islands should be related to Oceanic Region of some authors). In these cases the oceans for island location are named. One species is mainly found around the Poles, but also in islands and continental territories close to them and this distribution is defined as circumpolar.

The information is related to theories of tick evolution focusing on the clade of Australasian *Ixodes + uriae* (also named as "Australian *Ixodes*", "Australasian *Ixodes*" or "*Ixodes tasmani* group" by others) and related species with notes on evolutionary events occurring before and after the hypothetical origin of this tick clade.

Results

The vast majority of the 32 species whose all parasitic stages feed on Aves are Prostriata; only 2 of the 11 extant genera of Metastratiata have species with larvae, nymphs and adult ticks feeding on Aves for a total of 7 species, 1 *Amblyomma* and 6 *Haemaphysalis*. The species of Ixodidae with all parasitic stages feeding on Aves, their distribution, hosts and comments are listed below.

METASTRIATA

Amblyomma loculosum Neumann, 1907: this species is mainly found on islands close to the Afrotropical, Australasian and Oriental Zoogeographic Regions. All parasitic stages feed on Charadriiformes: Fregatidae and Sulidae; nymphs and adult ticks were recovered

from Charadriiformes: Laridae and Procellariiformes: Procellariidae. Dietrich et al. (2011) stated that *A. loculosum* is occasionally found on NMB. All parasitic stages have been found on Squamata: Scincidae which appear to be important hosts for *A. loculosum* larvae, but the absence of skinks do not imperil the cycle of this tick; therefore, we still consider this tick as bound to MB. *Amblyomma loculosum* has been exceptionally found on Artiodactyla: Bovidae and also on humans. Main references: Hoogstraal et al. (1976), Ramos et al. (2002), Dietrich et al. (2011), Guglielmone et al. (2014).

Haemaphysalis chordeilis (Packard, 1869): a Nearctic species with all parasitic stages found on Galliformes: Phasianidae and Passeriformes: Icteridae; adult ticks has been found on Anseriformes: Anatidae and Caprimulgiformes: Caprimulgidae, and larvae and nymphs on several families of Passeriformes. Nymphs were also recovered from Accipitriformes: Accipitridae. There are also some unusual records of *H. chordeilis* adults on mammals including humans. Main references: Bequaert (1945), Bishopp and Trembley (1945), Cooley (1946), Gregson (1956), Keirans (1967, 1985), Wilson and Kale (1972), Guglielmone et al. (2014).

Haemaphysalis doenitzi Warburton and Nuttall, 1909: an Australasian-Oriental-Palearctic species. The usual hosts for larvae, nymphs and adult ticks are Cuculiformes: Cuculidae and Galliformes: Phasianidae, but the avian host range is ample. All parasitic stages of *H. doenitzi* have been found on several families of Passeriformes; adults and nymphs on Accipitriformes: Accipitridae, Falconiformes: Falconidae, and Strigiformes: Strigidae, just adult ticks on Coraciiformes: Coraciidae, Upupidae, and Gruiformes: Rallidae; and nymphs on Piciformes: Capitonidae. There are also some exceptional records on mammals (including humans) and reptilian (Testudines). Main references: Hoogstraal and Wassef (1973), Tanskul et al. (1983), Guglielmone et al. (2014).

Haemaphysalis hoodi Warburton and Nuttall, 1909: an Afrotropical species, whose all parasitic stages have been found on Cuculiformes: Cuculidae, Galliformes: Phasianidae and Passeriformes: Muscicapidae; adults and nymphs on Galliformes: Numididae and Passeriformes: Laniidae, and just adult ticks on Accipitriformes: Accipitridae, Ciconiiformes: Ciconiidae, Coraciiformes: Bucorvidae, Cuculiformes: Musophagidae, Falconiformes: Falconidae, Gruiformes: Rallidae and Passeriformes: Corvidae. Nymphs and/or larvae of *H. hoodi* have been recovered from Columbiformes and Passeriformes. There are also some unusual records of *H. hoodi* from mammals. Main references: Santos Dias (1958), Theiler (1962), Elb and Anastos (1966), Aeschlimann (1967), Matthyse and Colbo (1987), Cornet (1995), Horak et al. (1995), Guglielmone et al. (2014).

Haemaphysalis megalaimae Rajagopalan, 1963: an Oriental species with all parasitic stages feeding on Piciformes: Capitonidae (Rajagopalan 1963; Guglielmone et al. 2014).

Haemaphysalis minuta Kohls, 1950: an Oriental species whose parasitic stages usually feed on Galliformes: Phasianidae with nymphal records from several families of Passeriformes as well as from Cuculiformes: Cuculidae. There is also a record of larvae of *H. minuta* on Passeriformes: Timaliidae, and some exceptional records from mammals. Main references: Rajagopalan et al. (1968), Rajagopalan (1972), Rao et al. (1973), Hoogstraal and Kim (1985), Guglielmone et al. (2014).

Haemaphysalis wellingtoni: an Australasian-Oriental species with larvae, nymphs and adults usually feeding on Galliformes: Phasianidae but also recovered from Cuculiformes: Cuculidae and Passeriformes (five families). Additionally larvae, nymphs or adult ticks were found on Accipitriformes: Accipitridae, Charadriiformes: Charadriidae, Coraciiformes: Bucerotidae, Gruiformes: Rallidae and ten families of Passeriformes. There are also records of *H. wellingtoni* from five orders of mammals plus humans. Guglielmone et al. (2014) did not classify *H. wellingtoni* as a species that feed exclusively on Aves after the exclusion of exceptional hosts but this criterion is not applied here. Main references: Trapido et al. (1964), Boshell and Rajagopalan (1968), Hoogstraal et al. (1972), Rajagopalan (1972), Bhat and Sreenivasan (1981), Tanskul et al. (1983), Xu and Li (1997), Parola et al. (2003), Durden et al. (2008), Guglielmone et al. (2014).

PROSTRIATA

Ixodes anatis Chilton, 1904: an Australasian species with all parasitic stages found on Struthioniformes: Apterygidae, while adults and nymphs have been detected on Anseriformes: Anatidae (Dumbleton 1953, 1961; Heath 2010; Guglielmone et al. 2014; Swift et al. 2015). This bird is the only representative of the clade Palaeognathae from all the 32 species of Ixodidae strictly bound to Aves.

