

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

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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. Several changes to the nomenclature of ticks have been made or are likely to be made in the near future. 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 Australasian 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 valid genus and species names of ticks as at February 2007.

## INTRODUCTION

Hoogstraal & Aeschlimann (1982) were apparently the first people to publish a phylogenetic tree for the ticks (sub-order 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 over 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.* (1995*a, 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, Barges & Mas-Coma (1998*a, b*); Dobson & Barker (1999); Murrell, Campbell & Barker (1999); Norris, Klompen & Black (1999); Fukunaga *et al.* (2000); Klompen *et al.* (2000); Murrell, Campbell & Barker (2000, 2001*a, b*, 2003); Beati & Keirans (2001); Ushijima *et al.* (2003); Xu *et al.* (2003); Murrell *et al.* (2005); Shao *et al.* (2005); Szabo *et al.* (2005); and Miller *et al.* (2007). 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 nine 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); and Murrell *et al.* (2001*b*).

The first part 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

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about many tick relationships. The second part of the review deals with the taxonomy and nomenclature of ticks. Table 1.1 (see below, pp. 3–25) is a list of the 907 valid genus and species names as at February 2007.

### 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. All three of the tests of these hypotheses indicate that the sister-group of the Ixodida is the Holothyrida: Dobson & Barker (1999) and Murrell *et al.* (2005) (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 chapter.

#### 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. 1.1). 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 group and the Barker

group 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; Shao *et al.*, 2005). Our working hypothesis has the genus *Ixodes* as a monophyletic lineage (Fig. 1.1). 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* (Klompen *et al.*, 1997, 2000; Dobson & Barker, 1999). 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 of the extant *Ixodes* species 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* and *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 (see below, and Shao *et al.*, 2005). 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. eudyptidis*, *I. feicalis*, *I. hydromyidis*, *I. jacksoni*, *I. kohlsi*, *I. laysanensis*, *I. luxuriosus*, *I. prisciollaris*, *I. steimi*, *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: five species of Bothriocrotoninae Klompen, Dobson & Barker, 2002. This group was first recognized by Kaufman (1972) as one of the three groups of *Aponomma*

Table 1.1 *A current list of valid genus and species names (in alphabetical order except for the five species that were previously in the genus Boophilus – these species are now at the top of the list of Rhipicephalus species)*

Family	Genus	Species
IXODIDA (907 valid species names)		
NUTTALLIELLIDAE (1 valid species name)	<i>Nuttalliella</i> (1 species)	<i>N. namaqua</i> Bedford, 1931 <sup>K,CHAM,HCK</sup>
ARGASIDAE (186 valid species names)	<i>Argas</i> (58 species)	<i>A. abdussalami</i> Hoogstraal & McCarthy, 1965 <sup>K,CHAM,HCK</sup> <i>A. acinus</i> (Whittick, 1938) <sup>K,CHAM,HCK</sup> <i>A. africanus</i> Hoogstraal, Kaiser, Walker, Ledger, Converse & Rice, 1975 <sup>K,CHAM,HCK</sup> <i>A. arboreus</i> Kaiser, Hoogstraal & Kohls, 1964 <sup>K,CHAM,HCK</sup> <i>A. assimilis</i> Teng & Song, 1983 <sup>K,CHAM,HCK</sup> <i>A. beijingensis</i> Teng, 1983 <sup>K,CHAM,HCK</sup> <i>A. beklemischevi</i> Pospelova-Shtrom, Vasil'eva & Semashko, 1963 <sup>K,CHAM,HCK</sup> <i>A. brevipes</i> Banks, 1908 <sup>K,CHAM,HCK</sup> <i>A. brumpti</i> Newmann, 1907 <sup>K,CHAM,HCK</sup> <i>A. bureschi</i> Dryenski, 1957 <sup>K,CHAM,HCK</sup> <i>A. canestrinii</i> Birula, 1895 <sup>K,HCK</sup> <i>A. cooleyi</i> (McIvor, 1941) <i>nec A. cooleyi</i> Kohls & Hoogstraal, 1960 <sup>K,CHAM,HCK</sup> <i>A. cooleyi</i> Kohls & Hoogstraal, 1960 <i>nec A. cooleyi</i> (McIvor, 1941) <sup>K,CHAM,HCK</sup> <i>A. cucumerinus</i> Neumann, 1901 <sup>K,CHAM,HCK</sup> <i>A. dalei</i> Clifford, Keirans, Hoogstraal & Corwin, 1976 <sup>K,CHAM,HCK</sup> <i>A. delanoi</i> (Roubaud & Colas-Belcour, 1931) <sup>K,CHAM,HCK</sup> <i>A. dulus</i> Keirans, Clifford & Capriles, 1971 <sup>K,CHAM,HCK</sup> <i>A. eboris</i> (Theiler, 1959) <sup>K,CHAM</sup> <i>A. echinops</i> Hoogstraal, Uilenberg & Blanc, 1967 <sup>K,CHAM,HCK</sup> <i>A. falco</i> Kaiser & Hoogstraal, 1974 <sup>K,CHAM,HCK</sup> <i>A. foleyi</i> (Parrot, 1928) <sup>K,CHAM,HCK</sup> <i>A. giganteus</i> Kohls & Clifford, 1968 <sup>K,CHAM,HCK</sup> <i>A. gilcolladoi</i> Estrada-Peña, Lucientes & Sánchez, 1987 <sup>K,CHAM,HCK</sup> <i>A. hermanni</i> Audouin, 1827 <sup>K,CHAM,HCK</sup> <i>A. himalayensis</i> Hoogstraal & Kaiser, 1973 <sup>K,CHAM,HCK</sup> <i>A. hoogstraali</i> Morel & Vassiliades, 1965 <sup>K,CHAM,HCK</sup> <i>A. japonicus</i> Yamaguti, Clifford & Tipton, 1968 <sup>K,CHAM,HCK</sup> <i>A. keiransi</i> Estrada-peña, Venzal, Gonzalez-Acuna & Gugliemone, 2003 <sup>RD</sup> <i>A. lagenoplastis</i> Froggatt, 1906 <sup>K,CHAM,HCK</sup> <i>A. lahorensis</i> (Neumann, 1908) <sup>K,CHAM,HCK</sup> <i>A. latus</i> Filippova, 1961 <sup>K,CHAM,HCK</sup>

