**An overview of systematics and evolution of ticks**

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## 1. ABSTRACT

All species of ticks (Acari: Ixodida) are grouped into three families: Argasidae (186 species), Ixodidae (692 species) and Nuttalliellidae (monotypic). Molecular markers have been developed and applied for tick studies along with conventional techniques. The origin of ticks is during the pre-mid Cretaceous period (with both the Argasidae and Ixodidae being established in the middle Cretaceous). Primeval hosts were probably reptiles or amphibians. The Argasidae contains two to five subfamilies according to authors but relationships among its members are far from resolved. The Ixodidae were formed by the basal Prostriata group (genus *Ixodes* subfamily Ixodinae) and the Metastriata group (all others genera). Conventional classifications considered Metastriata to be divided into Amblyomminae, Haemaphysalinae, Hyalomminae and Rhipicephalinae but evidences shows that part of Amblyomminae (species considered previously as "indigenous Australian Aponomma") are now members of the basal Metastriata subfamily Bothriocrotinae, and Hyalomminae are part of Rhipicephalinae. The former genus *Boophilus* is included as a subgenus within *Rhipicephalus*. The validity of tick names is discussed in relation to latest world list of ticks.

## 2. INTRODUCTION

Ticks (Acari: Ixodida) are blood-feeding ectoparasites second only in importance to mosquitoes as vectors of human diseases, and their importance as vectors of animal diseases is widely recognized (1, 2, 3). Ticks are distributed worldwide as parasites of wild and domestic vertebrates except fishes. These parasites belong to Phylum Arthropoda, Class Arachnida, Subclass Acari, Order Parasitiformes and Suborder Ixodida. Ticks share the Order Parasitiformes with the suborders Holothyrida, Mesostigmata (commonly known as mites) and Opilioacarida. Ixodida contains three families: Argasidae (soft ticks which have dorsum without chitin), Ixodidae (hard ticks which have a dorsum totally or partially covered with chitin) and Nuttalliellidae (an ill known monotypic family represented by *Nuttalliella namaqua*). In turn, according to morphological characters, the family Ixodidae is subdivided into the Prostriata group (genus *Ixodes*) and Metastriata group (all other genera in Ixodidae).

Traditionally, classifications and phylogenetics inferences for Ixodida were based on morphological, biological and ecological characteristics (4, 5, 6, 7, 8, 9). Tick classification is a consequence of phylogenetic criteria still based largely on morphological characteristics, and the value given to differences and similarities among groups of ticks, resulting in non-homogeneous tick arrangements. The "Soviet" and "American" schools for Argasidae classification (8) are good examples. Nevertheless, in the last fifteen years considerable modifications were applied to the previous classifications when molecular markers were incorporated for phylogenetics analysis. Thus, the taxonomic status and the phylogenetic position of numerous tick species were reconsidered. The molecular taxonomy associated with conventional morphological cataloging will be useful to obtain a more homogeneous and independent criterion for classification, although in the short term this may not be obvious.

Below, we will discuss in broad terms some aspects of the classification and phylogenetic relationships of Argasidae and Ixodidae. Also, tick fossil records and hypotheses on the origin of ticks are summarized, and a revision of the molecular markers used for systematic and ecological studies is given. Finally, we present an update with remarks for tick names. Abbreviations of genera used throughout this article are listed at the end of reference section.

## 3. MOLECULAR MARKERS IN THE STUDY OF THE SYSTEMATICS AND ECOLOGY OF TICKS

Conventional techniques (morphology-ecology) for species determination are limited when taxa are morphologically very similar (e.g. *I. ricinus-I. pararicinus*), specimens are damaged, and in the frequent cases where immature stages are not described or are engorged. Molecular techniques, especially those based on DNA sequences analysis offer an alternative approach for the characterization of species, population studies and phylogenetic inferences. A revision of molecular data used

in tick studies was made by Navajas & Fenton (10) and Cruickshank (11), but difficulties arise comparing results in which when different markers are used.

Diverse molecular markers have been applied in tick studies. Those markers considered for phylogenetics approach are also mentioned in the "Phylogeny" section.

Two main types of molecular markers can be distinguished, nuclear ribosomal genes and mitochondrial DNA. In the nuclear ribosomal DNA, the main locus in eukaryotic organisms consists of three genes encoding the 5.8S, 18S and 28S rRNA subunits of the ribosome. Among these genes are intercalated the internal transcribed spacers 1 (ITS1) and internal transcribed spacers 2 (ITS2) (12). The ribosomal genes are reiterated in tandem for more than one hundred copies on a chromosome. Therefore, PCR amplification of the rRNA genes is considerably easier than for single copy genes.

Different nuclear rRNA genes are more appropriate for different purposes. Klompen *et al. (*13) used the entire sequence of 18S rDNA and partial sequences of 28S rDNA in the study of relationships at the suborder and infraorder level of Parasitiformes. Others papers relied on the use of partial or entire sequences of 18S rDNA and 28S rDNA to infer the phylogenetic relationships for family and subfamily levels of ticks (14, 15, 16, 17, 18, 19). Norris *et al. (*20) concluded that the sequence of 18S rDNA is more conserved and better than mitochondrial 12S and 16S rDNA sequences for resolution at this taxonomic level.

The animal mitochondrial genome has been widely used in systematic and population studies and the patterns of evolution are well-understood (21, 22). The advantages of the mtDNA reside mainly in the high number of copies per cell, the strictly maternal inheritance and the lack of recombination. Most taxa have two ribosomal RNA genes, 22 transfer RNA genes, 13 protein-coding genes and the control regions. The mitochondrial rRNA genes are 12S and 16S rRNA; they are not separated by internal transcribed spacers. In mitochondrial protein-coding genes generally, the third codon positions evolve more quickly than the ribosomal genes but it may be possible to use the first and second positions at deeper taxonomic levels. Significant advances in this topic were reached during the last ten years. The mitochondrial genome of soft ticks as *O. capensis (*also named as *C. capensis*)*, O. moubata*, and hard ticks *I. hexagonus*, *H. flava*, *R. microplus (*also named as *B. microplus*) and *R. sanguineus* have been sequenced and the gene arrangements were characterized (23, 24, 25). Moreover, there are projects to sequence the complete genome of *I. scapularis* (26) and *R. (B) microplus (*27).

The molecular markers most used in studies at population level and to infer inter and intra-specific variation of ticks were the ITS1 and ITS2 (28, 29, 30, 31, 32, 33, 34, 35, 36, 37, 38, 39) and the mitochondrial genes 16S (34, 40, 41, 42, 43, 44, 45, 46, 47, 48, 49, 50, 51, 52, 53, 54), 12S (38, 42, 43, 55), cytochrome oxidase I (COI) (36) and cytochrome oxidase III (COIII) (56). Others genetic markers used to infer variation at inter and intra-

specific levels were microsatellites (57, 58, 59, 60, 61, 62, 63), allozyme polymorphism (64, 65, 66), random amplified polymorphic DNA (RAPD) (67), polymorphism of the bm86 gene (68) and 28S rDNA gene (69).

The sequences of both mitochondrial rDNA genes appear suitable markers for tick species identification. However, some particularity makes that 16S rDNA sequence more appropriate than 12S rDNA. For example, useful primers have been developed for a wide variety of taxa and the sequence was found to be more variable and informative than 12S rDNA. On the other hand, the database of 16S rDNA tick sequences available in GenBank is larger than for 12S rDNA, and includ more than thirty sequences of soft ticks. An effort is needed to obtain 16S rDNA sequence for most species to be deposited in the GenBank. We also suggest the inclusion of DNA sequencing data in descriptions of new species, immature stages and re-descriptions.

## 4. PHYLOGENY, CLASSIFICATION AND EVOLUTION

### 4.1. Fossil records and hypotheses on the origin of ticks

It is difficult to construct hypotheses on the origin of ticks because fossil evidences are few. Useful fossils of ticks that allow the observation of microscopical details occur mostly in amber (70). The oldest fossils are a larva described under the name *C. jerseyi* (we included this taxon in *Ornithodoros*) found in Cretaceous New Jersey amber, 90-94 million years ago (mya) (71), a larva of *Amblyomma* found in Cretaceous Burmese amber (70) and the Cretaceous fossil genus *Cornupalpatum* described from larvae also found in Burmese amber, probably from upper Albian, 100 mya (72). This fossil genus is characterized by the presence of claws on palpal segment 3, which is a distinctive character for Ixodida, and palpi with a distinct and apical segment four, similar to extant Ixodidae feeding on reptiles. This finding along with the larvae of *Amblyomma* in Burmese amber indicates that two lines of Metastriata ticks (one extant) were soundly established in middle Cretaceous (*ca.* 100 mya) (72).

All the remaining records were made in deposits of the Tertiary period. *O. antiquus* was determined from a male and a female obtained from Tertiary Dominican Republic amber, 30-40 mya (73). This species appears to share some characters with members of the subgenus *Pavloskyella* and *Alectorobius* sensu Clifford *et al.* (4). Fossils for four genera of hard ticks are documented. One female of *I. succineus*, larvae of *Ixodes* sp. and one male of *Hyalomma* sp. were found in Baltic amber, 35-50 mya (74, 75). Larvae of *Amblyomma* sp., close to *A. dissimile* and a male of *Amblyomma* close to *A. argentinae* (cited as *A. testudinis*) were recorded from Dominican amber, 14-40 mya (75, 76, 77), and Schille (78) described a male of *Dermacentor* close to *D. reticulatus* collected from the exterior auditory canal of a wholly rhinoceros, *Trichorhinus antiquitatis* from a Pliocene deposit, 2-5 mya.