Ixodes arboricola Schulze and Schlottke, 1929: an Oriental-Palaearctic species with all parasitic stages found on Passeriformes (seven families), Piciformes: Picidae and Strigiformes: Strigidae. Adult ticks have been recovered from Charadriiformes: Burhinidae and Falconiformes: Falconidae and larvae from Accipitriformes: Accipitridae and Columbiformes: Columbidae, while adults and nymphs of *I. arboricola* have been found on several families of Passeriformes. There are also some exceptional records from Mammalia. Main references: Clifford and Hoogstraal (1965), Gembitsky (1966), Sixl and Nosek (1972), Filippova (1977), Martyn (1988), Jaenson et al. (1994), Yu et al. (1997), Papadopoulos et al. (2001), Chen et al. (2010), Moneris et al. (2011), Guglielmone et al. (2014).

Ixodes auritulus Neumann, 1904: a species with a wide range including Afrotropical, Australasian, Nearctic and Neotropical Zoogeographic Regions with an ample hosts records from MB and NMB from different orders, with exceptional records from rodents and a mammalian carnivore. All parasitic stages of *I. auritulus* have been found on Falconiformes: Falconidae, Galliformes: Cracidae and Passeriformes (eight families). Larvae, nymphs or adults have been recovered from 11 families of Passeriformes, while nymphs and adult ticks have been found on Columbiformes: Columbidae, Galliformes: Phasianidae, Procellariiformes: Pelecanoididae and Procellariidae, and Tinamiformes: Tinamidae. Nymphs and larvae of *I. auritulus* were determined as parasite of Apodiformes: Apodidae, and adult ticks on Accipitriformes: Accipitridae, Charadriiformes: Stercorariidae, Galliformes: Odontophoridae, Piciformes: Picidae, and Sphenisciformes: Spheniscidae. Undetermined stages of *I. auritulus* were found on Charadriiformes: Laridae and Scolopacidae, Gruiformes: Rallidae, Procellariiformes: Diomedidae and Psittaciformes: Strigopidae. Important articles referring to MB as hosts of *I. auritulus* do not mention tick stages found on them but there is no doubt that there are population of this species bound to MB. Main references: Bequaert (1945), Cooley and Kohls (1945), Arthur (1960), Dumbleton (1961), Roberts (1964), González-Acuña et al. (2005, 2009), Heath (2010), Dietrich et al. (2011), Heath et al. (2011), Guglielmone et al. (2014), Bermúdez et al. (2015), Flores et al. (2014).

Ixodes baergi Cooley and Kohls, 1942: a Nearctic species whose larvae, nymphs and adults have been found on Passeriformes: Hirundinidae, with a record from humans (Keirans et al. 1993; Durden and Keirans 1996; Walker et al. 1998; Guglielmone et al. 2014).

Ixodes berlesei Birula, 1895: a Palaearctic species with all parasitic stages usually found on Apodiformes: Apodidae. Larvae and adult ticks were also found on Passeriformes: Emberizidae; nymphs and larvae of *I. berlesei* were recovered from Passeriformes: Corvidae and Passeridae. Undetermined stages of this species were found on Columbiformes: Columbidae; Falconiformes: Falconidae, and several families of Passeriformes. Main references: Emchuk (1960), Chunikhin (1967), Clifford et al. (1975), Filippova (1977), Prokop'ev et al. (1979), Voltzit (1997), Guglielmone et al. (2014).

Ixodes brunneus Koch, 1844: a Nearctic-Neotropical species whose larvae, nymphs and adults usually feed on several families of Passeriformes, but adults and nymphs were also found on Galliformes: Odontophoridae, adult ticks on Piciformes: Rhampastidae and Strigiformes: Strigidae, and larvae on Galliformes: Phasianidae. Undetermined stages of *I. brunneus* have been recovered from Columbiformes: Columbidae, and it was also found on humans. Main references: Bishopp and Trembley (1945), Cooley and Kohls

(1945), Anastos and Smith (1957), Sonenshine and Stout (1970), Furman and Loomis (1984), Mullen et al. (1999), Williams et al. (1999), Scott et al. (2012), Guglielmone et al. (2014).

Ixodes caledonicus: a Palearctic species with all parasitic stages found on Apodiformes: Apodidae, Columbiformes: Columbidae, Falconiformes: Falconidae and Passeriformes: Corvidae; adult ticks also found on MB (Procellariiformes: Procellariidae). Main references: Filippova (1977), Jaenson et al. (1994), Jaenson and Jensen (2007), Guglielmone et al. (2014).

Ixodes colloclaliae Nuttal, 1910: an Australasian-Oriental species whose larvae, nymphs and adults have been found on Apodiformes: Apodidae (Wilson 1964b, 1970a; Petney and Keirans 1994; Guglielmone et al. 2014).

Ixodes eudyptidis Maskell, 1885: an Australasian species with all parasitic stages found on Charadriiformes: Laridae and Sphenisciformes: Spheniscidae; nymphs and larvae on Suliformes: Phalacrocoracidae, and nymphs on Suliformes: Sulidae. Undetermined stages of *I. eudyptidis* have been also found on Anseriformes: Anatidae, Charadriiformes: Sternidae and Procellariiformes: Pelecanoididae and Procellariidae. Main references: Dumbleton (1961), Roberts (1960, 1964, 1970), Heath (2006, 2010), Heath and Cane (2010), Guglielmone et al. (2014).

Ixodes frontalis (Panzer, 1798): a Palearctic species whose usual hosts for all parasitic stages are Passeriformes: Turdidae, but also recovered from Passeriformes: Acrocephalidae, Muscicapidae and Passeridae. Nymphs of *I. frontalis* were found on Piciformes: Picidae and one or two parasitic stages from 18 families of Passeriformes. There are records of this species from Accipitriformes: Accipitridae, Anseriformes: Anatidae, Charadriiformes: Haematopodidae, Columbiformes: Columbidae, Falconiformes: Falconidae, Galliformes: Phasianidae, Gruiformes: Rallidae and Strigiformes: Strigidae but we were unable to discern if all parasitic stages of *I. frontalis* were found on them. There are exceptional records from Carnivora: Mustelidae and humans. Main references: Filippova (1977), Gilot (1984), Tovornik (1991), Doby (1998), Guglielmone et al. (2014), Norte et al. (2015).

