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ARTHROPODA

Acari (Order): Ticks

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Order Acari

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Chapter 66

Acari (Order): Ticks

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Tick Biology and Life Cycles

Ticks (order Ixodida Leach, 1815) are blood-feeding ectoparasites of vertebrates representing important vectors of pathogens that cause diseases in humans and other animals (see Figure 1). They are obligate parasites at 1 or more developmental stages and may parasitize different classes of terrestrial vertebrates including mammals, birds, reptiles, and amphibians. All species of ticks have 4 stages in their life cycle, including the **embryonated egg** and 3 active stages: **Larva**, **nymph** (one or more instars), and **adult** (male and female). The tick life cycle may have many variations depending on the family and species. Depending on the number of hosts on which they feed, the tick may have a 1-host, 2-host, 3-host, or multi-host life cycle. During their off-host development phases, they can persist for long periods in the environment without feeding, particularly ticks in the family Argasidae (the soft ticks; see Sonenshine, 1991).

Ixodid ticks (family Ixodidae, the hard ticks) have a single nymphal instar and of them are **non-nidicolous**, meaning living in open and exposed habitats. In some species, only females result from the nymphal stage. These females reproduce **parthenogenetically**, that is, they do not need to mate to produce eggs (Sonenshine, 1991). Larvae and nymphs take a blood meal before molting to the next stage. Females lay several hundreds or thousands of eggs after engorging. Larvae, nymphs, and females may feed for several days, whereas males are usually intermittent feeders, taking small blood meals at each feeding and may remain on the host for long periods of time (Oliver, 1989; Sonenshine, 1991; 2013). Ixodid females have a single **gonotrophic cycle**. After completing feeding, they detach from the host to initiate oviposition in a secluded place, such as under vegetation, at the base of tree trunks, animal burrows, or even in cracks and crevices on the walls of human houses and animal sheds. Once oviposition is complete, the female dies. Males of Metastriata may stay on the hosts for long periods, mating with several females. These males usually mate on the host and need a blood meal to produce viable sperm. Males of the genus *Ixodes* (Prostriata) typically mate off the host, which is typical of nidocolous tick species. Most ixodids have a 3-host life cycle, where each stage falls to the ground after feeding. Engorged larvae detach from a host to molt in the environment, the same occurring with resulting nymphs that seek another host to feed and detach as engorged nymphs to molt into males or females, which in turn will complete the parasitic life cycle onto another host (Oliver, 1989; Sonenshine, 1991).

Other species of ixodids have a 2-host tick life cycle, characterized by larvae that feed and molt on the same host, whereas the nymphs feed and detach after engorgement. Nymphs molt in the environment and the resulting males or females attach to another host to complete the parasitic life cycle. There are a few species, including some of economic importance, that have a 1-host life cycle. They molt on the host (from larva to nymph and then to adult) and detach from the host as engorged females (Oliver, 1989; Sonenshine, 1991).

Almost all argasid species (family Argasidae, the soft ticks) are **nidicolous**, meaning living in the protected habitat of a nest of a bird or mammal, and usually have more than 1 nymphal instar in their life cycle. Many species have a multi-host life cycle, with the exception of some species, such as

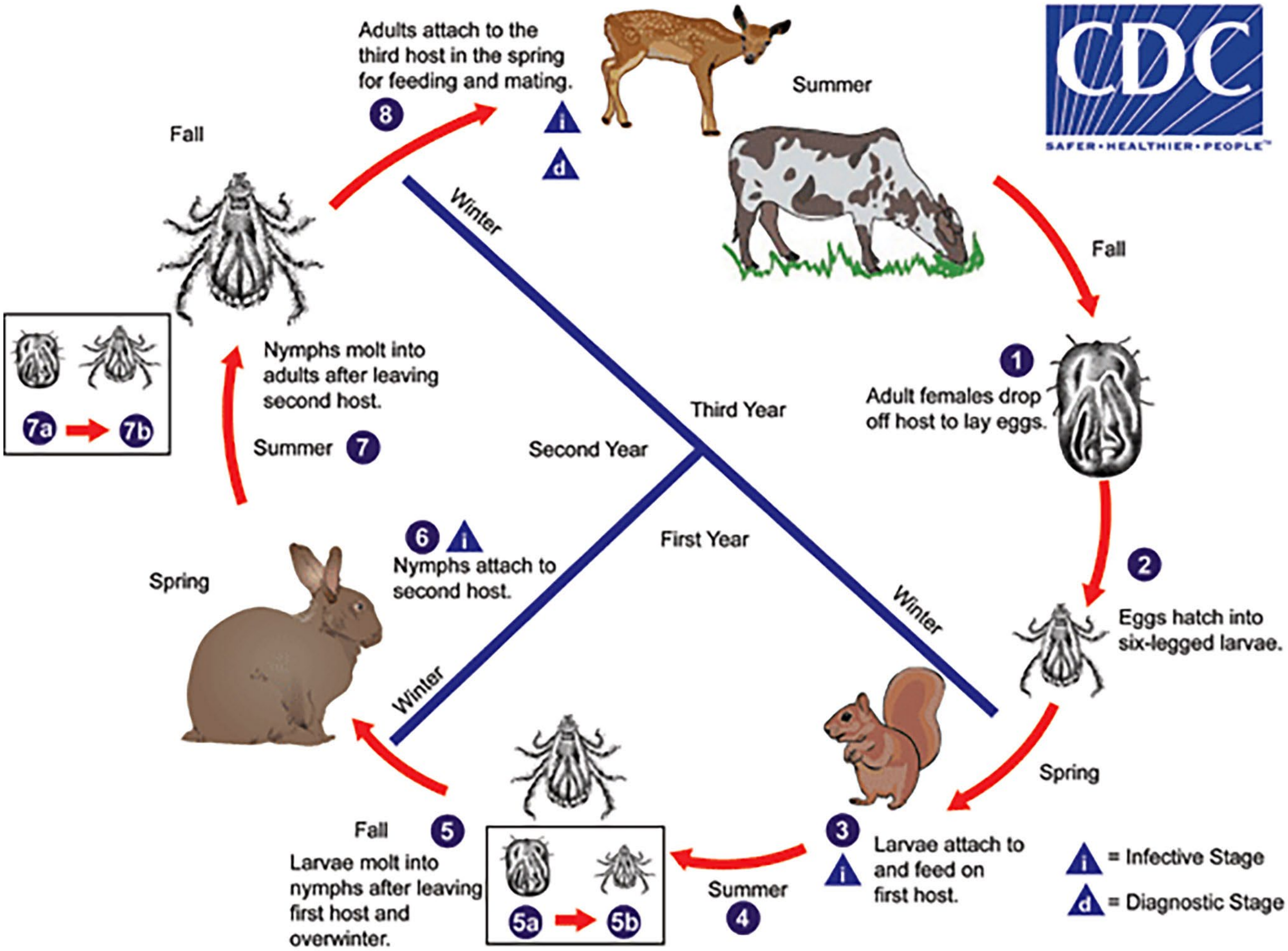

Figure 1. Life cycle of 3-host ixodid (hard) ticks. The adult is considered the diagnostic stage, as identification to the species level is best achieved with adults. Most ticks of public health importance follow this pattern, including members of the genera *Ixodes* (Lyme borreliosis, babesiosis, human granulocytic ehrlichiosis), *Amblyomma* (tularemia, ehrlichiosis, and Rocky Mountain spotted fever), *Dermacentor* (Rocky Mountain spotted fever, Colorado tick fever, tularemia, tick paralysis), and *Rhipicephalus* (Rocky Mountain spotted fever, boutonneuse fever). — Three-host ixodid ticks have a life cycle that usually spans 3 years, although some species can complete the cycle in only 2 years. Adult females drop off the third host to lay eggs after feeding (1), usually in the fall. Eggs hatch into 6-legged larvae (2) and overwinter in the larval stage. In the spring, the larvae seek out and attach to the first host, usually a small rodent (3). Later in the summer, engorged larvae leave the first host (4) and molt into nymphs (5), usually in the fall. The ticks overwinter in this stage. During the following spring, the nymphs seek out and attach to the second host (6), usually another rodent or lagomorph. The nymphs feed on the second host and drop off later in the summer (7). Nymphs molt into adults (7a–7b) off the host in the late summer or fall and overwinter in this stage. The next spring, adults seek out and attach to a third host, which is usually a larger herbivore (including cervids and bovids), carnivore, or human (8). The adults feed and mate on the third host during the summer. Females drop off the host in the fall to continue the cycle. Females may reattach and feed multiple times. The 3 hosts do not necessarily have to be different species, or even different individuals. Also, humans may serve as first, second, or third hosts. Source: United States Centers for Disease Control and Prevention, Division of Parasitic Diseases and Malaria, 2017. Public domain.

Ornithodoros lahorensis Neumann, 1908 that has a 2-host life cycle, and *O. megnini* that is a 1-host tick. In most argasid species, nymphs and adults are rapid feeders (generally taking around 30 to 40 minutes to complete a meal), but larvae usually remain feeding on a host for several days (Oliver, 1989; Sonenshine, 1991; 2013). Each immature stage feeds before molting to the next stage, but in some species of the genus *Ornithodoros*, such as *O. brasiliensis* Aragão, 1923, larvae molt to nymphs without feeding (Ramirez et al., 2016).

Some species of *Argas* and *Ornithodoros* may reproduce by **autogeny** (for example, *A. persicus* (Oken, 1818), *O. lahorensis*, *O. tholozani* (Laboulbène and Mégnin, 1882), *O. tartakovskyi* Olenev, 1931, and *O. parkeri* Cooley, 1936) (see Feldman-Muhsam, 1973; Oliver, 1989), and nymphs of some species (for example, *O. fonsecai* (Labruna and Venzal, 2009) and *Nothoaspis amazoniensis*) molt from the first to the second instar without feeding (Nava et al., 2010). Facultative autogeny may occur in the absence of a host. Females present multiple gonotrophic cycles and can feed many times, usually before mating and oviposition (Sonenshine, 1991). But for some species, the feeding behavior remains unknown.

Mating takes place off-host, and the female can lay a few hundred eggs after each meal, in each gonotrophic cycle. This is a survival mechanism, especially for nest dwelling species that depend on the presence, not always frequent, of their hosts. Exceptions may occur, for example, in adults of *Antricola* and *Otobius* that have vestigial mouthparts and a female may even lay eggs without feeding (this is called obligate autogeny) (Oliver, 1989; Sonenshine, 1991; 2013).

The biological life cycle involving multiple hosts is typical of argasids, which inhabit restricted environments and feed on the same individual host several times or in several hosts (of the same species or not) during their lifetime. Their habitat is intimately associated with that of their hosts. However, they can be found in remote locations far from human habitations such as loose soil, tree bark, animal burrows, caves, and in nests of wild and marine birds. Those that inhabit animal nests live in relatively stable microhabitats, feeding and reproducing continuously throughout the year. In this group, as in ixodids that inhabit nests, the development can be adapted seasonally, and a generation can take a year or more to develop in temperate climates (Oliver, 1989; Sonenshine, 1991; 2013).

The life cycle of the only species of family Nuttalliellidae is still unknown and the main hosts for each stage are uncertain. As an ixodid tick, *Nuttalliella namaqua* has a single nymphal instar and recently it has been shown that *N. namaqua* females may feed multiple times, like argasid females (Latif et al., 2012; Mans et al., 2012). Potential hosts already described for *N. namaqua* include mammals, reptiles, and birds (Mans et al., 2014). Larvae have been found parasitizing different species of rodents (Horak et al., 2012), and adults have been found in nests of birds (Keirans et al., 1976). Results of DNA analysis of the gut meals of females indicated that the ticks had fed on lizards of different species. Nymphs and adult females, therefore, have been shown to successfully feed on lizards in an experimental setting (Mans et al., 2011; 2014). Nymphs and adult females have been found in a variety of microhabitats in different regions of Africa (Mans et al., 2014). Although larvae may generally feed on rodents, the nymphal and adult stages seem to prefer reptiles, it is still premature to conclude that natural hosts of immature individuals or adults may feed exclusively on either mammals or reptiles. All these data may suggest a wider geographic distribution as well as host preference for *N. namaqua.*

Host Range

Ticks have variable degrees of specificity for their hosts, with some species parasitizing very different groups of animals. Some species of ticks only feed on a narrow range of host groups or on a specific host species (host-specific = narrow host range), whereas others are less selective (generalists), using a wide range (broad host range) of vertebrates as hosts (Sonenshine, 2013). Mammals serve as hosts for more tick species than birds, reptiles, and amphibians. Among mammals, rodents are one of the most common host groups, particularly for immature stages of hard ticks.

In general, immature stages of species that have a 2- or 3-host life cycle feed on small animals (for example, rodents), whereas adults prefer medium- and large-sized animals. In ticks that use more than 1 host, as happens with most species of the genus *Amblyomma*, immature stages are less specific than the adults, and may parasitize a greater diversity of hosts (Sonenshine, 2013). Host specificity is influenced by several factors, including host defense mechanisms against tick infestations, such as physical barriers in the body, self-cleaning behavior, and immunological responses.

Both passive and active questing methods are used by ticks to find their hosts. Passive species, such as most nidicolous ticks, remain in their habitat (for example, grassy fields, brushy areas, animal burrows, nests) and depend upon contact with vertebrate animals that invade their space incidentally. Most non-nidicolous ticks are hunters; they use ambush behavior (called questing), referring to ticks living in grass or brush-covered habitats typically climbing to the tips of stems or branches of vegetation where they wait for passing hosts to brush against them (Sonenshine, 2013). The success of a tick in finding a host depends on several factors, including the height of the vegetation on which ticks of different stages are waiting for a host, as well as the response of ticks to specific stimuli, such as body odor, body heat, and carbon dioxide (CO_2), which are emitted from the host. Also, the type of environment has a direct influence on the qualitative and quantitative availability of hosts for the ticks.