Due to insufficient information gained from fossil records, the hypotheses about origins of ticks were mostly based on phylogenetics, host associations, biological, morphological and biogeographical evidences from present-day tick species. The hypothesis of Hoogstraal (79) was constructed considering tick-host associations as the main driven force for tick evolution. According to this author, the ticks associated with reptiles evolved along two lines in the late Paleozoic (*ca.* 300 mya) or early Mesozoic (*ca.* 200 mya) eras, in a warm, humid climate. One was ancestral ticks like-current Argasidae. The second line was ixodid represented by primitive members of the genera *Ixodes* and *Haemaphysalis*, and another branch that gradually evolved was one containing *Amblyomma* and *Aponomma (*we currently consider this genus non-valid). The Hyalomminae (a family we no longer recognize) appeared later close to the Cretaceous, and Rhipicephalinae in the Tertiary, both on mammals. Other proposals that argued that tick origin was in the Paleozoic era (Devonian, 408-362 mya) are those of Oliver (80) and Dobson & Barker (17) who state that the original hosts were not reptiles but amphibians. The rest of the hypotheses locate the origin of ticks in two periods of the Mesozoic era, Triassic (250-208 mya) (81, 82, 83) and Cretaceous (18, 84, 85).

Some authors proposed, with differences, an Australian origin of Ixodidae. Dobson & Barker (17) speculate with an origin in the part of Gondwana that became Australia on Devonian amphibians. They justify this view on the fact that the alleged sister group of ticks, Holothyrida, has Gondwana distribution, and that the most "primitive" family (Allothyridae) is restricted to Australia and New Zealand. Klompen *et al. (*18, 85) places the origin of hard ticks after complete isolation of the Australian island in the mid-to late Cretaceous, and then dispersed. The justification of this hypothesis is that the "basal" lineage of the Metastriata, the subfamily Bothriocrotoninae, and the Australasian *Ixodes* (Australia-New Guinea) (see section "Phylogeny of Ixodidae") are almost exclusive of Australia. Nevertheless, Shao *et al. (*86) presented evidences that Argasidae and non Australian *Ixodes* have one control regions in mitochondrial genome while Australian-New Guinean *Ixodes* and species of the Metastriata group have two control regions. Although this phenomenon may have occurred independently, it does not either support the consideration of Australian-New Guinean *Ixodes* as basal within the genus *Ixodes*. Regarding to genome size of ticks, Geraci *et al. (*87) found that species of Ixodidae have larger genomes than the Argasidae, and within the Ixodidae, the metastriate species had larger genomes than the prostriate species, indicating a general trend toward larger genome size in more recent species of the Ixodida.

With respect to the evolution of Rhipicephalinae ticks, Murrell *et al. (*19) using ecological, morphological and molecular evidence proposed that the ancestor of the *Dermacentor-Anocentor* lineage evolved in the Afrotropical region, the *Nosomma-Hyalomma* lineage evolved from an ancestor that lived in the Oriental region, the *Rhipicephalus* lineage evolved and radiated in Africa, and the *Rhipicentor* lineage evolved and remained in Africa.

Mans *et al. (*88) and Mans & Neitz (89) focused tick evolution from a functional perspective, considering blood-feeding aspects. They reach the conclusion that the inhibitors of blood coagulation and platelet aggregation of hard and soft ticks do not share a common origin, and that the main tick families have evolved different antihemostatic strategies during independent adaptation to a blood-feeding environment. Consequently, the adaptation to blood-feeding was an independent event for hard and soft ticks. Additionally, Mans *et al. (*88) propose that the emergence of hematophagy in ticks was triggered by the independent radiation of placental mammals and birds between 120 and 92 mya ago and that the hemostatic system of the hosts played a decisive role in the evolution of this crucial event. More recently Mans *et al. (*90) showed that anti-hemostatic mechanisms are conserved between *Argas* and *Ornithodoros* genera, and they stated that the time between the proposed origin of ticks in the late cretaceous (110 mya) (18, 85) and the divergence of ticks into the main soft tick genera was too short to allow the divergence of genera and evolution of anti-hemostatic factors within the soft tick family. Mans *et al. (*90) place a lower limit on the origins of anti-hemostatic factors in soft ticks at least at 96 mya, but probably as far back as 250-145 mya.

Evidently, more information is needed to assert tick origin and evolution. Nevertheless, fossil records indicate that the origin of ticks is most probably pre-middle Cretaceous, because in middle cretaceous the two principal lineages of ticks, Argasidae and Ixodidade, were well differentiated. Thus, fossil tick records defy the hypotheses that postulate the origin of ticks in middle or late Cretaceous. The first hosts were possibly amphibian or reptilian being premature, in our perspective, to argue where these events occurred. Discerning the driving forces that influenced tick evolution is clearly difficult considering our meager knowledge of the ecology of most tick species. Klompen *et al. (*85) do not agree with Hoogstraal´s theory and support the view that biogeography and ecological specificity had a more important role than host-association in tick evolution. Cumming (91, 92) presents quantitative data set for host-preferences of African ticks, and conclude that both host specificity and ecological specificity may be important within the Ixodida but evaluation of these ecological aspects are extremely difficult. We coincide with Cumming's vision.

### 4.2. Phylogeny of Argasidae

The systematic studies of the family Argasidae goes back to the beginning of the 20<sup>th</sup> century (93), but the firsts hypotheses about phylogenetic affinities among members of this family were proposed by Pospelova-Shtrom (5, 94), Filippova (95), and Clifford *et al. (*4). The classification of Pospelova-Shtrom (5, 94) contains the subfamilies Ornithodorinae and Argasinae. Ornithodorinae has two tribes, Ornithodorini, which includes the genera *Ornithodoros*, *Alectorobius* and *Antricola*, and Otobiini, that includes the genera *Otobius* and *Alveonasus*, while, Argasinae, has a single tribe, Argasini, with two genera, *Argas* and *Carios*. The scheme of Filippova (95) is similar

to the classification proposed by Pospelova-Shtrom (5, 94) but considers *Alectorobius* as subgenus of *Ornithodoros*. In the classification of Clifford *et al. (*4), the division of the family in two subfamilies has been maintained but not the tribes, and the recognized genera are *Ornithodoros*, *Antricola*, *Otobius* (Ornithodorinae) and *Argas* (Argasinae). *Alectorobius* and *Alveonasus* are considered subgenera of *Ornithodoros* and *Carios* subgenus of *Argas*. The classification of Hoogstraal (96) is similar to Clifford *et al. (*4), but includes the monospecific genus *Nothoaspis* described by Keirans & Clifford (97) and each genus has its own subfamily (*Argas*: Argasinae; *Ornithodoros*: Ornithodorinae; *Otobius*: Otobinae; *Antricola*: Antricolinae; *Nothoaspis*: Nothoaspinae). This classification was widely used and still is recognized by workers dealing with argasid ticks, including the authors. Nevertheless, in recent years scientists have also started to apply the arrangement proposed by Klompen & Oliver (8) (see below).

Camicas & Morel (6) present a classification of soft ticks where Argasinae has three genera, *Argas*, *Carios* and *Ogadenus*, and Ornithodorinae has seven genera, *Alectorobius*, *Alveonasus*, *Antricola*, *Nothoaspis*, *Ornithodoros*, *Otobius* and *Parantricola*. Contrary to the authors cited above, Camicas & Morel (6) do not present evidences to support their views making it difficult to evaluate the merits of this classification.

Klompen (98) carried out the first phylogenetic study of Argasidae using a cladistic methodology based on shared derived characters to infer evolutionary history. This author makes a preliminary analysis using comparative morphology of larvae, principally characters of setation of the appendages, and suggests that bat-associated taxa of the genera *Argas* and *Ornithodoros*, all species of *Antricola* and possibly *Nothoaspis* form a monophyletic group, implying that the genera *Argas* and *Ornithodoros* are not natural groups. Afterward, Klompen & Oliver (8) conducted a phylogenetic analysis of the relationships at the generic and subgeneric level using 83 characters, most from larval morphology, but adult morphology, development and behavioral characters were also included. This study confirms the monophyly of the family Argasidae and the validity of subfamilies Argasinae and Ornithodorinae, but introduced several modifications in respect to earlier classifications: - Within the subfamily Argasinae a single genus, *Argas*, with five subgenera, *Argas* (that includes the previous recognized subgenera *Argas* and *Persicargas*), *Secretargas*, *Ogadenus*, *Proknekallia* and *Alveonasus* – Within the subfamily Ornithodorinae three genera, *Ornithodoros (*with the subgenera *Ornithodoros*, *Pavlovskyella*, *Ornamentum* and *Microargas*), *Otobius* (consisting in *Otobius s.s* plus the addition of the species previously known as *O. sparnus*), and *Carios* (containing the species from the previous subgenera of the genus *Argas*: *Carios* and *Chiropterargas* plus species from the previous subgenera of the genus *Ornithodoros*: *Alectorobius*, *Reticulinasus* and *Subparmatus*, and all members of the genera *Antricola* and *Nothoaspis*). Finally, Klompen & Oliver (8) affirm that their classification is superior to the previous ones due to

**Table 1.** Classifications proposed for the family Argasidae

| Pospelova-Shtrom (5, 94) and Filippova (95) | Clifford *et al.* (4) and Hoogstraal (96)[3] | Klompen & Oliver (8) |
|---|---|---|
| Subfamily Argasinae | Subfamily Argasinae | Subfamily Argasinae |
| Tribe Argasini | | |
| *Argas* | *Argas* | *Argas* |
| *Carios*[1] | | |
| Subfamily Ornithodorinae | Subfamily Ornithodorinae | SubfamilyOrnithodorinae |
| Tribe Onithodorini[2] | | |
| *Ornithodoros* | *Ornithodoros* | *Ornithodoros* |
| *Antricola* | *Antricola* | *Otobius* |
| Tribe Otobiini | *Otobius* | *Carios* |
| *Otobius* | *Nothoaspis* | |
| *Alveonasus* | | |

[1]*Carios* is considered a subgenus of *Argas* by Filippova (170). [2] Pospelova-Shtrom (94) includes *Alectorobius* as a genus belonging to the tribe Ornithodorini. [3] In the Hoogstraal's study each genus has its own subfamily.

the superior fit to the data and because it recognized only monophyletic taxa, but they also accept a weakness in the relatively poor support for *Ornithodoros*, *Carios* and *Argas* (*Secretargas*). Table 1 contains a summary of the classification proposals for Argasidae.