Ixodes howelli Cooley and Kohls, 1938: a Nearctic species with larvae, nymphs and adults usually found on Passeriformes: Hirundinidae, with records of larvae and nymphs on Passeriformes: Fringillidae and nymphs on Falconiformes: Falconidae (Kohls and Ryckman 1962; Webb et al. 1990; Durden and Keirans 1996; Guglielmone et al. 2014).

Ixodes jacksoni Hoogstraal, 1967: an Australasian species with all parasitic stages found on Suliformes: Phalacrocoracidae (Hoogstraal 1967; Dumbleton 1973; Dietrich et al. 2011; Guglielmone et al. 2014).

Ixodes kerguelenensis André and Colas-Belcour, 1942: a species established in Australasia and islands in the Atlantic, Indian and Pacific Oceans with all stages usually feeding on Procellariiformes: Procellariidae and Sphenisciformes: Spheniscidae, but adults and nymphs were also recovered from Procellariiformes: Diomedidae, and adult ticks on Procellariiformes: Pelecanoididae. An undetermined stage of *I. kerguelenensis* has been found on Psittaciformes: Strigopidae. Main references: Wilson (1970b), Dietrich et al. (2011), Guglielmone et al. (2014).

Ixodes kohlsi Arthur, 1955: an Australasian species with all parasitic stages usually found on Sphenisciformes: Spheniscidae, with records of adult ticks on Suliformes: Phalacrocoracidae and Procellariiformes: Procellariidae. Undetermined stages of *I. kohlsi* have been found on Pelecaniformes: Sulidae and Charadriiformes: Sternidae. It was also found on humans. Main references: Roberts (1960, 1970), Dietrich et al. (2011), Guglielmone et al. (2014).

Ixodes laysanensis Wilson, 1964: a species established in Central Pacific islands where their adults and nymphs feed on Charadriiformes: Scolopacidae and Procellariiformes: Diomedidae. Adult ticks were also found on Charadriiformes: Laridae, Suliformes: Fregatidae, Sulidae, and Phaethontiformes: Phaethontidae, while larvae were determined on Charadriiformes: Sternidae but also on a NMB (Passeriformes: Fringillidae). Main references: Wilson (1964a), Kohls and Clifford (1967), Dietrich et al. (2011), Guglielmone et al. (2014).

Ixodes lividus Koch, 1844: a Palearctic species whose larvae, nymphs and adults are usually found on Passeriformes: Hirundinidae; adults and larvae on Coraciiformes: Alcedinidae, nymphs and larvae on Coraciiformes: Meropidae, Passeriformes: Paridae, larvae on Passeriformes: Passeridae. Undetermined stages of *I. lividus* were recovered from Passeriformes: Alaudidae, Sturnidae and Turdidae. Main references: Fedorov (1972), Filippova (1977), Ulmanen et al. 1977, Gilot (1984), Trilar (2004), Guglielmone et al. (2014).

Ixodes mitchelli Kohls, Clifford and Hoogstraal, 1970: a Palearctic species whose larvae, nymphs and adults are found on Galliformes: Phasianidae (Clifford et al. 1975; Guglielmone et al. 2014).

Ixodes paranaensis Barros-Battesti, Arzua, Pichorim and Keirans, 2003: a Neotropical species whose larvae, nymphs and adults feed on Apodiformes: Apodidae (Barros-Battesti et al. 2003; Dantas-Torres et al. 2009; Tolesano-Pascoli et al. 2014; Luz et al. 2016).

Ixodes percavatus Neumann, 1906: a species established in islands in the Atlantic and Indian Oceans. All parasitic stages were found on Procellariiformes: Diomedidae (ANL). Undetermined tick stages were found on Procellariiformes: Pelecanoididae and Hydrobatidae; Sphenisciformes: Spheniscidae. One

larva was found on NMB (Passeriformes: Turdidae). Main references: Anastos (1954), Dietrich et al. (2011), Guglielmone et al. (2014).

Ixodes rothschildi Nuttall and Warburton, 1911: a Palearctic species whose larvae, nymphs and adults are found on Procellariiformes: Procellariidae and Charadriiformes: Alcidae, and adults and nymphs also recovered from Charadriiformes: Laridae. Undetermined specimens of *I. rothschildi* were also collected from Suliformes: Phalacrocoracidae. Main references: Arthur (1953, 1955, 1958), Zumpt (1952), Dietrich et al. (2011), Guglielmone et al. (2014).

Ixodes signatus Birula, 1895: a Nearctic-Palearctic species whose larvae, nymphs and adults usually feed on Suliformes: Phalacrocoracidae but also found on Charadriiformes: Alcidae and Laridae. Nymphs and adults of *I. signatus* have been recovered from the NMB (Passeriformes: Fringillidae) and adult ticks from Carnivora: Otariidae. Main references: Gregson (1954, 1956), Kozlovskaya et al. (1968), Yamaguti et al. (1971), Filippova (1977), Schwan and Kelly (1981), Dietrich et al. (2011), Guglielmone et al. (2014).

Ixodes subterraneus Filippova, 1961: a Palearctic species with larvae, nymphs and adult ticks found on Passeriformes: Passeridae. Undetermined tick stages were found on Passeriformes (six families), Coraciiformes: Coraciidae, Falconiformes: Falconidae, Galliformes: Phasianidae and Strigiformes: Strigidae. Main references: Filippova (1961, 1977), Guglielmone et al. (2014).

Ixodes turdus Nakatsudi, 1942: a Palearctic species with larvae, nymphs and adults ticks found on Galliformes: Phasianidae and Passeriformes (eight families); adults and larvae were also recovered from Strigiformes: Strigidae. There is also an odd larval record of *I. turdus* on Rodentia: Muridae and this tick has been also found biting humans. Main references: Asanuma and Kosaka (1955), Yamaguti et al. (1971), Miyamoto et al. (2000), Yamauchi (2001), Kim et al. (2009), Kang et al. (2013), Guglielmone et al. (2014).