The seasonal variation in the biological cycles and development of a species of tick is determined by the host and by abiotic factors, such as temperature, photoperiod, and relative humidity. Temperature plays an important role in determining the duration of each off-host development phase such as: For example, oviposition, egg incubation, larvae hatching, and ecdysis (molting from one stage to another). The photoperiod has a direct influence in the induction of diapause, mainly in nonequatorial regions, modulating the cycles in seasonal rhythms that assure the ticks the synchronization of their activities with the appropriate climatic conditions (Oliver, 1989; Sonenshine, 2013).

Two types of diapause are known: Behavioral (suppression of host-seeking activity or delay of engorgement) and morphogenetic or developmental (delay during embryogenesis) in the ecdysis of immature stages or in the oviposition (egg laying) of females (Sonenshine, 2013). This is an important strategy in the biology of both nidicolous and non-nidicolous ticks, such as *Amblyomma sculptum*, that use both larval and behavioral diapause (Labruna et al., 2002; 2003).

Taxonomic History

Millions of years ago, during the Paleozoic Era, ticks diverged from other Acari Leach, 1817, probably as parasites of the ancestors of modern vertebrates such as reptiles and amphibians (Dantas-Torres, 2018). Therefore, ticks disappeared when their conquering continental hosts went extinct. Fossil evidence indicates that modern tick lineages originated and diverged during the Mesozoic Era (Mans et al., 2016).

There are 2 fossil species in the family Argasidae Koch, 1844 (soft ticks), both of which are in the genus *Ornithodoros* Koch, 1844, namely, *O. antiquus* Poinar, 1995 and *O. jerseyi* (Klompen and Grimaldi, 2001). The third argasid fossil with an adequate morphological description corresponds to a male of *Ornithodoros* sp. found in Dominican amber from about 25 Ma (= million years ago) (Estrada-Peña and De La Fuente, 2018). These authors suggested that many of the lineage splits were produced when the landmasses were still forming the supercontinent Pangea, or Laurasia and Gondwanaland. Fossil species in the family Ixodidae Koch, 1844 (hard ticks) include *Amblyomma birmitum* Chitimia-Dobler, Araujo, Ruthensteiner, Pfeffer and Araujo, 2017, *Cornupalpatum burmanicum* Poinar and Brown, 2003, *Compluriscutula vetulum* Poinar and Buckley, 2008, *Ixodes succineus* Weidner, 1964, and *Haemaphysalis cretacea* Chitimia-Dobler, Pfeffer and Dunlop, 2018. The only fossil of the genus *Haemaphysalis* Koch, 1844 may actually belong to another genus (Guglielmone et al., 2016; see also Dantas-Torres, 2018). Recently, a fossil species, namely *Deinocroton draculi* Peñalver, Arillo, Anderson and De la Fuente, 2017, was described in a recently proposed fossil family Deinocrotonidae Peñalver, Arillo, Anderson and Pérez-de la Fuente, 2017. This species resembles *Nuttalliella namaqua* Bedford, 1931, which represents a basal lineage within the order Ixodida.

Current Taxonomic Position of Tick Genera

The Ixodida is currently represented by 956 species (948 extant and 8 fossil species) (see the supplementary material for more about this), which we now consider to be distributed into 4 families: **Argasidae** (215 species), **Ixodidae** (733 species), **Nuttalliellidae** Bedford, 1931 (monospecific), and **Deinocrotonidae** (monospecific) (Dantas-Torres, 2018; Du et al., 2018; Kwak, 2018; Barker, 2019; Tomlinson and Apanaskevich, 2019).

Excluding the monospecific families, the genus-level classification of ticks has been a long issue of debate and changes are constantly proposed, particularly in the family Argasidae.

Following are detailed descriptions of some groups of ticks.

Family Argasidae: The Soft Ticks

The family Argasidae, or the soft ticks, includes 215 extant and 2 fossil species (Dantas-Torres, 2018), many of which have not been yet adequately described. Estrada-Peña and colleagues (2010) suggest that there is still a long way to go to achieve an accurate view of the main evolutionary lines of the family. The soft ticks are so-named because they have no hard plate on their back (called the scutum in hard ticks; see below). They also commented that there is no consensus about the relevant morphological features for the determination of argasid species nor there is consensus on the appropriate genus for many species. According to Venzal and colleagues (2008), only larval morphological features have been adequately defined for a specific determination, mainly in the absence of DNA sequence data.

In this chapter, the genus-level classification adopted by the last lists of ticks of the world is used (Guglielmone et al., 2010; Dantas-Torres, 2018). Also included are 2 recent genera proposed by Barker and Burger (2018) and new species described in 2019 (Barker, 2019; Martins et al., 2019; Tomlinson and Apanaskevich, 2019; Sun et al., 2019). However, the genus-level classification of argasids is still controversial, with some subgenera perhaps deserving to be elevated to the rank of genera (Burger et al., 2014; Mans et al., 2019). Based on 4 classification schemes for the argasid genera (the Soviet, American, French, and Cladistic schools), the subfamily Argasinae (Trouessart, 1892, pro parte) Pospelova-Shtrom, 1946 (ectoparasites of chickens and wild birds) is well supported by molecular data (Burger et al., 2014). However, this is not true for the subfamily Ornithodorinae Pospelova-Shtrom, 1946. After sequencing the mitochondrial genomes of 12 species, Burger and colleagues (2014) concluded that there is a clade of Neotropical species within the Ornithodorinae that includes the genera *Antricola* Cooley and Kohls, 1942 and *Nothoaspis* Keirans and Clifford, 1975, and the subgenera *Alectorobius* Pocock, 1907, *Parantricola* Cerny, 1966, and *Subparmatus* Clifford, Kohls and Sonenshine, 1964. On the other hand, the genera and subgenera of the Neotropical Ornithodorinae clade were placed in the genus *Carios* Latreille, 1796, as previously proposed by Klompen and Oliver (1993). Probably, the generic classification of argasids adopted here (Guglielmone et al., 2010) will change in the future, considering that new genomic data are becoming available, shedding new light onto this issue. For instance, Mans and colleagues (2019) generated a total of 83 whole mitochondrial genomes, 18S rRNA and 28S rRNA genes and proposed a revised genus-level classification for the family Argasidae. The new classification corresponds broadly with the morphological cladistic analysis of Klompen and Oliver (1993), however, with the erection of different subgenera to the genus level.

The genus *Antricola* is represented by 17 species distributed in the Neotropical region, most of them being restricted to Cuba. Besides Cuba, some species have been described from Mexico, Puerto Rico, Brazil, and Venezuela (Jones et al., 1972; De La Cruz, 1973; 1976; 1978; De La Cruz and Estrada-Peña, 1995; Camicas et al., 1998; Estrada-Peña et al., 2004; Guglielmone et al., 2010). The main contributions to the taxonomy of this genus were produced by De La Cruz, during the 1970s (De La Cruz, 1973; 1976; 1978). The number of species described from 1910 to 2004 is shown in Figure 2A. A key for the currently known species of *Antricola* is available in Estrada-Peña and colleagues (2004).

The genus *Argas* Latreille, 1795 is currently represented by 62 species, distributed in the Afrotropical, Australasian, Neotropical, and Oriental regions (Camicas et al., 1998). The number of species described from 1795 to 2012 is shown in Figure 2B. Most of the species have been described in the last century, and half of them from 1960 to 1980 (35 species). The main contributions were those of Kohls and Hoogstraal (1961), Kohls and colleagues (1970), and Keirans and colleagues (1979). According to Muñoz-Leal (2018), the morphology of nymphs and adults of *Argas* are less informative taxonomically, but some integumental dorsal features may be useful for a specific identification.

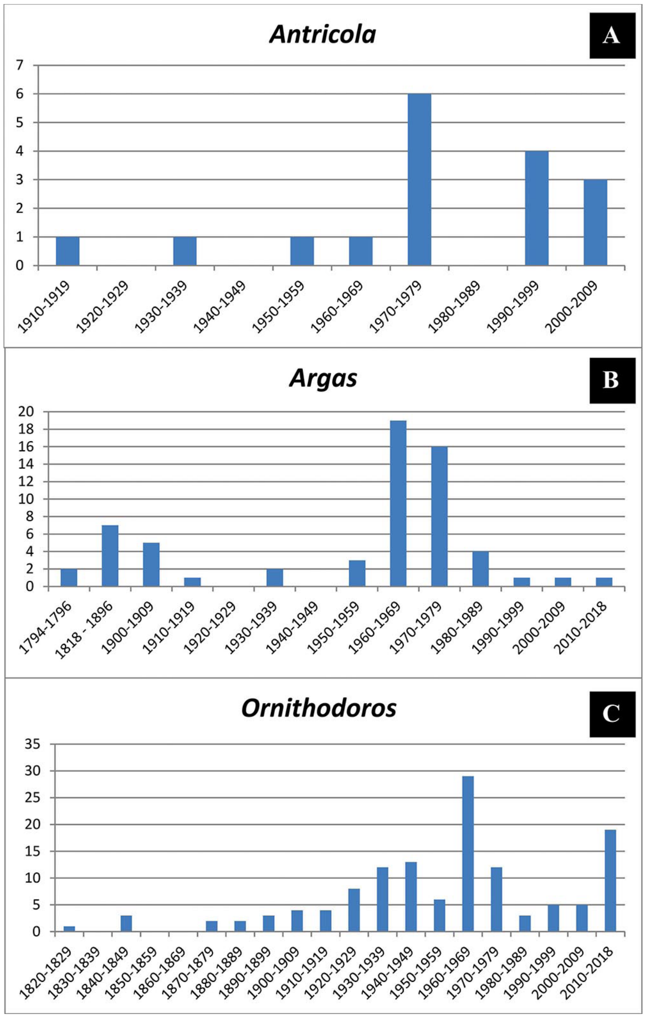

Figure 2. Argasidae genera. A) Number of *Antricola* species chronologically described from 1910 to 2004; B) number of *Argas* species chronologically described from 1795 to 2012; C) number of *Ornithodoros* species chronologically described from 1820 to 2019. Source: D. Moraes Barros-Battesti, V. Castilho Onofrio, and F. Dantas-Torres. License: CC BY.

The genus *Nothoaspis* is composed of 3 species (*N. reddelli* Keirans and Clifford, 1975 in Mexico; *N. amazoniensis* Nava, Venzal and Labruna, 2010 in Brazil; and *N. setosus* (Kohls, Clifford & Jones, 1969) n. comb. (Muñoz-Leal et al., 2019). The last species was previously assigned to the genus *Ornithodoros*, but the morphological and molecular analysis of *O. setosus* larvae recently collected of the local type of this species showed that it belongs to the genus *Nothoaspis.* This genus is restricted to the Neotropical region (Keirans and

