

Systematics and evolution of ticks with a list of valid genus and species names

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SUMMARY

In recent years there has been much progress in our understanding of the phylogeny and evolution of ticks, in particular the hard ticks (Ixodidae). Indeed, a consensus about the phylogeny of the hard ticks has emerged which is quite different to the working hypothesis of 10 years ago. So that the classification reflects our knowledge of ticks, several changes to the nomenclature of ticks are imminent or have been made. One subfamily, the Hyalomminae, should be sunk, while another, the Bothriocrotoninae, has been created (Klompen, Dobson & Barker, 2002). Bothriocrotoninae, and its sole genus *Bothriocroton*, have been created to house an early-diverging ('basal') lineage of endemic Australian ticks that used to be in the genus *Aponomma*. The remaining species of the genus *Aponomma* have been moved to the genus *Amblyomma*. Thus, the name *Aponomma* is no longer a valid genus name. The genus *Rhipicephalus* is paraphyletic with respect to the genus *Boophilus*. Thus, the genus *Boophilus* has become a subgenus of the genus *Rhipicephalus* (Murrell & Barker, 2003). Knowledge of the phylogenetic relationships of ticks has also provided new insights into the evolution of ornateness and of their life cycles, and has allowed the historical zoogeography of ticks to be studied. Finally, we present a list of the 899 valid genus and species names of ticks as of February 2004.

Key words: Ixodida, ticks, phylogeny, evolution, nomenclature.

INTRODUCTION

Hoogstraal & Aeschlimann (1982) were apparently the first people to publish a phylogenetic tree for the ticks (suborder Ixodida); however, hypotheses about the evolutionary relationships of ticks had been proposed well before this (e.g. Pomerantsev, 1948; Camicas & Morel, 1977). The Hoogstraal and Aeschlimann phylogeny was inferred from intuition about the relative 'primitiveness' of the morphology and life cycles of ticks, and their hosts. An alternative phylogeny was proposed by Filippova (1993, 1994), but the trees of Hoogstraal & Aeschlimann (1982) and Filippova (1993, 1994) were not tested until the mid 1990s. The phylogeny of ticks was first studied with molecular characters in the 1990s; there have been 30 papers on the molecular phylogeny and evolution of ticks and, although they have not always agreed, a consensus on phylogenetic relationships of ticks has emerged: Wesson & Collins (1992); Wesson *et al.* (1993); Black & Piesman (1994); Caporale *et al.* (1995); McLain *et al.* (1995a, b); Rich *et al.* (1995); Crampton, McKay & Barker (1996); Klompen *et al.* (1996); Norris *et al.* (1996, 1997); Black, Klompen & Keirans (1997); Zahler *et al.* (1997); Barker (1998); Black & Roehrdanz (1998); Crosbie, Boyce & Rodwell (1998); Mangold, Bargues & Mas-Coma (1998a, b);

Dobson & Barker (1999); Murrell, Campbell & Barker (1999); Norris, Klompen & Black (1999); Fukunaga *et al.* (2000); Klompen *et al.* (2000); Murrell, Campbell & Barker (2000, 2001a, b, 2003); Beati & Keirans (2001); Ushijima *et al.* (2003); Xu *et al.* (2003). Cuticular hydrocarbon composition has also been used to infer phylogenies of populations of ticks (Estrada-Peña, Castellá & Morel, 1994; Estrada-Peña, Castellá & Moreno, 1994; Estrada-Peña *et al.* 1997), and Hutcheson *et al.* (2000) reviewed progress in tick molecular systematics. At least eight papers have been published on the phylogeny and evolution of ticks inferred from morphology and other phenotypes: Klompen (1992); Klompen & Oliver (1993); Hutcheson *et al.* (1995); Klompen *et al.* (1997, 2000); Borges *et al.* (1998); Klompen (1999); Beati & Keirans (2001); Murrell *et al.* (2001b).

Part I of this review draws together recent advances in our understanding of the phylogeny of ticks and shows how robust phylogenetic trees can help us to interpret the evolution of ticks and make informed changes to their taxonomy and nomenclature. Phylogenies of tick groups inferred from different sets of characters have not always been congruent; however, consensus has emerged about many tick relationships. Part II of the review deals with the taxonomy and nomenclature of ticks. Table 1 is a list of the valid genus and species names as at February 2004.

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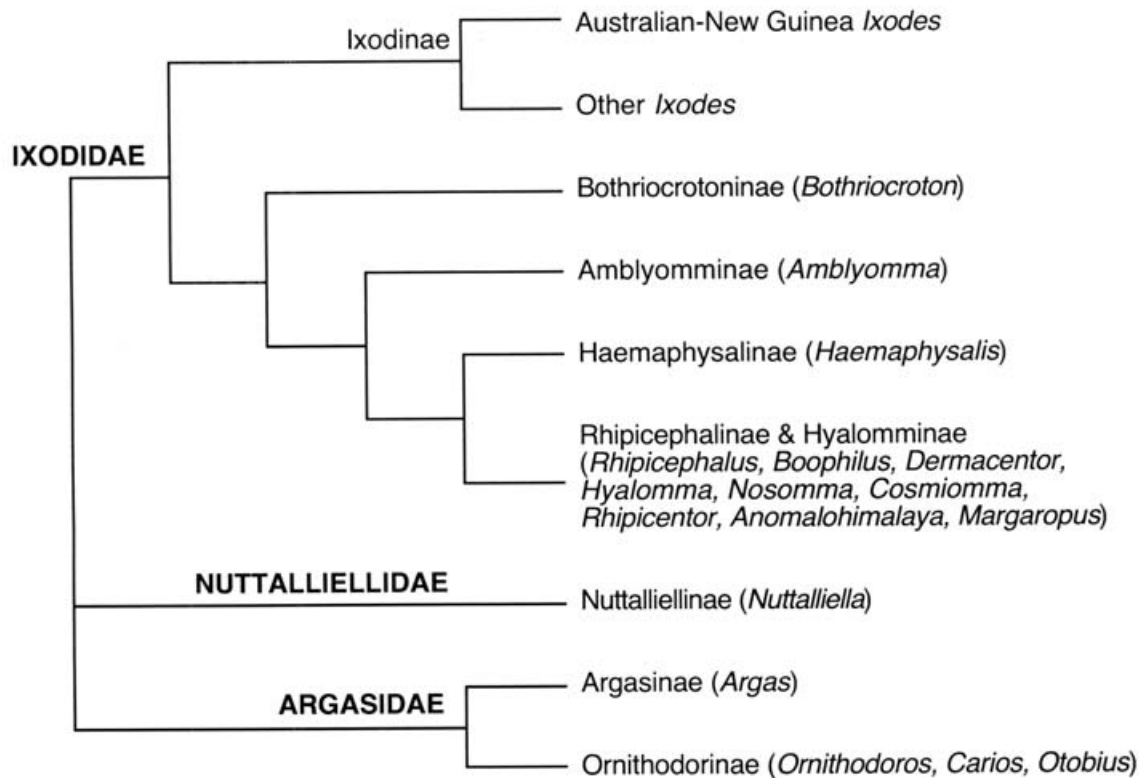


Fig. 1. Working hypothesis of the phylogeny of the subfamilies of ticks (Suborder Ixodida). This hypothesis was proposed from analyses of nucleotide sequences and phenotypes by Black & Piesman (1994); Crampton *et al.* (1996); Black *et al.* (1997); Dobson & Barker (1999); Klompen *et al.* (2000) and Murrell *et al.* (2001 *b*). [Note added in press: 'Australian-New Guinea *Ixodes*' should read 'Australasian *Ixodes*'.] The genus *Boophilus* is now a subgenus of the genus *Rhipicephalus*.

PHYLOGENETICS OF TICKS – RECENT ADVANCES

The sister-group of the ticks

Discovery of the sister-group, the nearest relatives, of the ticks will reveal much about the evolution of the ticks; then we will be able to root our phylogenetic trees with confidence. There are two main competing hypotheses: (1) that the sister-group of the Ixodida is the Order Holothyrida (Lehtinen, 1991) ((Ixodida, Holothyrida), Mesostigmata) Opilioacariformes); and (2) that the sister-group of the Ixodida is the Order Mesostigmata (Krantz, 1978) ((Ixodida, Mesostigmata), Holothyrida), Opilioacariformes). The presence of Haller's organ, the ability to retract the gnathosoma, and a similar type of musculature at the base of the gnathosoma in ticks and holothyrid mites, which are putatively derived characters for the Acari, was the basis of Lehtinen's (1991) hypothesis that the sister-group of the ticks is the Holothyrida. Both of the tests of these hypotheses indicate that the sister-group of the Ixodida is the Holothyrida: Dobson & Barker (1999) (small subunit (SSU) rDNA) and Klompen *et al.* (2000) (total evidence analysis of morphology, SSU rDNA, large subunit (LSU) rDNA, 16S rDNA (mitochondrial)). However, it is still not certain that the sister-group of the ticks is the Holothyrida. More data are needed.

Phylogeny of the Ixodida

Here is our interpretation of the working hypothesis of the phylogeny of the subfamilies of ticks in use by many current tick systematists. This tree is based on information from the papers cited in the introduction to this paper.

We highlight five features of the tree.

The phylogenetic relationships of the three tick families are unresolved. The phylogeny of the three families of ticks, Ixodidae (hard ticks), Argasidae (soft ticks) and Nuttalliellidae, is still unresolved (Fig. 1). This is due to the fact that *Nuttalliella namaqua*, the only species in the Nuttalliellidae, has not been collected for many years. Attempts to amplify DNA from museum specimens by the Black and Barker groups resulted only in the amplification of DNA from fungi that had infected the specimens either before or after their death (unpublished data).

The Rhipicephalinae is paraphyletic. The subfamily Hyalomminae is embedded within the Rhipicephalinae (see below for a more detailed description of phylogenetic relationships in Rhipicephalinae).

Monophyly or paraphyly of Ixodes? There is evidence that the genus *Ixodes* has two main lineages, the

Australasian *Ixodes* and the other *Ixodes* (Klompen, 1999; Klompen *et al.* 2000). Our working hypothesis has the genus *Ixodes* as a monophyletic lineage (Fig. 1). This is the traditional view; however, it is far from certain that this is correct. Indeed, morphological and molecular characters provide only weak evidence for monophyly of the genus *Ixodes* (Dobson & Barker, 1999; Klompen *et al.* 1997, 2000). The Australasian *Ixodes* may even be the sister-group to the rest of the Metastriata, but this idea is based at this stage on analysis of rDNA alone (Dobson & Barker, 1999; Klompen *et al.* 2000). The evolutionary relationships of most *Ixodes* species have not been studied so it is not known exactly how many species of the extant *Ixodes* belong to the Australasian *Ixodes* lineage. Analyses of morphology and nucleotides indicated that *I. tasmani*, *I. holocyclus* and *I. uriae* (=the *I. tasmani* group sensu Klompen *et al.* 2000) and *I. antechini*, *I. ornithorhynchi* belong to this lineage (Klompen *et al.* 2000). The presence of two control regions in their mitochondrial genomes indicates that *I. cordifer*, *I. cornuatus*, *I. hirsti*, *I. myrmecobii* and *I. trichosuri* also belong to this lineage (below and Shao, Aoki, Fukunaga and Barker, unpublished data). Until contrary evidence is found we presume that the remaining *Ixodes* that are endemic to, and/or evolved in Australasia (at least Australia, New Guinea and New Zealand) also belong to this lineage i.e. *I. amersoni*, *I. apteridis*, *I. australiensis*, *I. confusus*, *I. dendrolagi*, *I. eudypitidis*, *I. fecialis*, *I. hydromyidis*, *I. jacksoni*, *I. kohlsi*, *I. laysanensis*, *I. luxuriosus*, *I. prisciollaris*, *I. steini*, *I. vestitus*, *I. victoriensis*, *I. zaglossi* and *I. zealandicus*. Thus, at present the Australasian *Ixodes* lineage has 28 extant species.

A new lineage of Australian ticks. Dobson & Barker (1999) and Klompen, Dobson & Barker (2002) reported a new lineage of ticks that infest reptiles in Australia: the five species of Bothriocrotoninae (Klompen, Dobson & Barker, 2002). This group was first recognized by Kaufman (1972) as one of the three groups of *Aponomma* species, the 'indigenous Australian *Aponomma* species', primarily on the basis of morphology. Analyses of SSU rDNA (Dobson & Barker, 1999) and evidence from morphological characters (Klompen *et al.* 1997) indicate that this lineage is the sister-group to the rest of the Metastriata rather than being one of the three lineages of the genus *Aponomma*. Klompen *et al.* (2000) also had the endemic Australian *Aponomma* species in a separate lineage to the other *Aponomma* and *Amblyomma* species (Amblyomminae) but this lineage was the sister-group to three species of *Haemaphysalis* in their trees, rather than to the rest of the Metastriata.

Phylogeny of the Argasidae. There has been little molecular study of the Argasidae, but Klompen (1992) and Klompen & Oliver (1993) studied the

morphology and systematics of these ticks and confirmed that there were two lineages (=subfamilies Argasinae and Ornithodorinae). The species and genera in these subfamilies were revised by Klompen & Oliver (1993). Black & Piesman (1994) and Crampton *et al.* (1996) found evidence of paraphyly of the Argasidae from 16S rDNA, 18S (SSU) V4 rDNA and 28S (LSU) rDNA (the two studies differed in the type of paraphyly) but subsequent study with complete 18S (SSU) rDNA sequences indicate that the Argasidae is monophyletic (Black *et al.* 1997).

Phylogenetic relationships within the genus Ixodes. Despite the fact that many *Ixodes* species are important parasites and vectors of pathogens to humankind, domestic animals and wildlife, there has been little study of the phylogeny of the group (16–18 subgenera, 249 valid species names). Klompen (1999) inferred the phylogeny of the subgenera of *Ixodes* from morphological characters whereas Fukunaga *et al.* (2000) inferred relationships among a few subgenera of *Ixodes* from internal transcribed spacer 2 (ITS2) rDNA sequences. It is not even certain that the genus is monophyletic (see above). However, robust phylogenies are known for some groups of closely related species of *Ixodes*, particularly some of the ticks that may transmit *Borrelia burgdorferi*: Caporale *et al.* (1995); McLain *et al.* (1995a,b); Rich *et al.* (1995, 1997); Norris *et al.* (1996, 1997). Xu *et al.* (2003) found evidence that the 11 species in the *I. ricinus* complex were not monophyletic unless three other species, *I. muris*, *I. minor* and *I. granulatus*, were added to this complex.

Phylogeny and evolution of rhipicephaline ticks. There has been much recent progress in our understanding of the taxonomy and phylogeny of the Rhipicephalinae, so we review this work in detail. Murrell *et al.* (1999, 2000, 2001a,b) and Beati & Keirans (2001) used molecular and morphological characters to infer the phylogeny of the group. Here is our working hypothesis of the Rhipicephalinae (Fig. 2, after Murrell *et al.* 2001b).