Ixodes unicavatus Neumann, 1908: a Palearctic species with larvae, nymphs and adults usually found on Suliformes: Phalacrocoracidae; larvae were also recovered from Passeriformes: Motacillidae. Undetermined stages of *I. unicavatus* have been found on Charadriiformes: Alcidae and Falconiformes: Falconidae. Main references: Filippova (1977), Guiguen et al. (1987), Martyn (1988), Jaenson et al. (1994), Dietrich et al. (2011), Guglielmone et al. (2014).

Ixodes uriae: a species with a circumpolar distribution including localities in the Afrotropical, Australasian, Nearctic and Neotropical Regions. Larvae, nymph and adults of *I. uriae* feed on a great variety of Aves as

Charadriiformes: Alcidae and Lariidae, Procellariiformes: Diomedidae, Sphenisciformes: Spheniscidae and Suliformes: Phalacrocoracidae. Nymphs and adult ticks were recovered from Charadriiformes: Stercorariidae, Procellariiformes: Procellariidae and Hydrobatidae. Unknown stages of *I. uriae* were also found on Anseriformes: Anatidae, Charadriiformes: Scopelidae, Passeriformes (four families), Suliformes: Sulidae with some exceptional records on mammals of the orders Carnivora and Rodentia plus humans: Main references: Eley (1977), Jaenson and Jensen (2007), Baggs et al. (2011), Dietrich et al. (2011), Guglielmone et al. (2014), Muñoz-Leal and González-Acuña (2015).

ANALYSIS BY HOST TAXA

Only one species (*I. anatis*) is strictly bound to Palaeognathae. The six species of *Haemaphysalis* and 14 of the 25 species of *Ixodes* feed on NMB (table 1). Four species of *Haemaphysalis* are found exclusively (*H. megalaimae*, *H. minuta*) and non-exclusively (*H. doenitzi*, *H. wellingtoni*) in the Oriental Region, while *H. chordeilis* is a Nearctic species and *H. hoodi* an Afrotropical taxon. The majority of the 14 species of *Ixodes* that feed on NMB are found in the Palearctic, seven exclusively there as follows: *I. berlesei*, *I. caledonicus* (with some records on MB), *I. frontalis*, *I. lividus*, *I. mitchelli*, *I. subterraneus*, *I. turdus*, while *I. arboricola* is established in the Oriental and Palearctic regions; three are Nearctic species, *I. baergi* and *I. howelli* (exclusively) plus *I. brunneus* which is a Nearctic-Neotropical tick, *I. anatis* is an Australasian species, *I. collocaliae* is an Australasian-Oriental taxon, and *I. paranaensis* is found exclusively in the Neotropical region. One species, the cosmopolitan (Australasian-Afrotropical-Nearctic-Neotropical) *I. auritulus* feeds on MB and NMB (table 1).

Amblyomma loculosum (Afrotropical-Australasian-Oriental) and ten species of *Ixodes* parasitize exclusively MB. Five of these ten species are established in the Australasian Region, three only there (*I. egyptidis*, *I. jacksoni*, *I. kohlsi*), *I. kerguelensis* is found in Australasian and islands in the Atlantic, Indian and Pacific Oceans, while *I. uriae* is circumpolar with records at localities of the adjacent zoogeographical regions including Australasian. Two species, *I. rothschildi* and *I. unicavatus*, are Palearctic, *I. signatus* is a Nearctic-Palearctic taxon; *I. percavatus* is established in islands in the Atlantic and Indian Oceans and, finally, *I. laysanensis* is established in islands of the Pacific Ocean. There are a few record of immatures stages of *I. laysanensis*, *I. signatus* and *I. unicavatus* from NMB that do not defy the condition of these species as bound to MB.

Table 1. Orders of marine (M) and non-marine (NM) Aves crucial for larvae, nymphs and adult ticks of species of Ixodidae.