(cont.)

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Table 1.1 (*cont.*)

Family	Genus	Species
		<i>A. lowryae</i> Kaiser & Hoogstraal, 1975 <sup>K,CHAM,HCK</sup>
		<i>A. macrostigmatus</i> Filippova, 1961 <sup>K,CHAM,HCK</sup>
		<i>A. magnus</i> Neumann, 1896 <sup>K,CHAM,HCK</sup>
		<i>A. miniatus</i> Koch, 1844 <sup>K,CHAM,HCK</sup>
		<i>A. monachus</i> Keirans, Radovsky & Clifford, 1973 <sup>K,CHAM,HCK</sup>
		<i>A. monolakensis</i> Schwan, Corwin, & Brown, 1992 <sup>KR,CHAM,HCK</sup>
		<i>A. moreli</i> Keirans, Hoogstraal & Clifford, 1979 <sup>K,CHAM,HCK</sup>
		<i>A. neghmei</i> Kohls & Hoogstraal, 1961 <sup>K,CHAM,HCK</sup>
		<i>A. nullarborensis</i> Hoogstraal & Kaiser, 1973 <sup>K,CHAM,HCK</sup>
		<i>A. peringueyi</i> (Bedford & Hewitt, 1925) <sup>K,CHAM,HCK</sup>
		<i>A. persicus</i> (Oken, 1818) <sup>K,CHAM,HCK</sup>
		<i>A. peusi</i> (Schulze, 1943) <sup>K,CHAM,HCK</sup>
		<i>A. polonicus</i> Siuda, Hoogstraal, Clifford & Wassef, 1979 <sup>K,CHAM,HCK</sup>
		<i>A. radiatus</i> Railliet, 1893 <sup>K,CHAM,HCK</sup>
		<i>A. reflexus</i> (Fabricius, 1794) <sup>K,CHAM,HCK</sup>
		<i>A. ricei</i> Hoogstraal, Kaiser, Clifford & Keirans, 1975 <sup>K,CHAM,HCK</sup>
		<i>A. robertsi</i> Hoogstraal, Kaiser & Kohls, 1968 <sup>K,CHAM,HCK</sup>
		<i>A. sanchezi</i> Dugès, 1887 <sup>K,CHAM,HCK</sup>
		<i>A. streptopelia</i> Kaiser, Hoogstraal & Homer, 1970 <sup>K,CHAM,HCK</sup>
		<i>A. striatus</i> Bedford, 1932 <sup>K,CHAM,HCK</sup>
		<i>A. theilerae</i> Hoogstraal & Kaiser, 1970 <sup>K,CHAM,HCK</sup>
		<i>A. transgaripepinus</i> White, 1846 <sup>K,CHAM,HCK</sup>
		<i>A. tridentatus</i> Filippova, 1961 <sup>K,CHAM,HCK</sup>
		<i>A. vansomereni</i> (Keirans, Hoogstraal & Clifford, 1977) <sup>K,CHAM,HCK</sup>
		<i>A. vulgaris</i> Filippova, 1961 (?= <i>A. delicatus</i> Neumann, 1910) <sup>K,CHAM,HCK</sup>
		<i>A. walkerae</i> Kaiser & Hoogstraal, 1969 <sup>K,CHAM,HCK</sup>
		<i>A. zumpti</i> Hoogstraal, Kaiser & Kohls, 1968 <sup>K,CHAM,HCK</sup>
	<i>Antricola</i> (3 species)	<i>A. delacruzii</i> Estrada-Pena, Venzal, Barros-Battesti, Onofrio, Trajano, Firmino 2004 <sup>RD</sup>
		<i>A. guglielmoniei</i> Estrada-Pena, Venzal, Barros-Battesti, Onofrio, Trajano & Firmino 2004 <sup>RD</sup>
		<i>A. inexpectata</i> Estrada-Pena, Venzal, Barros-Battesti, Onofrio, Trajano & Firmino 2004 <sup>RD</sup>
	<i>Carios</i> (88 species)	<i>C. amblus</i> (Chamberlain, 1920) <sup>K,CHAM,HCK</sup>
		<i>C. aragoi</i> (Fonseca, 1960) <sup>HCK,CHAM</sup>
		<i>C. armasi</i> (de la Cruz & Estrada-Peña, 1995) <sup>KR,CHAM,HCK</sup>
		<i>C. australiensis</i> (Kohls & Hoogstraal, 1962) <sup>K,CHAM,HCK</sup>