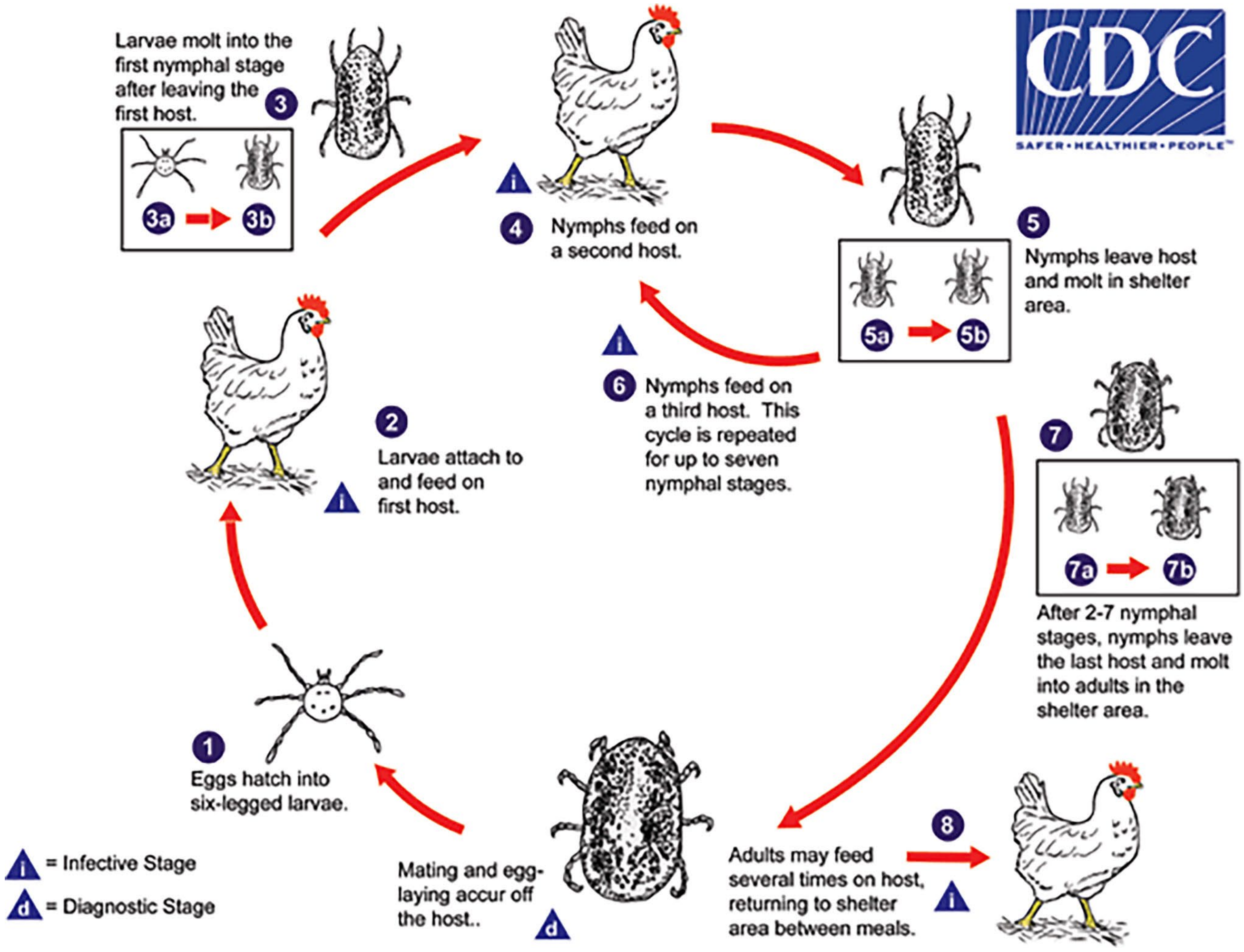

Figure 3. Multihost life cycle for argasid (soft) ticks. Unlike the Ixodidae, members of the family Argasidae have 2 or more nymphal stages, each of which requires a blood meal. This pattern is referred to as the multihost life cycle. Two species of public health concern in the United States, *Ornithodoros hermsi* and *O. turicata*, are vectors of tick-borne relapsing fever (TBRF) spirochetes. In Africa and Asia, *O. moubata* is a vector of TBRF spirochetes. Members of the genus *Carios* are vectors of TBRF spirochetes in Central America and South America. — Mating usually occurs, and egg-laying always occurs, off the host in a sheltered area (usually an animal nest). Eggs hatch into 6-legged larvae (1) in the parents' sheltered area. They quest for a host in the vicinity of the sheltered area. Once a suitable host is found, they feed for anywhere from 1 hour to several days, depending on the species (2). After feeding, the larvae leave the host and molt into the first nymphal instars in the sheltered area (3a–3b). The nymphs quest for, and feed on, the second host (4) rapidly (usually about an hour). The second host is usually the same species, and often the same individual, as the first host. The first nymphal instars leave the host and molt into the next nymphal instars in the sheltered area (5a–5b). This cycle can continue to accommodate up to 7 nymphal instars (6), depending on the species. After the last nymphal instar has fed, it leaves the host and molts into an adult (7a–7b) in the sheltered area. Adults may continue to feed on the host (8), feeding rapidly and detaching after each blood meal. Females of some species lay egg batches after each meal. Humans are usually only incidental hosts for argasid ticks and may be fed upon by any of the stages. Source: United States Centers for Disease Control and Prevention, Division of Parasitic Diseases and Malaria, 2017. Public domain.

Clifford, 1975; Nava et al., 2010; Muñoz-Leal et al., 2019). Note that *N. setosus* is referred to as *O. setosus* in the supplementary list for this chapter.

The genus *Ornithodoros* is the most speciose in the family Argasidae and comprises 131 extant and 2 fossil species (note that the fossil species are not included in the supplementary list for this chapter). They are distributed in the Afrotropical, Australasian, Oriental, Nearctic, Neotropical, and Palearctic regions (Camicas et al., 1998). The number of species described from 1820 to 2019 is shown in Figure 2C. As for *Argas*, most of them were described from 1960–1969 (29 species), and the main contributions are those of Clifford and colleagues (1964), Kohls and Clifford (1964), Kohls and colleagues (1965; 1969a), followed by those described from 2010–2019 (20 species) (Dantas-Torres et al., 2012a; Trape et al., 2013; Venzal et al., 2012; 2013; 2015; Barros-Battesti et al., 2015; Labruna et al., 2016; Muñoz-Leal et al, 2016; 2017; Bakkes et al., 2018; Sun et al., 2019).

The nymphs and adults of *Ornithodoros* are very similar and no reliable keys are currently available for their identification. On the other hand, larvae can be reliably separated by chaetotaxy of dorsum and venter, morphology of hypostome and, if present, dorsal plate.

The genus *Otobius* (Banks, 1912) includes 2 species, namely *O. megnini* (Dugès, 1883) and *O. lagophilus* Cooley and Kohls, 1940. The species *O. megnini* is thought to have had its original center of distribution in the arid lands of southwestern North America (Keirans and Pound, 2003). It was probably introduced into Central America and South America on both cattle and horses, and it was imported into South Africa in the ears of horses from South America or, perhaps, Mexico (Keirans and Pound, 2003). Currently, it is distributed worldwide, occurring in Afrotropical, Nearctic, Neotropical and Oriental regions (Camicas et al., 1998; Flores and Solís, 2018; Hosseini-Chegeni et al., 2018). The species *O. lagophilus* is restricted to the Nearctic region, parasitizing wild rabbits, occurring in Canada and the United States (Herrin and Beck, 1965).

Family Ixodidae: The Hard Ticks

The family Ixodidae currently comprises 733 extant and 5 fossil species. This family is divided into 2 lineages (that is, Prostriata and Metastriata) found in all zoogeographic regions of the world (Guglielmone et al., 2014). The ixodids are called hard ticks because they have a big plate on their back called the scutum. The Prostriata (anal groove curves anterior to anus) contains only 1 genus, whereas the Metastriata (when present, anal groove curves posterior to anus) contains 14 genera (Burger et al., 2012; Barker and Burger, 2018). In contrast to what occurs with the family Argasidae, the genus-level classification of Ixodidae is more stable and consensual (Barker and Murrell, 2002; Guglielmone et al., 2014; Dantas-Torres, 2018). Nonetheless, some systematic issues (for example, paraphyly of the genus *Amblyomma* Koch, 1844) are still under debate (Barker and Burger, 2018), but the 2 genera proposed by these authors are here included with the new combinations.

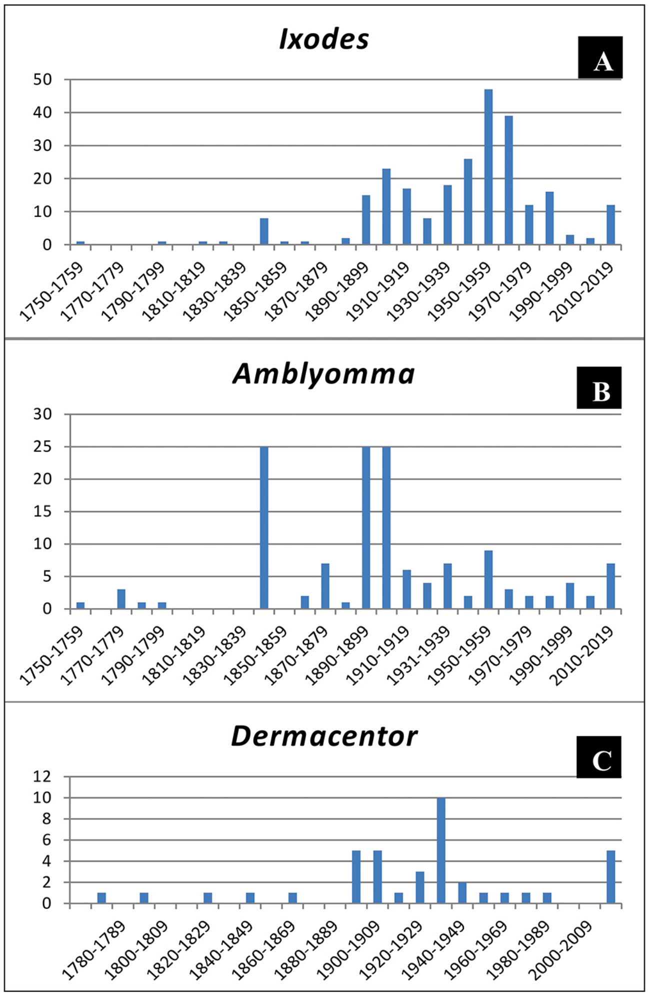

Figure 4. Ixodidae genera. A) Number of *Ixodes* species chronologically described from 1758 to 2019; B) number of *Amblyomma* species chronologically described from 1758 to 2019; C) number of *Dermacentor* species chronologically described from 1776 to 2016. Source: D. Moraes Barros-Battesti, V. Castilho Onofrio, and F. Dantas-Torres. License: CC BY.

The genus *Ixodes* Latreille, 1795 comprises 255 extant species and 1 fossil species. They are distributed in the Afrotropical, Australasian, Nearctic, Neotropical, Oriental, and Palearctic regions, and combinations of these regions including remote islands, and the polar area (circumpolar)

(Guglielmone et al., 2014; Estrada-Peña et al., 2014; Hornok et al., 2014, 2016; Ash et al., 2017; Apanaskevich and Bermúdez, 2017; Guo et al., 2017; Heath and Palma, 2017; Kwak et al., 2018; Barker, 2019). This is the largest tick genus, and most of the species originated on Gondwanaland (the southern continental landmass that began to break up in the early Jurassic around 184 million years BCE) (Guglielmone et al., 2014). The number of species described from 1758 to 2019 is shown in Figure 4A. The highest number of species were described during the 1950s and 1960s, with 47 and 39 species, respectively, mainly due to the contributions of Arthur (1956; 1960a), Kohls (1953; 1956a; 1956b; 1957; 1969), Kohls and Clifford (1962; 1966; 1967), and Kohls and colleagues (1969b).

The genus *Archaeocroton* Barker and Burger, 2018 was proposed for *Amblyomma sphenodonti* (Dumbleton, 1943), the tuatara tick of New Zealand. This new combination was mainly because this species in *Amblyomma* leaves this genus polyphyletic, and indeed, taxonomically unstable (Barker and Burger, 2018). The species was named *Archaeocroton sphenodonti* (Dumbleton, 1943).

The genus *Amblyomma* is 1 of the largest genera and comprises 137 extant and 1 fossil species, distributed in the Afrotropical, Australasian, Nearctic, Neotropical, and Oriental regions. Some species are found in more than 1 region, presenting Afrotropical-Neotropical, Afrotropical-Oriental, Afrotropical-Palearctic, Australasian-Oriental, Nearctic-Neotropical, Oriental-Palearctic, Afrotropical-Australasian-Oriental, or Australasian-Oriental-Palearctic distributions (Guglielmone et al., 2014; Nava et al., 2014a; 2014b; Krawczak et al., 2015; Apaneskevich and Apaneskevich, 2018). Chitimia-Dobler et al. (2017) commented that the genus *Amblyomma* was split in Gondwanaland, with a concurrent spread into what are now known as Africa, Australia, Asia, and South America. No species occurs exclusively in the Palearctic region (Guglielmone et al., 2014). The Neotropical region is home to the largest number of species within this genus, followed by the Afrotropical region. The number of species described from 1758–2019 is shown in Figure 4B. The highest number of species was described from 1840–1849 and 1890–1899, with 25 taxa each of those decades. The greatest contributions were those of Koch (1844) and Neumann (1899), who described 20 and 21 species of *Amblyomma*, respectively, during those years. In the first 10 years of the last century, Neumann (1901; 1904; 1905; 1906; 1907; 1911) described 16 species belonging to this genus.

The genus *Anomalohimalaya* Hoogstraal, Kaiser and Mitchel, 1970 is represented by 3 species, namely *A. lamai* Hoogstraal, Kaiser and Mitchell, 1970 from Nepal, *A.lotozkyi* Filippova and Panova, 1978 from Tajikistan, and *A. cricetuli* Teng and Huang, 1981 from China. They are exclusive to the Palearctic region and found in lands that once constituted Laurasia (Hoogstraal et al., 1970; Filippova and Panova, 1978; Filippova and Bardzimashvily, 1992; Guglielmone et al., 2014).

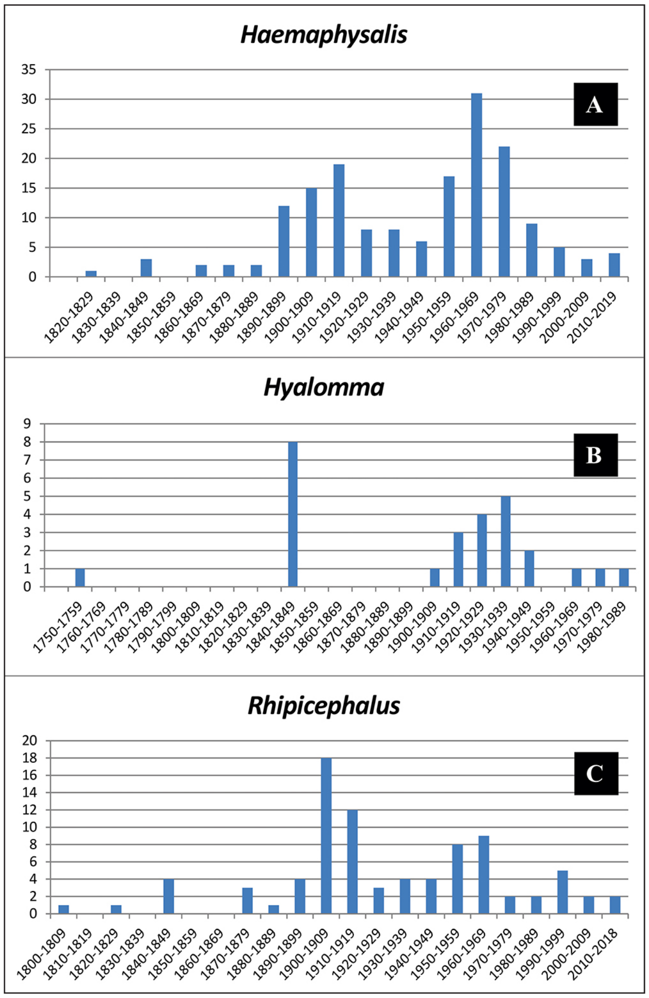

Figure 5. Ixodidae genera. A) Number of *Haemaphysalis* species chronologically described from 1826 to 2019; B) number of *Hyalomma* species chronologically described from 1758 to 1982; C) number of *Rhipicephalus* species chronologically described from 1806 to 2013. Source: D. Moraes Barros-Battesti, V. Castilho Onofrio, and F. Dantas-Torres. License: CC BY.