We highlight five features of the tree: (1) *Anocentor nitens* is embedded in the genus *Dermacentor* Koch, 1844; (2) *Hyalomma aegyptium*, the only species in the subgenus *Hyalommasta* Schulze, 1930, is embedded in the lineage of the subgenus *Hy.* (*Hyalomma*) so the subgenus *Hyalommasta* should not be retained. *Hyalomma aegyptium* is the type species of the genus *Hyalomma* so the subgenus *Hyalommasta* is invalid (Robbins *et al.* 1998); (3) Molecular data are not yet available for *Cosmiomma* Schulze, 1919 (1 species ex rhinoceros and antelopes), *Margaropus* Karsch, 1879 (3 species ex horse, other livestock and giraffes) and *Anomalohimalaya* Hoogstraal *et al.* 1970 (3 species ex rodents, shrews and hares from Nepal, Tibet, China, Russia and environs); (4) There is strong molecular

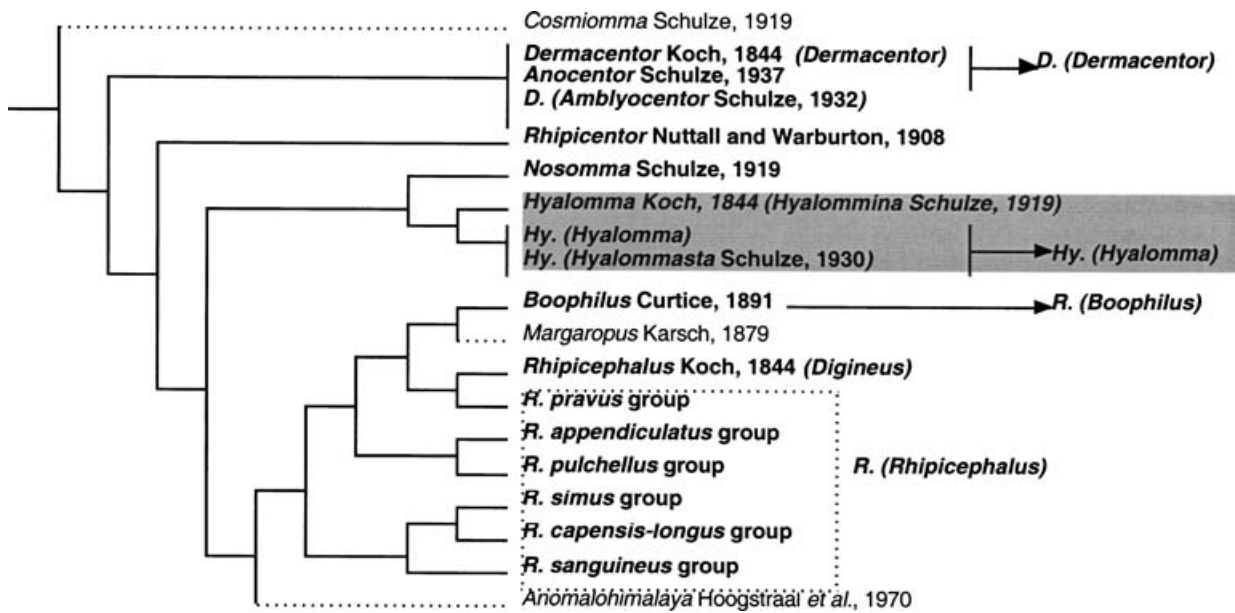


Fig. 2. Working hypothesis of the phylogeny of the Rhipicephalinae sensu lato from Murrell *et al.* (2001b). The taxa in plain text at the ends of broken lines have not been studied with molecular markers; their phylogenetic positions were inferred from the morphological analyses of Klompen *et al.* (1997). Shading indicates the subfamily Hyalomminae sensu stricto, which Murrell *et al.* (2001b) suggested should be synonymised with the Rhipicephalinae. Arrows indicate proposed taxonomic changes to the taxa that are apparently paraphyletic i.e. incomplete or unnatural taxa. Taxa in brackets are subgenera. Six of the species-groups that constitute the subgenus *R.* (*Rhipicephalus*) are in a box (broken line). Reproduced with permission from Murrell *et al.* (2001b).

and morphological evidence that the subgenus *Rhipicephalus* (*Boophilus*) (5 species) is monophyletic (Murrell *et al.* 2001a,b); and (5) There is substantial molecular and morphological evidence that the sister-group to the subgenus *Rhipicephalus* (*Digineus*) (= *R. evertsi* group) plus the *R. prævus* group, is the subgenus *R.* (*Boophilus*) plus perhaps the genus *Margaropus* (Mangold *et al.* 1998b; Murrell *et al.* 2000, 2001b; Beati & Keirans, 2001). This makes the genus *Rhipicephalus* paraphyletic with respect to the subgenus *R.* (*Boophilus*).

Phylogeny inferred from the mitochondrial genomes of ticks

Nucleotide sequences of three of the 37 genes of the mitochondrial genomes of ticks, 12S rRNA, 16S rRNA and cytochrome C oxidase I, have been a mainstay of tick molecular phylogenetics. The rest of the nucleotide sequence of the mitochondrial genome of tick species has been ignored. However, recent work shows that mitochondrial genomes contain much unexploited potential for the inference of the phylogeny and evolution of ticks.

Mitochondrial genomes are circular and have 37 genes in most metazoa: 13 protein-coding genes, 2 ribosomal RNA genes, 22 transfer RNA genes and a non-coding (control) region. The mitochondrial genomes of most metazoa, including the ticks that have been studied so far, are 14–16 kb long. Two types of information from mitochondrial genomes have contributed, and are likely to continue to

contribute, to our understanding of the phylogeny and evolution of ticks: (1) the nucleotide sequences of these genomes, or at least the nucleotide sequences of the 13 protein-coding genes and two rRNA genes, which together constitute 13–13.5 kb; and (2) idiosyncratic markers (sensu Murrell, Campbell & Barker, 2003). Translocations and inversions of genes are the best known idiosyncratic markers. Duplications of genes and parts of genes, and changes to the secondary structures of tRNAs and rRNAs are other types of idiosyncratic markers. Nucleotide substitutions in tRNA motifs that are usually highly conserved are also markers that can be phylogenetically informative (Murrell *et al.* 2003).

What we know about the mitochondrial genomes of ticks. The mitochondrial genomes of eight species of ticks have been sequenced entirely (Genbank Nos. are given in parentheses): (1) *Rhipicephalus sanguineus* and *Ixodes hexagonus* (NC002010 and NC002074; Black & Roehrdanz, 1998); (2) *Haemaphysalis flava*, *Carios capensis* and *Ornithodoros moubata* (AB075954, AB075955 and AB073679; Shao *et al.* in press) and (3) *I. persulcatus*, *I. holocyclus* and *I. uriae* (NC004470, AB075953 and AB087746; Shao, Mitani, Fukunaga & Barker, unpublished). In addition, we know the arrangement of genes in the mitochondrial genome of *R.* (*Boophilus*) *microplus* (Campbell & Barker, 1998, 1999) and part of the arrangement of these genes in the following 51 species of hard and soft ticks: *Amblyomma americanum*, *A. cajennense*, *A. hebraeum*, *A. fimbriatum*, *A. latum*, *A. maculatum*,

A. varanensis, *A. variegatum*, *A. vikirri*, *Argas lagenoplastis*, *A. persicus*, *Rhipicephalus (Boophilus) annulatus*, *R. (Boophilus) decoloratus*, *R. (Boophilus) geigy*, *R. (Boophilus) kohlsi*, *Bothriocroton concolor*, *B. glebopalma*, *B. undatum*, *Dermacentor andersoni*, *D. reticulatus*, *D. variabilis*, *Haemaphysalis humerosa*, *H. inermis*, *H. leporispalustris*, *H. longicornis*, *Hyalomma aegyptium*, *Hy. dromedarii*, *Hy. marginatum*, *Hy. truncatum*, *Ixodes affinis*, *I. auritulus*, *I. cookei*, *I. pilosus*, *I. ricinus*, *I. simplex*, *I. tasmani*, *Nosomma monstrosum*, *Ornithodoros turicata*, *Otobius megnini*, *Rhipicentor muttalli*, *Rhipicephalus appendiculatus*, *R. compositus*, *R. evertsi*, *R. maculatus*, *R. pulchellus*, *R. punctatus*, *R. pravus*, *R. simus*, *R. turanicus*, *R. zambeziensis* and *R. zumpti* (Black & Roehrdanz, 1998; Campbell & Barker, 1998; Murrell *et al.* 2003; Roehrdanz, Degrugillier & Black, 2002).

Translocation and inversion of genes that are synapomorphies for groups of ticks. Black & Roehrdanz (1998) and Campbell & Barker (1998) simultaneously discovered a major rearrangement of mitochondrial genes that was synapomorphic for *R. sanguineus* and *R. (Boophilus) microplus*: a section of the genome that contains the genes ND5, ND4, ND4L, ND6, Cyt b and five tRNAs has 'swapped' positions with a section that contains ND1, 16S, 12S, CR and four tRNA genes. In addition, Black & Roehrdanz (1998), Campbell & Barker (1998, 1999) and Roehrdanz, Degrugillier & Black (2002) showed by PCR that this translocation was in fact synapomorphic for the known Metastriata since 28 species from eight genera, which were from all of the subfamilies of metastriate ticks, had this rearrangement too. The translocation of tRNA Leu (CUN) and the translocation and inversion of tRNA Cys are also synapomorphies for the Metastriata (27 species in eight genera; Black & Roehrdanz, 1998; Campbell & Barker, 1998, 1999; Murrell *et al.* 2003).

Other idiosyncratic markers from the mitochondrial genomes of ticks. Murrell *et al.* (2003) assessed the value of idiosyncratic markers and changes to nucleotide sequences in tRNAs that are usually highly conserved for inference of the phylogeny of hard ticks. Many markers were informative. Moreover, parallel and convergent evolution of these markers was rare. Here are some examples of idiosyncratic markers that are synapomorphic for groups of ticks: (1) a region of tandemly repeated sequence (composed of tRNA Glu and 60 bp of the 3' end of ND1) unites *R. (Boophilus) microplus* and *R. (Boophilus) annulatus* to the exclusion of the other three *R. (Boophilus)* species; (2) a region of 25 bp repeats between the 5' end of ND1 and 16S and is synapomorphic for the Metastriata; and (3) a 15 bp insertion between tRNA Ala and tRNA Arg is synapomorphic for the genus *Hyalomma*.

Intriguingly, some species of hard ticks, but not others, have two control regions. On the one

hand *I. hexagonus* (Black & Roehrdanz, 1998) and *I. acutitarsus*, *I. asanumai*, *I. bricatus*, *I. nipponensis*, *I. ovatus*, *I. pavlovskyi*, *I. persulcatus*, *I. pilosus*, *I. ricinus*, *I. scapularis*, *I. simplex* and *I. turdus* (Shao, Mitani, Fukunaga, & Barker, unpublished) have one control region like the hypothetical ancestor of the arthropods. On the other hand, all 8 of the 28 species examined from the putative Australasian *Ixodes* lineage (*I. antechini*, *I. cordifer*, *I. cornuatus*, *I. hirsti*, *I. holocyclus*, *I. myrmecobii*, *I. trichosuri* and *I. uriae*; Shao, Fukunaga, Murrell & Barker, unpublished) and all known metastriate ticks (Black & Roehrdanz 1998; Campbell & Barker 1998, 1999; Murrell *et al.* 2003) have two control regions. Two control regions might be a synapomorphy for the Australasian *Ixodes* plus the Metastriata. However, it is equally parsimonious that the presence of two control regions is plesiomorphic for the Australasian *Ixodes* plus the Metastriata.

Whole mitochondrial genome sequences. Whole genome sequences, or at least the nucleotide or amino acid sequences of the 13 protein-coding genes (*ca.* 12 kbp), have been used to infer the phylogeny of a range of vertebrates (e.g. Broughton, Milam & Roe, 2001; Haring *et al.* 2001; Inoue *et al.* 2001; Maca-Meyer *et al.* 2001; Miya, Kawaguchi & Nishida, 2001; Schmitz, Ohme & Zischler, 2002) and invertebrates (e.g. Black & Roehrdanz, 1998; Wilson *et al.* 2000; Hwang *et al.* 2001). Entire nucleotide sequences are available for eight species of ticks (above). Sequencing of mitochondrial genomes of a further three species of ticks and the alternative sister-groups of the ticks is underway. Once the nucleotide sequences of mitochondrial genomes from each of the major lineages of ticks are obtained the first whole mitochondrial-genome phylogeny of the ticks will be attempted.

Using phylogeny to understand how ticks have evolved

Accurate phylogenies allow us to study the evolution of phenotypes (e.g. morphological and life history traits) and to infer historical zoogeography e.g. where the first tick might have evolved. When traits are mapped onto a phylogeny we may discover, for example, how many times and in which environments a particular trait evolved. Below, we show how accurate phylogenies have contributed to our understanding of ornateness, life cycles, the archetypal host of ticks, where particular groups of ticks, and indeed the first tick, evolved, and the evolution of haematophagy in ticks.

Evolution of ornateness in rhipicephaline ticks. A number of ticks in the subfamily Rhipicephalinae have ornate (patterned) scuta. By mapping ornateness onto the phylogeny of Murrell *et al.* (2001b) we can infer how ornateness might have evolved in the Rhipicephalinae sensu lato (Rhipicephalinae

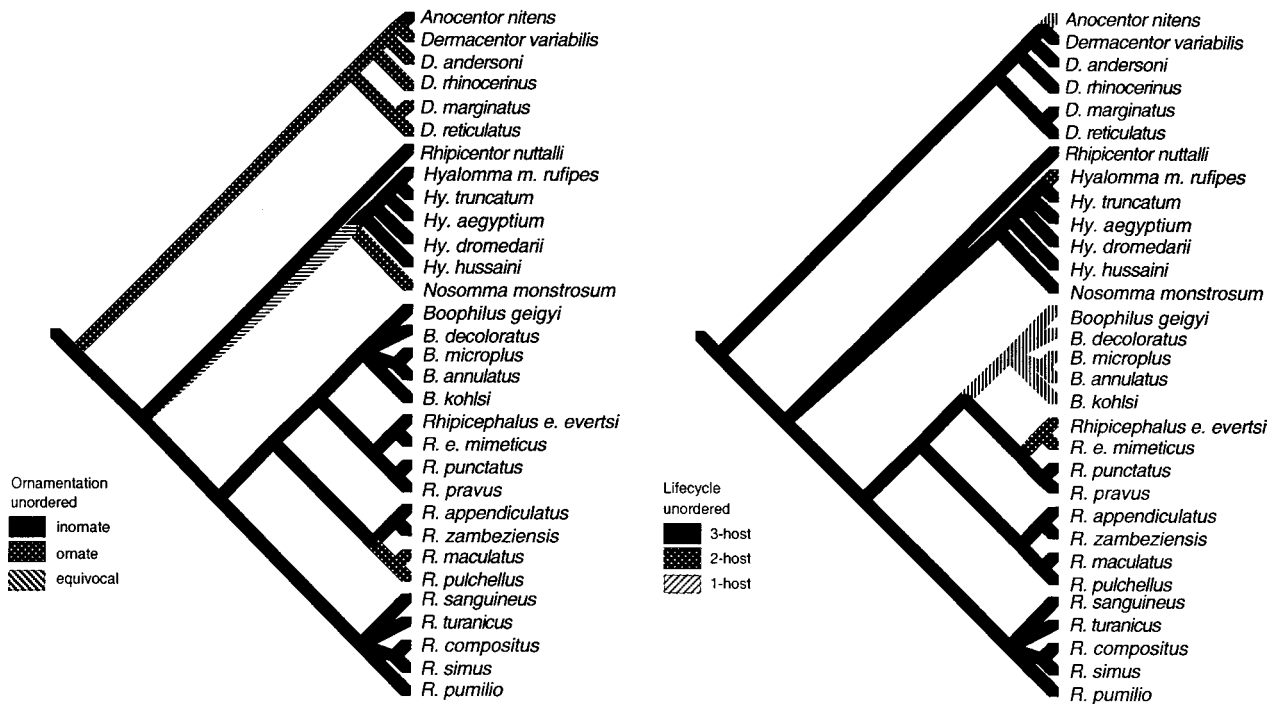


Fig. 3. A strict consensus of the 8 shortest maximum parsimony trees from a total-evidence analysis of nucleotide sequences from 4 genes (12S, COI, ITS2, SSU rRNA) and morphology from Murrell *et al.* (2001*b*). Ornamentation of the scutum and the number of hosts required to complete life cycles have been mapped onto this tree. Note that *Hy. dromedarii* has 1, 2 and 3-host life cycles and that the genus *Boophilus* is now a subgenus of the genus *Rhipicephalus*.

and Hyalomminae; Fig. 3) based on the species in that study. We propose that an inornate scutum (not patterned) is the ancestral (plesiomorphic) character-state for the Rhipicephalinae since inornate scuta predominate in a putative sister-group of the Rhipicephalinae, the Haemaphysalinae, and in the early diverging ('basal') lineages of hard ticks. Even if the Amblyomminae (members of which are both ornate and inornate) is the sister-group of the Rhipicephalinae, as proposed by Klompen *et al.* (2000), the most parsimonious explanation is still that an inornate scutum is plesiomorphic for the Rhipicephalinae. If an inornate scutum is plesiomorphic for the Rhipicephalinae, then the simplest interpretation of Fig. 3 is that ornate scuta have evolved at least three times in the Rhipicephalinae s.l.: (1) in the ancestor of the *Dermacentor* and *Anocentor* species (all *Dermacentor* species are ornate but note that the most recent ancestor of *A. nitens* apparently reverted to the plesiomorphic state); (2) in *N. monstrosom*; and (3) in *R. maculatus* and *R. pulchellus*. Note that Klompen *et al.* (1997) found some support from morphological characters for *Cosmiomma* being the earliest diverging lineage of Rhipicephalinae. If this is correct then it is just as parsimonious that ornateness is plesiomorphic for the Rhipicephalinae and that ornateness has been lost twice and secondarily gained twice in the Rhipicephalinae. In either scenario, ornateness has evolved more than once and been lost at least once in the rhipicephaline ticks.

The function, if any, of ornate scuta is unknown. However, it has been speculated that these ticks are advertising something, perhaps that they are unpalatable. Indeed, it is possible that the ornate rhipicephaline species from Africa are mimicking other ornate ticks from the genus *Amblyomma*, which may be unpalatable to tickbirds (Ivan Horak, personal communication).