Species of tick	Hosts		
	Adults	Nymphs	Larvae
<i>Amblyomma loculosum</i>	Charadriiformes (M) Suliformes (M)	Charadriiformes (M) Procellariiformes (M) Suliformes (M)	Charadriiformes (M) Suliformes (M)
<i>Haemaphysalis chordeilis</i>	Anseriformes (NM) Caprimulgiformes (NM) Galliformes (NM) Passeriformes (NM)	Accipitriformes (NM) Galliformes (NM) Passeriformes (NM)	Galliformes (NM) Passeriformes (NM)
<i>H. doenitzi</i>	Accipitriformes (NM) Coraciiformes (NM) Cuculiformes (NM) Falconiformes (NM) Galliformes (NM) Gruiformes (NM) Passeriformes (NM) Strigiformes (NM)	Accipitriformes (NM) Cuculiformes (NM) Falconiformes (NM) Galliformes (NM) Passeriformes (NM) Piciformes (NM) Strigiformes (NM)	Cuculiformes (NM) Galliformes (NM) Passeriformes (NM)
<i>H. hoodi</i>	Accipitriformes (NM) Ciconiiformes (NM) Coraciiformes (NM) Cuculiformes (NM) Falconiformes (NM) Galliformes (NM) Gruiformes (NM) Passeriformes (NM)	Columbiformes (NM) Cuculiformes (NM) Galliformes (NM) Passeriformes (NM)	Columbiformes (NM) Cuculiformes (NM) Galliformes (NM) Passeriformes (NM)
<i>H. megalaimae</i>	Piciformes (NM)	Piciformes (NM)	Piciformes (NM)
<i>H. minuta</i>	Galliformes (NM)	Cuculiformes (NM) Galliformes (NM) Passeriformes (NM)	Galliformes (NM) Passeriformes (NM)
<i>H. wellingtoni</i>	Accipitriformes (NM) Coraciiformes (NM) Cuculiformes (NM) Galliformes (NM) Passeriformes (NM)	Accipitriformes (NM) Cuculiformes (NM) Galliformes (NM) Passeriformes (NM)	Charadriiformes (NM) Cuculiformes (NM) Galliformes (NM) Gruiformes (NM) Passeriformes (NM)
<i>Ixodes anatis</i>	Anseriformes (NM) Struthioniformes (NM)	Anseriformes (NM) Struthioniformes (NM)	Struthioniformes (NM)
<i>I. arboricola</i>	Charadriiformes (NM) Falconiformes (NM) Passeriformes (NM) Piciformes (NM) Strigiformes (NM)	Passeriformes (NM) Piciformes (NM) Strigiformes (NM)	Accipitriformes (NM) Columbidae (NM) Passeriformes (NM) Piciformes (NM) Strigiformes (NM)
<i>I. auritulus</i>	Accipitriformes (NM) Charadriiformes (M) Columbiformes (NM) Falconiformes (NM) Galliformes (NM) Passeriformes (NM) Piciformes (NM) Procellariiformes (M) Sphenisciformes (M) Tinamiformes (NM)	Apodiformes (NM) Columbiformes (NM) Falconiformes (NM) Galliformes (NM) Passeriformes (NM) Procellariiformes (M) Tinamiformes (NM)	Apodiformes (NM) Falconiformes (NM) Galliformes (NM) Passeriformes (NM)
<i>I. baergi</i>	Passeriformes (NM)	Passeriformes (NM)	Passeriformes (NM)
<i>I. berlesei</i>	Apodiformes (NM) Passeriformes (NM)	Apodiformes (NM) Passeriformes (NM)	Apodiformes (NM) Passeriformes (NM)
<i>I. brunneus</i>	Galliformes (NM) Passeriformes (NM) Piciformes (NM) Strigidae (NM)	Galliformes (NM) Passeriformes (NM)	Galliformes (NM) Passeriformes (NM)
<i>I. caledonicus</i>	Apodiformes (NM) Columbiformes (NM) Falconiformes (NM) Passeriformes (NM) Procellariiformes (M)	Apodiformes (NM) Columbiformes (NM) Falconiformes (NM) Passeriformes (NM)	Apodiformes (NM) Columbiformes (NM) Falconiformes (NM) Passeriformes (NM)
<i>I. collocaliae</i>	Apodiformes (NM)	Apodiformes (NM)	Apodiformes (NM)
<i>I. eudyptidis</i>	Charadriiformes (M) Sphenisciformes (M)	Charadriiformes (M) Sphenisciformes (M) Suliformes (M)	Charadriiformes (M) Sphenisciformes (M) Suliformes (M)
<i>I. frontalis</i>	Passeriformes (NM)	Passeriformes (NM) Piciformes (NM)	Passeriformes (NM)
<i>I. howelli</i>	Passeriformes (NM)	Passeriformes (NM) Falconiformes (NM)	Passeriformes (NM)
<i>I. jacksoni</i>	Suliformes (M)	Suliformes (M)	Suliformes (M)
<i>I. kerguelenensis</i>	Procellariiformes (M) Sphenisciformes (M)	Procellariiformes (M) Sphenisciformes (M)	Procellariiformes (M) Sphenisciformes (M)
<i>I. kohlsi</i>	Procellariiformes (M) Sphenisciformes (M) Suliformes (M)	Sphenisciformes (M)	Sphenisciformes (M)
<i>I. laysanensis</i>	Charadriiformes (M) Phaethontiformes (M) Procellariiformes (M) Suliformes (M)	Charadriiformes (M) Procellariiformes (M)	Charadriiformes (M) Passeriformes (NM)
<i>I. lividus</i>	Coraciiformes (NM) Passeriformes (NM)	Coraciiformes (NM) Passeriformes (NM)	Coraciiformes (NM) Passeriformes (NM)
<i>I. mitchelli</i>	Galliformes (NM)	Galliformes (NM)	Galliformes (NM)
<i>I. paranaensis</i>	Apodiformes (NM)	Apodiformes (NM)	Apodiformes (NM)
<i>I. percavatus</i>	Procellariiformes (M)	Procellariiformes (M)	Procellariiformes (M) Passeriformes (NM)
<i>I. rothschildi</i>	Charadriiformes (M) Procellariiformes (M)	Charadriiformes (M) Procellariiformes (M)	Charadriiformes (M) Procellariiformes (M)
<i>I. signatus</i>	Charadriiformes (M) Suliformes (M)	Charadriiformes (M) Passeriformes (NM) Suliformes (M)	Charadriiformes (M) Passeriformes (NM) Suliformes (M)
<i>I. subterraneus</i>	Passeriformes (NM)	Passeriformes (NM)	Passeriformes (NM)
<i>I. turdus</i>	Galliformes (NM) Passeriformes (NM) Strigiformes (NM)	Galliformes (NM) Passeriformes (NM)	Galliformes (NM) Passeriformes (NM) Strigiformes (NM)
<i>I. unicavatus</i>	Suliformes (M)	Suliformes (M)	Suliformes (M) Passeriformes (NM)
<i>I. uriae</i>	Charadriiformes (M) Procellariiformes (M) Sphenisciformes (M) Suliformes (M)	Charadriiformes (M) Procellariiformes (M) Sphenisciformes (M) Suliformes (M)	Charadriiformes (M) Procellariiformes (M) Sphenisciformes (M) Suliformes (M)

ANALYSIS BY REGION

The Australasian *I. jacksoni* is close to *I. uriae* according to Hoogstraal (1967) and some workers treated these species as the only members of the genus *Ceratixodes*, while others included them in the subgenus *Ceratixodes*. All Australasian species above except *I. kerguelenensis* are included in the Australasian *Ixodes + uriae* by Barker and Murrell (2004) who added *I. laysanensis* (central Pacific Islands) to this group; however this assemblage is controversial as all these species but *I. jacksoni* belong to the worldwide distributed subgenus *Multidentatus* and were included in the Australasia *Ixodes + uriae* just because their relationship with the Australasian Zoogeographic Region without morphological considerations. Nevertheless, the Australasian contribution of *Ixodes* that feed on MB is noteworthy considering that there are only 28 species found exclusively and non-exclusively in this zoogeographic region versus 63 species in the Palearctic Region (61 species in Guglielmone et al., 2014 plus *I. ariadnae* and *I. inopinatus*). The genus *Ixodes* is best represented in the Afrotropical Region; there are 69 species of *Ixodes* in this region (68 in Guglielmone et al. 2014 plus *I. microgalei*), 64 are found only there, but birds are irrelevant to support all parasitic stages of African *Ixodes*.