The genus *Bothriocroton* Keirans, King and Sharrad, 1994 includes 7 species: *B. undatum* (Fabricius, 1775), *B. hydrosauri* (Denny, 1843), *B. concolor* (Neumann, 1899), *B. oudemansi* (Neumann, 1910), *B. auruginans* (Schulze, 1936), *B. tachyglossi* (Roberts, 1953), and *B. glebopalma* (Keirans, King and Sharrad, 1994). They are found exclusively in the

Australasian region (Klompen et al., 2002; Beati et al., 2008; Burger et al., 2012; Barker and Walker, 2014).

The monospecific genus *Cosmiomma* Schulze, 1919 is found in the Afrotropical region and it is represented only by *C. hippopotamensis* (Denny, 1843) (Arthur, 1960b).

The genus *Dermacentor* Koch, 1844 is represented by 40 species, which are of Afrotropical, Nearctic, Neotropical, Oriental, Palearctic, Australasian-Oriental, Nearctic-Neotropical, and Nearctic-Palearctic distribution (Guglielmone et al., 2014; Rubel et al., 2016; Vongphayloth et al., 2018). According to Nava and colleagues (2017), the species are more prevalent in lands of Laurasian origin than in Gondwanan lands. The number of species described from 1776–2016 is shown in Figure 4C. Most species were described during the 1930s, with 10 taxa described during that decade. The main contributions to this genus were those of Schulze (1933; 1935; 1937; 1939). In the last 5 years, 1 species was described in Central America (Apanaskevich and Bermúdez, 2013a) and 4 taxa were described to in the Oriental region (Apanaskevich and Apanaskevich, 2015a; 2015b; 2015c; 2016).

The genus *Haemaphysalis* comprises 169 extant species and 1 fossil species, distributed in the Afrotropical, Australasian, Nearctic, Neotropical, Oriental, and Palearctic regions, and combinations of these regions: Afrotropical-Neotropical, Afrotropical-Palearctic, Australasian-Oriental, Nearctic-Neotropical, Oriental-Palearctic, Afrotropical-Oriental-Palearctic, and Australasian-Oriental-Palearctic (Guglielmone et al., 2014). This genus is poorly represented in the Nearctic and Neotropical regions, with the majority of species occurring exclusively in the Oriental region. The inclusion of the fossil species *H. cretacea* in this genus (Chitimia-Dobler et al., 2018) has been questioned (Dantas-Torres, 2018). The number of species described from 1826–2019 is shown in Figure 5A. The greatest numbers of species were described during the 1960s with 31 taxa, followed by the 1970s with 22 species. The greatest contributions were those of Hoogstraal and colleagues (1965; 1969), Hoogstraal and Trapido (1966), and Hoogstraal and Kim (1985). In the last decade, 6 species were described (Tomlinson and Apanaskevich, 2019).

The genus *Hyalomma* Koch, 1844 is represented by 27 species, distributed in the Afrotropical, Oriental, Palearctic, Afrotropical-Palearctic, Oriental-Palearctic, and Afrotropical-Oriental-Palearctic regions (Guglielmone et al., 2014). The greatest number of species is found in the Afrotropical, followed by the Palearctic regions. According to these authors, the genus is absent in the Australasian, Nearctic, and Neotropical regions. The highest numbers of species were described during the 1840s with 8 taxa described, and the main contributions were those of Koch (1844) who described 7 species during that decade. The number of species described from 1758–1982 is shown in Figure 5B.

The genus *Margaropus* Karsch, 1879 is represented by 3 species, namely *M. reidi* Hoogstraal, 1956, *M. wileyi* Walker and Laurence, 1973, and *M. winthemi* Karsch, 1879, which occur only in the Afrotropical region (Arthur, 1960b; Walker and Laurence, 1973; Guglielmone et al., 2014).

The genus *Nosomma* Schulze, 1919 is represented only by 2 species, namely *N. monstrosum* (Nuttall and Warburton, 1908) and *N. keralensis* Prakasan and Ramani, 2007. Both species are exclusively from the Oriental region (Guglielmone et al., 2014).

The genus *Rhipicentor* Nuttall and Warburton, 1908 is represented by 2 species, namely *R. bicornis* Nuttall and Warburton, 1908 and *R. nuttalli* Cooper and Robinson, 1908, both of which are exclusively found in the Afrotropical region (Guglielmone et al., 2014).

The genus *Rhipicephalus* Koch, 1844 includes 85 species. According to Guglielmone and colleagues (2014), 63 species are exclusively found in the Afrotropical region, 7 species occur exclusively in the Palearctic region, and 3 are found only in the Oriental region. The remaining species are distributed in the Australasian, Nearctic, and Neotropical regions, but they are not exclusively from these regions. The number of species described from 1806–2013 is shown in Figure 5C. The highest numbers of species described were from 1900–1910 with 18 taxa, followed by the 1910s with 12 species. The greatest contributions were those of Neumann (1899; 1901; 1904; 1905; 1906; 1907; 1911; 1913). The 2 latest species described in this genus were in 2013 (Apanaskevich et al., 2013b; Horak et al., 2013).

The genus *Robertsicus* Barker and Burger, 2018 was proposed for *Amblyomma elaphensis* (Price, 1959), from the Chihuahuan Desert of Mexico and the southeastern United States. This new combination was meant to solve for the polyphyly of the genus *Amblyomma* that is in the same situation (Barker and Burger, 2018). These authors named the species *Robertsicus elaphensis* (Price, 1959).

Family Nuttalliellidae

Nuttalliellidae is a monospecific family, which presently is restricted to the Afrotropical region (Bedford, 1931; Keirans et al., 1976; Camicas et al., 1998; Mans et al., 2011; 2016). Based on analysis of mitochondrial genome and nuclear ribosomal RNA (18S and 28S) sequence data, Mans and colleagues (2011; 2019) suggested that the Nuttalliellidae is basal to other tick families, representing the closest extant lineage to the last common ancestral tick lineage.

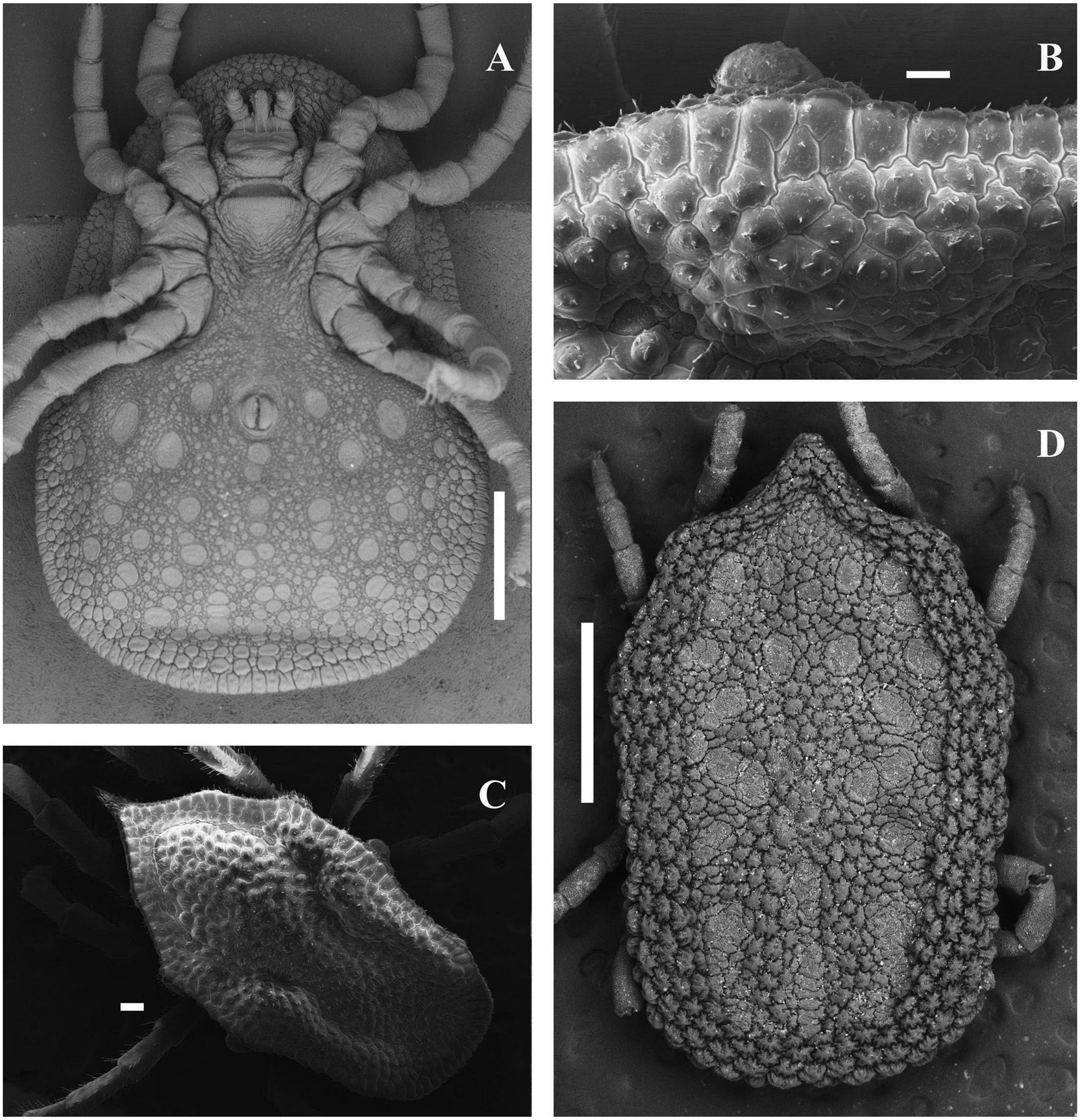

Figure 6. Adults of Argasidae genera. A) *Argas miniatus* female, ventral view; B, C) *Antricola guglielmonei*, spiracular plate and dorsal view; D) *Ornithodoros* sp., dorsal view. Scale bars: A, D = 1,000 µm; B = 100 µm; C = 200 µm. Source: D. Moraes Barros-Battesti, V. Castilho Onofrio, and F. Dantas-Torres. License: CC BY-NC-SA 4.0.

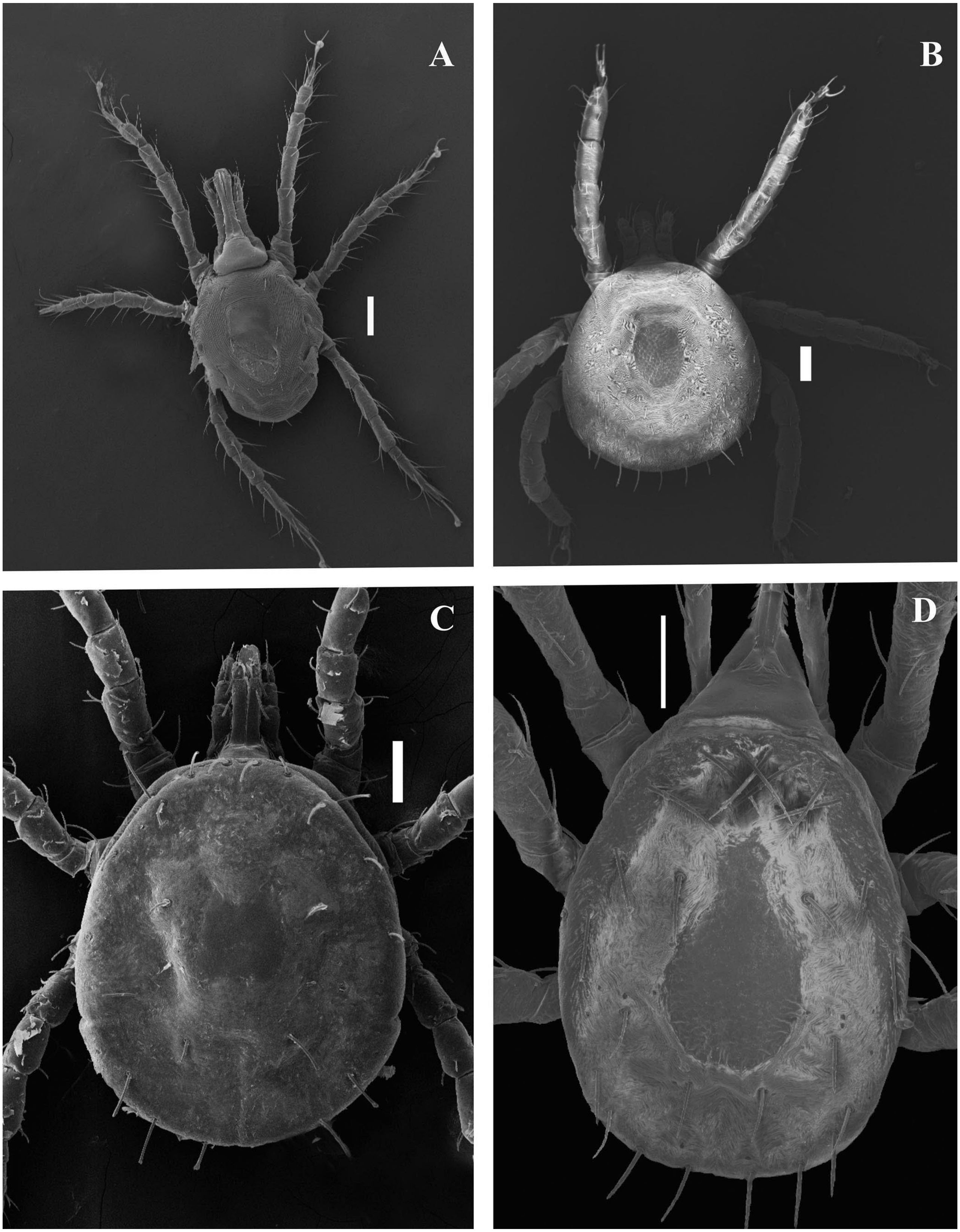

Figure 7. Larvae of Argasidae genera. A) *Otobius megnini*, dorsal view; B) *Argas miniatus*, dorsal view; C) *Ornithodoros brasiliensis*, dorsal view; D) *Or. fonsecai*, dorsal view. Scale bars: A–C = 100 µm; D = 120 µm. Source: D. Moraes Barros-Battesti, V. Castilho Onofrio, and F. Dantas-Torres. License: CC BY-NC-SA 4.0.