Truncation of life cycles in rhipicephaline ticks. Most hard ticks have a three-host life cycle: each of the three mobile stages in the life cycle (larvae, nymphs and adults) leave the host to moult to the next stage (Hoogstraal, 1978). In some ticks, moulting from larvae to nymphs takes place without leaving the host: the two-host ticks (all *Rhipicephalus* (*Digineus*) species and some *Hyalomma* spp.). In the most extreme case, all of the mobile stages remain on the one host: the one-host ticks (all *R. (Boophilus)* species, *A. nitens* and *D. albipictus*). There is much evidence that the plesiomorphic life cycle of the Rhipicephalinae s.l. is a three-host life cycle, since all known life cycles in the putative sister-groups of the Rhipicephalinae s.l., the Haemaphysalinae, and indeed in all other Ixodidae, are three-host life cycles. Murrell *et al.* (2001*b*) found that when the number of stages in the life cycle is mapped onto their phylogeny, a life cycle with a reduced number of hosts (two or one) has evolved as many as four times: in *R. evertsi*, in *A. nitens*, in some *Hyalomma* species (life cycles may vary within a species; Hoogstraal, 1978; Sonenshine,

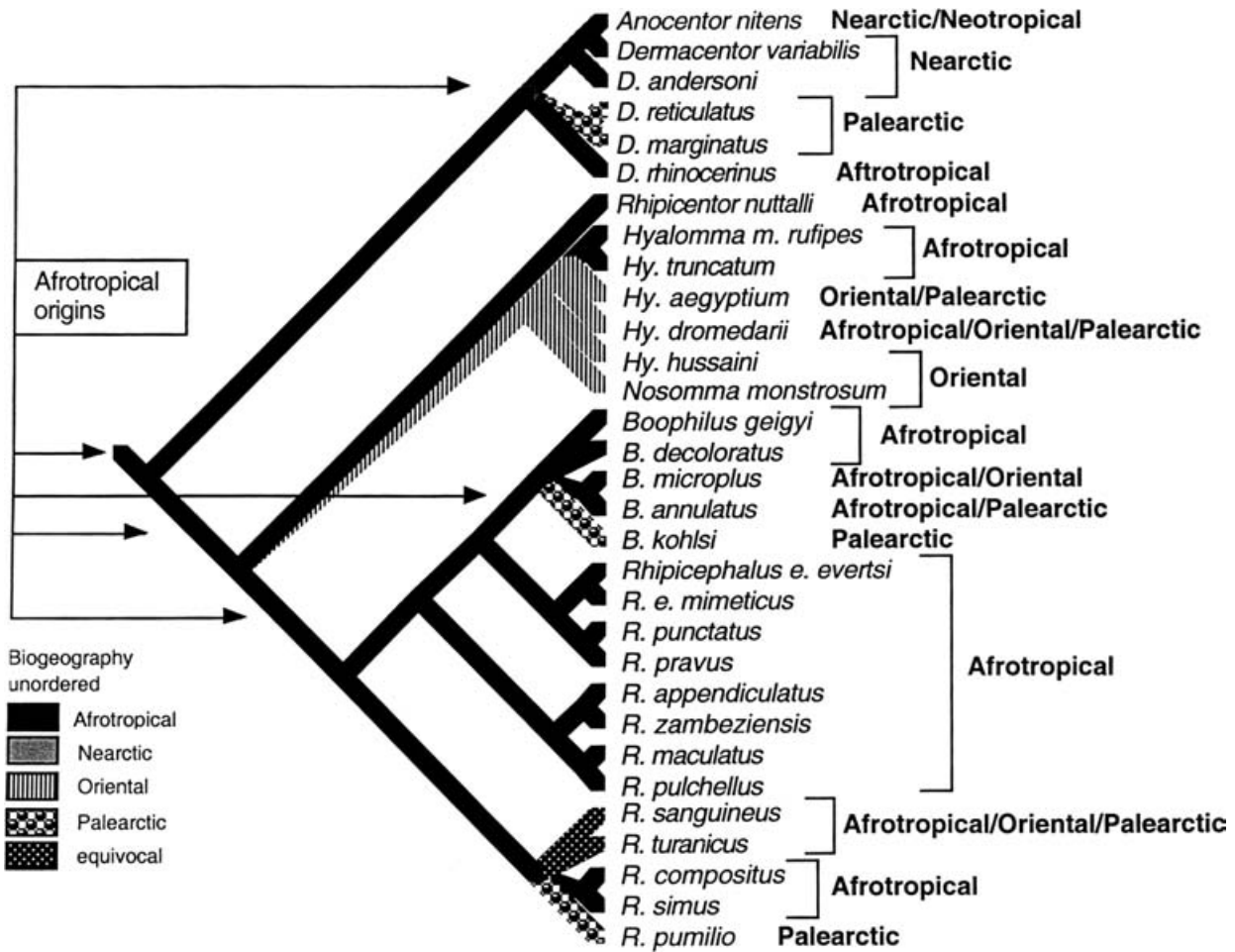


Fig. 4. Historical zoogeography of ticks of the subfamily Rhipicephalinae sensu lato Murrell *et al.* (2001 *b*). Information on the geographical distribution of ticks is from Camicas *et al.* (1998). Introductions of *B. microplus*, *B. annulatus* (cattle ticks) and *R. sanguineus* (dog ticks) to biogeographical regions by humans were excluded. Reproduced with permission from Murrell *et al.* (2001 *b*). The genus *Boophilus* is now a subgenus of the genus *Rhipicephalus*.

1993) and in the *R. (Boophilus)* species (Fig. 3). It is unclear whether the evolution of a two-host life cycle in *Rhipicephalus (Digineus)* species (e.g. *R. evertsi*) and a one-host life cycle in *R. (Boophilus)* species are linked evolutionarily. Despite being phylogenetically close to *R. (Boophilus)* species, *R. evertsi* is apparently closer, phylogenetically, to species from the *R. pravus* group which are three-host ticks (refer to Fig. 2).

Hoogstraal (1978) discussed the evolution of reductions in the number of hosts in life cycles and concluded that the survival of larvae is more precarious than survival of other life stages, so the larvae are the ‘weak link’ in the life cycles of ticks. Hoogstraal (1978) concluded that selection pressure for two-host and one-host life cycles would be strong in ticks that are associated with hosts that wander, but weak in ticks with hosts that have a nest or localized breeding site. In ticks of hosts that wander, it would be more difficult for larvae and nymphs to find a host than for ticks with hosts that do not wander. As far as we know the only ixodid ticks with truncated life cycles, either with one or two hosts, are in the Rhipicephalinae.

Historical zoogeography of rhipicephaline ticks. The regions inhabited by ticks may also be mapped onto the phylogeny of ticks. To demonstrate this approach we highlight the zoogeographical analysis of Murrell *et al.* (2001 *b*). This analysis shows that the *Dermacentor–Anocentor* clade, the *Rhipicephalus–Boophilus–Hyalomma–Nosomma–Rhipicentor* clade, the *Rhipicephalus–Boophilus* clade, the subgenus *R. (Boophilus)*, and the hypothetical ancestors of the Rhipicephalinae s.l. probably evolved in the Afrotropical region (Fig. 4) but note that they did not study some lineages such as the oriental *Dermacentor* and *Rhipicephalus* species. Only a handful of rhipicephaline species seem to have evolved in a region other than the Afrotropical region: the clade with *Anocentor nitens* plus some *Dermacentor* species, *Hy. aegyptium* (ex tortoises), *Hy. dromedarii* (ex camels), *Hy. hussaini* (ex ungulates), *N. monstrosus* (ex buffalo and others), *R. (Boophilus) kohlsi* (ex goats and sheep) and *R. pumilio* (ex wide range of mammals). It is not clear where *R. sanguineus* (ex dogs) and *R. turanicus* (ex dogs and other large mammals) evolved. *R. turanicus* occurs in Africa and many European

countries whilst *R. sanguineus* can now be found on dogs throughout the world.

Fig. 4 also allows us to speculate about the history of the rhipicephaline ticks. Murrell *et al.* (2001b) proposed that: (1) The ancestor of the *Dermacentor–Anocentor* lineage evolved in the Afrotropical region. Then ticks of this lineage dispersed into Eurasia, probably in the Eocene (50 Mya) a period for which there is evidence for migration of mammals between Africa and Eurasia (Cox & Moore, 1993). After the Eocene, Africa became isolated and most dispersal and cladogenesis was in and between the Palearctic and Nearctic regions where most *Dermacentor* species are found today. Only two species from the *Dermacentor–Anocentor* lineage are found in Africa today, either because there has been little speciation in this lineage in Africa or because species from this lineage became extinct. During the Oligocene (~35 Mya) dispersal between Eurasia and the Nearctic was possible via the Bering land-bridge and movement between Europe and the Nearctic via Greenland (Cox & Moore, 1993). Much later (2.5 Mya) dispersal between the Nearctic and Neotropical regions was via the Isthmus of Panama. Hypotheses of an African origin of the genus *Dermacentor* contrast with previous ideas about the origin of this genus which have centred around arguments over whether *Dermacentor* evolved in the Nearctic region and moved into the Palearctic and Oriental regions, or whether the *Dermacentor* species evolved in the Palearctic and then dispersed to Nearctic and Oriental regions (Balashov, 1994; Berdyevev, 1989; Crosbie *et al.* 1998); (2) The *Nosomma–Hyalomma* lineage appears to have evolved from an ancestor that lived in the Oriental region, perhaps in the early Miocene (~19 Mya) when movement from Africa into Asia was possible for the ancestor of these species via a land bridge (Cox & Moore, 1993). Movement from Asia to Eurasia became possible and then there was probably dispersal back into Africa after Africa and Eurasia were joined by a land bridge 14 Mya (Cox & Moore, 1993). This proposal is consistent with Balashov (1994); he proposed an Asian origin for the genus *Hyalomma*; (3) The *Boophilus–Rhipicephalus* lineage probably evolved and radiated in Africa i.e. when Africa was mostly isolated from the Palearctic and Oriental regions before the formation of the land bridge between Africa and Eurasia (14 Mya). Dispersal and radiation into Eurasia and Asia probably occurred after the land bridge formed between Africa and Eurasia in the Miocene. Balashov (1994) proposed that the genus *Rhipicephalus* evolved in Africa but thought it likely that the subgenus *R. (Boophilus)* evolved in Europe. However, the phylogeny of Murrell *et al.* (2001b) indicates that the subgenus *R. (Boophilus)* evolved in Africa (also see Murrell *et al.* 2000); and (4) The *Rhipicentor* lineage (2 species) appears to have evolved in, and then remained in, Africa, although the possibility that

species from this lineage evolved in, or dispersed to, other regions but then became extinct in those regions cannot be ruled out. *Anomalohimalaya* species live in the Palearctic and Oriental regions but not until the phylogenetic position of this genus is resolved can its historical biogeography be inferred.

Where did the first hard ticks evolve and how did their descendants spread around the globe? Two main hypotheses have been proposed that address this question. On the one hand, Dobson & Barker (1999) proposed that hard ticks, and indeed all ticks, may have evolved in Australia, or more precisely in that part of Gondwana that became Australia, on early crocodile-like amphibians (Labyrinthodonts, which are now extinct) in the Devonian *ca.* 390 Mya. On the other hand, Klompen *et al.* (1996, 2000) proposed that the first hard ticks evolved in Australia much later (120 Mya), when Australia and Antarctica had separated from the other landmasses of Gondwana. The two proposals differ in the proposed time of origin of the hard ticks (*ca.* 390 Mya *vs.* *ca.* 120 Mya). Three hundred and ninety Mya Gondwana was intact, so land animals could have moved between Australia, Antarctica, South America, Africa and India. However, 120 Mya, Australia was connected to Antarctica but not to South America, Africa and India: these three land masses had become island continents. Klompen *et al.* (2000) argued against the origin of ticks 390 Mya on labyrinthodont amphibians since modern-day Australian amphibians do not have ticks. [We know of only one amphibian that is regularly infested with ticks: *Bufo marinus* (cane toad infested by *Amblyomma rotundatum* in South America).] However, the labyrinthodont amphibians belonged to a 'distinct evolutionary radiation to that which produced our modern amphibian fauna' (Vickers-Rich & Rich, 1993). So we would not necessarily expect modern amphibians to be infested with the direct descendants of the ticks that infested labyrinthodont amphibians. Labyrinthodont amphibians lived alongside reptiles and mammal-like reptiles well into the Cretaceous *ca.* 65–140 Mya. So there was ample time for ticks to infest lineages of reptiles and/or mammal-like reptiles before the labyrinthodont amphibians became extinct (see Vickers-Rich & Rich, 1993 for an account of these terrestrial amphibians).

The evidence that the Ixodida evolved in that part of Gondwana that became Australia, is that the putative sister-group of the ticks, the Holothyrida (Lehtinen, 1991), has a Gondwanan distribution (Australia, New Zealand, South and Central America, and islands in the Caribbean Sea and Indian Ocean) (Walter & Proctor, 1998, 1999) and that the most 'primitive' family of holothyrid mites is restricted to Australia and New Zealand (Allothyridae) (D. E. Walter personal communication). The evidence that the Ixodidae evolved in

Australia is that the earliest-diverging ('basal') lineage of the Metastrata, the Bothriocrotoninae, and one of the two putative lineages of the *Ixodes*, the Australasian *Ixodes*, live almost exclusively in Australasia (but note that *I. uriae* of the Australasian *Ixodes* lineage has a worldwide distribution on sea birds). Questions about where the first ticks evolved, and indeed the first hard ticks, are still far from resolved.

What were the first hosts of ticks: reptiles, amphibians or birds? Alas, the oldest fossil ticks are only about 90–94 Mya old (Cretaceous) (Klompen & Grimaldi, 2001; Poinar & Brown, 2003). Prior to Klompen & Grimaldi (2001) and Poinar & Brown (2003), records of ticks were restricted to the Miocene (15–20 Mya; Lane & Poinar, 1986), the Oligocene (~30 Mya) and the Eocene (35–40 Mya; reviewed in Klompen & Grimaldi, 2001 and in Fuente, 2003). So it seems that inference of the archetypal host will have to rely on estimates of the age of the Ixodida clade and knowledge of the potential hosts that were available at that time. Hoogstraal (1978) thought that the reptiles were the first hosts of ticks; Oliver (1989) proposed amphibians; whereas Stothard & Fuerst (1995) suggested birds. Dobson & Barker (1999) argued for labyrinthodont amphibians (which evolved in that part of Gondwana that became Australia) as the archetypal host (see also above).

How did haematophagy (blood-feeding behaviour) evolve in ticks? To feed efficiently haematophagous arthropods adapt to the haemostatic system of their hosts (see Mans, Louw & Neitz, 2002). Mans, Louw & Neitz (2002) compared the sequences of inhibitors of blood coagulation and platelet aggregation in hard and soft ticks and insects and found that the inhibitors from hard and soft ticks did not share a common origin. This indicates independent adaptation to blood-feeding by hard and soft ticks, rather than adaptation to blood-feeding prior to the divergence of hard and soft ticks.

TAXONOMY AND NOMENCLATURE OF THE TICKS—THE INFLUENCE OF PHYLOGENY

Since Linnaeus described the first tick in 1746, a veritable army of biologists have contributed to the current taxonomic scheme of the ticks. Latreille was the first to classify the 'tiques' and in 1795 divided them into 11 genera, two of which were *Argas* and *Ixodes* (see Nuttall & Warburton, 1911). It is highly desirable that taxa are monophyletic and thus that classifications reflect accurately our knowledge of the evolutionary history (phylogeny) of organisms. A number of changes to the taxonomy of ticks have occurred or have been proposed recently to account for recent advances in our knowledge of the phylogeny of ticks.

Revision of the Argasidae

Klompen & Oliver (1993) revised the genera of the Argasidae. These authors reduced the number of genera from five to four: *Carios*, *Ornithodoros*, *Otobius* and *Argas*. Some species were moved from one genus to another and *Carios* was elevated from subgenus to genus. This revision is not universally accepted, however, a phylogeny inferred from SSU rDNA by Black *et al.* (1997) was consistent with the revision of Klompen & Oliver (1993). Ushijima *et al.* (2003) also concluded that their analyses of part of mitochondrial 16S rRNA of *Carios capensis* were consistent with Klompen & Oliver (2003). [However, we note that there was <50% bootstrap support for monophyly of *C. capensis*, *C. marginatus* and *C. mexicanus*.] We, like Horak, Camicas & Keirans (2002), incorporated the revision of Klompen & Oliver (1993) into our list of valid genus and species names (Table 1).

A new subfamily of hard ticks

A new subfamily, Bothriocrotoninae and a new genus *Bothriocroton* were described for the lineage of five species of Australian endemic ticks that predominantly infest reptiles (Klompen, Dobson & Barker, 2002).

Synonymy of Amblyomma and Aponomma. The genus *Aponomma*, or remains thereof, was synonymised with the genus *Amblyomma* because *Amblyomma* is paraphyletic without the inclusion of *Aponomma* (Klompen *et al.* 2002). Klompen *et al.* (2002) stated that 'the status of the "primitive *Aponomma*" remains unclear' and therefore *Aponomma sphenodonti* and *A. elaphense* were 'tentatively placed with the "typical *Aponomma*" in *Amblyomma*, until further evidence relating them to other ixodid lineages is generated'.