Discussion

IXODIDAE AND AVES

Many species of Prostriata and Metastriata feed on birds, but avian-feeding is probably not relevant for survival because avian records are exceptional. For some other taxa the situation is uncertain due insufficient field data (Guglielmone et al., 2014). Conversely, Aves are vital for the existence of some species because the immature stages feed mainly on Aves and adult ticks feed largely on Mammalia, a host-parasite relationships that will not be treated here. The analysis involved only those species whose larvae, nymphs and adult ticks feed on Aves. Surely there are more than 32 species treated here that depend on Aves for survival of all parasitic stages, but hosts are unknown for one or two parasitic stages in several taxa mostly known as parasites of birds. This is especially evident for *Ixodes* with 17 species under this condition but not relevant for Metastriata (Guglielmone et al. 2014). The proportion of *Ixodes* with all parasitic stages feeding on Aves (19%) is substantially higher than for *Haemaphysalis*, with 7% of all species with stages feeding on birds. All the species that feed exclusively on MB are *Ixodes* with the exception of *A. loculosum*. Conversely the modern Ixodidae (Rhipicephalinae), which contains the genera *Anomalohimalaya*, *Cosmiomma*, *Dermacentor*, *Hyalomma*,

Nosomma, *Rhipicentor* and *Rhipicephalus*, have no species with all parasitic stages bound to Aves, a condition which may have evolutionary importance and already noted by Zumpt (1952) in relation to seabirds ticks. Evidently Aves are more important as hosts for Prostriata than for Metastriata, probably indicating an old host-parasitic relationship with evolutionary implications as already emphasized by other workers mentioned in the Introduction.

The six species of *Haemaphysalis* feeding on a variety of NMB are predominantly from the Oriental Region but jointly encompasses all zoogeographic regions except the Neotropical region. These species are classified in three subgenera, four in *Ornithophysalis* (*H. doenitzi*, *H. hoodi*, *H. megalaimae*, *H. minuta*), one (*H. wellingtoni*) in *Kaiseriana*, and one (*H. chordeilis*) in *Aboimissalis*; the first two subgenera are “structurally advanced” and the third “structurally primitive” according to Hoogstraal and Kim (1985) but this subgeneric division of *Haemaphysalis* has shown inconsistencies (Burger et al. 2013). The relevance of these species of *Haemaphysalis* for the origin and evolution of this genus remains unclear.

At first sight the scenario for the 14 species of *Ixodes* from NMB is similar to the scenario depicted for *Haemaphysalis* above. These *Ixodes* shows a Palearctic predominance but jointly encompasses all zoogeographic regions. According to the subgeneric division of Clifford et al. (1973) these 14 species represent five subgenera (*Ixodes*, *Multidentatus*, *Pholeoixodes*, *Scaphixodes* and *Sternalixodes*) and one species (*I. collocaliae*) is left without subgeneric status although others classified it as *Xiphixodes*. The subgeneric division in *Ixodes* is not resolved as shown by Klompen (1999) and Guglielmone et al. (2006), as is not resolved either for several genera forming Metastriata. Nevertheless, a clade formed by the Palearctic *I. berlesei*, *I. caledonicus*, *I. mitchelli* and the Nearctic *I. howelli* (all from NMB) plus the parasites of MB *I. unicavatus* (Palearctic) and *I. signatus* (Nearctic-Palearctic) form a rather homogeneous group in Clifford et al. (1973) under the subgenus *Scaphixodes* and Filippova (1977) agreed, which is not irrelevant because there is disagreement in the subgeneric division of *Ixodes* between these authors. Filippova (1977) also includes *I. rothschildi* (Palearctic) into *Scaphixodes*. It should be of value to explore if this Palearctic-Nearctic group of *Ixodes* is basal for *Ixodes sensu stricto* (or Prostriata not included in the Australasian *Ixodes + uriae*).

The *Ceratixodes I. uriae* and *I. jacksoni* plus eight species of *Ixodes* feed on MB and all receive the treatment of “primitive” *Ixodes* by Zumpt (1951, 1952), Morel (1969), Filippova (1977), Balashov (1994) and Kolonin (2008). They are currently parasites of Neognathae that were established before the K-Pg boundary (Pacheco et al., 2011) and these tick species (or their ancestors) probably surpassed this boundary along with these types of hosts. The eight species with the exclusion of *I. uriae* and *I. jacksoni* are found in the

Australasian, Nearctic and Palearctic Zoogeographic Regions, and islands of the Atlantic, Indian and Pacific Oceans; five of them (*I. eudyptidis*, *I. kerguelensis*, *I. kohlsi*, *I. laysanensis* and *I. percavatus*) are included in the subgenus *Multidentatus*, two (*I. signatus* and *I. univatus*) are *Scaphixodes* and *I. rothschildi* is classified as *Multidentatus* by Clifford et al. (1973) and as *Scaphixodes* by Filippova (1977). All or some of these species may belong to a same hypothetical lineage that radiated from Australasia to colonize oceanic islands and the northern hemisphere in a similar way as it is proposed for *I. uriae* by Dietrich et al. (2014), or eventually, may be part of the hypothetical Palearctic-Nearctic basal tick clade discussed above.

HYPOTHESIS ABOUT EVOLUTION OF THE AUSTRALASIAN *IXODES* + *URIAE* AND PROSTRIATA

By definition the lineage of Australasian *Ixodes* + *uriae* should have originated in Australasia, but Mans et al. (2012) did not discard its occurrence in South American. Dietrich et al. (2014) stated that *I. uriae* and *I. holocyclus* split 97 ± 21 mya (Cretaceous). Hypothetically, it should be inferred that the ancestor of *I. uriae* was a parasite of feathered dinosaurs of the clade Avialae (Theropoda) that continued its evolutionary path to reach Neornithes, while alleged *I. holocyclus*-like species shifted to ancient mammal hosts. Actually *I. holocyclus* is a catholic feeder with a strong presence as a parasite of Australasian marsupials (Guglielmo et al., 2014). The earliest date for the onset of *I. holocyclus*-marsupials relationship is about 70 mya (Mitchell et al., 2014; Gallus et al., 2015) and probably consolidated after the K-Pg boundary. Dietrich et al. (2014) dated the split of *I. uriae* and *I. holocyclus* when Australia and Antarctic was still connected and available mammal hosts there were monotremes (Archer et al., 1985; Musser, 2003). Avialae was established by early Cretaceous in Australasia (Chiappe, 1996; Close et al., 2009; Fitzgerald et al., 2012; Martin et al., 2014) and by late Cretaceous in Antarctica (Chiappe, 1996; Clarke et al., 2005) therefore this split event should have occurred in Australasia coinciding with the origin of *I. uriae* proposed by Dietrich et al. (2014). Probably Australasian *Ixodes uriae* passed the K-Pg boundary feeding on MB and *Ixodes holocyclus* or their ancestors, surpassed it as a parasite of Monotremata (eventually on early Australian marsupials or both).