According to these authors, nuttalliellids almost became extinct during the great end-Permian mass extinction event, leaving *Nuttalliellia namaqua* as the closest living relative to the ancestral tick lineage.

Family Deinocrotonidae (Fossil)

Deinocrotonidae is a fossil tick family recently described based on fossil material retrieved in 99-million-year-old Cretaceous amber from Myanmar (Peñalver et al., 2017). *Deinocroton draculi* was found in association with *Cornupalpatum burmanicum*, suggesting that both deinocrotonids and ixodids fed on blood from feathered dinosaurs (Peñalver et al., 2017). Morphologically, deinocrotonids resemble nuttalliellids, but no DNA sequences from the former are available to assess their phylogenetic relationship.

Descriptions of Selected Tick Genera

In this section, morphological descriptions are presented for the identification of several tick genera as used in scientific papers. The fossil family Deinocrotonidae and the fossil genera *Deinocroton*, *Cornupalpatum*, and *Compluriscutula* are not included.

ARGASID TICK GENERA

Genus *Argas*

The following morphological descriptions are based on Cooley and Kohls (1944) and Kohls and colleagues (1970).

Larva: Dorsal surface with around 25–30 pairs of setae, dorsal plate oval and elongated; ventral surface with less than 7 pairs of setae and 1 pair on valves; posteromedial seta present or absent; 2 pairs of short post-hypostomal setae; hypostome rounded at apex, dentition 2/2 at basis to 3/3 at apex. *Nymph*: Outline oval, discs present, distributed more or less symmetrically dorsally; idiosoma mamillated, flattened dorsoventrally, with suture and lateral margin demarcating the dorsal and ventral surfaces; Haller's organ with transversely slit-like aperture, placed slightly laterally. *Adults*: Idiosoma flattened, dorsal and ventral surface equal, margin distinct flattened, made up a radial striae or quadrangular plates; sutural line present; flattened margin not obliterated even when tick is fully fed; capitulum ventral; integument leathery, minutely wrinkled in folds, of many shapes often intermingled with small, rounded, buttons each with a pit on top and often bearing a hair in the pit; discs present on both dorsal and ventral surfaces and placed in more or less radial lines; eyes absent.

Genus *Antricola*

The following morphological descriptions are based on Cooley and Kohls (1944), Estrada-Peña and colleagues (2004), and Barros-Battesti and colleagues (2013).

Larva: Dorsal surface with 14 pairs of setae, typically 14 (11 dorsolateral, 3 central dorsal); dorsal plate, large and elongated with lateral margins parallel, narrowing anteriorly; eyes absent; ventral surface with 11 pairs of setae (3 sternal setae, 3 post-coxal setae, 4 circumanal + 1 on valves), and 1 posteromedial seta; 2 pairs of long post hypostomal setae, hypostome pointed, dentition 3/3 in anterior three-fourths, then 2/2 posteriorly to basis; palps with 18 setae, number of setae on palpal article 1–4, respectively 0, 4, 5 and 9; pulvilli large, claws absent (except in *A. marginatus*); dorsal hump absent; Haller's organ with a rounded capsule, open only in a small central portion. *Nymph*: Body outline suboval, pointed anteriorly, covered by tubercles, most of them bearing short setae, some single, others in groups; hypostome short, broad and rounded apically, with small denticles on anterior and lateral margins; cheeks absent; spiracular plates oval, relatively large, expanded and dorsally visible in some specimens, with numerous minute pores. *Adults*: Dorsal surface flattened and marginated; cuticle semi-translucent and smooth, shining, and with tubercles and tufts of setae; dorsomarginal grooves well defined; transverse post-anal groove present. Basis capituli slightly longer than wide, rounded laterally, hypostome small, slightly longer than wide, scoop-like, without denticles.

Genus *Ornithodoros*

The following morphological descriptions are based on Venzal and colleagues (2006) and Barros-Battesti and colleagues (2013).

Larva: Dorsal surface of idiosoma usually with 13–14 pairs of setae (with some exceptions); dorsal plate absent in few species, but present in the majority, varying in shape, from triangular to pyriform (bat-associated group) to elongated sub-rectangular with anterior extremity narrowed; venter with 7–8 pairs + 1 pair on anal valves, and 1 posteromedial seta (which may be absent). Basis capituli with lateral angles slightly rounded, lateral auriculae present or absent, hypostome with apex rounded or pointed, dental formula: 5/5 to 2/2 at apex, 4/4 to 2/2 in medial portion and 2/2 at basis; Haller's organ with capsule aperture transversely slit-like, large, occupying all of the dorsum with many small setae, or small occupying part of the dorsum. *Nymph*: Body outline oval, slightly pointed anteriorly, idiosoma covered by tile-like mammillae; presence of 4 pairs of bulging lateral structures resembling large mammillae on supracoxal

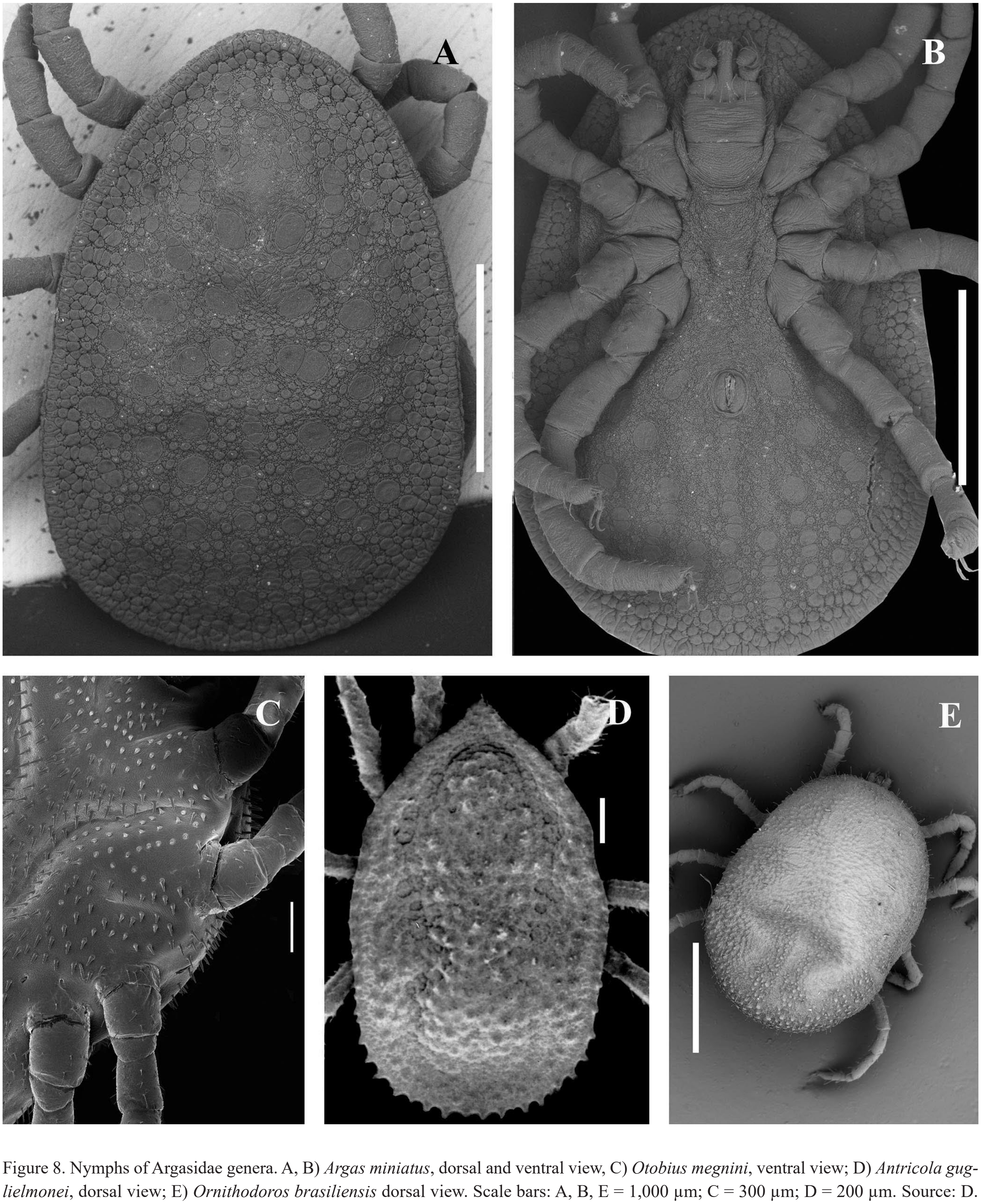

Figure 8. Nymphs of Argasidae genera. A, B) *Argas miniatus*, dorsal and ventral view, C) *Otobius megnini*, ventral view; D) *Antricola guglielmonei*, dorsal view; E) *Ornithodoros brasiliensis* dorsal view. Scale bars: A, B, E = 1,000 µm; C = 300 µm; D = 200 µm. Source: D. Moraes Barros-Battesti, V. Castilho Onofrio, and F. Dantas-Torres. License: CC BY-NC-SA 4.0.

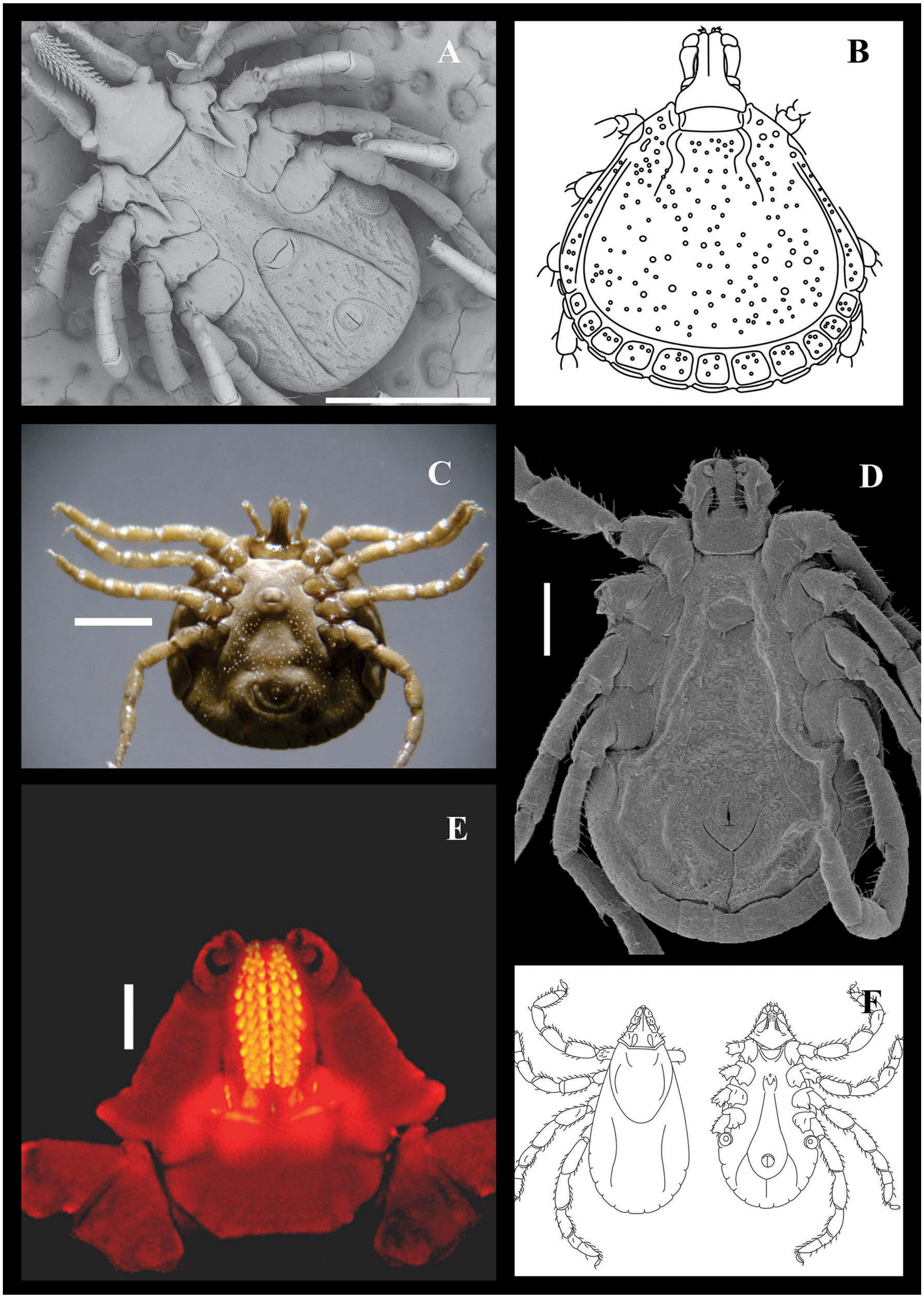

Figure 9. Adults of Ixodidae genera. A) *Ixodes aragaoi* female, ventral view; B) *Bothriocroton* male, dorsal view; C) *Amblyomma (Aponomma) quadricavum* female, ventral view; D) *Haemaphysalis juxtakochi* male, ventral view; E) *H. leporipalustris,* gnatosoma ventral view; F) *Anomalohimalaya* female, dorsal and ventral view. Scale bars: A = 500 µm; C = 1,000 µm; D = 300 µm; E = 100 µm. Sources: A, C–E) D. Moraes Barros-Battesti, V. Castilho Onofrio, and F. Dantas-Torres; B) adapted from Baker and Walker, 2004; F) adapted from Hoogstraal et al., 1970. License: CC BY-NC-SA 4.0.

folds between legs I–IV (soil-living group) or absent (bat-associated group), hypostome rounded on apex; humps present (only in the soil-living group) or absent (bat-associated group), Haller's organ similar to the larvae. *Adults*: Idiosoma suboval, with rounded margins, without marginal lateral sutures; well-developed hypostome with well-defined rows of denticles; hood present; sometimes cheeks present; eyes, when present are arranged anterolaterally to the supracoxaal folds; integument leathery, with tiny mammillated elevations, interspersed by discs on both the dorsal and ventral surfaces.