Black & Piesman (84) incorporated molecular evidence (16S rDNA sequences) to study of Argasidae to reach five significant conclusions: 1) the derived phylogeny failed to support a monophyletic relationship among members of the subfamily Ornithodorinae (up to 68 %) and supported the monophyly of subfamily Argasinae (97-100%); 2) the species of *Argas* analyzed (*A. monolakensis*, *A. reflexus* and *A. persicus*) formed a monophyletic group basal to Ixodidae; 3) the members of the *Ornithodoros moubata* complex formed a clade with 100 % support; 4) the two *Antricola* species (*An. marginatus* and *An. mexicanus*) constituted a branch with 90-100 % support. Crampton *et al.* (14) showed evidence of paraphyly in the family Argasidae using nucleotide sequences of the D1 domain of large subunit (28S) ribosomal DNA (rDNA), the V4 region of small subunit (18S) rDNA and sequences immediately adjacent to these, and contrarily to Black & Piesman (84), they locate Ornithodorinae as sister group of Ixodidae. On the other hand, the phylogeny obtained by Black *et al.* (15) with the sequences of the 18S nuclear rDNA gene, which is more conserved than the 16S rDNA, has strong support for the monophyly of Argasidae and for the two subfamilies, Argasinae and Ornithodorinae, and the branch that connects *O. puertoricensis* (named as *C. puertoricensis*) with *O. moubata* has low support. Sequences of mitochondrial 16S gene were used by Ushijima *et al.* (99) and Estrada-Peña *et al.* (100), who located *O. capensis* (mentioned as *C. capensis* in Ushijima *et al.* (99)) in a clade with *An. mexicanus*, *An. marginatus* (mentioned as *C. mexicanus* and *C. marginatus* in Ushijima *et al.* (99)), *O. puertoricensis* and *O. mimon* (these two species only included in the work of Estrada-Peña *et al.* (100) separated from other clade that contains *O. moubata* and two subspecies of *O. porcinus*. Petney *et al.* (48) and Estrada-Peña *et al.* (100) used 16S rDNA sequences to study the genus *Argas*. The taxa analyzed form a monophyletic group with two sub-groups: 1) a clade (100 % and 91 % bootstrap support, respectively) formed by species belonging to the subgenus *Persicargas* (*Ar. persicus*, *Ar. robersti*, *Ar. keiransi*), and 2) a clade with low bootstrap supports (48 % and 54 %, respectively) constituted by species of the subgenus *Argas*.

A phylogenetic analysis using 16S rDNA sequences belonging to several species of soft ticks, including some that were not considered previously, was performed. To construct this tree we consider as sister group of Ixodida the Holothyrida (large scavenger mites with Gondwanan distribution), because the morphological and molecular evidences for this position are sound (13, 101, 102). The rooted neighbor-joining tree is depicted in Figure 1 (the tree obtained with maximum parsimony method showed a similar topology). Genus *Argas* constitutes a natural group. Nevertheless, this result has to be considered cautiously because only species of the subgenera *Argas* and *Persicargas* were used for this analysis. The species of *Persicargas*, *Ar. keiransi*, *Ar. persicus* and *Ar. robersti* form a monophyletic group with 95 % bootstrap support but, the species of the subgenus *Argas* do not constitute a natural group. The subfamily Ornithodorinae (genera *Antricola*, *Ornithodoros* and *Otobius*) is not monophyletic, *O. moubata*, *O. porcinus domesticus* and *O. p. porcinus* form a monophyletic clade (100 % bootstrap support) separated of the remaining Ornithodorinae species, and the clade formed by the *Antricola* species (*An. delacruzi*, *An. guglielmonei*, *An. marginatus* and *An. mexicanus*), *O. capensis* and *O. sawai*, *O. mimon* and *O. puertoricensis* is monophyletic (bootstrap support 97 %), but three groups can be differentiated in this clade, 1) *An. delacruzi*, *An.guglielmonei*, *An. marginatus* and *An. mexicanus*, 2) *O. capensis* and *O. sawai* and 3) *O. mimon* and *O. puertoricensis*. The evidences provided by our analysis and by previous studies allow us to reach these general conclusions: 1) the genus *Argas* is monophyletic when considering species of the subgenera *Argas* and *Persicargas*, 2) the genus *Ornithodoros* as presented by Clifford *et al.* (4) and Hoogstrall (96) has low support, thus, the species of the subgenus *Ornithodoros*, *Pavloskyella* and *Ornamentum* sensu Clifford *et al.* (4) and Hoogstrall (96) should be located in a genus separated from the rest of *Ornithodoros* species, coinciding with the suggestion of Klompen & Oliver (8), 3) the genus *Carios* proposed by Klompen & Oliver (8) seems not to be justified *in toto*. Probably, the invalidation of the basically Neotropical genus *Antricola* is unjustified. The grouping of *Antricola* species (Figure 1) may be considered an indication of generic status. Moreover, *Antricola* ticks are characterized by peculiar aspects as: 1) larvae feeding on bats in humid-hot caves, with long, bulbous pulvilli (claws absent) adapted to climb caves with the exception of *An. marginatus*, 2) it is uncertain if the nymphs feed on blood,
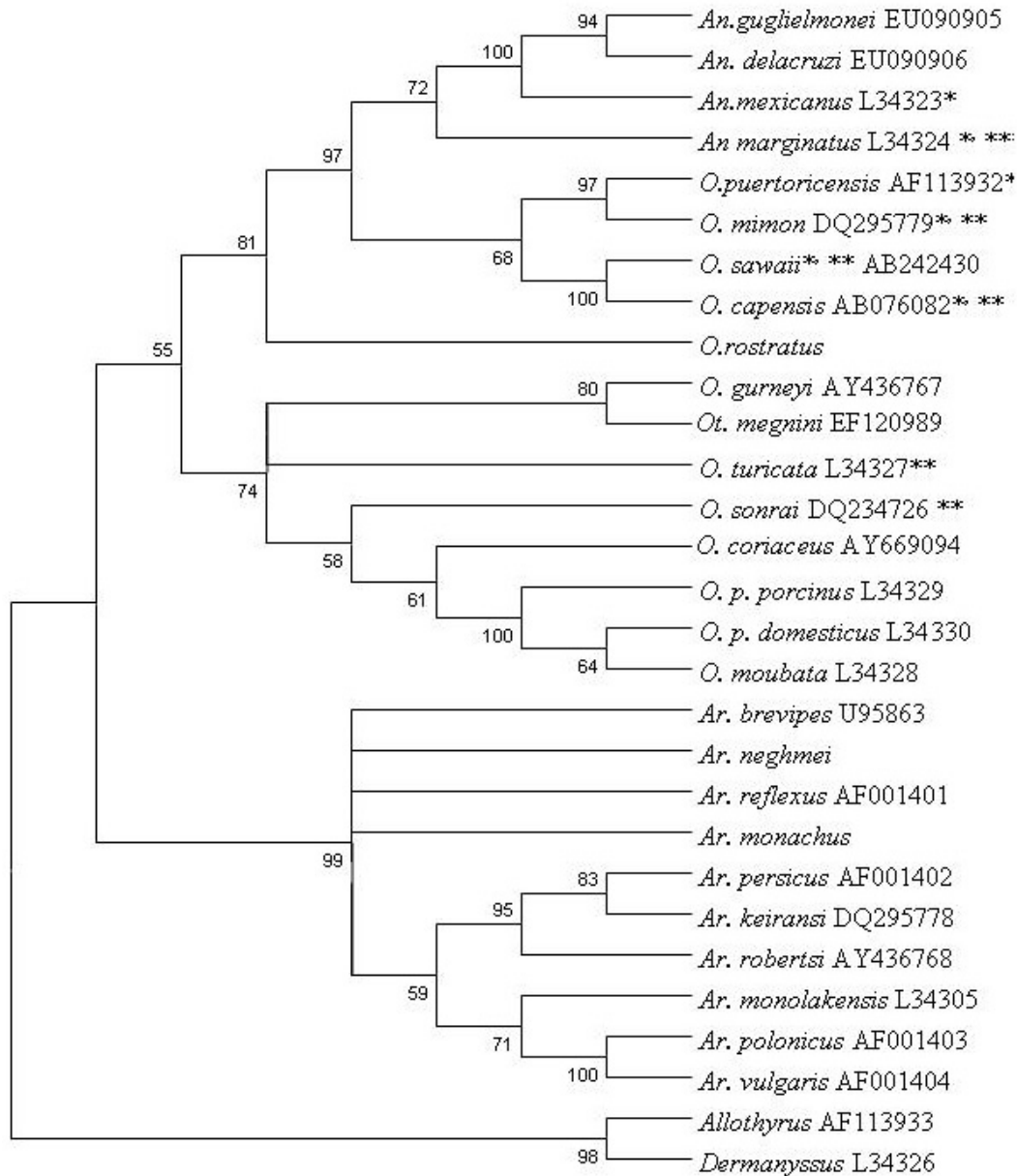
**Figure 1.** Neighbor-joining condensed tree showing the phylogentic relationships among Argasidae species and GenBank accession numbers The tree was made with 16S rDNA sequences and the Kimura two-parameter model was used. Numbers represent bootstrap support generated from 1000 replications. Only bootstraps > 50 % are presented. All positions containing alignment gaps and missing data were eliminated only in pairwise sequence comparisons. * Horak *et al. (*104) consider these species to belong to *Carios* ** Camicas *et al. (*112) consider these species to belong to the genus *Alectorobius* *** Belong to *Parantricola*

3) males and females show sexual dimorphism unusual for Argasidae, 4) morphology of nymphs and adults is also unusual for the family. The length of larvae feeding period, the number of nymphal stages and the life cycle of *Antricola* are unknown.