The Hyalomminae and Rhipicephalinae should be synonymised. Many authors have suggested that the subfamily Hyalomminae Schulze, 1940 should be synonymised with the subfamily Rhipicephalinae Banks, 1908 because the Rhipicephalinae is paraphyletic without the inclusion of members of the Hyalomminae (Murrell *et al.* 2001b; Klompen *et al.* 2000, 2002). However, some authors still use this name (e.g. Horak, Camicas & Keirans, 2002) and thus, presumably, are not convinced by the evidence of Murrell *et al.* (2001b) and Klompen *et al.* (2000, 2002).

Rhipicephalus and Boophilus have been synonymised (Murrell & Barker, 2003). Murrell *et al.* (2001b) then Barker & Murrell (2003) proposed that the genus *Boophilus* Curtice, 1891 be relegated to a subgenus of *Rhipicephalus* Koch, 1844 because, as outlined in the previous section, the genus *Rhipicephalus* is

paraphyletic without the inclusion of the species of *Boophilus*. The alternative was to elevate some species or species groups of *Rhipicephalus* to the rank of genus. This was undesirable, first because it increases greatly the number of genus names and second because not enough is known about the phylogeny of the *Rhipicephalus* species to warrant splitting the genus into a number of new genera. By placing the *Boophilus* species in a subgenus of *Rhipicephalus*, *Rhipicephalus* (*Boophilus*), the name *Boophilus* can still be used for the five species that were in the genus *Boophilus*. It was desirable that the name *Boophilus* be available, since there is a lot of literature on the *Boophilus* species and hundreds, perhaps thousands of people use these names regularly (Murrell *et al.* 2001b).

A current list of the valid genus and species names of ticks

The most recent and pertinent taxonomic schemes and lists of names of ticks are: (1) Keirans, (1992) for species names as at 1992; (2) Camicas *et al.* (1998) for species names as at the end of 1995; (3) Keirans & Robbins (1999), a list of species described between 1973 and 1997; (4) Horak, Camicas & Keirans (2002); and (5) Walker, Keirans & Horak (2000), which is a comprehensive taxonomy of 74 species of the genus *Rhipicephalus* [note that a subsequent revision by Murrell & Barker (2003) moved all five species from the genus *Boophilus* to the genus *Rhipicephalus* so there are now 79 species in the genus *Rhipicephalus*]. Table 1 is a compilation of the genus and species of Keirans (1992), Camicas *et al.* (1998), Keirans & Robbins (1999), Horak, Camicas & Walker (2002) plus the three species, including one new genus, *Cornupalpatum*, that have been described since 2002. For the *Rhipicephalus* species we list only the species in Walker, Keirans & Horak (2000) since this was a comprehensive taxonomic treatment of the group. We ignored the plethora of subgenera, species groups and subspecies with one exception *Rhipicephalus* (*Boophilus*) – see discussion above. We also ignored the genus-level taxonomy of Camicas *et al.* (1998) because it differs markedly with the genus-level taxonomy of Keirans (1992), Keirans & Robbins (1999) and Horak, Camicas & Keirans (2002). For example, Camicas *et al.* (1998) has the *Ixodes* species of Keirans (1992), Keirans & Robbins (1999) and Horak, Camicas & Keirans (2002) in six different genera: *Ixodes*, *Ceratixodes*, *Eschatocephalus*, *Lepidixodes*, *Pholeoixodes* and *Scaphixodes*. Since Camicas is an author of the most recent of the above lists, Horak, Camicas & Keirans (2002), which ignores these genus names, this omission seems to be justified. The superscripts in Table 1 show the paper(s) in which each name appears: Keirans (1992)^K; Camicas, Hery, Adam & Morel (1998)^{CHAM}; Keirans & Robbins (1999)^{KR}; Walker,

Keirans & Horak (2000)^{WKH}; and Horak *et al.* (2002)^{HCK}. You will notice that these lists differ. Most species names are in all possible lists for that particular species e.g. *I. holocyclus* Neumann, 1899 which is in Keirans (1992), Camicas *et al.* (1998) and Horak *et al.* (2002). However, some names appear in two of three possible lists (e.g. *I. anatis* Chilton, 1904 which is in Keirans (1992) and Horak *et al.* (2002) but not in Camicas *et al.* (2002)) or one of three possible lists (e.g. *I. apteridis* Maskell, 1897 which is in Camicas *et al.* (1998) but not Keirans (1992), Keirans & Robbins (1999) nor Horak *et al.* (2002)). We trust that our list will lay the foundation for a new list of valid names with evidence and arguments for the removal and/or addition of names from the literature. The three species and one genus described since the last list of species names (Horak *et al.* 2002) have the superscript RD (recent description): *Cornupalpatum burmanicum* Poinar & Brown, 2003; *Ixodes paranaensis* Barros-Battesti, Arzua, Pichorim and Keirans, 2003; and *Ixodes dicei* Keirans and Ajohola, 2003. *Cornupalpatum burmanicum* Poinar & Brown, 2003 was described from tick larva found in amber from the Cretaceous Era (Poinar & Brown, 2003). There is only one species in the genus *Cornupalpatum*. This tick resembles some species of *Amblyomma* (formerly *Aponomma* spp. that infest reptiles). Note that *Argas cooleyi* (McIvor, 1941) is a homonym of *Argas cooleyi* Kohls & Hoogstraal, 1960, and *vice versa*. These homonyms were inadvertently created when Klompen & Oliver (1993) moved the subgenus *Ornithodoros* (*Alveonanus*) from the genus *Ornithodoros* to the genus *Argas*.

CONCLUSIONS

Taxonomic schemes provide the evolutionary framework that all tick biologists use to help interpret the biology and phenotypes of the species of ticks they study. Fortunately, there has been much progress in our understanding of the phylogeny of ticks since the mid 1990s when modern methods were first applied to the study of tick phylogeny. There is now consensus among many workers in the field about many clades of ticks, e.g. that the five species of endemic Australian ticks that were in the former genus *Aponomma* that infest reptiles are a distinct lineage of ticks, that the Hyalomminae is embedded in the Rhipicephalinae and that some species of the genus *Rhipicephalus* are more closely related to the *Boophilus* species than they are to the other *Rhipicephalus* species. Yet there is disagreement, or more often a lack of information, about the relationships of other ticks (e.g. the phylogenetic position of the Haemaphysalinae and whether or not the genus *Ixodes* is monophyletic) and where and when the ticks evolved. Study of the mitochondrial genomes of ticks has also provided insight into the phylogeny and evolution of ticks. Entire

Table 1. A current list of valid genus and species names (in alphabetical order except for the 5 species that were previously in the genus *Boophilus*—these species are now at the top of the list of *Rhipicephalus* species).

IXODIDA (899 valid species names)

NUTTALLIELLIDAE (1 valid species name)

Nuttalliella (1 species)

N. namaqua Bedford, 1931^{K,CHAM,HCK}

ARGASIDAE (185 valid species names)

Argas (57 species)

A. abdussalami Hoogstraal & McCarthy, 1965^{K,CHAM,HCK}

A. acinus (Whittick, 1938)^{K,CHAM,HCK},

A. africanus Hoogstraal, Kaiser, Walker, Ledger, Converse & Rice, 1975^{K,CHAM,HCK}

A. arboreus Kaiser, Hoogstraal & Kohls, 1964^{K,CHAM,HCK}

A. assimilis Teng & Song, 1983^{K,CHAM,HCK}

A. beijingensis Teng, 1983^{K,CHAM,HCK}

A. beklemischevi Pospelova-Shtrom, Vasil'eva & Semashko, 1963^{K,CHAM,HCK}

A. brevipes Banks, 1908^{K,CHAM,HCK}

A. brumpti Newmann, 1907^{K,CHAM,HCK}

A. bureschi Dryenski, 1957^{K,CHAM,HCK}

A. canestrinii Birula, 1895^{K,HCK}

A. cooleyi (McIvor, 1941) *nec A. cooleyi* Kohls & Hoogstraal, 1960^{K,CHAM,HCK}

A. cooleyi Kohls & Hoogstraal, 1960 *nec A. cooleyi* (McIvor, 1941)^{K,CHAM,HCK}

A. cucumerinus Neumann, 1901^{K,CHAM,HCK}

A. dalei Clifford, Keirans, Hoogstraal & Corwin, 1976^{K,CHAM,HCK}

A. delanoei (Roubaud & Colas-Belcour, 1931)^{K,CHAM,HCK}

A. dulus Keirans, Clifford & Capriles, 1971^{K,CHAM,HCK}

A. eboris (Theiler, 1959)^{K,CHAM}

A. echinops Hoogstraal, Uilenberg & Blanc, 1967^{K,CHAM,HCK}

A. falco Kaiser & Hoogstraal, 1974^{K,CHAM,HCK}

A. foleyi (Parrot, 1928)^{K,CHAM,HCK}

A. giganteus Kohls & Clifford, 1968^{K,CHAM,HCK}

A. gilcolladoi Estrada-Peña, Lucientes & Sánchez, 1987^{K,CHAM,HCK}

A. hermanni Audouin, 1827^{K,CHAM,HCK}

A. himalayensis Hoogstraal & Kaiser, 1973^{K,CHAM,HCK}

A. hoogstraali Morel & Vassiliades, 1965^{K,CHAM,HCK}

A. japonicus Yamaguti, Clifford & Tipton, 1968^{K,CHAM,HCK}

A. lagenoplastis Froggatt, 1906^{K,CHAM,HCK}

A. lahorensis (Neumann, 1908)^{K,CHAM,HCK}

A. latus Filippova, 1961^{K,CHAM,HCK}

A. lowryae Kaiser & Hoogstraal, 1975^{K,CHAM,HCK}

A. macrostigmatus Filippova, 1961^{K,CHAM,HCK}

A. magnus Neumann, 1896^{K,CHAM,HCK}

A. miniatus Koch, 1844^{K,CHAM,HCK}

A. monachus Keirans, Radovsky & Clifford, 1973^{K,CHAM,HCK}

A. monolakensis Schwan, Corwin, & Brown, 1992^{KR,CHAM,HCK}

A. moreli Keirans, Hoogstraal & Clifford, 1979^{K,CHAM,HCK}

A. neghmei Kohls & Hoogstraal, 1961^{K,CHAM,HCK}

A. nullarborensis Hoogstraal & Kaiser, 1973^{K,CHAM,HCK}

A. peringueyi (Bedford & Hewitt, 1925)^{K,CHAM,HCK}

A. persicus (Oken, 1818)^{K,CHAM,HCK}

A. peusi (Schulze, 1943)^{K,CHAM,HCK}

A. polonicus Siuda, Hoogstraal, Clifford & Wassef, 1979^{K,CHAM,HCK}

A. radiatus Railliet, 1893^{K,CHAM,HCK}

A. reflexus (Fabricius, 1794)^{K,CHAM,HCK}

A. ricei Hoogstraal, Kaiser, Clifford & Keirans, 1975^{K,CHAM,HCK}

A. robertsi Hoogstraal, Kaiser & Kohls, 1968^{K,CHAM,HCK}

A. sanchezi Dugès, 1887^{K,CHAM,HCK}

A. streptopelia Kaiser, Hoogstraal & Homer, 1970^{K,CHAM,HCK}

A. striatus Bedford, 1932^{K,CHAM,HCK}

A. theilerae Hoogstraal & Kaiser, 1970^{K,CHAM,HCK}

A. transgarepinus White, 1846^{K,CHAM,HCK}

A. tridentatus Filippova, 1961^{K,CHAM,HCK}

A. vansomeri (Keirans, Hoogstraal & Clifford, 1977)^{K,CHAM,HCK}

A. vulgaris Filippova, 1961 (? = *A. delicatus* Neumann, 1910)^{K,CHAM,HCK}

A. walkerae Kaiser & Hoogstraal, 1969^{K,CHAM,HCK}

A. zumpti Hoogstraal, Kaiser & Kohls, 1968^{K,CHAM,HCK}

Carios (88 species)

C. amblus (Chamberlain, 1920)^{K,CHAM,HCK}

C. aragaoi (Fonseca, 1960)^{HCK,CHAM}

C. armasi (de la Cruz & Estrada-Peña, 1995)^{KR,CHAM,HCK}

C. australiensis (Kohls & Hoogstraal, 1962)^{K,CHAM,HCK}

C. azteci (Matheson, 1935)^{K,CHAM,HCK}

C. batuenis (Hirst, 1929)^{K,CHAM,HCK}

C. boueti (Roubaud & Colas-Belcour, 1933)^{K,CHAM,HCK}

C. brodyi (Matheson, 1935)^{K,CHAM,HCK}

C. camicasi (Sylla, Cornet & Marchand, 1997)^{KR,HCK}

C. capensis (Neumann, 1901)^{K,CHAM,HCK}

C. casebeeri (Jones & Clifford, 1972)^{K,CHAM,HCK}

C. centralis (de la Cruz & Estrada-Peña, 1995)^{KR,CHAM,HCK}

C. cernyi (de la Cruz, 1978)^{K,CHAM,HCK}

C. ceylonensis (Hoogstraal & Kaiser, 1968)^{K,CHAM,HCK}

C. cheikhi (Vermeil, Michel & Vermeil, 1997)^{HCK}

C. chironectes (Jones & Clifford, 1972)^{K,CHAM,HCK}

C. chiropterphila (Dhanda & Rajagopalan, 1971)^{K,CHAM,HCK}

C. clarki (Jones & Clifford, 1972)^{K,CHAM,HCK}

C. colloccaliae (Hoogstraal, Kadarsan, Kaiser & Van Peenan, 1974)^{K,CHAM,HCK}

C. concanensis (Cooley & Kohls, 1941)^{K,CHAM,HCK}

C. confusus (Hoogstraal, 1955)^{K,CHAM,HCK}

C. coniceps (Canestrini, 1890)^{K,CHAM,HCK}

C. coprophilus (McIntosh, 1935)^{K,CHAM,HCK}

C. cordiformis (Hoogstraal & Kohls, 1967)^{K,CHAM,HCK}

C. cycluriae (de la Cruz, 1984)^{K,CHAM,HCK}

C. darvini (Kohls, Clifford & Hoogstraal, 1969)^{K,CHAM,HCK}

C. daviesi (Kaiser & Hoogstraal, 1973)^{K,CHAM,HCK}

C. denmarki (Kohls, Sonenshine & Clifford, 1965)^{K,CHAM,HCK}

C. dewae (Kaiser & Hoogstraal, 1974)^{K,CHAM,HCK}

C. dusbabeki (Černý, 1967)^{K,CHAM,HCK}

C. dyeri (Cooley & Kohls, 1940)^{K,CHAM,HCK}

C. echimys (Kohls, Clifford & Jones, 1969)^{K,CHAM,HCK}

C. elongatus (Kohls, Clifford & Sonenshine, 1965)^{K,CHAM,HCK}

C. eptesicus (Kohls, Clifford & Jones, 1969)^{K,CHAM,HCK}

C. faini (Hoogstraal, 1960)^{K,CHAM,HCK}

Table 1. (Cont.)