Table 1.1 (*cont.*)

Family	Genus	Species
		<i>C. azteci</i> (Matheson, 1935) <sup>K,CHAM,HCK</sup>
		<i>C. batuensis</i> (Hirst, 1929) <sup>K,CHAM,HCK</sup>
		<i>C. boueti</i> (Roubaud & Colas-Belcour, 1933) <sup>K,CHAM,HCK</sup>
		<i>C. brodyi</i> (Matheson, 1935) <sup>K,CHAM,HCK</sup>
		<i>C. camicasi</i> (Sylla, Cornet & Marchand, 1997) <sup>KR,HCK</sup>
		<i>C. capensis</i> (Neumann, 1901) <sup>K,CHAM,HCK</sup>
		<i>C. casebeerii</i> (Jones & Clifford, 1972) <sup>K,CHAM,HCK</sup>
		<i>C. centralis</i> (de la Cruz & Estrada-Peña, 1995) <sup>KR,CHAM,HCK</sup>
		<i>C. cernyi</i> (de la Cruz, 1978) <sup>K,CHAM,HCK</sup>
		<i>C. ceylonensis</i> (Hoogstraal & Kaiser, 1968) <sup>K,CHAM,HCK</sup>
		<i>C. cheikhi</i> (Vermeil, Marjolet & Vermeil, 1997) <sup>HCK</sup>
		<i>C. chironectes</i> (Jones & Clifford, 1972) <sup>K,CHAM,HCK</sup>
		<i>C. chiropterphila</i> (Dhanda & Rajagopalan, 1971) <sup>K,CHAM,HCK</sup>
		<i>C. clarki</i> (Jones & Clifford, 1972) <sup>K,CHAM,HCK</sup>
		<i>C. collocaliae</i> (Hoogstraal, Kadarsan, Kaiser & Van Peenan, 1974) <sup>K,CHAM,HCK</sup>
		<i>C. concanensis</i> (Cooley & Kohls, 1941) <sup>K,CHAM,HCK</sup>
		<i>C. confusus</i> (Hoogstraal, 1955) <sup>K,CHAM,HCK</sup>
		<i>C. coniceps</i> (Canestrini, 1890) <sup>K,CHAM,HCK</sup>
		<i>C. coprophilus</i> (McIntosh, 1935) <sup>K,CHAM,HCK</sup>
		<i>C. cordiformis</i> (Hoogstraal & Kohls, 1967) <sup>K,CHAM,HCK</sup>
		<i>C. cycluræ</i> (de la Cruz, 1984) <sup>K,CHAM,HCK</sup>
		<i>C. darwini</i> (Kohls, Clifford & Hoogstraal, 1969) <sup>K,CHAM,HCK</sup>
		<i>C. daviesi</i> (Kaiser & Hoogstraal, 1973) <sup>K,CHAM,HCK</sup>
		<i>C. denmarki</i> (Kohls, Sonenshine & Clifford, 1965) <sup>K,CHAM,HCK</sup>
		<i>C. demæ</i> (Kaiser & Hoogstraal, 1974) <sup>K,CHAM,HCK</sup>
		<i>C. dusbabeki</i> (Cérny, 1967) <sup>K,CHAM,HCK</sup>
		<i>C. dyeri</i> (Cooley & Kohls, 1940) <sup>K,CHAM,HCK</sup>
		<i>C. echimys</i> (Kohls, Clifford & Jones, 1969) <sup>K,CHAM,HCK</sup>
		<i>C. elongates</i> (Kohls, Clifford & Sonenshine, 1965) <sup>K,CHAM,HCK</sup>
		<i>C. eptesicus</i> (Kohls, Clifford & Jones, 1969) <sup>K,CHAM,HCK</sup>
		<i>C. faini</i> (Hoogstraal, 1960) <sup>K,CHAM,HCK</sup>
		<i>C. fischeri</i> (Audouin, 1827) <sup>CHAM</sup>
		<i>C. galapagensis</i> (Kohls, Clifford & Hoogstraal, 1969) <sup>K,CHAM,HCK</sup>
		<i>C. granasi</i> (de la Cruz, 1973) <sup>K,CHAM,HCK</sup>
		<i>C. habanensis</i> (de la Cruz, 1976) <sup>K,CHAM,HCK</sup>
		<i>C. hadiæ</i> Klompen, Keirans & Durden, 1995 <sup>KR,CHAM,HCK</sup>
		<i>C. hasei</i> (Schulze, 1935) <sup>K,CHAM,HCK</sup>
		<i>C. hummelincki</i> (de la Cruz & Estrada-Peña, 1995) <sup>KR,CHAM,HCK</sup>