We analyzed only one gene sequence for 26 of 185 species of Argasidae with poor representation of several family groups. A broad species analysis is essential

to validate the proposal of Klompen & Oliver (8). This is especially relevant for the genus *Carios* which contains about 40 % of the current Argasidae species and for about 70 % of species with low data support (those species included in *Ornithodoros*, *Carios* and partially in the genus *Argas*) according to Klompen & Oliver (8). Therefore, we provisionally still adhere to the traditional Argasidae classification of Hoogstraal (96) (Table 1) which has weaknesses as has the proposal of Klompen & Oliver (8).

Nevertheless, we acknowledge the contribution of these authors to phylogeny of Argasidae. Incoming information will probably aid to sustain partly or totally their proposal currently with low data support.

## 4.3. Phylogeny of Ixodidae

Hoogstraal & Aeschlimann (7) published the first phylogenetic tree for Ixodidae , based on morphology, life cycles and host associations, where they recognize four subfamilies, Amblyomminae (genera *Amblyomma* and *Aponomma*), Haemaphysalinae (genus *Haemaphysalis*), Hyalomminae (genus *Hyalomma*) and Rhipicephalinae (genera *Anomalohimalaya*, *Boophilus*, *Cosmiomma*, *Dermacentor*, *Margaropus*, *Nosomma*, *Rhipicentor* and *Rhipicephalus*). Filippova (9) presented an alternative classification which was constructed from chaetotaxy of the anal valves, and proposes two subfamilies, Amblyomminae and Ixodinae, with tribe subdivisions. More recent studies used morphological and molecular evidences to understand the phylogeny of hard ticks. They present considerable differences in respect to the proposals of Hoogstraal & Aeschlimann (7) and Filippova (9). A compilation of the proposed hypotheses by different authors plus unpublished information (SN & AJM) on phylogenetic relationships for each subfamily of Ixodidae[1] is presented thereafter.

### 4.3.1. Ixodinae

The monophyly of the genus *Ixodes* is under discussion. Klompen (103) and Klompen *et al. (*18) indicate two lineages, one formed by Australasian *Ixodes* (*I. tasmani*, *I. holocyclus*, *I. uriae* (these taxa conform the *tasmani* group *sensu* Klompen *et al. (*18)**)**, *I. antechini* and *I. ornithorhynchi*) and a second lineage formed for the remainder *Ixodes*. The control regions in the mitochondrial genomes of *Ixodes* species also conform to an Australasian group (with two control regions) constituted by *I. antechini*, *I. cordifer*, *I. cornuatus*, *I. hirsti*, *I. holocyclus*, *I. myrmecobii*, *I. trichosuri* and *I. uriae*, separated from others *Ixodes* ticks with one control region: namely, *I. acutitarsus*, *I. asanumai*, *I. hexagonus*, *I. loricatus*, *I. ovatus*, *I. persulcatus*, *I. pilosus*, *I. ricinus*, *I. scapularis*, *I. simplex* and *I. turdus* (86). Fukunaga *et al. (*105), Xu *et al. (*106), Guglielmone *et al. (*107) and Mitani *et al. (*108) used ITS, 16S rDNA and COI sequences to find  that *I. holocyclus* and *I. uriae* (southern populations) form a basal clade distinctive from the remainder species of *Ixodes*. In contrast, Murrell *et al. (*109) used tRNAs sequences and found support for monophyly of Prostriata. These authors also examined the data used by Klompen *et al. (*18) to carry out a combined analysis to conclude that the results were more robust when gaps were treated as missing than when gaps were treated as a fifth base.

In the same way, the subgeneric status of several *Ixodes* species is uncertain (110, 111, 112). For example, Xu *et al. (*106) found that the subgenus *Ixodes* is not a monophyletic group, and Guglielmone *et al. (*107) reached the conclusion that *I. stilesi* and several species from southern Neotropics do not belong to the subgenus *Ixodes* as designated by Clifford *et al. (*110). Consequently, the re-evaluation of the subgeneric position of *Ixodes* species is necessary. For this aim, it would be convenient to use multiple molecular data and morphological comparisons of immature and adults stages.

### 4.3.2. Amblyomminae and Bothriocrotoninae

Traditionally, the genera *Amblyomma* and *Aponomma* were included in the subfamily Amblyomminae (7) or in the subtribe Amblyommini (9). However, Dobson & Barker (17) with the use of 18S rDNA sequences found that the genus *Aponomma* was paraphyletic, and consequently also the subfamily Amblyomminae. Endemic Australian species of *Aponomma* (*Ap. concolor* and *Ap. undatum*) formed a monophyletic group with 100 % boostrap support and they were the sister group to the rest of Metastriata. Other *Aponomma* species (*Ap. fimbriatum* and *Ap.latum*) were located in a monophyletic clade that contained the *Amblyomma* species. Therefore, the species previously named as *Ap. auruginans*, *Ap. concolor*, *Ap. glebopalma*, *Ap. hydrosauri* and *Ap. undatum* ("the indigenous Australian *Aponomma*" sensu Kaufman (113)) were transferred to the genus *Bothriocroton* and located in the new subfamily Bothriocrotoninae by Klompen *et al. (*114), who based their analysis in molecular, morphological, ecological and cytogenetics evidences. The rest of the previous recognized *Aponomma* ("the primitive" and "the typical" sensu Kaufman (113)) were transferred to the genus *Amblyomma*, and the genus *Aponomma* was invalidated. Recently, Miller *et al. (*115) showed that the phylogenetic position of *A. sphenodonti* ("primitive *Aponomma*" sensu Kaufman (113)) in relation to other *Amblyomma* and *Bothriocroton* species evaluated by using 18S rRNA sequences is peculiar because *A. sphenodonti* does not form a monophyletic clade with neither *Amblyomma* nor *Bothriocroton* species included in the tree. They suggest that *A. sphenodonti* might be placed in a separate genus and indicate that the relationship of *A. sphenodonti* with the other "primitive *Aponomma*" *A. elaphense* is unknown; a situation that deserves additional consideration.

Recent studies about interrelationships among *Amblyomma* species showed differences with subgeneric classification (112, 116), which is particularly weak for *Amblyomma*. For instance, the subgenus *Anastosiella* was created by Santos Dias (116) considering the coxae structure of males. This subgenus includes the Neotropical *A. brasiliense*, *A. maculatum*, *A. tigrinum*, *A. triste*, *A. parvitarsum*, *A. pecarium*, and others five species distributed in the Ethiopian, Nearctic and Australian zoogeographic regions (*A. albolimbatum*, *A. eburneum*, *A. moyi*, *A. paulopunctatum* and *A. rhinocerotis*). Camicas *et al. (*112) modified that scheme and bring together in *Anastosiella A. maculatum*, *A. neumanni*, *A. parvitarsum*, *A. tigrinum*, *A. triste*, ("the *maculatum* group"), *A. aureolatum* and *A. ovale* ("the *ovale* group"). The work of Estrada-Peña *et al. (*117) based on 16S rDNA sequences and morphological characters of immature stages reject partially those classifications because they conclude that the subgenus *Anastosiella* comprises *A. maculatum*, *A. tigrinum* and *A. triste*, being excluded of this group *A. neumanni*, *A. parvitarsum* and the two species of the *ovale* group.

We consider that the erection of the genus *Bothriotocoton* and the corresponding subfamily is soundly validated including historical information and additional research will probably confirm that at least the species known as *A. sphenodonti* represents a new genus. The weakness of the subgeneric classification of *Amblyomma* is obvious and an extensive study is needed to understand the natural groups within this genus.

### 4.3.3. Haemaphysalinae and Hyalomminae

The phylogenetic position of the genus *Haemaphysalis* (Haemaphysalinae) is controversial. Hoogstraal & Aeschlimann (7) positioned Haemaphysalinae with Hyalomminae and Rhipicephalinae based on the shared morphological characters such as spines on the legs and palps, but in the phylogeny constructed with sequences of 16S rDNA (84) the species of Amblyomminae and Haemaphysalinae occur on a common branch. It is clear that the relationship of *Haemaphysalis* with others genera of Ixodidae is still uncertain as shown by Black *et al. (*15), Klompen *et al. (*118) Norris *et al. (*43), Mangold *et al. (*16), Klompen *et al. (*18) and Barker & Murrell (119).