<i>C. fischeri</i> (Audouin, 1827) ^{CHAM}	<i>C. rudis</i> (Karsch, 1880) ^{K,CHAM,HCK}	<i>O. nattereri</i> Warburton, 1927 ^{K,HCK}
<i>C. galapagensis</i> (Kohls, Clifford & Hoogstraal, 1969) ^{K,CHAM,HCK}	<i>C. salahi</i> (Hoogstraal, 1953) ^{K,CHAM,HCK}	<i>O. nicolleti</i> Mooser, 1932 ^{K,CHAM,HCK}
<i>C. granasi</i> (de la Cruz, 1973) ^{K,CHAM,HCK}	<i>C. savaii</i> (Kitaoka & Suzuki, 1973) ^{K,CHAM,HCK}	<i>O. normandi</i> Larrousse, 1923 ^{K,CHAM,HCK}
<i>C. habanensis</i> (de la Cruz, 1976) ^{K,CHAM,HCK}	<i>C. setosus</i> (Kohls, Clifford & Jones, 1969) ^{HCK,CHAM}	<i>O. parkeri</i> Cooley, 1936 ^{K,CHAM,HCK}
<i>C. hadiae</i> Klompen, Keirans & Durden, 1995 ^{KR,CHAM,HCK}	<i>C. siboneyi</i> (de la Cruz & Estrada-Peña, 1995) ^{KR,CHAM,HCK}	<i>O. porcinus</i> Walton, 1962 ^{K,CHAM,HCK}
<i>C. hasei</i> (Schulze, 1935) ^{K,CHAM,HCK}	<i>C. silvai</i> (Černý, 1967) ^{K,CHAM,HCK}	<i>O. procaviae</i> Theodor & Costa, 1960 ^{K,CHAM,HCK}
<i>C. hummelincki</i> (de la Cruz & Estrada-Peña, 1995) ^{KR,CHAM,HCK}	<i>C. sinensis</i> (Jeu & Zhu, 1982) ^{K,CHAM,HCK}	<i>O. rostratus</i> Aragão, 1911 ^{K,CHAM,HCK}
<i>C. jerseyi</i> Klompen & Grimaldi, 2001 ^{HCK}	<i>C. solomonis</i> (Dumbleton, 1959) ^{K,CHAM,HCK}	<i>O. savignyi</i> (Audouin, 1827) ^{K,CHAM,HCK}
<i>C. jul</i> (Schulze, 1940) ^{HCK,CHAM}	<i>C. spheniscus</i> (Hoogstraal, Wassef, Hays & Keirans, 1985) ^{K,CHAM,HCK}	<i>O. steini</i> (Schulze, 1935) ^{K,HCK}
<i>C. kelleyi</i> (Cooley & Kohls, 1941) ^{K,HCK}	<i>C. stageri</i> (Cooley & Kohls, 1941) ^{K,CHAM,HCK}	<i>O. sonrai</i> Sautet & Witkowski, 1943 ^{K,CHAM,HCK}
<i>C. kohlsi</i> (Guglielmone & Keirans, 2002) ^{HCK}	<i>C. tadaridae</i> (Černý & Dusbábek, 1967) ^{K,CHAM,HCK}	<i>O. tartakovskyi</i> Olenov, 1931 ^{K,CHAM,HCK}
<i>C. macrodermae</i> (Hoogstraal, Moorhouse, Wolf & Wassef, 1977) ^{K,CHAM,HCK}	<i>C. talaje</i> (Guérin-Ménil, 1849) ^{K,CHAM,HCK}	<i>O. tholozani</i> (Laboulbène & Méglin, 1882) ^{K,CHAM,HCK}
<i>C. madagascariensis</i> (Hoogstraal, 1962) ^{K,CHAM,HCK}	<i>C. tiptoni</i> (Jones & Clifford, 1972) ^{K,CHAM,HCK}	<i>O. transversus</i> (Banks, 1902) ^{K,CHAM,HCK}
<i>C. marginatus</i> (Banks, 1910) ^{K,CHAM,HCK}	<i>C. tuttlei</i> (Jones & Clifford, 1972) ^{K,CHAM,HCK}	<i>O. turicata</i> (Dugès, 1876) ^{K,CHAM,HCK}
<i>C. marinkellei</i> (Kohls, Clifford & Jones, 1969) ^{K,CHAM,HCK}	<i>C. vesperilionis</i> Latreille, 1796 ^{K,CHAM,HCK}	<i>O. zumpti</i> Heisch & Guggisberg, 1953 ^{K,CHAM,HCK}
<i>C. maritimus</i> (Vermeil & Marguet, 1967) ^{K,CHAM,HCK}	<i>C. vignerasi</i> (Cooley & Kohls, 1941) ^{K,CHAM,HCK}	Otobius (3 species)
<i>C. marmosae</i> (Jones & Clifford, 1972) ^{K,CHAM,HCK}	<i>C. yumatensis</i> (Cooley & Kohls, 1941) ^{K,CHAM,HCK}	<i>O. lagophilus</i> Cooley & Kohls, 1940 ^{K,CHAM,HCK}
<i>C. martelorum</i> (de la Cruz, 1978) ^{K,CHAM,HCK}	<i>C. yunkeri</i> (Keirans, Clifford & Hoogstraal, 1984) ^{K,CHAM,HCK}	<i>O. megnini</i> (Dugès, 1883) ^{K,CHAM,HCK}
<i>C. mexicanus</i> (Hoffman, 1959) ^{K,CHAM,HCK}	Ornithodoros (37 species)	<i>O. sparmus</i> (Kohls & Clifford, 1963) ^{K,CHAM,HCK}
<i>C. mimon</i> (Kohls, Clifford & Jones, 1969) ^{K,CHAM,HCK}	<i>O. alactagalis</i> Issaakjan, 1936 ^{K,CHAM,HCK}	IXODIDAE (713 species)
<i>C. mormoops</i> (Kohls, Clifford & Jones, 1969) ^{K,CHAM,HCK}	<i>O. antiquus</i> Poinar, 1995 ^{KR,CHAM,HCK}	Amblyomma (142 species)
<i>C. muesebecki</i> (Hoogstraal, 1969) ^{K,CHAM,HCK}	(known only as a fossil)	<i>A. acutangulatum</i> Neumann, 1899 ^{CHAM}
<i>C. multisetosus</i> Klompen, Keirans & Durden, 1995 ^{KR,CHAM,HCK}	<i>O. apertus</i> Walton, 1962 ^{K,CHAM,HCK}	<i>A. albolimbatum</i> Neumann, 1907 ^{K,CHAM,HCK}
<i>C. naomiae</i> (de la Cruz, 1978) ^{K,CHAM,HCK}	<i>O. arenicolous</i> Hoogstraal, 1953 ^{K,CHAM,HCK}	<i>A. albopictum</i> Neumann, 1899 ^{K,CHAM,HCK}
<i>C. natalinus</i> (Černý & Dusbábek, 1967) ^{HCK,CHAM}	<i>O. asperus</i> Warburton, 1918 ^{K,CHAM,HCK}	<i>A. americanum</i> (Linnaeus, 1758) ^{K,CHAM,HCK}
<i>C. occidentalis</i> (de la Cruz, 1978) ^{K,CHAM,HCK}	<i>O. brasiliensis</i> Aragão, 1923 ^{K,CHAM,HCK}	<i>A. antillorum</i> Kohls, 1969 ^{K,CHAM,HCK}
<i>C. papuensis</i> Klompen, Keirans & Durden, 1995 ^{KR,CHAM,HCK}	<i>O. boliviensis</i> (Kohls & Clifford, 1964) ^{K,CHAM}	<i>A. arcanum</i> Karsch, 1879 ^{CHAM,HCK}
<i>C. peropteryx</i> (Kohls, Clifford & Jones, 1969) ^{K,CHAM,HCK}	<i>O. cholodkovskiyi</i> Pavlovsky, 1930 ^{K,CHAM,HCK}	<i>A. argentinae</i> Neumann, 1905 ^{CHAM,HCK}
<i>C. peruvianus</i> (Kohls, Clifford & Jones, 1969) ^{K,CHAM,HCK}	<i>O. compactus</i> Walton, 1962 ^{K,CHAM,HCK}	<i>A. arianae</i> Keirans & Garris, 1986 ^{KR}
<i>C. piriformis</i> (Warburton, 1918) ^{K,CHAM,HCK}	<i>O. coriaceus</i> Koch, 1844 ^{K,CHAM,HCK}	<i>A. astrion</i> Dönitz, 1909 ^{K,CHAM,HCK}
<i>C. puertoricensis</i> (Fox, 1947) ^{K,CHAM,HCK}	<i>O. eremicus</i> Cooley & Kohls, 1941 ^{K,CHAM,HCK}	<i>A. aureolatum</i> (Pallas, 1772) ^{HCK}
<i>C. pusillus</i> (Kohls, 1950) ^{K,CHAM,HCK}	<i>O. erraticus</i> (Lucas, 1849) ^{K,CHAM,HCK}	<i>A. auricularium</i> (Conil, 1878) ^{K,CHAM,HCK}
<i>C. reddelli</i> (Keirans & Clifford, 1975) ^{K,CHAM,HCK}	<i>O. furcosus</i> Neumann, 1908 ^{K,CHAM,HCK}	<i>A. australiense</i> Neumann, 1905 ^{K,CHAM,HCK}
<i>C. remmellensis</i> (Clifford & Sonenshine, 1962) ^{K,CHAM,HCK}	<i>O. graingeri</i> Heisch & Guggisberg, 1953 ^{K,CHAM,HCK}	<i>A. babirussae</i> Schulze, 1933 ^{K,CHAM,HCK}
<i>C. rossi</i> (Kohls, Sonenshine & Clifford, 1965) ^{K,CHAM,HCK}	<i>O. grenieri</i> Klein, 1965 ^{K,CHAM,HCK}	<i>A. bibroni</i> (Gervais, 1842) ^{CHAM}
	<i>O. gurneyi</i> Warburton, 1926 ^{K,CHAM,HCK}	<i>A. boulegeri</i> Hirst & Hirst, 1910 ^{K,CHAM,HCK}
	<i>O. hermsi</i> Wheeler, Herms & Meyer, 1935 ^{K,CHAM,HCK}	<i>A. brasiliense</i> Aragão, 1908 ^{K,CHAM,HCK}
	<i>O. indica</i> Rau & Rao, 1971 ^{K,CHAM,HCK}	<i>A. breviscutatum</i> Neumann, 1899 ^{HCK}
	<i>O. knoxjonesi</i> Jones & Clifford, 1972 ^{K,HCK}	<i>A. cajennense</i> (Fabricius, 1787) ^{K,CHAM,HCK}
	<i>O. macmillani</i> Hoogstraal & Kohls, 1966 ^{K,CHAM,HCK}	<i>A. calabyi</i> Roberts, 1963 ^{K,CHAM,HCK}
	<i>O. maroccanus</i> Velu, 1919 ^{K,HCK}	<i>A. calcaratum</i> Neumann, 1899 ^{K,CHAM,HCK}
	<i>O. moubata</i> (Murray, 1877) ^{K,CHAM,HCK}	<i>A. chabaudi</i> Rageau, 1964 ^{K,CHAM,HCK}
		<i>A. clypeolatum</i> Neumann, 1899 ^{K,CHAM,HCK}
		<i>A. coelebs</i> Neumann, 1899 ^{K,CHAM,HCK}

A. cohaerens Dönitz, 1909^{K,CHAM,HCK}
A. colasbelcouri (Santos Dias, 1958)^{K,HCK}
A. compressum (Macalister, 1872)^{K,CHAM,HCK}
A. cooperi Nuttall & Warburton, 1908^{K,HCK}
A. cordiferum Neumann, 1899^{K,CHAM,HCK}
A. crassipes (Neumann, 1901)^{K,HCK}
A. crassum Robinson, 1926^{K,CHAM,HCK}
A. crenatum Neumann, 1899^{K,CHAM,HCK}
A. cruciferum Neumann, 1901^{K,CHAM,HCK}
A. curraca Schulze, 1936^{CHAM}
A. cyprium Neumann, 1899^{K,HCK}
A. darvini Hirst & Hirst, 1910^{K,CHAM,HCK}
A. decorosum (Koch, 1867)^{K,CHAM}
A. dissimile Koch, 1844^{K,HCK}
A. dubitatum Neumann, 1899^{HCK}
A. eburneum Gerstäcker, 1873^{K,CHAM,HCK}
A. echidnae Roberts, 1953^{K,HCK}
A. elaphense (Price, 1959)^{K,CHAM,HCK}
A. exornatum Koch, 1844^{K,CHAM,HCK}
A. extraoculatum Neumann, 1899^{K,CHAM,HCK}
A. falsomarmoreum Tonelli-Rondelli, 1935^{K,CHAM,HCK}
A. fimbriatum Koch, 1844^{K,CHAM,HCK}
A. flavomaculatum (Lucas, 1846)^{K,CHAM,HCK}
A. fulvum Neumann, 1899^{K,CHAM,HCK}
A. fuscolineatum (Lucas, 1847)^{K,CHAM,HCK}
A. fuscum Neumann, 1907^{CHAM}
A. geayi Neumann, 1899^{K,HCK}
A. gemma Dönitz, 1909^{K,CHAM,HCK}
A. geochelone Durden, Keirans & Smith, 2002^{HCK}
A. geoemydae (Cantor, 1847)^{K,CHAM,HCK}
A. gervaisi (Lucas, 1847)^{K,CHAM,HCK}
A. glauerti Keirans, King & Sharrad, 1994^{KR,CHAM,HCK}
A. goeldii Neumann, 1899^{K,CHAM,HCK}
A. hainanense Teng, 1981^{K,CHAM,HCK}
A. hebraeum Koch, 1844^{K,CHAM,HCK}
A. helvolum Koch, 1844^{K,CHAM,HCK}
A. hirtum Neumann, 1906^{HCK}
A. humerale Koch, 1844^{K,CHAM,HCK}
A. imitator Kohls, 1958^{K,CHAM,HCK}
A. incisum Neumann, 1906^{K,CHAM,HCK}
A. inopinatum (Santos Dias, 1989)^{HCK}
A. inornatum (Banks, 1909)^{K,CHAM,HCK}
A. integrum Karsch, 1879^{K,CHAM,HCK}
A. javanense (Supino, 1897)^{K,CHAM,HCK}
A. komodoense (Oudemans, 1929)^{K,CHAM,HCK}
A. kraneveldi (Anastos, 1956)^{K,CHAM,HCK}
A. laticaudae Warburton, 1933^{K,CHAM,HCK}
A. latum Koch, 1844^{K,CHAM,HCK}

A. lepidum Dönitz, 1909^{K,CHAM,HCK}
A. limbatum Neumann, 1899^{K,CHAM,HCK}
A. loculosum Neumann, 1907^{K,CHAM,HCK}
A. longirostre (Koch, 1844)^{K,CHAM,HCK}
A. macfarlandi Keirans, Hoogstraal & Clifford, 1973^{K,CHAM,HCK}
A. macropi Roberts, 1953^{K,CHAM,HCK}
A. maculatum Koch, 1844^{K,CHAM,HCK}
A. marmoreum Koch, 1844^{K,CHAM,HCK}
A. moreliae (Koch, 1867)^{K,CHAM,HCK}
A. moyi Roberts, 1953^{K,CHAM,HCK}
A. multipunctum Neumann, 1899^{K,CHAM,HCK}
A. naponense (Packard, 1869)^{K,CHAM,HCK}
A. neumanni Ribaga, 1902^{K,CHAM,HCK}
A. nitidum Hirst & Hirst, 1910^{K,CHAM,HCK}
A. nocens Robinson, 1912 sensu Theiler & Salisbury, 1959^{CHAM}
A. nodosum Neumann, 1899^{K,CHAM,HCK}
A. nuttalli Dönitz, 1909^{K,CHAM,HCK}
A. oblongoguttatum Koch, 1844^{K,CHAM,HCK}
A. orlovi (Kolonin, 1992)^{KR,CHAM,HCK}
A. oudemansi (Neumann, 1910)^{K,HCK}
A. ovale Koch, 1844^{K,CHAM,HCK}
A. pacae Aragão, 1911^{K,CHAM,HCK}
A. papuanum Hirst, 1914^{K,CHAM,HCK}
A. parkeri Fonseca & Aragão, 1952^{CHAM}
A. parvitarum Neumann, 1901^{K,CHAM,HCK}
A. parvum Aragão, 1908^{K,CHAM,HCK}
A. pattoni (Neumann, 1910)^{K,CHAM,HCK}
A. paulopunctatum Neumann, 1899^{K,CHAM,HCK}
A. pecarium Dunn, 1933^{K,CHAM,HCK}
A. perpunctatum (Packard, 1869)^{CHAM}
A. personatum Neumann, 1901^{K,CHAM,HCK}
A. pictum Neumann, 1906^{K,CHAM,HCK}
A. pilosum Neumann, 1899^{K,CHAM,HCK}
A. pomposum Dönitz, 1909^{K,CHAM,HCK}
A. postoculatum Neumann, 1899^{K,CHAM,HCK}
A. pseudoconcolor Aragão, 1908^{K,HCK}
A. pseudoparvum Guglielmo, Mangold & Keirans, 1990^{K,CHAM,HCK}
A. quadricavum (Schulze, 1941)^{K,CHAM,HCK}
A. rhinocerotis (de Geer, 1778)^{K,CHAM,HCK}
A. robinsoni Warburton, 1927^{K,CHAM,HCK}
A. rotundatum Koch, 1844^{K,CHAM,HCK}
A. sabanerae Stoll, 1890^{K,CHAM,HCK}
A. scalpturatum Neumann, 1906^{K,CHAM,HCK}
A. scutatatum Neumann, 1899^{K,CHAM,HCK}
A. soembawensis (Anastos, 1956)^{K,CHAM,HCK}

A. sparsum Neumann, 1899^{K,CHAM,HCK}
A. sphenodonti (Dumbleton, 1943)^{K,CHAM,HCK}
A. splendidum Giebel, 1877^{K,CHAM,HCK}
A. squamosum Kohls, 1953^{K,CHAM,HCK}
A. striatum Koch, 1844^{K,HCK}
A. superbum Santos Dias, 1953^{CHAM}
A. supinoi Neumann, 1905^{K,CHAM,HCK}
A. sylvaticum (de Geer, 1778)^{K,CHAM,HCK}
A. tapirellum Dunn, 1933^{K,CHAM,HCK}
A. testudinarium Koch 1844^{K,CHAM,HCK}
A. testudinis (Conil, 1877)^{K,HCK}
A. tholloni Neumann, 1899^{K,CHAM,HCK}
A. tigrinum Koch, 1844^{K,CHAM,HCK}
A. torrei Pérez Viqueiras, 1934^{K,CHAM,HCK}
A. transversale (Lucas, 1844)^{K,CHAM,HCK}
A. triguttatum Koch, 1844^{K,CHAM,HCK}
A. trimaculatum (Lucas, 1878)^{K,CHAM,HCK}
A. trinitatus Turk, 1948^{CHAM}
A. triste Koch, 1844^{K,CHAM,HCK}
A. tuberculatum Marx, 1894^{K,CHAM,HCK}
A. usingeri Keirans, Hoogstraal & Clifford, 1973^{K,CHAM,HCK}
A. varanense (Supino, 1897)^{K,CHAM,HCK}
A. variegatum (Fabricius, 1794)^{K,CHAM,HCK}
A. varium Koch, 1844^{K,CHAM,HCK}
A. vikirri Keirans, Bull, & Duffield, 1996^{KR,HCK}
A. williamsi Banks, 1924^{K,CHAM,HCK}
Anomalohimalaya (3 species)
A. cricetuli Teng & Huang, 1981^{K,CHAM,HCK}
A. lamai Hoogstraal, Kaiser & Mitchell, 1970^{K,CHAM,HCK}
A. lotzkyi Filippova & Panova, 1978^{K,CHAM,HCK}
Bothriocroton (5 species)
B. auruginans (Schulze, 1936)^{CHAM,HCK}
B. concolor (Neumann, 1899)^{CHAM,HCK}
B. gleopalma (Keirans, King, & Sharrad, 1994)^{CHAM,HCK}
B. hydrosauri (Denny, 1843)^{CHAM,HCK}
B. undatum (Fabricius, 1775)^{HCK}
Cosmiomma (1 species)
C. hippopotamensis (Denny, 1843)^{K,CHAM,HCK}
Cornupalpatum (1 species)
C. burmanicum Poinar & Brown, 2003ND
Dermacentor (36 species)
D. abaensis Teng, 1963^{CHAM,HCK}
D. albipictus (Packard, 1869)^{K,CHAM,HCK}

Table 1. (Cont.)