*(cont.)*

Table 1.1 (*cont.*)

Family	Genus	Species
		<i>C. jerseyi</i> Klompen & Grimaldi, 2001 <sup>HCK</sup>
		<i>C. jul</i> (Schulze, 1940) <sup>HCK, CHAM</sup>
		<i>C. kelleyi</i> (Cooley & Kohls, 1941) <sup>K, HCK</sup>
		<i>C. kohlsi</i> (Guglielmone & Keirans, 2002) <sup>HCK</sup>
		<i>C. macrodermae</i> (Hoogstraal, Moorhouse, Wolf & Wassef, 1977) <sup>K, CHAM, HCK</sup>
		<i>C. madagascariensis</i> (Hoogstraal, 1962) <sup>K, CHAM, HCK</sup>
		<i>C. marginatus</i> (Banks, 1910) <sup>K, CHAM, HCK</sup>
		<i>C. marinkellei</i> (Kohls, Clifford & Jones, 1969) <sup>K, CHAM, HCK</sup>
		<i>C. maritimus</i> (Vermeil & Marguet, 1967) <sup>K, CHAM, HCK</sup>
		<i>C. marmosae</i> (Jones & Clifford, 1972) <sup>K, CHAM, HCK</sup>
		<i>C. martelorum</i> (de la Cruz, 1978) <sup>K, CHAM, HCK</sup>
		<i>C. mexicanus</i> (Hoffman, 1959) <sup>K, CHAM, HCK</sup>
		<i>C. mimon</i> (Kohls, Clifford & Jones, 1969) <sup>K, CHAM, HCK</sup>
		<i>C. mormoops</i> (Kohls, Clifford & Jones, 1969) <sup>K, CHAM, HCK</sup>
		<i>C. muesebecki</i> (Hoogstraal, 1969) <sup>K, CHAM, HCK</sup>
		<i>C. multisetosus</i> Klompen, Keirans & Durden, 1995 <sup>KR, CHAM, HCK</sup>
		<i>C. naomiae</i> (de la Cruz, 1978) <sup>K, CHAM, HCK</sup>
		<i>C. natalinus</i> (Cerný & Dusbábek, 1967) <sup>HCK, CHAM</sup>
		<i>C. occidentalis</i> (de la Cruz, 1978) <sup>K, CHAM, HCK</sup>
		<i>C. papuensis</i> Klompen, Keirans & Durden, 1995 <sup>KR, CHAM, HCK</sup>
		<i>C. peroptyx</i> (Kohls, Clifford & Jones, 1969) <sup>K, CHAM, HCK</sup>
		<i>C. peruvianus</i> (Kohls, Clifford & Jones, 1969) <sup>K, CHAM, HCK</sup>
		<i>C. piriformis</i> (Warburton, 1918) <sup>K, CHAM, HCK</sup>
		<i>C. puertoricensis</i> (Fox, 1947) <sup>K, CHAM, HCK</sup>
		<i>C. pusillus</i> (Kohls, 1950) <sup>K, CHAM, HCK</sup>
		<i>C. reddelli</i> (Keirans & Clifford, 1975) <sup>K, CHAM, HCK</sup>
		<i>C. rennellensis</i> (Clifford & Sonenshine, 1962) <sup>K, CHAM, HCK</sup>
		<i>C. rossi</i> (Kohls, Sonenshine & Clifford, 1965) <sup>K, CHAM, HCK</sup>
		<i>C. rudis</i> (Karsch, 1880) <sup>K, CHAM, HCK</sup>
		<i>C. salahi</i> (Hoogstraal, 1953) <sup>K, CHAM, HCK</sup>
		<i>C. sawaii</i> (Kitaoka & Suzuki, 1973) <sup>K, CHAM, HCK</sup>
		<i>C. setosus</i> (Kohls, Clifford & Jones, 1969) <sup>HCK, CHAM</sup>
		<i>C. siboneyi</i> (de la Cruz & Estrada-Peña, 1995) <sup>KR, CHAM, HCK</sup>
		<i>C. silvai</i> (Černý, 1967) <sup>K, CHAM, HCK</sup>
		<i>C. sinensis</i> (Jeu & Zhu, 1982) <sup>K, CHAM, HCK</sup>
		<i>C. solomonis</i> (Dumbleton, 1959) <sup>K, CHAM, HCK</sup>
		<i>C. spheniscus</i> (Hoogstraal, Wassef, Hays & Keirans, 1985) <sup>K, CHAM, HCK</sup>
		<i>C. stageri</i> (Cooley & Kohls, 1941) <sup>K, CHAM, HCK</sup>
		<i>C. tadaridae</i> (Černý & Dusbábek, 1967) <sup>K, CHAM, HCK</sup>
		<i>C. talaje</i> (Guérin-Méville, 1849) <sup>K, CHAM, HCK</sup>