Hoogstraal & Aeschlimann (7) considered Hyalomminae primitive and basal to Rhipicephalinae because Hyalomminae has elongated hypostome and palps (primitive characters according to these authors), but Black & Piesman (84) locate Hyalomminae on a common branch with Rhipicephalinae. Black *et al. (*15), using sequences of 18S nuclear rDNA gene, and Klompen *et al. (*118) using a combination of morphological and developmental characters also found that Hyalomminae is located within Rhipicephalinae. Currently there is consensus that *Hyalomma* species form a monophyletic clade with Rhipicephalinae, and consequently Hyalomminae should be embedded in the subfamily Rhipicepahlinae (16, 17, 18, 19, 114, 120,121, 122).

Indeed, the Hoogstraal´s contribution to understand the Haemaphysalinae ticks is relevant. However, his opinion to merge Hyalomminae with Haemaphysalinae ticks as rather primitive groups within Metastriata appears currently unsound as Hyalomminae appears to be more closely related to Rhipicephalinae than to Haemaphysalinae. There is no ground to consider Hyalomminae as a subfamily of Ixodidae.

### 4.3.4. Rhipicephalinae

Several phylogenetic studies were performed with members of the subfamily Rhipicephalinae. The classifications of Camicas & Morel (6), Hoogstraal & Aeschlimann (7) and Fillipova (9) were significantly modified when molecular information was added to traditional characters for phylogenetic studies.

The paraphyly of the genus *Rhipicephalus* without the inclusion of species belonging to genus *Boophilus* was indicated by Murrell *et al. (*123, 124) and Beati & Keirans (125) who used COI plus 12S rDNA sequences, ITS2 rDNA sequences and 12S rDNA sequences plus morphological characters, respectively, and

Mangold *et al. (*120) found in a phylogeny based on mitochondrial 16S rDNA seuquences that *R. bursa* was more closely related to *R. microplus* and *R. annulatus (*cited as *B. microplus* and *B. annulatus*) than to other *Rhipicephalus* species. Therefore, the genus *Boophilus* was synonymized with the genus *Rhipicephalus*, and the name *Boophilus* was retained as subgenus (126). Moreover, in several works about Rhipicephalinae phylogeny the species of *Rhipicephalus* belonging to *R. pravus* species-group and to subgenus *Digineus* were more closely related to *Boophilus* species than to other *Rhipicephalus* species (19, 123, 125, 126).

Several studies were performed on *Rhipicephalus* species with economic relevance. Figure 2 show an analysis on *R. microplus* using 12S rDNA sequences from specimens of American, African, Asian and Australian populations. The specimens of America (obtained from populations of Argentina, Bolivia, Brazil, Costa Rica, Paraguay and Uruguay) form a clade with African specimens collected in South Africa and Tanzania (99 % bootstrap support) whereas the Australian specimens grouped in other clade (78 % bootstrap support). Surprisingly, the specimen from Nepal was associated with *R. annulatus* from Egypt, although with a relatively low bootstrap support (51 %). The nucleotide divergence between American and African populations was substantially low (0.2%), but the divergence between ticks of these population and the *R. microplus* from Australia and Nepal was 1.3 % and 2.5 %, respectively. In contrast, Barker (127) found that the analysis with ITS2 sequences provide low support for this hypothesis, since the divergence between Australian and South African *R. microplus* (0.8 %) was not bigger than the nucleotide divergence among populations from Australia, Brazil, Kenya and South Africa (mean 1 %). However, Spickett & Malan (128) found that crossings between *R. microplus* from Australia and South Africa were unsuccessful, and recently Labruna *et al. (*129) carried out a study where the crossings between specimens belonging to populations of *R. microplus* from America and Africa were successful, but not the crossings between specimens from Australia and America and between specimens from Australia and Africa. These results were also supported by analyses of microsatellites and mitochondrial 16S rDNA sequences. Probably, *R. microplus* was introduced in America with cattle from Africa, and ticks from America-Africa and specimens from Australia might be different species.

Another species of *Rhipicephalus* distributed around the world with a considerable sanitary importance is *R. sanguineus*. There is strong evidence of the close relationship between *R. sanguineus* and *R. turanicus*. Both species are morphologically similar (130), and numerous phylogenetics studies where molecular markers such as ITS2 rRNA, 16S rDNA, 12S rDNA and tRNA sequences were used (31, 109, 120, 125, 127), showed results of the close relationship between these taxa. In fact, molecular data and cross-breeding experiments where "fertile progeny" (131) and "normal offspring" (132) were obtained indicate conspsecificity for some populations. A tree obtained with 12S rDNA sequences of specimens
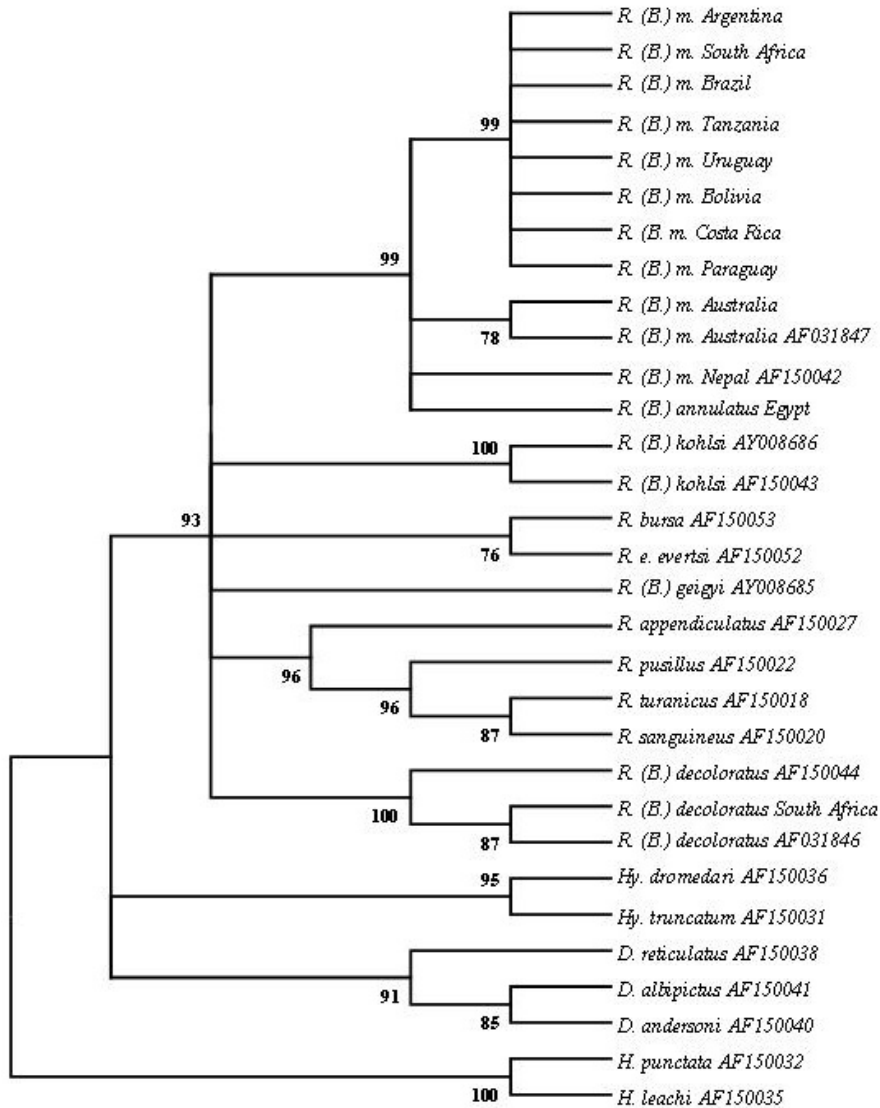
**Figure 2.** Neighbor-joining condensed tree showing the phylogentic relationships among *R. (B.) microplus (R. (B.) m*) ticks from different countries and GenBank accession numbers The tree was made with 12S rDNA sequences and the Kimura two-parameter model was used. Numbers represent bootstrap support generated from 1000 replications. Only bootstraps > 50 % are presented. All positions containing alignment gaps and missing data were eliminated only in pairwise sequence comparisons. Some authors considered these species to belong to the genus *Boophilus*.

identified as *R. sanguineus* and *R. turanicus* from several countries is presented in Figure 3, where three groups can be distinguished: the first group (71 % bootstrap support) contains *R. turanicus* from Italy, Turkey and Israel; the second group (99 % bootstrap support) contains *R. turanicus* from Costa Rica and Zimbabwe and *R. sanguineus* from Paraguay, Peru and Brazil; and the third group (100 % bootstrap support) contains *R. turanicus* from France and *R. sanguineus* from Argentina, Uruguay, France, Israel and Egypt. In view of this, the *R. sanguineus*-like ticks from Argentina, Uruguay, France, Israel and Egypt (plus a specimen determined as *R. turanicus* from France) appear to be the same species, which is almost certainly distinct from the *R. sanguineus*-like ticks from

Brazil, Paraguay and Peru plus ticks determined as *R. turanicus* from Zimbabwe and Costa Rica. Probably, the *Rhipicephalus* from Brazil, Paraguay, Peru and Central America were introduced from Africa, and the *Rhipicephalus* from Argentina and Uruguay were introduced from Europe. In agreement with these results, differences in the morphology, biology and 12S rDNA sequences between two strains of *R. sanguineus* from Argentina and Brazil were notorious, and cross-mating of both tick strains produced non-fertile females (133, 134).