<i>D. andersoni</i> Stiles, 1908 ^{K,CHAM,HCK}	<i>H. asiatica</i> (Supino, 1897) ^{K,CHAM,HCK}	<i>H. goral</i> Hoogstraal, 1970 ^{K,CHAM,HCK}
<i>D. asper</i> Arthur, 1960 ^{K,CHAM,HCK}	<i>H. atheruri</i> Hoogstraal, Trapido & Kohls, 1965 ^{K,CHAM,HCK}	<i>H. grochovskajae</i> Kolonin, 1992 ^{KR,CHAM,HCK}
<i>D. atrosignatus</i> Neumann, 1906 ^{K,CHAM,HCK}	<i>H. bancrofti</i> Nuttall & Warburton, 1915 ^{K,CHAM,HCK}	<i>H. heinrichi</i> Schulze, 1939 ^{K,CHAM,HCK}
<i>D. auratus</i> Supino, 1897 ^{K,CHAM,HCK}	<i>H. bandicota</i> Hoogstraal & Kohls, 1965 ^{K,CHAM,HCK}	<i>H. himalaya</i> Hoogstraal, 1966 ^{K,HCK}
<i>D. circumguttatus</i> Neumann, 1897 ^{K,CHAM,HCK}	<i>H. bartelsi</i> Schulze, 1938 ^{K,CHAM,HCK}	<i>H. hirsuta</i> Hoogstraal, Trapido & Kohls, 1966 ^{K,CHAM,HCK}
<i>D. compactus</i> Neumann, 1901 ^{K,CHAM,HCK}	<i>H. bequaerti</i> Hoogstraal, 1956 ^{K,CHAM,HCK}	<i>H. hispanica</i> Gil Collado, 1938 ^{K,CHAM,HCK}
<i>D. confractus</i> (Schulze, 1933) ^{CHAM}	<i>H. birmaniae</i> Supino, 1897 ^{K,CHAM, HCK}	<i>H. hoodi</i> Warburton & Nuttall, 1909 ^{K,CHAM,HCK}
<i>D. daghestanicus</i> Olenov, 1928 ^{CHAM}	<i>H. bispinosa</i> Neumann, 1897 ^{K,CHAM, HCK}	<i>H. hoogstraali</i> Kohls, 1950 ^{K,CHAM,HCK}
<i>D. dispar</i> Cooley, 1937 ^{K,CHAM,HCK}	<i>H. borneata</i> Hoogstraal, 1971 ^{K,CHAM,HCK}	<i>H. houyi</i> Nuttall & Warburton, 1915 ^{K,CHAM,HCK}
<i>D. dissimilis</i> Cooley, 1947 ^{K,CHAM,HCK}	<i>H. bremneri</i> Roberts, 1963 ^{K,CHAM,HCK}	<i>H. howletti</i> Warburton, 1913 ^{K,CHAM,HCK}
<i>D. everestianus</i> Hirst, 1926 ^{K,CHAM,HCK}	<i>H. calcarata</i> Neumann, 1902 ^{K,CHAM,HCK}	<i>H. humerosa</i> Warburton & Nuttall, 1909 ^{K,CHAM,HCK}
<i>D. halli</i> McIntosh, 1931 ^{K,CHAM,HCK}	<i>H. calva</i> Nuttall & Warburton, 1915 ^{K,CHAM,HCK}	<i>H. hylobatis</i> Schulze, 1933 ^{K,CHAM,HCK}
<i>D. hunteri</i> Bishopp, 1912 ^{K,CHAM,HCK}	<i>H. campanulata</i> Warburton, 1908 ^{K,CHAM,HCK}	<i>H. hyracophila</i> Hoogstraal, Walker & Neitz, 1971 ^{K,CHAM,HCK}
<i>D. imitans</i> Warburton, 1933 ^{K,CHAM,HCK}	<i>H. canestrinii</i> (Supino, 1897) ^{K,CHAM,HCK}	<i>H. hystricis</i> Supino, 1897 ^{K,CHAM,HCK}
<i>D. latus</i> Cooley, 1937 ^{K,CHAM,HCK}	<i>H. capricornis</i> Hoogstraal, 1966 ^{K,CHAM,HCK}	<i>H. ias</i> Nakamura & Yajima, 1937 ^{K,CHAM,HCK}
<i>D. marginatus</i> (Sulzer, 1776) ^{K,CHAM,HCK}	<i>H. caucasica</i> Olenov, 1928 ^{K,CHAM,HCK}	<i>H. indica</i> Warburton, 1910 ^{K,CHAM,HCK}
<i>D. montanus</i> Filippova & Panova, 1974 ^{K,CHAM,HCK}	<i>H. celebensis</i> Hoogstraal, Trapido & Kohls, 1965 ^{K,CHAM,HCK}	<i>H. indoflava</i> Dhanda & Bhat, 1968 ^{K,CHAM,HCK}
<i>D. nigrolineatus</i> (Packard, 1869) ^{CHAM}	<i>H. chordeilis</i> (Packard, 1869) ^{K,CHAM,HCK}	<i>H. inermis</i> Birula, 1895 ^{K,CHAM,HCK}
<i>D. nitens</i> Neumann, 1897 ^{K,CHAM,HCK}	<i>H. cinnabarina</i> Koch, 1844 ^{CHAM}	<i>H. intermedia</i> Warburton & Nuttall, 1909 ^{K,CHAM,HCK}
<i>D. niveus</i> Neumann, 1897 ^{K,CHAM,HCK}	<i>H. colasbelcouri</i> (Santos Dias, 1958) ^{CHAM,HCK}	<i>H. japonica</i> Warburton, 1908 ^{K,CHAM,HCK}
<i>D. nuttalli</i> Olenov, 1928 ^{K,CHAM,HCK}	<i>H. concinna</i> Koch, 1844 ^{K,CHAM,HCK}	<i>H. juxtakochi</i> Cooley, 1946 ^{K,CHAM,HCK}
<i>D. occidentalis</i> Marx, 1892 ^{K,CHAM,HCK}	<i>H. cooleyi</i> Bedford, 1929 ^{K,CHAM,HCK}	<i>H. kadarsani</i> Hoogstraal & Wassef, 1977 ^{K,CHAM,HCK}
<i>D. parumapertus</i> Neumann, 1901 ^{K,CHAM,HCK}	<i>H. cornigera</i> Neumann, 1897 ^{K,CHAM,HCK}	<i>H. kashmirensis</i> Hoogstraal & Varma, 1962 ^{K,CHAM,HCK}
<i>D. pavlovskiyi</i> Olenov, 1927 ^{K,CHAM,HCK}	<i>H. cornupunctata</i> Hoogstraal & Varma, 1962 ^{K,CHAM,HCK}	<i>H. kinneari</i> Warburton, 1913 ^{K,CHAM,HCK}
<i>D. pomerantzevi</i> Serdyukova, 1951 ^{K,CHAM,HCK}	<i>H. cuspidata</i> Warburton, 1910 ^{K,CHAM,HCK}	<i>H. kitaokai</i> Hoogstraal, 1969 ^{K,CHAM,HCK}
<i>D. raskemensis</i> Pomerantsev, 1946 ^{K,CHAM,HCK}	<i>H. dangi</i> Phan Trong, 1977 ^{CHAM,HCK}	<i>H. koningsbergeri</i> Warburton & Nuttall, 1909 ^{K,CHAM,HCK}
<i>D. reticulatus</i> (Fabricius, 1794) ^{K,CHAM,HCK}	<i>H. danieli</i> Černý & Hoogstraal, 1977 ^{K,CHAM,HCK}	<i>H. kopetdaghica</i> Kerbabaev, 1962 ^{K,CHAM,HCK}
<i>D. rhinocerimus</i> (Denny, 1843) ^{K,CHAM,HCK}	<i>H. darjeeling</i> Hoogstraal & Dhanda, 1970 ^{K,CHAM,HCK}	<i>H. kutchensis</i> Hoogstraal & Trapido, 1963 ^{K,CHAM,HCK}
<i>D. silvarum</i> Olenov, 1931 ^{K,CHAM,HCK}	<i>H. davisii</i> Hoogstraal, Dhanda & Bhat, 1970 ^{K,CHAM,HCK}	<i>H. kyasamurensis</i> Trapido, Hoogstraal & Rajagopalan, 1964 ^{K,CHAM,HCK}
<i>D. sinicus</i> Schulze, 1932 ^{K,CHAM,HCK}	<i>H. demidovae</i> Emel'yanova, 1978 ^{KR,CHAM,HCK}	<i>H. lagostrophii</i> Roberts, 1963 ^{K,CHAM,HCK}
<i>D. steini</i> Schulze, 1933 ^{K,CHAM,HCK}	<i>H. doenitzi</i> Warburton, & Nuttall, 1909 ^{K,CHAM,HCK}	<i>H. lagrangei</i> Larrousse, 1925 ^{K,CHAM,HCK}
<i>D. taiwanensis</i> Sugimoto, 1935 ^{K,CHAM,HCK}	<i>H. elliptica</i> (Koch, 1844) ^{CHAM,HCK}	<i>H. laocayensis</i> Phan Trong, 1977 ^{HCK}
<i>D. ushakovae</i> Filippova & Panova, 1987 ^{K,KR,HCK}	<i>H. elongata</i> Neumann, 1897 ^{K,CHAM,HCK}	<i>H. leachi</i> (Audouin, 1826) ^{K,CHAM,HCK}
<i>D. variabilis</i> (Say, 1821) ^{K,CHAM,HCK}	<i>H. erinacei</i> Pavesi, 1884 ^{K,CHAM,HCK}	<i>H. lemuris</i> Hoogstraal, 1953 ^{K,CHAM,HCK}
<i>Haemaphysalis</i> (166 species)	<i>H. eupleres</i> Hoogstraal, Kohls & Trapido, 1965 ^{K,CHAM,HCK}	<i>H. leporispalustris</i> (Packard, 1869) ^{K,CHAM,HCK}
<i>H. aborensis</i> Warburton, 1913 ^{K,CHAM,HCK}	<i>H. filippovae</i> Bolotin, 1979 ^{KR,HCK}	<i>H. lobachovi</i> Kolonin, 1995 ^{KR,CHAM,HCK}
<i>H. aciculifer</i> Warburton, 1913 ^{K,CHAM,HCK}	<i>H. flava</i> Newmann, 1987 ^{K,CHAM,HCK}	<i>H. longicornis</i> Neumann, 1901 ^{K,CHAM,HCK}
<i>H. aculeata</i> Lavarra 1904 ^{K,CHAM,HCK}	<i>H. formosensis</i> Neumann, 1913 ^{K,CHAM,HCK}	<i>H. luzonensis</i> Hoogstraal & Parrish, 1968 ^{K,CHAM,HCK}
<i>H. adleri</i> Feldman-Muhsam, 1951 ^{K,CHAM,HCK}	<i>H. fossae</i> Hoogstraal, 1953 ^{K,CHAM,HCK}	<i>H. madagascariensis</i> Colas-Belcour & Millot, 1948 ^{K,CHAM,HCK}
<i>H. anomala</i> Warburton, 1913 ^{K,CHAM,HCK}	<i>H. fujisana</i> Kitaoka, 1970 ^{K,CHAM,HCK}	
<i>H. anomalocerae</i> Teng & Cui, 1984 ^{KR,HCK}	<i>H. garhwalensis</i> Dhanda & Bhat, 1968 ^{K,CHAM,HCK}	
<i>H. anoplos</i> Hoogstraal, Uilenberg & Klein, 1967 ^{K,CHAM,HCK}		
<i>H. aponommoides</i> Warburton, 1913 ^{K,CHAM,HCK}		