The date of the split of *I. uriae* and *I. holocyclus*-like ticks should not be confused with the origin of the Australasian *Ixodes* + *uriae* clade. The oldest fossil record of Australasian Avialae is from early Cretaceous (125-113 mya) (Close et al., 2009) a date matching the age of the first fossil record of Monotremata (Musser, 2003). The latter author emphasized that early Cretaceous was a time of diversification of monotremes rather than a time of origin that according to van Rheede et al. (2006) occurred in late Triassic (231-

217 mya). Likely Australasian *Ixodes* + *uriae* clade evolved before the date of fossil records of Avialae and Monotremata listed above with some ticks probably radiating earlier than the time of split of *I. uriae* and *I. holocyclus*. It is uncertain if the origin of the clade has to be traced back to early Triassic in concordance with the origin of Monotremata although this time is in accord with the proposal of Mans et al. (2012). There are few records of *I. holocyclus* from monotremes (Roberts, 1970, Gofton et al., 2015) but *I. ornithorhynchi* (all tick stages known) has been found only on Ornithorhynchidae (platypus), while *I. zaglossi* feeds on Tachyglossidae (echidna) but only the female tick is known, *I. luxuriosus* and *I. tasmani* have been recorded as parasite of Monotremata: Tachyglossidae, among other hosts (Roberts, 1970, Guglielmo et al. 2014). *Ixodes ornithorhynchi*, the most "primitive" of Australasian *Ixodes* according to Morel (1969), and *I. tasmani* are members of the Australasian *Ixodes* + *uriae* group in Klompen et al. (2000) while *I. luxuriosus* and *I. zaglossi* are included in this clade by Barker and Murrell (2004). Perhaps, some of the actual Australasian *Ixodes* parasites of marsupials and eutherians are derived from ancestors that fed on ancient mammals with no choice than to feed on monotremes if their life history started in Australasia before than 70 mya, with species as *I. ornithorhynchi* still bound to Monotremata.

Neornithes basal divergences occurred before the K-Pg boundary with several orders and crown groups of Aves well represented before the catastrophic event (Pacheco et al., 2011). Some of these avian orders are actually important for the sustenance of *I. uriae* as presented in Muñoz-Leal and González-Acuña (2015). After surpassing the K-Pg boundary *I. uriae* remained an Australasian species that started to radiated in early Miocene (22 mya) to reach South Atlantic and Indian Ocean territories thereafter (Dietrich et al., 2014), in coincidence with strong avian radiation of Neornithes during this period (Benton, 2005).

Prostriata (*Ixodes*) originated in the Jurassic (196 ± 27 mya) according to Jeyaprakash and Hoy (2009) and supported by Dietrich et al. (2014), but it is a Triassic event that took place 217 ± 24 mya in Mans et al. (2012). Both dates of Prostriata origin correspond to epochs before Pangaea started to break apart encompassing a period of more than 130 million years until K-Pg boundary. Hypothetically during this period several lines of Ixodidae should have radiated to cover niches of terrestrial vertebrates and some become extinct along with their hosts, a force that shaped the current tick situation in the opinion of many workers from Hoogstraal (1978) to Barker et al. (2014) and Mans et al. (2014) among others. Under this speculative scenario, likely first successful Prostriata (proto *Ceratixodes*?) fed on theropod dinosaurs and their descendants through marine Neornithes, being uncertain where this hypothetical event occurred.

Nevertheless, if late Triassic ancestral monotremes were involved in the evolution of Prostriata an Australasian origin for this event seems plausible.

In brief, it is proposed that actual *I. uriae* is the final expression of a natural history that started in an undetermined place in late Triassic - early Jurassic feeding on Theropoda giving rise to the Australasian *Ixodes + uriae* in an uncertain time period from late Triassic to early Cretaceous. This was followed by the split of the ancestor of *I. uriae* in late Cretaceous which surpassed the K-Pg boundary on marine Neornithes to finally radiate to colonize coastal environment in northern and southern hemispheres alongside the radiation of its neognathan hosts.

HYPOTHESIS ABOUT THE ORIGIN OF IXODIDA AND IXODIDAE:

Guglielmone et al. (2014) stated that 67% of hard tick species are only found on lands of this former super continent and only 18 % in Laurasian territory; this biased distribution is considered here a result of the origin of Ixodida in Gondwanan lands. When it occurred is debatable and there are a vast arrange of hypothesis covering several periods of Paleozoic to Mesozoic epochs before, during and after Pangaea covering times when amphibians, dinosaurs and mammals originated and several massive extinctions of vertebrates occurred. Great part of the disagreement among theories is due to lack of tick fossils earlier than Cretaceous period.