Genus *Otobius*

The following morphological descriptions are based on Cooley and Kohls (1940; 1944), Guglielmone and colleagues (2006), and Barros-Battesti and colleagues. (2013).

Larva: Integument striated, dorsal surface with 7–10 pairs of setae, dorsal plate large, elongate tapering slightly posteriorly; 2 pairs of eyes; ventral surface with 5 pairs of setae + 1 pair on valves; pulvilli present on all tarsi, not enlarged, claws present, Haller's organ with capsule aperture large and rounded, with posterior projections; hypostome long without corona, dental formula 2/2. *Nymph*: Camerostome and hood absent; hypostomal dentition 4/4; idiosoma panduriform, integument striated and spinous; spiracular plate cone-shaped; Haller's organ with capsule aperture transversely slit-like, elevated and large, bordered with prolonged pointed projections and with small setae internally. *Adult*: Integument granulated and with no change of pattern at the sides; small discs present; hood and eyes absent; hypostome vestigial, not functional to the hematophagy. The morphology is very similar between the 2 species, but the distance between the dorsal small discs in *Otobius megnini* is larger than in *O. lagophilus.*

Genus *Nothoaspis*

The following morphological descriptions are based on Nava and colleagues (2010) and Barros-Battesti and colleagues (2013) and Muñoz-Leal and colleagues (2019).

Larva: Dorsal plate with isosceles triangle shape occupying entire length of the dorsum of unfed specimens with a curvy-notched posterior margin; lateral margins of basis capitulum provided with a small bulge dorsal; surface with 12–13 pairs of setae; hypostome with apex pointed, dental formula 2/2 with 20 denticles in each row, corona absent. *Nymphs*: Idiosoma twice as longer as wide, anteriorly more abruptly narrowing than posteriorly; false shield covered by cells (irregular in shape and size) occupying the anterocentral area of dorsum, most of them at least with 1 seta; setae short, except for posterior margin of idiosoma, where setae are larger. Ventral surface with integument also covered by cells (irregular in shape and size), except for a narrow area located between coxae I and III; spiracular plate small; basis capituli subrectangular in outline, with 1 pair of post-hypostomal setae and at least 7 pairs of sublateral setae, bordered posteriorly by integumental fold; postpalpal setae absent; hood large, broadly rounded, not entirely covering capitulum, cheliceral blades, palpal articles II–IV visible dorsally; ventrally, article I forms elongate flaps protecting the pointed hypostome, dental formula 4/4 apically, 5/5 at base. *Adults*: Presence of false shield or nothoaspis (pseudoscutum), an anteriorly projecting hood covering the capitulum, a medial extension of palpal article I (flaps), genital plate extending from coxa I to IV, absence of 2 setae on the internal margin of the flaps, a small hypostome without denticles, presence of a central pore in the base of hypostome, and a reticulate surface pattern on the posterior half of the nothoaspis in males.

IXODID TICK GENERA

Genus *Ixodes*

The following morphological descriptions are based on Coley and Kohls (1945), Clifford and Anastos (1960), Clifford and colleagues. (1973), Nava and colleagues (2017), Apaneskevich and Lemon (2018), and Kwuat and colleagues (2018).

Larva: Anal groove anterior to anus; sensilla sagittiformia absent; with 2 pairs of post-hypostomal setae; eyes and festoons absent; 6 legs. *Nymph*: Anal groove anterior to anus; eyes and festoons absent; genital pore absent; spiracular plates circular ; 8 legs; nymphs are smaller than adults. *Adults*: An anal groove is present anterior to the anus, forming an arch; eyes and festoons are absent; an inornate scutum is present; spiracular plates are semicircular or oval; and there is a spur on the coxae. Sexual dimorphism is pronounced. The male venter is largely covered by 7 sclerotized plates. Males have ventral plates. Females have porose areas. The denticles of the female hypostome are well developed, while those of the male are usually few and small, often appearing only as mild crenulations.

Genus *Dermacentor*

The following morphological descriptions are based on Arthur (1960b), Yunker and colleagues (1986), Apanaskevich and Bermúdez (2013a), and Barker and Walker (2014).

Larva: Sensilla sagittiformia present; eyes present; a pair of posthypostomal setae; anal groove absent; 3 marginal dorsal setae anterior to the sensilla sagittiformia on dor-

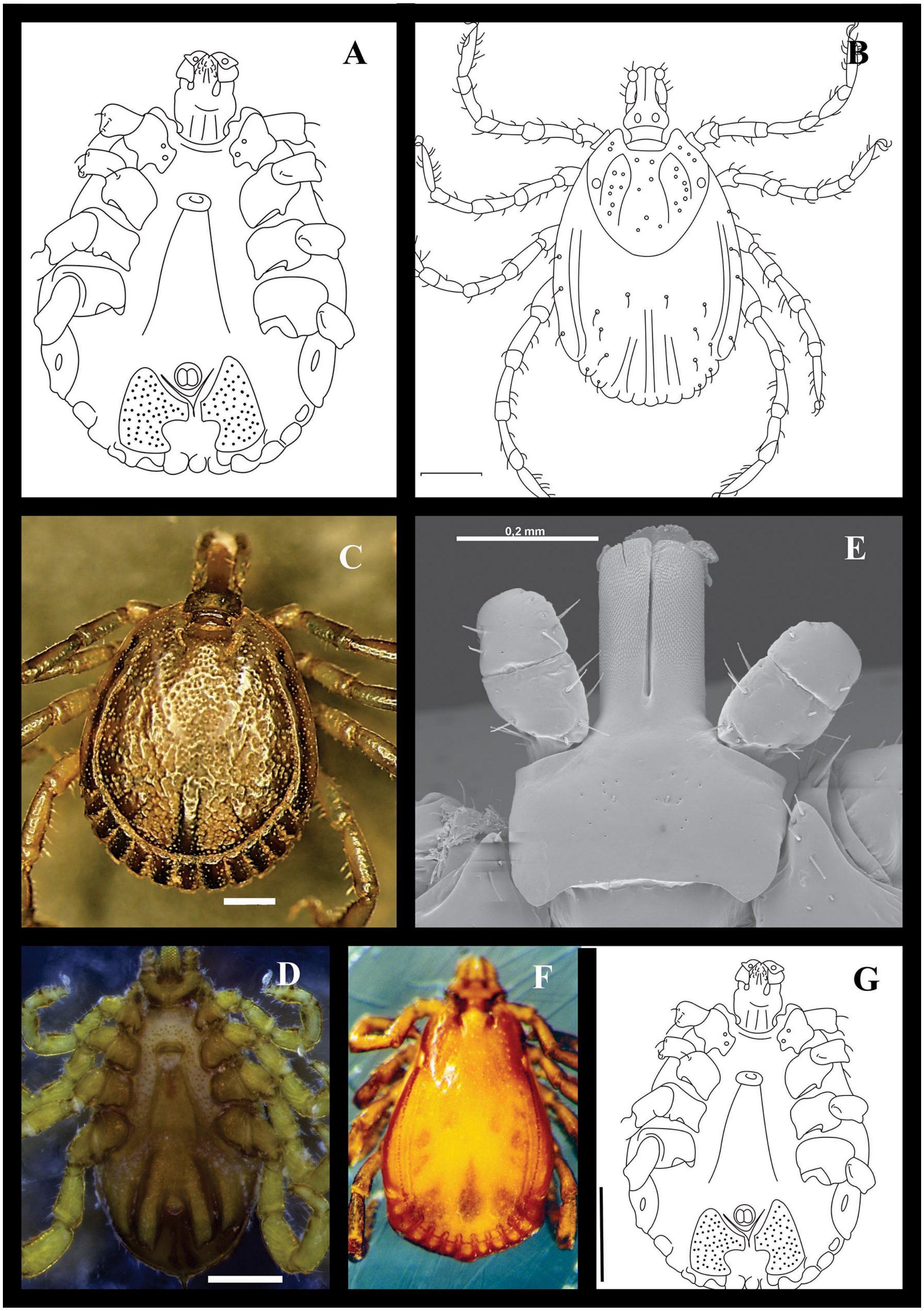

Figure 10. Adults of Ixodidae genera. A) *Nosomma* male, ventral view; B) *Hyalomma* female, dorsal view; C) *Amblyomma sculptum* male, dorsal view; D) *Rhipicephalus (Boophilus) microplus* male, ventral view; E) *Dermacentor* male, gnathosoma dorsal view; F) *Rhipicephalus sanguineus* s. l. male, dorsal view; G) *Rhipicentor* male, ventral view. Scale bars: C = 250 µm; D = 500 µm; E = 250 µm. Sources: A) Adapted from Prakasan and Ramani, 2007; B) adapted from Walker et al., 2003; C–F) D. Moraes Barros-Battesti, V. Castilho Onofrio, and F. Dantas-Torres; G)adapted from Nuttall and Warburton, 1908. License: CC BY-NC-SA 4.0.

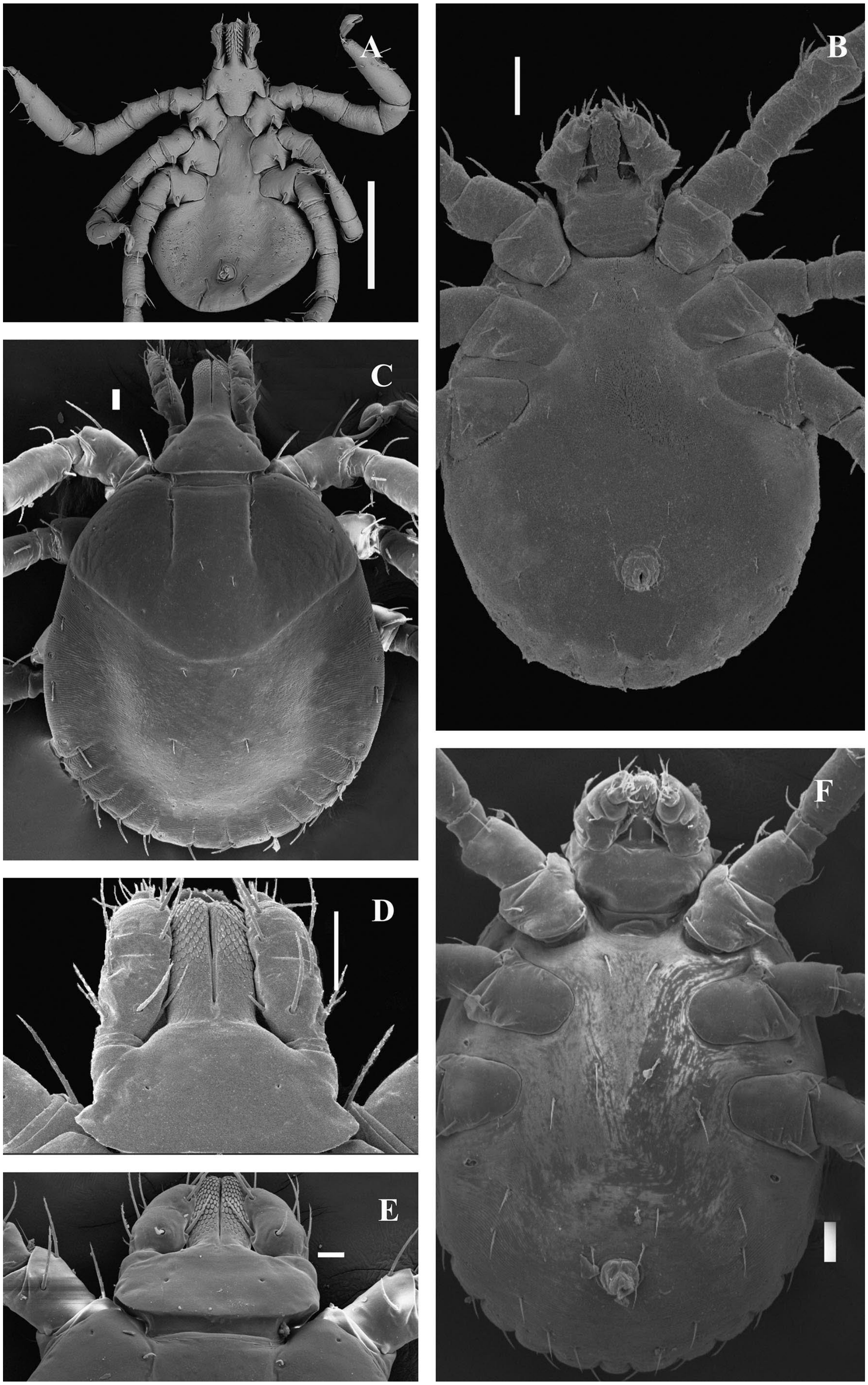

Figure 11. Larvae of Ixodidae genera. A) *Ixodes auritulus* group, ventral view; B) *Amblyomma romitii*, dorsal view; C) *Dermacentor nitens*, gnathosoma dorsal view; D) *Haemaphysalis juxtakochi*, ventral view; E) *Rhipicephalus microplus*, gnatosoma dorsal view; F) *Rhipicephalus sanguineus*, ventral view. Scale bars: A = 250 µm; B, F = 30 µm; C = 40 µm; D = 60 µm; E = 20 µm. Source: D. Moraes Barros-Battesti, V. Castilho Onofrio, and F. Dantas-Torres. License: CC BY-NC-SA 4.0.

sal surface; idiosoma with 9 festoons. *Nymphs*: Eyes present; anal groove absent; spiracular plate circular to suboval with few and large goblet cells. *Adults:* Scutum in females usually ornate (inornate in *Dermacentor nitens* Neumann, 1897); anal groove contouring the anus behind; spiracular plates subcircular to comma-shaped (subcircular in *D. nitens* with large goblet cells); basis capituli more broad than long, rectangular dorsally; eyes on the scutum usually present and distinct. *Males*: Scutum usually ornate (inornate in *D. nitens*); anal groove posterior to the anus; coxae I–IV increase progressively in size; dorsal and posterior margins with festoons.