Table 1.1 (*cont.*)

Family	Genus	Species
		<i>C. tiptoni</i> (Jones & Clifford, 1972) <sup>K,CHAM,HCK</sup>
		<i>C. tuttlei</i> (Jones & Clifford, 1972) <sup>K,CHAM,HCK</sup>
		<i>C. vespertilionis</i> Latreille, 1796 <sup>K,CHAM,HCK</sup>
		<i>C. viguerasi</i> (Cooley & Kohls, 1941) <sup>K,CHAM,HCK</sup>
		<i>C. yumatensis</i> (Cooley & Kohls, 1941) <sup>K,CHAM,HCK</sup>
		<i>C. yunkeri</i> (Keirans, Clifford & Hoogstraal, 1984) <sup>K,CHAM,HCK</sup>
	<i>Ornithodoros</i>	<i>O. alactagalis</i> Issaakjan, 1936 <sup>K,CHAM,HCK</sup>
	(37 species)	<i>O. antiquus</i> Poinar, 1995 <sup>KR,CHAM,HCK</sup> (known only as a fossil)
		<i>O. apertus</i> Walton, 1962 <sup>K,CHAM,HCK</sup>
		<i>O. arenicolous</i> Hoogstraal, 1953 <sup>K,CHAM,HCK</sup>
		<i>O. asperus</i> Warburton, 1918 <sup>K,CHAM,HCK</sup>
		<i>O. brasiliensis</i> Aragão, 1923 <sup>K,CHAM,HCK</sup>
		<i>O. boliviensis</i> (Kohls & Clifford, 1964) <sup>K,CHAM</sup>
		<i>O. chlodkovskyi</i> Pavlovsky, 1930 <sup>K,CHAM,HCK</sup>
		<i>O. compactus</i> Walton, 1962 <sup>K,CHAM,HCK</sup>
		<i>O. coriaceus</i> Koch, 1844 <sup>K,CHAM,HCK</sup>
		<i>O. eremicus</i> Cooley & Kohls, 1941 <sup>K,CHAM,HCK</sup>
		<i>O. erraticus</i> (Lucas, 1849) <sup>K,CHAM,HCK</sup>
		<i>O. furcosus</i> Neumann, 1908 <sup>K,CHAM,HCK</sup>
		<i>O. graingeri</i> Heisch & Guggisberg, 1953 <sup>K,CHAM,HCK</sup>
		<i>O. grenieri</i> Klein, 1965 <sup>K,CHAM,HCK</sup>
		<i>O. gurneyi</i> Warburton, 1926 <sup>K,CHAM,HCK</sup>
		<i>O. hermsi</i> Wheeler, Herms & Meyer, 1935 <sup>K,CHAM,HCK</sup>
		<i>O. indica</i> Rau & Rao, 1971 <sup>K,CHAM,HCK</sup>
		<i>O. knoxjonesi</i> Jones & Clifford, 1972 <sup>K,HCK</sup>
		<i>O. macmillani</i> Hoogstraal & Kohls, 1966 <sup>K,CHAM,HCK</sup>
		<i>O. maroccanus</i> Velu, 1919 <sup>K,HCK</sup>
		<i>O. moubata</i> (Murray, 1877) <sup>K,CHAM,HCK</sup>
		<i>O. nattereri</i> Warburton, 1927 <sup>K,HCK</sup>
		<i>O. nicolleti</i> Mooser, 1932 <sup>K,CHAM,HCK</sup>
		<i>O. normandi</i> Larrousse, 1923 <sup>K,CHAM,HCK</sup>
		<i>O. parkeri</i> Cooley, 1936 <sup>K,CHAM,HCK</sup>
		<i>O. porcinus</i> Walton, 1962 <sup>K,CHAM,HCK</sup>
		<i>O. procaviae</i> Theodor & Costa, 1960 <sup>K,CHAM,HCK</sup>
		<i>O. rostratus</i> Aragão, 1911 <sup>K,CHAM,HCK</sup>
		<i>O. savignyi</i> (Audouin, 1827) <sup>K,CHAM,HCK</sup>
		<i>O. sonrai</i> Sautet & Witkowski, 1943 <sup>K,CHAM,HCK</sup>
		<i>O. steini</i> (Schulze, 1935) <sup>K,HCK</sup>
		<i>O. tartakovskiyi</i> Olenov, 1931 <sup>K,CHAM,HCK</sup>
		<i>O. tholozani</i> (Laboulbène & Mégnin, 1882)
		<i>O. transversus</i> (Banks, 1902) <sup>K,CHAM,HCK</sup>