- H. mageshimaensis* Saito & Hoogstraal, 1973^{K,CHAM,HCK}
H. megalaimae Rajagopalan, 1963^{K,CHAM,HCK}
H. megaspinosa Saito, 1969^{K,CHAM,HCK}
H. menglaensis Pang, Chen & Xiang, 1982^{KR,HCK}
H. minuta Kohls, 1950^{K,CHAM,HCK}
H. mjoebergi Warburton, 1926^{K,CHAM,HCK}
H. montgomeryi Nuttall, 1912^{K,CHAM,HCK}
H. moreli Camicas, Hoogstraal & El Kammah, 1972^{K,CHAM,HCK}
H. moschisuga Teng, 1980^{KR,CHAM,HCK}
H. muhsamae Santos Dias, 1954^{CHAM,HCK}
H. nadchatrami Hoogstraal, Trapido & Kohls, 1965^{K,CHAM,HCK}
H. nepalensis Hoogstraal, 1962^{K,CHAM,HCK}
H. nesomys Hoogstraal, Uilenberg & Klein, 1966^{K,CHAM,HCK}
H. norvali Hoogstraal & Wassef, 1983^{K,CHAM,HCK}
H. novaeguineae Hirst, 1914^{K,CHAM,HCK}
H. obesa Larrousse, 1925^{K,CHAM,HCK}
H. obtusa Dönitz, 1910^{K,CHAM,HCK}
H. orientalis Nuttall & Warburton, 1915^{K,CHAM,HCK}
H. ornithophila Hoogstraal & Kohls, 1959^{K,CHAM,HCK}
H. palawanensis Kohls, 1950^{K,CHAM,HCK}
H. papuana Thorell, 1883^{K,CHAM,HCK}
H. paraleachi Camicas, Hoogstraal & El Kammah, 1983^{K,CHAM,HCK}
H. paraturturis Hoogstraal, Trapido & Rebello, 1963^{K,CHAM,HCK}
H. parmata Neumann, 1905^{K,CHAM,HCK}
H. parva Neumann, 1897^{K,CHAM,HCK}
H. pavlovskiyi Pospelova-Shtrom, 1935^{K,HCK}
H. pedetes Hoogstraal, 1972^{K,CHAM,HCK}
H. pentalagi Pospelova-Shtrom, 1935^{K,CHAM,HCK}
H. petrogalis Roberts, 1970^{K,CHAM,HCK}
H. phasiana Satto, Hoogstraal & Wassef, 1974^{K,CHAM,HCK}
H. pospelovashtroniae Hoogstraal, 1966^{K,CHAM,HCK}
H. primitiva Teng, 1982^{KR,CHAM,HCK}
H. psalidos Hoogstraal, Kohls & Parrish, 1967^{K,CHAM,HCK}
H. punctaleachi Camicas, Hoogstraal & El Kammah, 1973^{K,CHAM,HCK}
H. punctata Canestrini & Fanzago, 1878^{K,CHAM,HCK}
H. quadriaculeata Kolonin, 1992^{KR,CHAM,HCK}
H. qinghaiensis Teng, 1980^{KR,CHAM,HCK}
H. ramachandrai Dhanda, Hoogstraal & Bhat, 1970^{K,CHAM,HCK}
H. ratti Kohls, 1948^{K,CHAM,HCK}
H. renschi Schulze, 1933^{K,CHAM,HCK}
H. roubaudi Toumanoff, 1940^{K,CHAM,HCK}
H. rugosa Santos Dias, 1956^{K,CHAM,HCK}
H. rusae Kohls, 1950^{K,CHAM,HCK}
H. sambar Hoogstraal, 1971^{K,CHAM,HCK}
H. sciuri Kohls, 1950^{K,CHAM,HCK}
H. semermis Neumann, 1901^{K,CHAM,HCK}
H. shimoga Trapido & Hoogstraal, 1964^{K,CHAM,HCK}
H. silacea Robinson, 1912^{K,CHAM,HCK}
H. silvafelis Hoogstraal & Trapido, 1963^{K,CHAM,HCK}
H. simplex Neumann, 1897^{K,CHAM,HCK}
H. simplicima Hoogstraal & Wassef, 1979^{K,CHAM,HCK}
H. sinensis Zhang, 1981^{KR,HCK}
H. spinigera Neumann, 1897^{K,CHAM,HCK}
H. spinulosa Neumann, 1906^{K,CHAM,HCK}
H. subelongata Hoogstraal, 1953^{K,CHAM,HCK}
H. subterra Hoogstraal, El Kammah & Camicas, 1992^{K,CHAM,HCK}
H. sulcata Canestrini & Fanzago, 1878^{K,CHAM,HCK}
H. sumatraensis Hoogstraal, El Kammah, Kadarsan & Anastos, 1971^{K,CHAM,HCK}
H. sundrai Sharif, 1928^{K,CHAM,HCK}
H. suntzovi Kolonin, 1993^{KR,CHAM,HCK}
H. susphilippensis Hoogstraal, Kohls & Parrish, 1968^{K,CHAM,HCK}
H. taiwana Sugimoto, 1936^{K,CHAM,HCK}
H. tauffliebi Morel, 1965^{K,CHAM,HCK}
H. theilerae Hoogstraal, 1953^{K,CHAM,HCK}
H. tibetensis Hoogstraal, 1965^{K,CHAM,HCK}
H. tiptoni Hoogstraal, 1953^{K,CHAM,HCK}
H. toxopei Warburton, 1927^{K,CHAM,HCK}
H. traguli Oudemans, 1928^{K,CHAM,HCK}
H. traubi Kohls, 1955^{K,CHAM,HCK}
H. turturis Nuttall & Warburton, 1915^{K,CHAM,HCK}
H. verticalis Itagaki, Noda & Yamaguchi, 1944^{K,CHAM,HCK}
H. vidua Warburton & Nuttall, 1909^{K,CHAM,HCK}
H. vietnamensis Hoogstraal & Wilson, 1966^{K,HCK}
H. warburtoni Nuttall, 1912^{K,CHAM,HCK}
H. wellingtoni Nuttall & Warburton, 1908^{K,CHAM,HCK}
H. xinjiangensis Teng, 1980^{KR,CHAM,HCK}
H. yeni Toumanoff, 1944^{K,CHAM,HCK}
H. zumpti Hoogstraal & El Kammah, 1974^{K,CHAM,HCK}
Hyalomma (25 species)
H. aegyptium (Linnaeus, 1758)^{K,CHAM,HCK}
H. albiparatum Schulze, 1919^{K,CHAM,HCK}
H. anaticum Koch, 1844^{K,CHAM,HCK}
H. arabica Pegram, Hoogstraal & Wassef, 1982^{K,CHAM,HCK}
H. asiaticum Schulze & Schlottke, 1930^{K,CHAM,HCK}
H. brevipunctata Sharif, 1928^{K,CHAM,HCK}
H. detritum Schulze, 1919^{K,CHAM,HCK}
H. dromedarii Koch, 1844^{K,CHAM,HCK}
H. erythraeum Tonelli-Rondelli, 1932^{K,CHAM,HCK}
H. franchinii Tonelli-Rondelli, 1932^{K,CHAM,HCK}
H. hussaini Sharif, 1928^{K,CHAM,HCK}
H. hystricis Dhanda & Raja, 1974^{KR,CHAM,HCK}
H. impeltatum Schulze & Schlottke, 1930^{K,CHAM,HCK}
H. impressum Koch, 1844^{K,CHAM,HCK}
H. kumari Sharif, 1928^{K,CHAM,HCK}
H. lusitanicum Koch, 1844^{K,CHAM,HCK}
H. marginatum Koch, 1844^{K,CHAM,HCK}
H. nitidum Schulze, 1919^{K,CHAM,HCK}
H. punt Hoogstraal, Kaiser & Pedersen, 1969^{K,CHAM,HCK}
H. rhipicephaloides Neumann, 1901^{K,CHAM,HCK}
H. rufipes Koch, 1844^{K,HCK}
H. schulzei Olenev, 1931^{K,CHAM,HCK}
H. sinaii Feldman-Muhsam, 1960^{HCK}
H. truncatum Koch, 1844^{K,CHAM,HCK}
H. turanicum Pomerantsev, 1946^{HCK}
Ixodes (249 species)
I. abrocomae Lahille, 1917^{CHAM,HCK}
I. acuminatus Neumann, 1901^{K,CHAM,HCK}
I. acutitarsus (Karsch, 1880)^{K,CHAM,HCK}
I. affinis Neumann, 1899^{K,CHAM,HCK}
I. albignaci Uilenberg & Hoogstraal, 1969^{K,CHAM,HCK}
I. alluaudi Neumann, 1913^{K,CHAM,HCK}
I. amarali Fonseca, 1935^{K,CHAM,HCK}
I. amersoni Kohls, 1966^{K,HCK}
I. anatis Chilton, 1904^{K,HCK}
I. andimus Kohls, 1956^{K,CHAM,HCK}
I. angustus Neumann, 1899^{K,CHAM,HCK}
I. antechimi Roberts, 1960^{K,CHAM,HCK}
I. apteridis Maskell, 1897^{CHAM}
I. apronophorus Schulze, 1924^{K,CHAM,HCK}
I. arabukiensis Arthur, 1959^{K,HCK}
I. aragaii Fonseca, 1935^{CHAM,HCK}
I. arboricola Schulze & Schlottke, 1930^{K,CHAM,HCK}
I. arebiensis Arthur, 1956^{K,CHAM,HCK}
I. asanumai Kitaoka, 1973^{K,CHAM,HCK}
I. aulacodi Arthur, 1956^{K,CHAM,HCK}
I. auriculaelongae Arthur, 1958^{K,CHAM,HCK}
I. auritulus Neumann, 1904^{K,CHAM,HCK}

Table 1. (Cont.)

<i>I. australiensis</i> Neumann, 1904 ^{K,CHAM,HCK}	<i>I. djaronensis</i> Neumann, 1907 ^{K,CHAM,HCK}	<i>I. kerguelenensis</i> Andre & Colas-Belcour, 1942 ^{K,CHAM,HCK}
<i>I. baergi</i> Cooley & Kohls, 1942 ^{K,CHAM,HCK}	<i>I. domerguei</i> Uilenberg & Hoogstraal, 1965 ^{K,CHAM,HCK}	<i>I. kingi</i> Bishopp, 1911 ^{K,CHAM,HCK}
<i>I. bakeri</i> Arthur & Clifford, 1961 ^{K,CHAM,HCK}	<i>I. donarthuri</i> Santos Dias, 1980 ^{KR,CHAM}	<i>I. kohlsi</i> Arthur, 1955 ^{K,CHAM,HCK}
<i>I. banksi</i> Bishopp, 1911 ^{K,CHAM,HCK}	<i>I. downsi</i> Kohls, 1957 ^{K,CHAM,HCK}	<i>I. kopsteini</i> (Oudemans, 1926) ^{K,CHAM,HCK}
<i>I. bedfordi</i> Arthur, 1959 ^{K,CHAM,HCK}	<i>I. drakensbergensis</i> Clifford, Theiler & Baker, 1975 ^{K,CHAM,HCK}	<i>I. kuntzi</i> Hoogstraal & Kohls, 1965 ^{K,CHAM,HCK}
<i>I. bequaerti</i> Cooley & Kohls, 1945 ^{K,CHAM,HCK}	<i>I. eadsi</i> Kohls & Clifford, 1964 ^{K,CHAM,HCK}	<i>I. laguri</i> Olenev, 1929 <i>sensu</i> Olenev, 1931 ^{K,CHAM,HCK}
<i>I. berleseii</i> Birula, 1895 ^{K,CHAM,HCK}	<i>I. eastoni</i> Keirans & Clifford, 1983 ^{K,CHAM,HCK}	<i>I. lasallei</i> Mendez Arocha & Ortiz, 1958 ^{K,CHAM,HCK}
<i>I. bivari</i> Santos Dias, 1990 ^{KR,CHAM,HCK}	<i>I. eichhorni</i> Nuttall, 1916 ^{K,CHAM,HCK}	<i>I. latus</i> Arthur, 1958 ^{K,CHAM,HCK}
<i>I. boliviensis</i> Neumann, 1904 ^{K,HCK}	<i>I. eldaricus</i> Dzshaparidze, 1950 ^{K,CHAM,HCK}	<i>I. laysanensis</i> Wilson, 1964 ^{K,CHAM,HCK}
<i>I. brewsterae</i> Keirans, Clifford & Walker, 1982 ^{K,CHAM,HCK}	<i>I. elongatus</i> Bedford, 1929 ^{K,CHAM,HCK}	<i>I. lemuris</i> Arthur, 1958 ^{K,CHAM,HCK}
<i>I. browningi</i> Arthur, 1956 ^{K,CHAM,HCK}	<i>I. eudypitidis</i> Maskell, 1885 ^{K,CHAM,HCK}	<i>I. levisi</i> Arthur, 1965 ^{K,CHAM,HCK}
<i>I. brumpti</i> Morel, 1965 ^{K,CHAM,HCK}	<i>I. euplecti</i> Arthur, 1958 ^{K,CHAM,HCK}	<i>I. lividus</i> Koch, 1844 ^{K,CHAM,HCK}
<i>I. brunneus</i> Koch, 1844 ^{K,CHAM,HCK}	<i>I. evansi</i> Arthur, 1956 ^{K,CHAM,HCK}	<i>I. longiscutatus</i> Boero, 1944 ^{K,CHAM,HCK}
<i>I. calcarhebes</i> Arthur & Zulu, 1980 ^{K,CHAM,HCK}	<i>I. feicalis</i> Warburton & Nuttall, 1909 ^{K,CHAM,HCK}	<i>I. loricatus</i> Neumann, 1899 ^{K,CHAM,HCK}
<i>I. caledonicus</i> Nuttall, 1910 ^{K,CHAM,HCK}	<i>I. festai</i> Tonelli-Rondelli, 1926 ^{K,CHAM,HCK}	<i>I. loveridgei</i> Arthur, 1958 ^{K,CHAM,HCK}
<i>I. canisuga</i> Johnston, 1849 ^{K,CHAM,HCK}	<i>I. filippovae</i> Černý, 1961 ^{CHAM,HCK}	<i>I. luciae</i> Sénevet, 1940 ^{K,CHAM,HCK}
<i>I. capromydis</i> Černý, 1966 ^{K,CHAM,HCK}	<i>I. fossulatus</i> Neumann, 1899 ^{K,CHAM,HCK}	<i>I. lunatus</i> Neumann, 1907 ^{K,CHAM,HCK}
<i>I. catherinei</i> Keirans, Clifford & Walker, 1982 ^{K,CHAM,HCK}	<i>I. frontalis</i> (Panzer, 1798) ^{K,CHAM,HCK}	<i>I. luxuriosus</i> Schulze, 1932 ^{K,CHAM,HCK}
<i>I. cavipalpus</i> Nuttall & Warburton, 1908 ^{K,CHAM,HCK}	<i>I. fuscipes</i> Koch, 1844 ^{K,CHAM,HCK}	<i>I. macfarlanei</i> Keirans, Clifford & Walker, 1982 ^{K,CHAM,HCK}
<i>I. ceylonensis</i> Kohls, 1950 ^{K,CHAM,HCK}	<i>I. galapagoensis</i> Clifford & Hoogstraal, 1980 ^{K,CHAM,HCK}	<i>I. malayensis</i> Kohls, 1962 ^{K,CHAM,HCK}
<i>I. chilensis</i> Kohls, 1957 ^{K,CHAM,HCK}	<i>I. ghilarovi</i> Filippova & Panova, 1988 ^{K,CHAM,HCK}	<i>I. marmotae</i> Cooley & Kohls, 1938 ^{K,CHAM,HCK}
<i>I. colasbelcouri</i> Arthur, 1957 ^{K,CHAM,HCK}	<i>I. gibbosus</i> Nuttall, 1916 ^{K,CHAM,HCK}	<i>I. marxi</i> Banks, 1908 ^{K,CHAM,HCK}
<i>I. collocaliae</i> Schulze, 1937 ^{K,CHAM,HCK}	<i>I. granulatus</i> Supino, 1897 ^{K,CHAM,HCK}	<i>I. maslovi</i> Emel'yanova & Kozlovskaya, 1967 ^{K,HCK}
<i>I. columnae</i> Takada & Fujita, 1992 ^{KR,HCK}	<i>I. gregsoni</i> Lindquist, Wu & Redner, 1999 ^{HCK}	<i>I. matopi</i> Spickett, Keirans, Norval & Clifford, 1981 ^{K,CHAM,HCK}
<i>I. coneptati</i> Cooley & Kohls, 1943 ^{K,CHAM,HCK}	<i>I. guatemalensis</i> Kohls, 1956 ^{K,CHAM,HCK}	<i>I. mexicanus</i> Cooley & Kohls, 1942 ^{K,CHAM,HCK}
<i>I. confusus</i> Roberts, 1960 ^{K,CHAM,HCK}	<i>I. hearlei</i> Gregson, 1941 ^{K,CHAM,HCK}	<i>I. minor</i> Neumann, 1902 ^{K,CHAM,HCK}
<i>I. cookei</i> Packard, 1869 ^{K,CHAM,HCK}	<i>I. heinrichi</i> Arthur, 1962 ^{K,CHAM,HCK}	<i>I. minutae</i> Arthur, 1959 ^{K,CHAM,HCK}
<i>I. cooleyi</i> Aragão & Fonseca, 1951 ^{K,CHAM,HCK}	<i>I. hexagonus</i> Leach, 1815 ^{K,CHAM,HCK}	<i>I. mitchelli</i> Kohls, Clifford & Hoogstraal, 1970 ^{K,CHAM,HCK}
<i>I. copei</i> Wilson, 1980 ^{K,CHAM,HCK}	<i>I. himalayensis</i> Dhanda & Kulkarni, 1969 ^{K,CHAM,HCK}	<i>I. monospinosus</i> Saito, 1968 ^{K,CHAM,HCK}
<i>I. cordifer</i> Neumann, 1908 ^{K,CHAM,HCK}	<i>I. hirsti</i> Hassall, 1931 ^{K,CHAM,HCK}	<i>I. montoyanus</i> Cooley, 1944 ^{K,CHAM,HCK}
<i>I. cornuae</i> Arthur, 1960 ^{K,CHAM,HCK}	<i>I. holocyclus</i> Neumann, 1899 ^{K,CHAM,HCK}	<i>I. moreli</i> Arthur, 1957 ^{K,CHAM,HCK}
<i>I. cornuatus</i> Roberts, 1960 ^{K,HCK}	<i>I. hoogstraali</i> Arthur, 1955 ^{K,CHAM,HCK}	<i>I. moscharius</i> Teng, 1982 ^{KR,CHAM,HCK}
<i>I. corvini</i> Keirans, Clifford & Walker, 1982 ^{K,CHAM,HCK}	<i>I. howelli</i> Cooley & Kohls, 1938 ^{K,CHAM,HCK}	<i>I. moschiferi</i> Nemenz, 1968 ^{K,CHAM,HCK}
<i>I. cremulatus</i> Koch, 1844 ^{K,CHAM,HCK}	<i>I. hyatti</i> Clifford, Hoogstraal & Kohls, 1971 ^{K,CHAM,HCK}	<i>I. muniensis</i> Arthur & Burrow, 1957 ^{K,CHAM,HCK}
<i>I. cuernavacensis</i> Kohls & Clifford, 1966 ^{K,CHAM,HCK}	<i>I. hydromyidis</i> Swan, 1931 ^{K,CHAM,HCK}	<i>I. muris</i> Bishopp & Smith, 1937 ^{K,CHAM,HCK}
<i>I. cumulatimpunctatus</i> Schulze, 1943 ^{K,CHAM,HCK}	<i>I. jacksoni</i> Hoogstraal, 1967 ^{K,CHAM,HCK}	<i>I. murreleti</i> Cooley & Kohls, 1945 ^{K,CHAM,HCK}
<i>I. dampfi</i> Cooley, 1943 ^{K,CHAM,HCK}	<i>I. jellisoni</i> Cooley & Kohls, 1938 ^{K,CHAM,HCK}	<i>I. myospalacis</i> Teng, 1986 ^{K,CHAM,HCK}
<i>I. daveyi</i> Nuttall, 1913 ^{K,CHAM,HCK}	<i>I. jonesae</i> Kohls, Sonenshine & Clifford, 1969 ^{K,CHAM,HCK}	<i>I. myotomys</i> Clifford & Hoogstraal, 1970 ^{K,CHAM,HCK}
<i>I. dawesi</i> Arthur, 1956 ^{K,CHAM,HCK}	<i>I. kaiseri</i> Arthur, 1957 ^{K,CHAM,HCK}	<i>I. myrmecobii</i> Roberts, 1962 ^{K,CHAM,HCK}
<i>I. dendrolagi</i> Wilson, 1967 ^{K,CHAM,HCK}	<i>I. kashimiricus</i> Pomerantsev, 1948 ^{K,CHAM,HCK}	<i>I. nairobiensis</i> Nuttall, 1916 ^{K,CHAM,HCK}
<i>I. dentatus</i> Marx, 1899 ^{K,CHAM,HCK}	<i>I. kazakstani</i> Olenev & Sorokoumov, 1934 ^{K,CHAM,HCK}	<i>I. nchisiensis</i> Arthur, 1958 ^{K,CHAM,HCK}
<i>I. dicei</i> Keirans & Ajohola, 2003	<i>I. kempfi</i> Nuttall, 1913 ^{CHAM}	
<i>I. diomedae</i> Arthur, 1958 ^{K,CHAM,HCK}		
<i>I. diversifossus</i> Neumann, 1899 ^{K,CHAM,HCK}		