Genus *Amblyomma*

The following morphological descriptions are based on Klompen and colleagues (1996), Barbieri and colleagues (2007), and Nava and colleagues (2017).

Larva: Anal groove absent, sometimes indistinct; sensilla sagittiformia present on idiosomal dorsal segment VIII and sometimes on segment V; hypostome with denticles arranged in rows; with 1 pair of posthypostomal setae; eyes and festoons present. *Nymph*: Anal groove posterior to the anus; eyes and festoons present; spiracular plates comma-shaped. *Adults*: Scutum ornate with rare exceptions; anal groove posterior to the anus; eyes and festoons present; spiracular plates in comma shape; spurs on coxae usually present; ventral plates absent in most males; porose areas present in females.

Genus *Hyalomma*

The following descriptions are based on Apanaskevich and colleagues (2008).

Larva: Eyes present; portion of scutum posterior to eyes 1/5 to 1/4 of scutal length; apex of spur on coxae I directed posteriorly or medially; narrower palps and hypostome; shorter legs. *Nymph*: posterior margin of scutum broadly rounded with moderate posterolateral depressions on either side of its extremity; spiracular plates with relatively large, wide, blunt dorsal prolongation. *Adults:* Deep cervical grooves; in females scutum with sparse large punctations, small punctations usually very sparse or absent; narrow V-shaped genital operculum; preatrial fold of genital operculum flat or very slightly convex; posteromedial spur of coxa I broad and with blunt apex; males with broadly oval shape of conscutum; deep and long cervical grooves; short marginal grooves; large punctations sparse; smaller punctations normally sparse or absent; adanal plates distinctly curved medially; subanal plates moderate in size; dorsal prolongation of spiracular plates long.

Genus *Rhipicentor*

The following morphological descriptions are based on Cooper and Robinson (1908) and Clifford and Anastos (1960).

Larva: Palps short with 3 articles (article 1 absent); 3 marginal dorsal setae anterior to the sensilla sagittiformia; eyes present; idiosomal with 9 festoons. *Adults:* females with scutum as long as broad, with few punctations, posterior border sinuous; eyes present slightly anterior to the lateral angles; cervical grooves parallel; spiracular plates short, comma-shaped; basis capituli protuberant laterally, small cornua present. Male of *Rhipicentor nuttalli* has idiosoma oval, narrow in front, slightly concave just behind level of eyes; scutum covers entire dorsum, glabrous, polished, punctations not numerous, coarse and showing a tendency to arrange linearly; numerous fine punctations at posterior end of body immediately anterior to festoons; cervical grooves short and deep, crescentic with convexity outwards; marginal grooves well-defined, commencing a little distance behind the eyes and terminating at the external festoon on either side; posteromedian and accessory grooves shallow and ill-defined; eyes large and pale. Venter yellowish-brown with few scattered pale hairs; genital grooves parallel anteriorly, divergent behind coxae and extending to festoons; spiracles comma-shaped. Capitulum short (length 1.1 mm), basis capituli large, with pronounced lateral angles, cornua strong, short and blunt; palps short and broad; articles 2 and 3 rounded laterally; slight ventral retrograde tooth on article 3; hypostome slightly spatulate, dentition 3/3. Legs strong, coxa I with 2 strong spurs placed close together, the internal pointed, the external blunt; coxae II and III with very stumpy blunt spurs; coxa IV very large, with 2 long almost equal spurs, widely separated and slightly divergent.

Genus *Rhipicephalus*

The following morphological descriptions are based on Neumann (1900; 1901; 1904; 1905; 1907; 1911), Apanaskevich and colleagues (2013b), Horak and colleagues (2013), and Nava and colleagues (2018).

Larva: Eyes present, with 4 pairs of marginal dorsal setae anterior to the sensilla sagittiformia; idiosomal with 9 festoons; lateral sides of basis capituli acute or slightly angular. *Nymph*: Eyes present; basis capituli hexagonal, hypostomal dentition 3/3, small auriculae present in *Rhipicephalus sanguineus* (Latreille, 1806) and related species that forms the *R. sanguineus* group; anal groove distinct or indistinct. *Female*: Scutum inornate; eyes present; basis capituli dorsally hexagonal; palps short and round apically, dental formula 3/3 to 4/4;

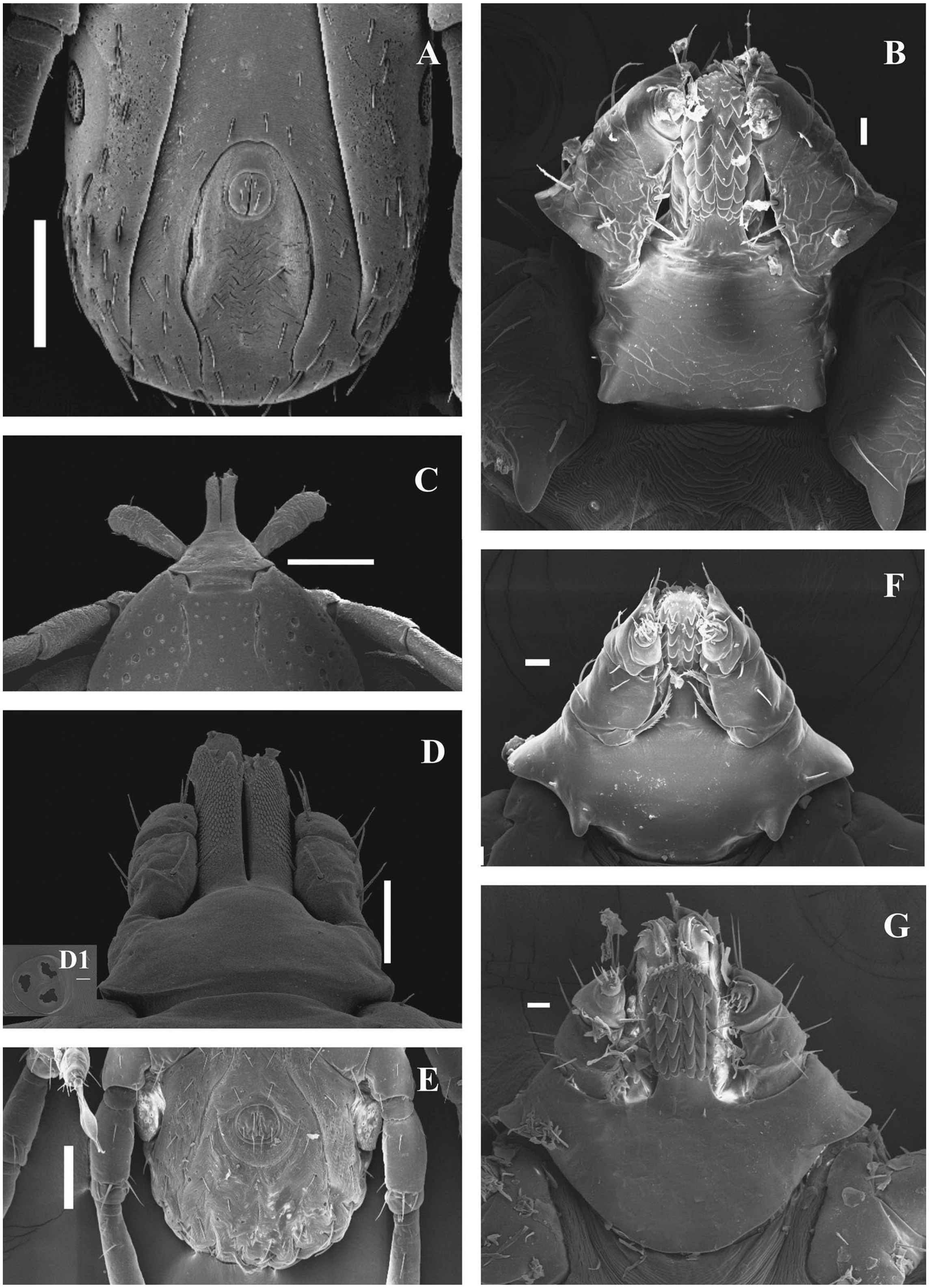

Figure 12. Nymphs of Ixodidae genera. A) *Ixodes luciae* anal groove, ventral view; B) *Haemaphysalis juxtakochi* gnathosoma, dorsal view; C) *Amblyomma longirostre*, dorsal view; D) *Dermacentor nitens* gnathosoma, dorsal view; d1) *Dermacentor nitens* spiracular plate; E) *Rhipicephalus sanguineus* s. l. anal groove, ventral view; F) *Rhipicephalus sanguineus* s. l. gnathosoma, ventral view; G) *Rhipicephalus microplus* gnathosoma, ventral view. Scale bars: A, E = 100 µm; B, G = 20 µm; C = 300 µm; D = 80 µm; d1 = 40 µm. Source: D. Moraes Barros-Battesti, V. Castilho Onofrio, and F. Dantas-Torres. License: CC BY-NC-SA 4.0.

anal groove distinct or indistinct; spiracular plates rounded to elongated. *Male*: Eyes present; basis capituli hexagonal dorsally; small cornua present or absent; palps short, palpal articles II and III with short, retrograde, internal process; dental formula 3/3 to 4/4; anal groove distinct or indistinct; spiracular plates round to elongated; adanal plates present, some species with caudal appendage.

Genus *Archaeocroton*

The description presented below was that proposed by Dumbleton (1943) and by Kaufman (1972) for *Archaeocroton sphenodonti.*

Larva: Large elongate cervical grooves. *Nymph*: not available. *Adults*: Idiosoma suboval in both, scutum light brown, inornate, with small and very numerous punctations evenly distributed; eyes absent. Male with cervical and marginal grooves, cervical grooves short, slightly divergent; lateral grooves distinct, incomplete, extending half the distance between the first festoons and scapulae; basis capitulum subtriangular, cornuae distinct, blunt; palps elongate and somewhat thickened; hypostome spatulate, dentition 3/3 distally and 2/2 proximally, with large corona; 2 files with about 5–6 stout denticles and partial innerfile with 5 very fine denticles; all coxae with a single subtriangular spur; tarsi very elongate. Female with scutum subcordiform, broader than long, cervical groove present; cervical pits deep, slightly concave externally; cervical grooves short and slightly divergent; cornua extremely broad, very blunt; palps elongate, thickened, article (segment) 2 about twice as long as article (segment) 3; a pair of very large conical spurs on either side of the midline of the ventral basis capituli; hypostome spatulate, dentition 3/3 distally and 2/2 proximally, with large corona; 2 files with circa 5–6 stout denticles and partial innerfile with 5 very fine denticles; genital aperture opposite level of coxae II; genital groove divergent; spiracular plate subcircular, as wide as long; all coxae with a subtriangular spur that is as long as broad, and tarsi very slightly humped, noticeably elongate and without spurs.

Genus *Anomalohimalaya*

The following morphological descriptions are based on Hoogstraal and colleagues (1970) and Filippova and Bardzimashvily (1992).

Larva: Basis capituli dorsally 3.5 times as broad as long, the ventrally posteroexternal junctures are at an angle; dorsally with 2 small sensilla hastiformia, ventrally 1 pair post-hypostomal setae, palps 2 times as long as broad; scutum 1.7 times as broad as long; anterior emargination broad, shallow; scapulae slightly rounded; external margin gradually diverging to convex posterior margin; eyes are large, slightly convex, pale area in each posteroexternal juncture; festoons present. *Nymph*: The nymph of *Anomalohimalaya cricetuli* has a smooth nitidous scutum with closely moved lateral and cervical grooves, forming a narrow deep short furrow, whereas in 2 other species the scutum is dull, the furrow between the lateral and cervical grooves is short and nearly reaches posterolateral margins of the scutum. Shape and location of the lateral projections of the basis capituli corresponds to those of female. Anal valves equally get narrow forward and backward, whereas in *A. lotozkyi* they are narrower anteriorly; eyes absent in *A. lamai*. *Adults*: Basis capituli dorsally broadly quadrangular, externally converging to narrower, straight posterior margin; anteroventrally flanged; palps clavate, 2 times as long as broad, article I extended ventrointernally; eyes absent; scutum broadly pyriform, rugose, lacking lateral grooves, cervical grooves indistinct, punctations especially large and numerous. Basis capituli hexagonal in females; the dorsal scutum in *A. cricetuli*, is pointed posteriorly and the genital opening is U-shaped, whereas in 2 other species the scutum is rounded posteriorly and the genital opening is V-shaped. *Anomalohimalaya cricetuli* differs from *A. lotozkyi* in that it has less pointed and shorter lateral projections of the gnathosoma basis, apexes of which are moved forward from the posterior margin, and by concave laterally porous area. It differs from *A. lama* by the absence of the dorsal process on the spiracular plate, and a short tooth on coxae IV.