*Rhipicephalus appendiculatus* and *R. zambeziensis* are also closely related, being morphologically very similar (130). However, in contrast with the results found for *R*
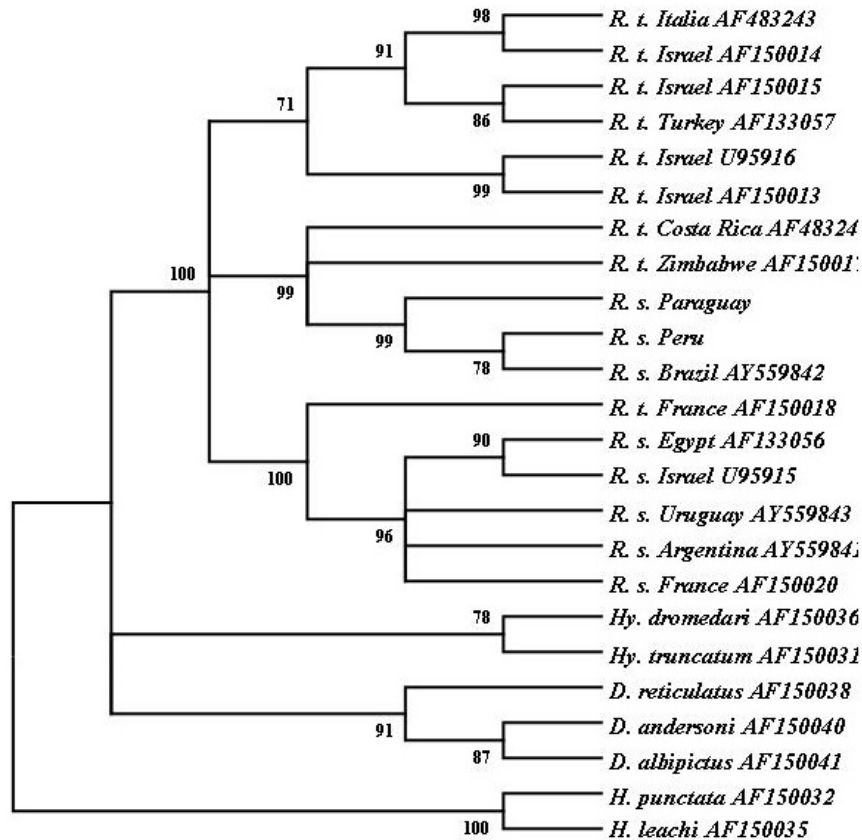
**Figure 3.** Neighbor-joining condensed tree showing the phylogentic relationships among *R. (B.) microplus (R. (B.) m*) ticks from different countries and GenBank accession numbers The tree was made with 12S rDNA sequences and the Kimura two-parameter model was used. Numbers represent bootstrap support generated from 1000 replications. Only bootstraps > 50 % are presented. All positions containing alignment gaps and missing data were eliminated only in pairwise sequence comparisons. Some authors considered these species to belong to the genus *Boophilus*.

*sanguineus-R. turanicus*, data from 12rDNA and ITS2 sequences revealed that both taxa are separate species (38). Wouters *et al. (*135), Barker (127) and Murrell *et al. (*19) using data from enzyme-electrophoresis and DNA sequences reach similar results. The two taxa have important differences in biological aspects such as host usage, life cycle and diapause behaviour (136, 137, 138).

The complexity of the taxonomic status and phylogenetic relationships of the *Rhipicephalus* species mentioned in the previous examples show the necessity of exhaustive and integrated studies for the rest of *Rhipicephalus* species, a genus that contains several taxa with relevance for human and animal health.

In regard to the genus *Dermacentor*, Estrada-Peña & Estrada-Peña (139) and Borges *et al. (*140) compared morphological characters to conclude that the genus *Anocentor* (*Anoc. nitens*) is valid. However, the results presented by Crosbie *et al. (*44) after using 16S rDNA sequences showed that *Anoc. nitens* is closely related to *D. albipictus*, and Murrell *et al. (*19) carrying out a phylogenetic analyses with morphological and molecular evidence, concluded that the genus *Dermacentor* was paraphyletic without the inclusion of

*Anoc. nitens*. In this sense, a 20-bp deletion in ITS2 sequences was discovered in *Anoc. nitens, D. variabilis* and *D. andersoni*, which was interpreted as a synapomorphy for these three species (124). We concur with the opinion that this species is a member of the genus *Dermacentor*.

A summary of the classifications of Ixodidae subfamilies and their genera are included in Table 2 following Hoogstraal & Aeschlimann (7), Filippova (9), Horak *et al* (104) and Barker & Murrell (122). We adhere with the proposal of the last authors.

**5. UPDATE OF TICK NAMES**

The role of ticks as vectors of human diseases is becoming increasingly relevant. Obviously, accurate identification and appropriate naming are essential to avoid confusion. As shown in previous sections of this article, tick classification and tick phylogeny are under discussion. We used the Argasidae classification of Hoogstraal (96) and consider for this update the list of names compiled by Keirans (141). For Ixodidae we use the classification of Barker & Murrell (122) and the list of names contained in Horak *et al. (*104). Therefore Argasidae contains the genera

**Table 2.** Classifications proposed for the family Ixodidae

| Hoogstraal & Aeschlimann (7) | Filippova (9) | Horak *et al.* (104) | Barker & Murrell (122) |
|---|---|---|---|
| Subfamily Ixodinae | Subfamily Ixodinae | Subfamily Ixodinae | Subfamily Ixodinae |
| *Ixodes* | *Ixodes* | *Ixodes* | *Ixodes* |
| Subfamily Amblyomminae | Subfamily Amblyomminae | Subfamily Bothriocrotoninae | Subfamily Bothriocrotoninae |
| *Amblyomma* | Tribe Amblyommini | *Bothriocroton* | *Bothriocroton* |
| *Aponomma* | Subtribe Haemaphysalini | Subfamily Amblyomminae | Subfamily Amblyomminae |
| Subfamily Haemaphysalinae | *Haemaphysalis* | *Amblyomma* | *Amblyomma* |
| *Haemaphysalis* | Subtribe Ambliommini | Subfamily Haemaphysalinae | Subfamily Haemaphysalinae |
| Subfamily Hyalomminae | *Amblyomma* | *Haemaphysalis* | *Haemaphysalis* |
| *Hyalomma* | *Aponomma* | Subfamily Hyalomminae | Subfamily Rhipicephalinae |
| Subfamily Rhipicephalinae | Subtribe Anomalohimalaini | *Hyalomma* | *Anomalohimalaya* |
| *Anomalohimalaya* | *Anomalohimalaya* | Subfamily Rhipicephalinae | *Cosmiomma* |
| *Boophilus* | Subtribe Dermacentorini | *Anomalohimalaya* | *Dermacentor* |
| *Cosmiomma* | *Dermacentor* | *Cosmiomma* | *Hyalomma* |
| *Dermacentor* | *Rhipicentor* | *Dermacentor* | *Margaropus* |
| *Margaropus* | Tribe Rhipicephalini | *Margaropus* | *Nosomma* |
| *Nosomma* | Subtribe Margaropini | *Nosomma* | *Rhipicentor* |
| *Rhipicentor* | *Margaropus* | *Rhipicentor* | *Rhipicephalus* |
| *Rhipicephalus* | *Boophilus* | *Rhipicephalus* | |
| | Subtribe Rhipicephalini | | |
| | *Rhipicephalus* | | |
| | *Hyalomma* | | |
| | *Nosomma* | | |
| | *Cosmiomma* | | |

Antricola, Argas, Nothoaspis, Ornithodoros and Otobius, while Ixodidae is formed by the genera Amblyomma, Anomalohimalaya, Bothriocroton, Cosmiomma, Dermacentor, Haemaphysalis, Hyalomma, Ixodes, Margaropus, Nosomma, Rhipicentor, Rhipicephalus but we also include the fossil genus Cornupalpatum. There is no universal agreement for these classifications. Nevertheless, here we focus on tick names of valid species, a concept generally undisputed contrary to higher hierarchy arrangements. In brief, some authors use the terms Bot. hydrosauri (Denny, 1843) while others use Ap. hydrosauri (Denny, 1843) for the same taxon. Although for the reasons cited above we use the name Bot. hydrosauri our objective is to remark that the name corresponds to a valid species. Contrary to others sections in this article, here we include the authorities and year of description when species are first mentioned to further clarify the status of the taxon.

**5.1. Lists of names for ticks of the world**

Keirans (141), Camicas *et al.* (112) and Horak *et al.* (104) published lists of ticks of the world. The work of Camicas *et al.* (112) is remarkable for the extensive work on tick synonyms (up to 1995) enhancing the contribution of French workers to comprehensive tick studies. The list of Horak *et al.* (104) is the result of consensus between views of recognized scientists involved in the constructions of the previous lists as stated in its preamble. Still, disagreement exists among the authors regarding the classification of Argasidae, especially with the genus *Carios*, which is in line with our concern stated above. The inclusion or exclusion of names as *D. nigreolineatus* (Packard, 1869), excluded from the list of Horak *et al.* (104) but included in Camicas *et al.* (112), or *D. abaensis* Teng, 1963, excluded in Keirans (141) and included in Camicas *et al.* (112), is a consequence of this consensus. Nevertheless, some disagreements continue since names as *Ar. fischeri* Audoin, 1826, a non-valid name in Horak *et al.* (104) is still used by authors that participated in the construction of the list (142).