- I. nectomys* Kohls, 1957^{K,CHAM,HCK}
I. neitzi Clifford, Walker & Keirans, 1977^{K,CHAM,HCK}
I. neotomae Cooley, 1944^{K,CHAM,HCK,a}
I. nesomys Uilenberg & Hoogstraal, 1969^{K,CHAM,HCK}
I. neuquenensis Ringuelet, 1947^{K,CHAM,HCK}
I. nicolasi Santos Dias, 1982^{KR,CHAM,HCK}
I. nipponensis Kitaoka & Saito, 1967^{K,CHAM,HCK}
I. nitens Neumann, 1904^{K,CHAM,HCK}
I. nuttalli Lahille, 1913^{K,CHAM,HCK}
I. nuttallianus Schulze, 1930^{K,CHAM,HCK}
I. occultus Pomerantsev, 1946^{K,CHAM,HCK}
I. ochotonae Gregson, 1941^{K,CHAM,HCK}
I. okapiae Arthur, 1956^{K,CHAM,HCK}
I. oldi Nuttall, 1913^{K,CHAM,HCK}
I. ornithorhynchi Lucas, 1846^{K,CHAM,HCK}
I. ovatus Neumann, 1899^{K,CHAM,HCK}
I. pacificus Cooley & Kohls, 1943^{K,CHAM,HCK}
I. paranensis Barros-Battesti, Arzua, Pichorim & Keirans, 2003
I. pararicinus Keirans & Clifford, 1985^{K,CHAM,HCK}
I. pavlovskiyi Pomerantsev, 1946^{K,CHAM,HCK}
I. percavatus Neumann, 1906^{K,CHAM,HCK}
I. peromysci Augustson, 1940^{K,CHAM,HCK}
I. persulcatus Schulze, 1930^{K,CHAM,HCK}
I. petauristae Warburton, 1933^{K,CHAM,HCK}
I. philipi Keirans & Kohls, 1970^{K,CHAM,HCK}
I. pilosus Koch, 1844^{K,CHAM,HCK}
I. pomerantzi Kohls, 1956^{K,CHAM,HCK}
I. pomeranzevi Serdyukova, 1941^{K,CHAM,HCK}
I. priscicollaris Schulze, 1932^{K,CHAM,HCK}
I. procaviae Arthur & Burrow, 1957^{K,CHAM,HCK}
I. prokopjevi (Emel'yanova, 1979)^{KR,CHAM,HCK}
I. radfordi Kohls, 1948^{K,CHAM,HCK}
I. rageaui Arthur, 1958^{K,CHAM,HCK}
I. randriansoloi Uilenberg & Hoogstraal, 1969^{K,CHAM,HCK}
I. rangtangensis Teng, 1973^{KR,HCK}
I. rarus Neumann, 1899^{K,CHAM,HCK}
I. redikorzevi Olenev, 1927^{K,CHAM,HCK}
I. rhabdomysae Arthur, 1959^{K,CHAM,HCK}
I. vicinus (Linnaeus, 1758)^{K,CHAM,HCK}
I. rothschildi Nuttall & Warburton, 1911^{K,CHAM,HCK}
I. rotundatus Arthur, 1958^{K,CHAM,HCK}
I. rubicundus Neumann, 1904^{K,CHAM,HCK}
I. rubidus Neumann, 1901^{K,CHAM,HCK}
I. rugicollis Schulze & Schlottke, 1930^{K,CHAM,HCK}
I. rugosus Bishopp, 1911^{K,CHAM,HCK}
I. sachalinensis Filippova, 1971^{K,HCK}
I. scapularis Say, 1821^{K,CHAM,HCK}
I. schillingsi Neumann, 1901^{K,CHAM,HCK}
I. schulzei Aragão & Fonseca, 1951^{K,CHAM,HCK}
I. sculptus Neumann, 1904^{K,CHAM,HCK}
I. semenovi Olenev, 1929^{K,CHAM,HCK}
I. shahi Clifford, Hoogstraal & Kohls, 1971^{K,CHAM,HCK}
I. siamensis Kitaoka & Suzuki, 1983^{KR,HCK}
I. sigelos Keirans, Clifford & Corwin, 1976^{K,HCK}
I. signatus Birula, 1895^{K,CHAM,HCK}
I. simplex Neumann, 1906^{K,CHAM,HCK}
I. sinaloa Kohls & Clifford, 1966^{K,CHAM,HCK}
I. sinensis Teng, 1977^{K,CHAM,HCK}
I. soricis Gregson, 1942^{K,CHAM,HCK}
I. spinae Arthur, 1958^{K,CHAM,HCK}
I. spinicoxalis Neumann, 1899^{K,CHAM,HCK}
I. spinipalpis Hadwen & Nuttall, 1916^{K,CHAM,HCK}
I. steini Schulze, 1932^{K,CHAM,HCK}
I. stilesi Neumann, 1911^{K,CHAM,HCK}
I. stromi Filippova, 1957^{K,CHAM,HCK}
I. subterraneus Filippova, 1961^{K,CHAM,HCK}
I. taglei Kohls, 1969^{K,CHAM,HCK}
I. tamaulipas Kohls & Clifford, 1966^{K,CHAM,HCK}
I. tancitarium Cooley & Kohls, 1942^{K,CHAM,HCK}
I. tanuki Saito, 1964^{K,CHAM,HCK}
I. tapirus Kohls, 1956^{K,CHAM,HCK}
I. tasmani Neumann, 1899^{K,CHAM,HCK}
I. tecpanensis Kohls, 1956^{K,CHAM,HCK}
I. texanus Banks, 1909^{K,CHAM,HCK}
I. theilerae Arthur, 1953^{K,CHAM,HCK}
I. thomasaе Arthur & Burrow, 1957^{K,CHAM,HCK}
I. tiptoni Kohls & Clifford, 1962^{K,CHAM,HCK}
I. tovari Cooley, 1945^{K,CHAM,HCK}
I. transvaalensis Clifford & Hoogstraal, 1966^{K,CHAM,HCK}
I. trianguliceps Birula, 1895^{K,CHAM,HCK}
I. trichosuri Roberts, 1960^{K,CHAM,HCK}
I. tropicalis Kohls, 1956^{K,CHAM,HCK}
I. turdus Nakatsuji, 1942^{K,CHAM,HCK}
I. ugandamus Neumann, 1906^{K,CHAM,HCK}
I. unicavatus Neumann, 1908^{K,CHAM,HCK}
I. uriae White, 1852^{K,CHAM,HCK}
I. vanidicus Schulze, 1943^{K,CHAM,HCK}
I. venezuelensis Kohls, 1953^{K,CHAM,HCK}
I. ventalloi Gil Collado, 1936^{K,CHAM,HCK}
I. vespertilionis Koch, 1844^{K,CHAM,HCK}
I. vestitus Neumann, 1908^{K,CHAM,HCK}
I. victoriensis Nuttall, 1916^{K,CHAM,HCK}
I. uruguayensis Kohls & Clifford, 1967^{K,CHAM}
I. walkerae Clifford, Kohls & Hoogstraal, 1968^{K,CHAM,HCK}
I. wernerii Kohls, 1950^{K,CHAM,HCK}
I. woodi Bishopp, 1911^{K,CHAM,HCK}
I. zaglossi Kohls, 1960^{K,CHAM,HCK}
I. zairensis Keirans, Clifford & Walker, 1982^{K,CHAM,HCK}
I. zealandicus (Dumbleton, 1953)^{CHAM}
I. zumpti Arthur, 1960^{K,HCK}
Margaropus (3 species)
M. reidi Hoogstraal, 1956^{K,CHAM,HCK}
M. wileyi Walker & Laurence, 1973^{K,CHAM,HCK}
M. winthemi Karsch, 1879^{K,CHAM,HCK}
Nosomma (1 species)
N. monstrosum (Nuttall & Warburton, 1908)^{K,CHAM,HCK}
Rhipicentor (2 species)
R. bicornis Nuttall & Warburton, 1908^{K,CHAM,HCK}
R. nuttalli Cooper & Robinson, 1908^{K,CHAM,HCK}
Rhipicephalus (79 species:– includes the 5 species that were in the genus *Boophilus*. These are now in the subgenus *Rhipicephalus* (*Boophilus*))
R. (Boophilus) annulatus (Say, 1821)^{K,CHAM,HCK}
R. (Boophilus) decoloratus (Koch, 1844)^{K,CHAM,HCK}
R. (Boophilus) geigyii (Aeschlimann & Morel, 1965)^{K,CHAM,HCK}
R. (Boophilus) kohlsi (Hoogstraal & Kaiser, 1960)^{K,CHAM,HCK}
R. (Boophilus) microplus (Canestrini, 1888)^{K,CHAM,HCK}
R. appendiculatus Neumann, 1901^{WKH}
R. aquatilis Walter, Keirans & Pegram, 1993^{WKH}
R. armatus Pocock, 1900^{WKH}
R. arnoldi Theiler & Zumpt, 1949^{WKH}
R. bequaerti Zumpt, 1949^{WKH}
R. bergeoni Morel & Balis, 1976^{WKH}
R. boueti Morel, 1957^{WKH}
R. bursa Canestrini & Fanzago, 1878^{WKH}
R. camicasi Morel, Mouchet & Rodhain, 1976^{WKH}
R. capensis Koch, 1844^{WKH}
R. carnivoralis Walker, 1966^{WKH}
R. complanatus Neumann, 1911^{WKH}
R. compositus Neumann, 1897^{WKH}
R. cuspidatus Neumann, 1906^{WKH}
R. deltoideus Neumann, 1910^{WKH}
R. distinctus Bedford, 1932^{WKH}

Table 1. (Cont.)

<i>R. duttoni</i> Neumann, 1907 ^{WKH}	<i>R. lumulatus</i> Neumann, 1907 ^{WKH}	<i>R. rossicus</i> Yakimov & Kol-Yakimova, 1911 ^{WKH}
<i>R. dux</i> Dönitz, 1910 ^{WKH}	<i>R. maculatus</i> Neumann, 1901 ^{WKH}	<i>R. sanguineus</i> (Latreille, 1806) ^{WKH}
<i>R. evertsi</i> Neumann, 1897 ^{WKH}	<i>R. masseyi</i> Nuttall & Warburton, 1908 ^{WKH}	<i>R. sculpturatus</i> Santos Dias, 1959 ^{WKH}
<i>R. exophthalmos</i> Keirans & Walker, 1993 ^{WKH}	<i>R. moucheti</i> Morel, 1965 ^{WKH}	<i>R. schulzei</i> Olenev, 1929 ^{WKH}
<i>R. follis</i> Dönitz, 1910 ^{WKH}	<i>R. muehlensi</i> Zumpt, 1943 ^{WKH}	<i>R. sculptus</i> Warburton, 1912 ^{WKH}
<i>R. fulvus</i> Neumann, 1913 ^{WKH}	<i>R. muhsamae</i> Morel & Vassiliades, 1965 ^{WKH}	<i>R. senegalensis</i> Koch, 1844 ^{WKH}
<i>R. gertrudae</i> Feldman-Muhsam, 1960 ^{WKH}	<i>R. neumanni</i> Walker, 1990 ^{WKH}	<i>R. serranoi</i> Santos Dias, 1950 ^{WKH}
<i>R. glabroscutatum</i> Du Toit, 1941 ^{WKH}	<i>R. nitens</i> Neumann, 1904 ^{WKH}	<i>R. simpsoni</i> Nuttall, 1910 ^{WKH}
<i>R. guilhoni</i> Morel & Vassiliades, 1963 ^{WKH}	<i>R. oculus</i> Neumann, 1901 ^{WKH}	<i>R. simus</i> Koch, 1844 ^{WKH}
<i>R. haemaphysaloides</i> Supino, 1897 ^{WKH}	<i>R. oreotragi</i> Walker & Horak, 2000 ^{WKH}	<i>R. sulcatus</i> Neumann, 1908 ^{WKH}
<i>R. humeralis</i> Tonelli-Rondelli, 1926 ^{WKH}	<i>R. pilans</i> Schulze, 1935 ^{WKH}	<i>R. supertritus</i> Neumann, 1907 ^{WKH}
<i>R. hurti</i> Wilson, 1954 ^{WKH}	<i>R. planus</i> Neumann, 1907 ^{WKH}	<i>R. theileri</i> Bedford & Hewitt, 1925 ^{WKH}
<i>R. interventus</i> Walker, Pegram & Keirans 1995 ^{WKH}	<i>R. praetextatus</i> Gerstäcker, 1873 ^{WKH}	<i>R. tricuspis</i> , Dönitz, 1906 ^{WKH}
<i>R. jeanneli</i> Neumann, 1913 ^{WKH}	<i>R. pravus</i> Dönitz, 1910 ^{WKH}	<i>R. turanicus</i> Pomerantsev, 1936 ^{WKH}
<i>R. kochi</i> Dönitz, 1905 ^{WKH}	<i>R. pseudolongus</i> Santos Dias, 1953 ^{WKH}	<i>R. warburtoni</i> Walker & Horak, 2000 ^{WKH}
<i>R. leporis</i> Pomerantsev, 1946 ^{WKH}	<i>R. pulchellus</i> (Gerstäcker, 1873) ^{WKH}	<i>R. zambeziensis</i> Walker, Norval & Corwin, 1981 ^{WKH}
<i>R. longiceps</i> Warburton, 1912 ^{WKH}	<i>R. pumilio</i> Schluze, 1935 ^{WKH}	<i>R. ziemanni</i> Neumann, 1904 ^{WKH}
<i>R. longicoxatus</i> Neumann, 1905 ^{WKH}	<i>R. punctatus</i> Warburton, 1912 ^{WKH}	<i>R. zumpti</i> Santos Dias, 1950 ^{WKH}
<i>R. longus</i> Neumann, 1907 ^{WKH}	<i>R. pusillus</i> Gil Collado, 1936 ^{WKH}	
<i>R. lounsburyi</i> Walker, 1990 ^{WKH}	<i>R. ramachandrai</i> Dhanda, 1966 ^{WKH}	

This list of valid names is a compilation of the genus and species names of Keirans (1992), Camicas *et al.* (1998), Keirans & Robbins (1999), Walker *et al.* (2000) and Horak, Camicas & Keirans (2002). The major revisions of Klompen & Oliver (1993) and Klompen *et al.* (2002), and species-level revisions and name changes of Venzal *et al.* (2001), Guglielmo & Keirans (2002) and Murrell & Barker (2003) have been incorporated. Superscripts show the lists that contain each name: Keirans (1992)^K; Keirans & Robbins (1999)^{KR}; Walker, Keirans & Horak (2000)^{WKH}; and Horak, Camicas & Keirans (2002)^{HCK}. Subspecies and subgenera were ignored except for the new subgenus *Rhipicephalus* (*Boophilus*) – see text. The four descriptions of species and one new genus since 2002 have the superscript RD (recent description). ^a*Ixodes neotomae* Cooley, 1944 is a valid species name. However, Norris *et al.* (1977) suggested that *I. neotomae* be reduced to a junior subjective synonym of *I. spinipalpis*. Although, analyses of 16S and 12S rRNA failed to recover reciprocal-monophyly for populations of *I. neotomae* and *I. spinipalpis* (Norris *et al.* 1997) we conclude that insufficient evidence has been produced to reject the hypothesis of two separate species: i.e. *I. neotomae* and *I. spinipalpis*. In any case *I. neotomae* has not been formerly made a subjective synonym of *I. spinipalpis* so both names are in our list.

mitochondrial genome sequences from each of the subfamilies of ticks and their potential sister-groups (holothyrid and mesostigmatid mites) are likely to reveal even more about the systematics of these fascinating arthropods. We have the tools to address many of the remaining outstanding questions but pivotal taxa may continue to be difficult to collect (e.g. *Nuttalliella namaqua* and *Anomalohimalaya* species). Nonetheless the tick–systematics community will continue to seek the answers to long-standing questions about the evolution of these fascinating parasites.

ACKNOWLEDGEMENTS

We thank Claire Ellender and Maree Schabe for invaluable help with the word processing. Jim Keirans, Dave Kemp, Dave Walter and Renfu Shao criticised the manuscript for us and Tom Cribb provided advice on nomenclature. Two anonymous referees also provided valuable suggestions.

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