*(cont.)*



Table 1.1 (*cont.*)

Family	Genus	Species
	<i>Otobius</i> (3 species)	<i>O. turicata</i> (Dugeš, 1876) <sup>K,CHAM,HCK</sup>
		<i>O. zumpti</i> Heisch & Guggisberg, 1953
IXODIDAE (720 species)	<i>Amblyomma</i> (143 species)	<i>O. lagophilus</i> Cooley & Kohls, 1940 <sup>K,CHAM,HCK</sup>
		<i>O. mégnini</i> (Dugeš, 1883) <sup>K,CHAM,HCK</sup>
		<i>O. sparnus</i> (Kohls & Clifford, 1963) <sup>K,CHAM,HCK</sup>
		<i>A. acutangulatum</i> Neumann, 1899 <sup>CHAM</sup>
		<i>A. albolimbatum</i> Neumann, 1907 <sup>K,CHAM,HCK</sup>
		<i>A. albopictum</i> Neumann, 1899 <sup>K,CHAM,HCK</sup>
		<i>A. americanum</i> (Linnaeus, 1758) <sup>K,CHAM,HCK</sup>
		<i>A. antillorum</i> Kohls, 1969 <sup>K,CHAM,HCK</sup>
		<i>A. arcanum</i> Karsch, 1879 <sup>CHAM,HCK</sup>
		<i>A. argentinae</i> Neumann, 1905 <sup>CHAM,HCK</sup>
		<i>A. arianae</i> Keirans & Garris, 1986 <sup>KR</sup>
		<i>A. astrion</i> Dönitz, 1909 <sup>K,CHAM,HCK</sup>
		<i>A. aureolatum</i> (Pallas, 1772) <sup>HCK</sup>
		<i>A. auricularium</i> (Conil, 1878) <sup>K,CHAM,HCK</sup>
		<i>A. australiense</i> Neumann, 1905 <sup>K,CHAM,HCK</sup>
		<i>A. babirussae</i> Schulze, 1933 <sup>K,CHAM,HCK</sup>
		<i>A. bibroni</i> (Gervais, 1842) <sup>CHAM</sup>
		<i>A. boulegeri</i> Hirst & Hirst, 1910 <sup>K,CHAM,HCK</sup>
		<i>A. brasiliense</i> Aragão, 1908 <sup>K,CHAM,HCK</sup>
		<i>A. breviscutatum</i> Neumann, 1899 <sup>HCK</sup>
		<i>A. cajennense</i> (Fabricius, 1787) <sup>K,CHAM,HCK</sup>
		<i>A. calabyi</i> Roberts, 1963 <sup>K,CHAM,HCK</sup>
		<i>A. calcaratum</i> Neumann, 1899 <sup>K,CHAM,HCK</sup>
		<i>A. chabaudi</i> Rageau, 1964 <sup>K,CHAM,HCK</sup>
		<i>A. clypeolatum</i> Neumann, 1899 <sup>K,CHAM,HCK</sup>
		<i>A. coelebs</i> Neumann, 1899 <sup>K,CHAM,HCK</sup>
		<i>A. cohaerens</i> Dönitz, 1909 <sup>K,CHAM,HCK</sup>
<i>A. colasbelcouri</i> (Santos Dias, 1958) <sup>K,HCK</sup>		
<i>A. compressum</i> (Macalister, 1872) <sup>K,CHAM,HCK</sup>		
<i>A. cooperi</i> Nuttall & Warburton, 1908 <sup>K,HCK</sup>		
<i>A. cordiferum</i> Neumann, 1899 <sup>K,CHAM,HCK</sup>		
<i>A. crassipes</i> (Neumann, 1901) <sup>K,HCK</sup>		
<i>A. crassum</i> Robinson, 1926 <sup>K,CHAM,HCK</sup>		
<i>A. crenatum</i> Neumann, 1899 <sup>K,CHAM,HCK</sup>		
<i>A. cruciferum</i> Neumann, 1901 <sup>K,CHAM,HCK</sup>		
<i>A. curraca</i> Schulze, 1936 <sup>CHAM</sup>		
<i>A. cyprium</i> Neumann, 1899 <sup>K,HCK</sup>		
<i>A. darwini</i> Hirst & Hirst, 1910 <sup>K,CHAM,HCK</sup>		
<i>A. decorosum</i> (Koch, 1867) <sup>K,CHAM</sup>		
<i>A. dissimile</i> Koch, 1844 <sup>K,HCK</sup>		
<i>A. dubitatum</i> Neumann, 1899 <sup>HCK</sup>		
<i>A. eburneum</i> Gerstäcker, 1873 <sup>K,CHAM,HCK</sup>		