Later, Barker & Murrell (122) published a compilation of allegedly valid tick species by listing not repeated names in Keirans (141), Camicas *et al.* (112), Keirans & Robbins (143) and Horak *et al.* (104) (not all indeed, i.e., *Ar. delicatus* Neumann, 1910, *A. concolor* Neumann, 1899, *I. robertsi* Camicas, Hervy, Adam & Morel, 1998, are exclusively mentioned in Camicas *et al.* (112), but not in this list) plus the species of *Rhipicephalus* contained in Walker *et al.* (130). This compilation of alleged valid tick names had a result contrary to the objective of the authors because, as the literature up to 2003 indicates, the list contains errors, especially duplication of names by the inclusion of valid names and some of their synonyms that generate confusion to an already confounding issue.

The users of the list of Barker & Murrell (122) have to be aware of the wrong inclusion of the following names: 1) *O. boliviensis* Kohls & Clifford, 1964 is *nomen nuda* (144); 2) *A. testudinis* (Conil 1877) is a synonym of *A. argentinae* Neumann, 1905 (145); 3) *A. arianae* Keirans & Garris, 1986 is a synonym of *A. quadricavum* (Schulze, 1941) (146); 4) *A. striatum* Koch, 1844 is a synonym of *A. aureolatum* (Pallas, 1772) (147); 5) *A. bibroni* (Gervais, 1842) is considered to prevail over *A. dissimile* Koch, 1844 according to Camicas *et al.* (112) while others do not adhere to this opinion for considering *A. dissimile* the valid name (104, 148) and one of these names does not warrant inclusion in the list; 6) *A. colasbelcouri* (Santos Dias, 1958) is a synonym of *H. colasbelcouri* (Santos Dias, 1958); 7) *A. cooperi* Nuttall & Warburton, 1908 is a synonym of *A. dubitatum* Neumann, 1899 (149); 8) *A. decorosum* (Koch, 1867) is a synonym of *Bot. undatum* (Fabricius, 1775) (114); 9) *A. geayi* Neumann, 1899 and *A. perpunctatum* (Packard, 1869) are both in the list. Some authors consider that the last name prevails over *A. geayi* (112, 150) but others do not (104, 148) and one name is incorrectly included; 10) *H. himalaya* Hoogstraal, 1966 is a synonym of *H. sundrai* Sharif, 1928 (112, 151); 11) *I. anatis* Chilton,

1904 is considered a probable synonym of *I. apteridis* Maskell, 1897 by Camicas *et al. (*112), while Horak *et al. (*104) considered *I. anatis* valid but not *I. apteridis*, both names are listed; 12) *I. uruguayensis* Kohls & Clifford, 1967 is a synonym of *I. longiscutatus* Boero, 1944 (152). The following names are misspelled: 1) *A. curruca* Schulze, 1936 is spelled *A. curraca* (n. syn.); 2) *A. trinitatis* Turk, 1948 is spelled *A. trinitatus* (n. syn.); 3) *I. paranaensis* Barros-Battesti, Arzua, Pichorim & Keirans, 2003 is spelled *I. paranensis* (n. syn.). Note: *A. curruca* and *A. trinitatis* are not considered valid in Horak *et al. (*104). The authorities of the following species have errors: 1) The authority of *A. torrei* Pérez Vigueras, 1934 is named as Pérez Viqueras; 2) the authority of *D. steini* (Schulze, 1933) is written Schulze, 1933; 3) the authority of *H. flava* Neumann, 1897 is named Newmann, 1987; 4) The authorities of *I. dicei* Keirans & Ajohda, 2003 are named as Keirans & Ajohola; 5) the authority of *I. zealandicus* Dumbleton, 1953 is named (Dumbleton, 1953); 6) the authorities of *R. masseyi* Nuttall & Warburton, 1908 are named as Nuttell & Warburton; 7) the authority of *R. pumilio* Schulze, 1935 is named Schluze; 8) the authority of *R. zumpti* Santos Dias, 1950 is named Santos Diaz. Note: *I. zealandicus* is not a valid species in Horak *et al. (*104).

**5.1.1. Update of names for Argasidae**

We consider that there are currently 186 species of Argasidae as follows:

**5.1.1.1. *Antricola***

17 species. The following species are added to the original list of 10 species in Keirans (141) following Guglielmone *et al. (*148) and Estrada-Peña *et al. (*153): 1) *An. armasi* de la Cruz & Estrada-Peña, 1995; 2) *An. centralis* de la Cruz & Estrada-Peña, 1995; 3) *An. delacruzi* Estrada-Peña, Barros-Battesti & Venzal, 2004; 4) *An. guglielmonei* Estrada-Peña, Barros-Battesti & Venzal, 2004; 5) *An. hummelencki* de la Cruz & Estrada-Peña, 1995; 6) *An. inexpectata* Estrada-Peña, Barros-Battesti & Venzal, 2004; 7) *An. siboneyi* de la Cruz & Estrada-Peña, 1995. All the species described by de la Cruz & Estrada-Peña (154) are included in Horak *et al. (*104) in the genus *Carios*.

**5.1.1.2. *Argas***

60 species. The following species are added to the original list of 58 species following Schwan *et al. (*155) and Estrada-Peña *et al. (*156): 1) *Ar. keiransi* Estrada-Peña, Venzal & González-Acuña, 2003; 2) *Ar. monolakiensis* Schwan, Corwin & Brown, 1992

**5.1.1.3. *Ornithodoros***

106 species following the additions of 11 species and deletions of two taxa for the total of 97 species (subspecies ignored) in the original list: Additions: 1) *O. antiquus* Poinar, 1995 (fossil); 2) *O. camicasi* Sylla, Cornet & Marchand, 1997 (n. syn.), originally named as *Al. camicasi*; 3) *O. cheikhi* Vermeil, Marjolet & Vermeil, 1997; 4) *O. jerseyi* (Klompen & Grimaldi, 2001) (n. syn.), a fossil species originally included in *Carios* but we located it in *Ornithodoros* because it shares morphological features with *O. rudis* Karsch, 1880 and *O. capensis* Neumann,

1901 (71), species included in *Ornithodoros* by Keirans (141); 5) *O. hadiae* (Klompen, Keirans & Durden, 1995) (n. syn.), a species originally included in the genus *Carios* but we included into *Ornithodoros* as the taxa is close to *Reticulinasus* (157), a subgenera which contains species belonging to *Ornithodoros* in Keirans (141); 6) *O. jul* Schulze, 1940, a species considered valid by Camicas *et al. (*112) (named as *Al. jul*), Horak *et al. (*104) (named as *C. jul*) and Guglielmone *et al. (*148); 7) *O. kohlsi* Guglielmone & Keirans, 2002; 8) *O. multisetosus* (Klompen, Keirans & Durden, 1995) (n. syn.) (same comments as in *O. hadiae*); 9) *O. natalinus* Černý & Dusbabek 1967, a species considered valid by Camicas *et al. (*112) (named as *Al. natalinus*), Horak *et al. (*104) (named *C. natalinus*) and Guglielmone *et al. (*148); 10) *O. papuensis* (Klompen, Keirans & Durden, 1995) (n. syn.) (same comments as in *O. hadiae*); 11) *O. setosus* Kohls, Clifford & Jones, 1969, a species considered valid by Camicas *et al. (*112) (named as *Al. setosus*), Horak *et al. (*104) (as *C. setosus*) and Guglielmone *et al. (*148). Deletions: 1) *O. boliviensis* Kohls & Clifford, 1964 was preoccupied by *O. boliviensis* Bacherer Gutiérrez, 1931 which represents a synonym of *Ot. megnini*, and the species was renamed as *O. kohlsi* Guglielmone & Keirans, 2002. *See O. boliviensis* in the amendments of Barker & Murrell (122); 2) *O. steini* (Schulze, 1935), a synonym of *O. batuensis* Hirst, 1929 as discussed by Klompen *et al. (*157) that include this taxon in *Carios*.

**5.1.1.4. *Nothoaspis and Otobius***

No change to the original list of one and two species, respectively.

**5.1.2. Update of names for Ixodidae**

The update is based on Horak *et al. (*104) plus the inclusion of the genus *Cornupalpatum* for a total of 692 species.

**5.1.2.1. *Amblyomma***

A total of 129 species considering the list of 126 species in Horak *et al. (*104) (subspecies ignored) with the addition of four species and deletion of one. Additions: 1) *A. fuscum* Neumann, 1907 is valid in Guglielmone *et al. (*148) and further validated by Barros-Battesti *et al. (*158); 2) *A. latepunctatum* Tonelli-Rondelli, 1939 was considered to be a synonym of *A. scalpturatum* Neumann, 1906 but finely resurrected by Labruna *et al. (*159); 3) *A. parkeri* Fonseca & Aragão, 1952 is considered a valid species by Guglielmone *et al. (*148) and further validated by Labruna *et al. (*160); 4) *A. romitii* Tonelli-Rondelli, 1939 was considered synonym of *A. extraoculatum* Neumann, 1899 but resurrected by Barros-Battesti *et al. (*161). Deletions: 1) *A. oudemansi* (Neumann, 1910) (formerly *Aponomma)* is a valid species in Horak *et al. (*104) but a synonym of *Bot. concolor* (Neumann, 1899) (formerly *Aponomma*) in Camicas *et al. (*112). Therefore, the correct name for the species is *Bot. oudemansi* (Neumann, 1910) as stated in Beati *et al* (162).