Black and Piesman (1994) analyzed 16S mitochondrial gene sequences and placed the origin of Ixodidae not earlier than 140 mya bound to appearance of first Aves in coincidence with the time proposal of Filippova (1977) who based her decision on morphological primitiveness of *Ixodes* subgenera such as *Ceratixodes*, *Exopalpiger*, *Scaphixodes* and *Sternalixodes*. Klompen et al. (2000) adhered to a Cretaceous origin of Ixodidae and placed it in Australia after the almost complete isolation of the country in mid-late time of this period. Balashov (1994) studied the current distribution of genera of Ixodidae and located the arisen of the family in late Triassic-early Jurassic well before Pangaea starts to break apart with most primitive mammals as ancestral hosts. Hoogstraal (1978), Hoogstraal and Aeschlimann (1982) and Hoogstraal and Kim (1985) hypothesized about Ixodida origin in late Permian-early Triassic as a parasite of reptiles that shortly diverged into Argasidae which mostly maintained the primitive morphological features and Ixodidae that shown a diverse morphological pattern from primitive to advanced species. Mans et al. (2011) analyzed phylogenetically 18S nuclear and 16S mitochondrial genes of *N. namaqua* to conclude that Ixodida originated in mid-late Permian (270-260 mya in Gondwanan lands, specifically in the Karoo Basin (currently Africa), as parasites of therapsids but later changed hosts to feed

on diapsids. Schulze (1937) claimed that Ixodida aroused during the Permian as a collateral branch of Anthracomarti (= Trigonotarbida) feeding on reptiles, while Morel (1969) also stated that Ixodida appeared during the Permian as parasites of reptiles. Jeyaprakash and Hoy (2009) used sequences of several mitochondrial genes to resolve the phylogeny of Chelicerata and located the origin of Ixodida at late Carboniferous-early Permian (327-273 mya) feeding on amphibians, followed by Ixodidae originated during late Permian-Triassic (269-213) as parasites of reptiles. Mans et al. (2012, 2016) presented a phylogenetic and time divergence analysis of Ixodida based on 16S, 18S and mitochondrial protein genes and a molecular clock with Xiphosura-Pycnogidae node dated 445 mya to calibrated the root of the tree and minimum age for Metastriata set up at 100 mya; These authors placed the origin of Ixodida in the Carboniferous Period in northern Gondwana (currently eastern Africa) and migration to the Karoo Basin in southern Africa during late Permian considering *N. namaqua* as the closest extant relative to the common ancestral tick lineage and placed the origin of Ixodidae in the Triassic. Oliver (1989) supported an origin of Ixodida in the Devonian feeding on amphibians based on a statement of Lindquist (1984) that Acarina ancestral stock have arisen in Late Silurian Period and a great radiation of Acarina in the Devonian; this view was supported by Dobson and Barker (1999) which located this event in territories of the actual Australia country, and by Barker et al. (2014) who disputed the basal nature of *N. namaqua* as well as the African Gondwanan origin of Ixodida, forwarding different hypothetical alternatives to the proposal in Mans et al. (2012).

From the many hypotheses above the proposals of Mans et al. (2012, 2016) and Barker et al. (2014) are more elaborated phylogenetically than the others, and present discussions quite specific about different sites for the origin of Ixodida in Gondwanan territories. These authors coincide in supporting holothyrid mites as the ancestors of Ixodida, conversely rejecting the competing theory that ticks evolved from mesostigmatid mites as proposed by Karg and Schorlemmer (2008, 2013) and some uncertainties of holothyrids basal position to Ixodida in Burger et al. (2014). Dunlop and Penney (2012) prefer the hypothesis of holothyrids basal to Ixodida but did not reject the second option showing that this matter is not resolved.

The ancient origin of *N. namaqua* in Mans et al. (2012) is accepted by Barker et al. (2014); this might favor a presumptive origin of Ixodida in the Carboniferous or perhaps earlier although additional evidence are needed to confirm it. Barker et al. (2014) based their hypothesis of a Devonian Australian origin of Ixodida on the presence there of six of eight main tick lineages (Amblyomminae, Argasinae, Bothriocrotinae, Haemaphysalinae, Ixodinae and Ornithodorinae) and the Australian endemism of holothyrid mites, but the

Afrotropical Zoogeographic Region contains seven of the eight subfamilies of ticks used in Barker et al. (2014) (Amblyomminae, Argasinae, Haemaphysalinae, Ixodinae, Nuttalliellinae, Ornithodorinae and Rhipicephalinae), and Holothyrida is not restricted to Australia (Walter and Proctor, 2013). Africa split from Gondwana about 130 mya carrying fauna originated in African Gondwana and derived fauna bringing some doubts about African origin of Nuttalliellidae postulated by Mans et al. (2011, 2012, 2016) as these authors supported their position by the actual limited distribution of *N. namaqua* in Africa, but its actual range may also be a relic of a former ampler distribution as stated in Barker et al. (2014). Notably, Mans et al. (2015) treated *N. namaqua* as a tick with a wide geographic distribution, but we are unaware of new reports apart from those records long known from South Africa and Tanzania. Barker et al. (2014) supported that labyrinthodont amphibians were the original hosts of Ixodida and this event occurred in the part of Gondwana that became the actual Australia country. The term labyrinthodont is taxonomical undefined for a group of paleo vertebrates non-restricted to the region occupied by Australia in Gondwana. Australia was connected with South America, Africa, Antarctic and India before the formation of Pangaea and maintained these connections when the continent split into Gondwana and Laurasia to become an island when finally Australia separated from Antarctic about 40 mya. Therefore, Ixodida may have arisen in Australia in Devonian or Carboniferous Periods and spread to other lands, or the opposite including a hypothetical introduction of Antarctic paleofauna. Most probably the Motherland of Ixodida is Gondwana but, as in the case of Prostriata, under current evidence is unknown where this event precisely occurred.

Prostriata emergence was followed by radiation of Metastrata in the Cretaceous according to Mans et al. (2012). Metastrata group has been considered of Australasian origin (Klompen et al. 1997) with almost no dispute but Mans et al. (2012) presented a South American alternative. Burger et al. (2012, 2013) soundly proposed that "*Amblyomma elaphense*" (formerly a "primitive" *Aponomma*) does not belong to *Amblyomma* but to a new still undefined genus. Burger et al. (2013) stated that probably "*A. elaphense*" is basal to Metastrata, conversely displaced *Bothriocroton* (Australasian) from this position, an outcome already anticipated by Keirans and Klompen (1996). "*Amblyomma elaphense*" is a Nearctic species parasite of Squamata: Colubridae in the Chihuahuan desert ecoregion (Guglielmo et al. 2014); perhaps the actual range of this species is a vestige of a clade originated in lands including in the actual Nearctic Region or a relict of an ample past range, bringing additional uncertainties where major evolutionary tick events (arisen of Ixodida, Ixodidae, Prostriata, Metastrata) occurred.

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