Table 1.1 (*cont.*)

Family	Genus	Species
		<i>A. echidnae</i> Roberts, 1953 <sup>K,HCK</sup>
		<i>A. elaphense</i> (Price, 1959) <sup>K,CHAM,HCK</sup>
		<i>A. exornatum</i> Koch, 1844 <sup>K,CHAM,HCK</sup>
		<i>A. extraoculatum</i> Neumann, 1899 <sup>K,CHAM,HCK</sup>
		<i>A. falsomarmoreum</i> Tonelli-Rondelli, 1935 <sup>K,CHAM,HCK</sup>
		<i>A. fimbriatum</i> Koch, 1844 <sup>K,CHAM,HCK</sup>
		<i>A. flavomaculatum</i> (Lucas, 1846) <sup>K,CHAM,HCK</sup>
		<i>A. fulvum</i> Neumann, 1899 <sup>K,CHAM,HCK</sup>
		<i>A. fuscolineatum</i> (Lucas, 1847) <sup>K,CHAM,HCK</sup>
		<i>A. fuscum</i> Neumann, 1907 <sup>CHAM</sup>
		<i>A. geayi</i> Neumann, 1899 <sup>K,HCK</sup>
		<i>A. gemma</i> Dönitz, 1909 <sup>K,CHAM,HCK</sup>
		<i>A. geocheilone</i> Durden, Keirans & Smith, 2002 <sup>HCK</sup>
		<i>A. geoemydae</i> (Cantor, 1847) <sup>K,CHAM,HCK</sup>
		<i>A. gervaisi</i> (Lucas, 1847) <sup>K,CHAM,HCK</sup>
		<i>A. glauerti</i> Keirans, King & Sharrad, 1994 <sup>KR,CHAM,HCK</sup>
		<i>A. goeldii</i> Neumann, 1899 <sup>K,CHAM,HCK</sup>
		<i>A. hainanense</i> Teng, 1981 <sup>K,CHAM,HCK</sup>
		<i>A. hebraeum</i> Koch, 1844 <sup>K,CHAM,HCK</sup>
		<i>A. helvolum</i> Koch, 1844 <sup>K,CHAM,HCK</sup>
		<i>A. hirtum</i> Neumann, 1906 <sup>HCK</sup>
		<i>A. humerale</i> Koch, 1844 <sup>K,CHAM,HCK</sup>
		<i>A. imitator</i> Kohls, 1958 <sup>K,CHAM,HCK</sup>
		<i>A. incisum</i> Neumann, 1906 <sup>K,CHAM,HCK</sup>
		<i>A. inopinatum</i> (Santos Dias, 1989) <sup>HCK</sup>
		<i>A. inornatum</i> (Banks, 1909) <sup>K,CHAM,HCK</sup>
		<i>A. integrum</i> Karsch, 1879 <sup>K,CHAM,HCK</sup>
		<i>A. javanense</i> (Supino, 1897) <sup>K,CHAM,HCK</sup>
		<i>A. komodoense</i> (Oudemans, 1929) <sup>K,CHAM,HCK</sup>
		<i>A. kraneveldi</i> (Anastos, 1956) <sup>K,CHAM,HCK</sup>
		<i>A. laticaudae</i> Warburton, 1933 <sup>K,CHAM,HCK</sup>
		<i>A. latum</i> Koch, 1844 <sup>K,CHAM,HCK</sup>
		<i>A. latepunctatum</i> Tonelli-Rondelli, 1939 <sup>RD</sup> (refer to Labruna <i>et al.</i> , 2005)
		<i>A. lepidum</i> Dönitz, 1909 <sup>K,CHAM,HCK</sup>
		<i>A. limbatum</i> Neumann, 1899 <sup>K,CHAM,HCK</sup>
		<i>A. loculosum</i> Neumann, 1907 <sup>K,CHAM,HCK</sup>
		<i>A. longirostre</i> (Koch, 1844) <sup>K,CHAM,HCK</sup>
		<i>A. macfarlandi</i> Keirans, Hoogstraal & Clifford, 1973 <sup>K,CHAM,HCK</sup>
		<i>A. macropi</i> Roberts, 1953 <sup>K,CHAM,HCK</sup>
		<i>A. maculatum</i> Koch, 1844 <sup>K,CHAM,HCK</sup>
		<i>A. marmoreum</i> Koch, 1844 <sup>K,CHAM,HCK</sup>