**5.1.2.2. *Bothriocroton***

A total of seven species considering two additions to the original list of five species. 1) *Bot.*

*oudemansi* (Neumann, 1910) see species deletion in *Amblyomma*; 2) *Bot. tachyglossi* (Roberts, 1953) (n. syn.) formerly considered a synonym of *Bot. hydrosauri* was resurrected by Andrews *et al. (*163) who redescribed all stages but included the species under the genus *Aponomma*.

### 5.1.2.3. *Cornupalpatum*

Fossil genus not included in Horak *et al. (*104) formed by *Cor. burmanicum* Poinar & Brown, 2003.

### 5.1.2.4. *Haemaphysalis*

164 species considering one addition and one deletion to the original list of 164 species (subspecies ignored). This list will be augmented in the near future by the description of new species from the *H. leachi* (Audouin, 1826) group (Apanaskevich, personal communication). Addition: 1) *H. cinnabarina* Koch, 1844, was revalidated by Hoogstraal (164) but Keirans & Restifo (165) considered it a synonym of *H. punctata* Canestrini & Fanzago, 1878. Recently, Barros-Battesti (personal communication) revised again the types of *H. cinnabarina* to coincide with the opinion of Hoogstraal (164). Deletion: 1) *H. vietnamensis* Hoogstraal & Wilson, 1966, is a valid species in Horak *et al. (*104) but is considered a synonym of *H. colasbelcouri* (Santos Dias, 1958) by Camicas *et al. (*112). J. Keirans (personal communication to I. Horak) considers that the opinion of Camicas *et al. (*112) is the correct one.

### 5.1.2.5. *Hyalomma*

25 species considering two additions and one deletion to the original list of 24 species (subspecies ignored). One name is changed. This genus is under revision and the list will be modified soon (Apanaskevich, D. personal communication). Additions: 1) *Hy. glabrum* Delpy, 1949, was soundly revalidated by Apanaskevich & Horak (166). See also *Hy. turanicum* Pomerantsev, 1946, below; 2) *Hy. excavatum* Koch, 1844, a name considered a subspecies of *Hy. anatolicum* Koch, 1844, was redescribed and given species status by Apanaskevich & Horak (167). Deletion: 1) *Hy. turanicum* Pomerantsev, 1946 is included in Horak *et al. (*104). This name is generally included as a subspecies of *Hy. marginatum* Koch, 1844, which has a distribution that encompasses Asia and southern Africa, where it was allegedly introduced with Persian sheep. However, Apanaskevich & Horak (166) demonstrated that the African populations corresponded to the resurrected species *Hy. glabrum* Delpy, 1949. Change of name: *Hy. scupense* Schulze, 1918 was considered a subspecies of *Hy. detritum* Schulze, 1919 but the former name has priority (168).

### 5.1.2.6. *Ixodes*

242 species considering the addition of two species to the original list of 241 species and one deletion. Additions: 1) *I. dicei* Keirans & Ajohda, 2003; 2) *I. paranaensis* Barros-Battesti, Arzua, Pichorim & Keirans, 2003. Deletion: *I. zumpti* Arthur 1960 is considered valid in Horak *et al. (*104) but not in Camicas *et al. (*112). Wilson (169) soundly demonstrates that it is a synonym of *I. kerguelensis* André & Colas-Belcour, 1942. Note: *I. serrafreirei* Amorim, Gazeta, Bossi & Linhares, 2003 is *nomen nuda* because of inadequate description.

### 5.1.2.7. *Rhipicephalus*

81 species considering two additions to the original list. 1) *R. aurantiacus* Neumann, 1907 is considered a synonym of *R. ziemanni* Neumann, 1904 by Walker *et al. (*130) but in the discussion of the latter species the situation is not so clear since the types were not compared and the authors stated that further studies are needed. We provisionally consider this taxon as valid; 2) *R. cliffordi* Morel, 1965 is considered a synonym of *R. pseudolongus* Santos Dias, 1953 by Walker *et al. (*130). Nevertheless, in the discussion of the latter species the situation is not so clear since the types of these and related species were not compared. We provisionally consider *R. cliffordi* as a valid name until the situation is clarified.

### 5.1.2.8. *Anomalohimalaya*, *Cosmiomma*, *Dermacentor*, *Margaropus*, *Nosomma* and *Rhipicentor*

No changes to the original list of one, three, 33, three, one and two species, respectively.

## 6. SUMMARY AND PERSPECTIVES

Molecular markers introduced new tools to study tick phylogenetics but also represent a valuable aid for tick identification. Indeed conventional techniques will be continuously applied in tick studies but molecular methods will be increasingly relevant to address many of still unsolved problems presented through this article.

The origin of ticks is most probably pre-middle Cretaceous, because fossil records of soft and hard ticks were made in deposits of the middle cretaceous, and some aspects of tick origin will be bound to find new fossil specimens from pre-middle Cretaceous periods to improve our meager knowledge on this matter. Indeed, many speculations can be made on tick origin but without robust evidence will be difficult to support any theory. There is no convincing information as to tick origins.

The two principal schemes of classification for Argasidae used in the last years were those of Clifford *et al. (*4) and Hoogstraal (96), with two subfamilies and five genera (Argasinae: *Argas*; Ornithodorinae: *Ornithodoros*, *Antricola*, *Otobius* and *Nothoaspis*) and Klompen & Oliver (8), with the same subfamilies but with four genera (Argasinae: *Argas*; Ornithodorinae: *Ornithodoros*, *Otobius* and *Carios*). New information on argasid ticks will be available in the next few years to solve its phylogenetics status that surely will be useful to modify traditional classifications as that of Hoogstraal (96) and to know the validity of proposal as that of Klompen & Oliver (8). Molecular phylogenetic analysis indicate that the genus *Ornithodoros* as presented by Clifford *et al. (*4) and Hoogstrall (96) has low support, but the genus *Carios* proposed by Klompen & Oliver (8) seems not to be justified *in toto* because probably the invalidation of the genus *Antricola* is unjustified. The molecular phylogenetic analysis was made with only one gene sequence for 26 of 185 species of Argasidae. Consequently, considering that the genus *Carios* contains about 40 % of the current Argasidae species, a broad analysis including

representative species of each subgenus is essential to validate or to reject the proposal of Klompen & Oliver (8).

Regarding to the phylogeny of the family Ixodidae, in both *Ixodes* and *Amblyomma* the results of the studies that incorporated molecular data in the phylogenetics analyses showed important differences with the previous subgeneric classifications based exclusively in morphological characters. For that reason, the subgeneric classification of these two genera should be re-evaluated. Also, the monophyly of the genus *Ixodes* is controversial. Some estudies (18, 103) found two phylogenetic lineages, one formed by Australasian *Ixodes* (*I. tasmani*, *I. holocyclus*, *I. uriae*, *I. antechini* and *I. ornithorhynchi*) and a second lineage formed for the remainder *Ixodes*.

The genus *Aponomma* was invalidated. The "indigenous Australian *Aponomma*" sensu Kaufman (113) were transferred to the genus *Bothriocroton* and located in the new subfamily Bothriocrotoninae (114), and "the primitive *Aponomma*" and "the typical *Aponomma*" sensu Kaufman (113) were transferred to the genus *Amblyomma*. However, the phylogenetic analysis carried out by Miller *et al. (*115) showed that *A. sphenodonti* ("primitive *Aponomma*" sensu Kaufman (113)) does not form a monophyletic clade with neither *Amblyomma* nor *Bothriocroton* species included in the tree. Therefore, morphological and molecular comparison between the Australasian (Gondwana origin) *A. sphenodonti* and the Nearctic (Laurasia origin) *A. elaphense (*morphological related species) will be relevant to understand the phylogeny of Metastriata.

Evidence indicates that Rhipicephalinae contains all the species of *Hyalomma*, consequently Hyalomminae is not a valid sub-family. *Anocentor* is in fact a member of *Dermacentor* and the former genus *Boophilus* represents a sub-genus of *Rhipicephalus*. There is no universal agreement for these views, especially with the inclusion of *Boophilus* within *Rhipicephalus*. However, analysis of morphological characters, biology and information from four molecular markers are important evidences to sustain this change. Evidence obtained from biological, morphological and molecular data suggest that the wordlwide distributed tick *R. sanguineus* could be a species group. In fact, the *R. sanguineus*-like ticks from Argentina, Uruguay, France, Israel and Egypt appear to be the same species, being distinguished of those *R. sanguineus*-like ticks from Brazil, Paraguay and Peru. Probably, the *Rhipicephalus* from Brazil, Paraguay, Peru and Central America were introduced in America from Africa, and the *Rhipicephalus* from Argentina and Uruguay were introduced in America from Europe. It is necessary to include in future phylogenetics studies several species of Rhipicephalinae to settle this and related topics.

Currently there are 186 species of Argasidae and 692 species of Ixodidae, but new or resurrected species will be continuously described. We hope that each article includes DNA sequences to aid species comparison but also valuable information to be complemented with ecological and morphological aspects to understand relationships among tick groups.

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**Footnote:** [1]The subfamily classification is according to Horak *et al.* (104).

**Abbreviations:** *A: Amblyomma; Al: Alectorobius; An: Antricola; Ar: Argas; Ap: Aponomma; Anoc: Anocentor; B: Boophilus; Bot: Bothriocroton; C: Carios; Cor: Cornupalpatum; D: Dermacentor; H: Haemaphysalis; Hy: Hyalomma; I: Ixodes; N: Nothoaspis; O: Ornithodoros;Ot: Otobius; R: Rhipicephalus*

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