*(cont.)*

Table 1.1 (*cont.*)

Family	Genus	Species
		<i>A. moreliae</i> (Koch, 1867) <sup>K,CHAM,HCK</sup>
		<i>A. moyi</i> Roberts, 1953 <sup>K,CHAM,HCK</sup>
		<i>A. multipunctum</i> Neumann, 1899 <sup>K,CHAM,HCK</sup>
		<i>A. naponense</i> (Packard, 1869) <sup>K,CHAM,HCK</sup>
		<i>A. neumanni</i> Ribaga, 1902 <sup>K,CHAM,HCK</sup>
		<i>A. nitidum</i> Hirst & Hirst, 1910 <sup>K,CHAM,HCK</sup>
		<i>A. nocens</i> Robinson, 1912 sensu Theiler & Salisbury, 1959 <sup>CHAM</sup>
		<i>A. nodosum</i> Neumann, 1899 <sup>K,CHAM,HCK</sup>
		<i>A. nuttalli</i> Dönitz, 1909 <sup>K,CHAM,HCK</sup>
		<i>A. oblongoguttatum</i> Koch, 1844 <sup>K,CHAM,HCK</sup>
		<i>A. orlovi</i> (Kolonin, 1992) <sup>KR,CHAM,HCK</sup>
		<i>A. ovale</i> Koch, 1844 <sup>K,CHAM,HCK</sup>
		<i>A. pacae</i> Aragão, 1911 <sup>K,CHAM,HCK</sup>
		<i>A. papuanum</i> Hirst, 1914 <sup>K,CHAM,HCK</sup>
		<i>A. parkeri</i> Fonseca & Aragão, 1952 <sup>CHAM</sup>
		<i>A. parvitarsum</i> Neumann, 1901 <sup>K,CHAM,HCK</sup>
		<i>A. parvum</i> Aragão, 1908 <sup>K,CHAM,HCK</sup>
		<i>A. pattoni</i> (Neumann, 1910) <sup>K,CHAM,HCK</sup>
		<i>A. paulopunctatum</i> Neumann, 1899 <sup>K,CHAM,HCK</sup>
		<i>A. pecarium</i> Dunn, 1933 <sup>K,CHAM,HCK</sup>
		<i>A. perpunctatum</i> (Packard, 1869) <sup>CHAM</sup>
		<i>A. personatum</i> Neumann, 1901 <sup>K,CHAM,HCK</sup>
		<i>A. pictum</i> Neumann, 1906 <sup>K,CHAM,HCK</sup>
		<i>A. pilosum</i> Neumann, 1899 <sup>K,CHAM,HCK</sup>
		<i>A. pomposum</i> Dönitz, 1909 <sup>K,CHAM,HCK</sup>
		<i>A. postoculatum</i> Neumann, 1899 <sup>K,CHAM,HCK</sup>
		<i>A. pseudoconcolor</i> Aragão, 1908 <sup>K,HCK</sup>
		<i>A. pseudoparvum</i> Guglielmone, Mangold & Keirans, 1990 <sup>K,CHAM,HCK</sup>
		<i>A. quadricavum</i> (Schulze, 1941) <sup>K,CHAM,HCK</sup>
		<i>A. rhinocerotis</i> (de Geer, 1778) <sup>K,CHAM,HCK</sup>
		<i>A. robinsoni</i> Warburton, 1927 <sup>K,CHAM,HCK</sup>
		<i>A. rotundatum</i> Koch, 1844 <sup>K,CHAM,HCK</sup>
		<i>A. sabanerae</i> Stoll, 1890 <sup>K,CHAM,HCK</sup>
		<i>A. sculpturatum</i> Neumann, 1906 <sup>K,CHAM,HCK</sup>
		<i>A. scutatatum</i> Neumann, 1899 <sup>K,CHAM,HCK</sup>
		<i>A. soembawensis</i> (Anastos, 1956) <sup>K,CHAM,HCK</sup>
		<i>A. sparsum</i> Neumann, 1899 <sup>K,CHAM,HCK</sup>
		<i>A. sphenodonti</i> (Dumbleton, 1943) <sup>K,CHAM,HCK</sup>
		<i>A. splendidum</i> Giebel, 1877 <sup>K,CHAM,HCK</sup>
		<i>A. squamosum</i> Kohls, 1953 <sup>K,CHAM,HCK</sup>
		<i>A. striatum</i> Koch, 1844 <sup>K,HCK</sup>
		<i>A. superbum</i> Santos Dias, 1953 <sup>CHAM</sup>