Genus *Bothriocroton*

The following morphological descriptions are based on Klompen and colleagues (2002), Barker and Walker (2014), and Beati and colleagues (2008).

Larva: Hypostomal dentition in the adults 2/2 or 3/3, internal row much smaller than other rows; 3 large wax glands lateral near setae s6 (= marginal dorsal setae Md3), and anterior to the first festoons; large wax glands on festoon 5 absent; eyes absent; idiosomal setation pattern generally as in other Metastriata; scutum more broad than long; leg and palpal chaetotaxy as in *Amblyomma* sensu lato *Nymph*: Scutum similar to the females, with conspicuous posterolateral indentations formed by confluence of larger punctations; eyes absent; anal groove posterior to the anus; spiracular plates extruding from lateral body margins in *Bothriocroton oudemansi*. *Adults*: Basis capituli subpentagonal in shape; eyes absent, but large punctations could be mistaken for an eye; hypostomal dentition 3/3 to 4/4; scutum of the males with partial or complete lateral grooves, with white ornamentation in some species; trochanters with a single subterminal ventral spur (absent in *B. glebopalma*); coxae I with anterior projection visible in some species; anal groove posterior to the anus; large spiracular plates anterior to first festoon, extruding from lateral body margin in male and female of *B. oudemansi.*

Genus *Cosmiomma*

The following morphological descriptions are based on adults (Arthur, 1960b); immature stages are unknown.

Adults: Basis capituli subtriangular dorsally; palpal article 2 appreciably narrower than article 3, and about twice as long; enamel pigmentation on the palps, basis capituli, scutum, and legs; eyes well developed; 11 festoons in the female more or less clearly defined, with large spiracular plate abutting against the margins of the anterior festoons; female with anal groove encircling the anus and produced behind in a median groove; male with 1 pair of adanal plates, accessory and subanal plates absent. Coxa I with long external spur and prominent internal spur, divergent.

Genus *Haemaphysalis*

The following descriptions are based on Apanaskevich and colleagues (2007).

Larva: Eyes absent; scutum inornate; 2 marginal dorsal setae anterior to the sensilla sagittiformia on each side; article II of palps laterally produced beyond the basis capituli; idiosoma with 11 festoons; anal groove posterior to the anus. *Nymphs*: Eyes absent; basis capituli rectangular dorsally; scutum inornate; article II of palps laterally produced; article III of palps with retrograde ventral spur; spiracular plate suboval; anal groove posterior to the anus. *Adults:* Article II of palps laterally produced; article III of palps with retrograde ventral spur; eyes absent; scutum inornate; article II of palps laterally produced; article III of palps with retrograde ventral spur; in females the scutum is 1.3 times as long as broad, cervical grooves narrow arcs extending 2/3 of total scutal length; posterior lip of genital aperture broadly U-shaped; spiracular plates varying in size, irregularly suboval or subcircular, dorsal projection short, broadly triangular; in males the spiracular plate is variable in size, usually slightly broader than long, suboval, dorsal projection triangular, submarginal row of perforations on spiracular plate complete; coxal pore absent. In male, the basis capituli rectangular dorsally; article II of palps laterally produced; article III of palps with retrograde ventral spur; marginal groove absent.

Genus *Margaropus*

The following morphological descriptions are based on Arthur (1960b), Clifford and Anastos (1960), Walker and Laurence (1973), and Walker and colleagues (2003).

Larva: 5 marginal dorsal setae, Md5, located anteriorly to the dorsal sensilla sagittiformia, all other larval morphology resembles those of the genera *Dermacentor* and *Rhipicephalus*. *Nymph*: Idiosoma with long setae; basis capituli 3 times as wide as long, with straight basal margin, rounded junctures, and divergent lateral margins; eyes present; palps 4 times as long as wide; segment I forming a slight pedicle; segments 2 and 3 of approximately equal length and subrectangular; apex more or less bluntly rounded; segment 3 ventrally with a short, wide spur not reaching basal margin of segment; hypostome similar with smaller corona and 3/3 dentition in files of 8 denticles; spiracular plates subcircular, with 6 large goblets in a circle. *Adults*: Festoons absent; in females the scutum is inornate, widest at midlength between the scapulae and the eyes, posterior margin bluntly pointed; eyes present which may be indistinct; porose areas vertically subtriangular; palpal articles 2 and 3 separated by a slight constriction; coxae conical, unarmed but for a small spur posteriorly on coxa I, tarsi elongate, narrow, tapering with a large apical hook-like projection; integument bears conspicuous hairs posteriorly; spiracular plate subcircular, 3 rows of large goblets around the ostium; males with expanded leg articles that are more or less deeply separated from each other; scutum with lateral margins convex, more strongly convergent anteriorly, bluntly rounded behind, about a third as long again as it is wide; spiracular plates similar to the females; a pair of adanal plates present; caudal appendage present in *Margaropus winthemi*, broad and has a hook on the ventral surface; hypostome about twice as long as broad, slightly notched in the mid-line distally, and behind a well-defined corona the dentition is 4/4. This species is distinguished from *Rhipicephalus* (*Boophilus*) by the thick legs that are very conspicuous in males.

Genus *Nosomma*

The following morphological descriptions are based on Arthur (1965), Singh (1968), and Prakasan and Ramani (2007).

Larva: Basis capituli triangular dorsally, posterior margin slightly convex, lateral margins slightly sinuous and meet posterior margin to form sharp lateral points; ventrally basis triangular with posterior margin bow shaped; palps long and slender, reaching to the apex of hypostome, hypostome slender, dentition 2/2; eyes flat; cervical grooves shallow, narrow anteriorly but broadening posteriorly to almost reach the hind margin of scutum; dorsally without marginal grooves but with 9 distinct festoons. *Nymph*: Basis capituli dorsally triangular; posterior margin almost straight; posterolateral angle sharp and pointed. Ventrally posterior margin bow shaped; palps long and slender, reaching to the tip of hypostome, article 2 twice as long as article 3, dentition 2/2; posterior margin of scutum broadly rounded; eyes flat and situated at posterolateral corners of scutum, cervical grooves subparallel anteriorly and diverging posteriorly reaching posterior margin; dorsal integument with faint marginal grooves and 11 well marked festoons; spiracular plates oval. *Adults: Nosomma* resembles *Dermacentor* in the shape of the capitulum and in having short palps; palpal articles 1, 2, and 3 of *Nosomma* are unlike those of known *Dermacentor* species in the possession of long, broad, strong sabre-like hairs on their infra-internal margin. Basis capituli of female is almost twice as broad as long; cornua prominent, basal breadth exceeding their length, broadly rounded; idiosomal with distinct median and paramedian grooves on the dorsal surface, posterior extremity of median groove continuous with depressions separating parma from adjacent festoons; 11 festoons present. Basis capituli of male is rectangular dorsally; palps conical lacking basolateral salience; median ridge like dorsal palpal spur; hypostome reaching apex of palps; hypostomal denticles formula 4/4; scutum outline elongated oval, brownish, whitish ornamentation present; cervical grooves short and deep; pseudoscutum well marked; eyes prominently colored; 11 festoons present, festoon 2 dorsally separated by well-marked sutures; palpal article III more broad than long with a stronger ventral process, hypostomal dentition 3/3; coxa I with 2 separated spurs; coxae II–IV with small spurs; tarsus IV with 2 ventral spurs, the distal one stronger than the proximal; ventral plates represented by adanal and accessory subadanal plates trilobed, middle lobes come close to each other behind the anal groove; anal groove posterior to the anus; spiracular plates comma-shaped.

Genus *Robertsicus*

Baker and Burger (2018) did not repeat the description for *Amblyomma elaphense* when the new combination for *Robertsicus elaphense* was proposed, but we present the one previously detailed by Keirans and Degenhardt (1985).

Larva: Outline suboval, widest at midlenght with 11 festoons; setae dorsally 13 pairs, all minute except for scutal central 1 (SC1); 2 central dorsal pairs; 8 marginal dorsal pairs, 2 of which are anterior to sensilla sagittiformia; supplementary setae absent; 3 scutal pairs; ventrally 15 pairs, 3 sternal pairs, 2 preanal pairs, 4–5 premarginal pairs, 5 marginal pairs, 1 pair on anal valves; palpal setae 10 on segment 4, 3 dorsally, 1 laterally, 2 ventrally on segment 3; 3 dorsally, 1 laterally, 2 ventrally on segment 2; 0 on segment 1; hypostome bluntly rounded apically with few minute hooklets, dental formula 2/2; scutum inornamented; eyes absent; cervical grooves and punctations absent; legs with small triangular external spur on coxae I–III, internal spurs absent; setae: coxa I with 3, coxae II and III with 2 setae each; Haller's organ with roof bifurcate; anterior pit setae: 1 porose, 2 fines, 1 fine or perhaps setiform. *Nymph*: Small, suboval, about as wide as long; scutum with scale-like markings over the surface, otherwise as in female; capitulum dorsally broadly triangular, corona absent; ventrally with hypostomal dentition 2/2, a small corona of minute denticles apically; legs each with a very small bluntly rounded spur on coxae I–IV; spiracular plate suboval, without dorsal prolongation. *Adults*: Inornate, light brown. Male with scutum smooth, without cervical or marginal grooves, setae and punctations minute, inapparent under binocular microscopy; capitulum dorsally subtriangular, lacking cornua; ventrally with hypostomal dentition 2/2 throughout, apically with a large corona of fine denticles; palps elongate; legs each with a single triangular spur on coxae I–IV; Haller's organ roof slit-like and slightly bifurcate medially, 5 anterior pit setae; spiracular plate suboval with a long narrow dorsal prolongation, globet cells minute. Female with scutum more broad than long, cordiform, smooth, without cervical grooves, setae and punctations minute; capitulum dorsally subtriangular, cornua absent; porose areas subcircular, shallow; ventrally with hypostomal dentition 2/2 (although the hypostome figured has a single supernumerary tooth between file 1 and 2 on the left side of the hypostome as viewed from above); legs with coxae as in male; genital aperture at level of coxae II; spiracular plate suboval with a short dorsal prolongation, goblet cells minute.

Genus *Nuttalliella*

The following morphological descriptions are based on Bedford (1931), Latif and colleagues (2012), and Mans and colleagues (2018).

Larva: Dorsum with a sclerotized scutum; cervical grooves and eyes absent; preanal groove present; anal plate with rows of denticles separated by the median post-anal groove; 5 posthypostomal setae present; apex of hypostome distinctly rounded, forming a ball-like structure, with 11 prominent denticles arranged in 2 rows. *Nymph*: Idiosoma circular; pseudoscutum with elevation between the cervical grooves; eyes absent; surface of alloscutum with dense-elevated and convoluted rosettes and setae in rosette pits; posthypostomal setae present; hypostomal denticles rudimentary; spiracular plates fenestrated and located posterior to coxa IV. *Female*: Idiosoma covered by leathery integument; scutum semi-sclerotized wider than long; preanal groove present; gnathosoma ventroapically, a pair of posthypostomal setae present; hypostomal denticles large and distinct arranged in 2 rows; palps 4-segmented; coxal organ absent; and spiracular plates fenestrated and located posterior to coxa IV. *Male*: Pseudoscutum present, covering most of the dorsum; chelicerae forming a unique rod-like structure similar to a spematodactyl in mites.

Medical and Veterinary Significance of Ticks

Ticks are obligate blood-sucking parasites with an almost worldwide distribution. As the second largest group of vectors of human disease agents (only trailing mosquitoes), ticks are among the most important vectors of pathogens causing disease in humans and other animals (Dantas-Torres et al., 2012). They are the most important ectoparasites of livestock in tropical and subtropical areas, and the diseases and direct damage caused by ticks are responsible for severe economic losses in livestock production (Jongejan and Uilenberg, 2004).

Human-tick interactions are extremely common, resulting in a great impact on human health. Due to saliva secretion during blood feeding, ticks transmit pathogens, such as viruses, bacteria, protozoa, and helminths, readily to hosts. Aside from mere irritation, their bite can also lead to allergy and even severe toxic conditions, such as paralysis and toxicosis in humans and other animals. Infection with multiple tick-transmitted pathogens can occur in an individual host after exposure to coinfected ticks or multiple ticks infected with different pathogens. The coinfection of individual ticks is a relatively frequent phenomenon and the same tick species may be a vector for different pathogens (Milutinovic et al., 2008; Nicholson et al., 2010), which may partially explain variations in clinical presentation, pathogenicity, and host response to therapy.

Pathogens ingested by a single larval tick may be passed through to subsequent developmental stages (that is, nymph and adult) through transstadial transmission from host to host (also called horizontal transmission) and, if a female is infected, may eventually be spread to her offspring through vertical or transovarial transmission. Female ticks are extremely fecund and may lay thousands of eggs, which enables effective dissemination of infectious agents.

Wildlife and ticks are the main reservoirs and vectors of tick-borne pathogens of medical and veterinary importance (Dantas-Torres et al., 2012b). Species of ticks that parasitize domestic animals are the most studied, while those that parasitize wildlife are still poorly understood as to their ability to transmit pathogens. Wild and domestic carnivores are considered the primary source of tick-borne zoonotic agents affecting humans (Otranto et al., 2015).

Ticks and tick-borne diseases have a zoogeographical range restricted by host movement and climatic factors. However, the increased mobility of humans and of domestic animals has resulted in a rapid extension of the zoogeographical ranges for many tick species and tick-transmitted pathogens. As such, the incidence of tick-borne diseases in humans and animals has increased in the 21st century (Estrada-Peña and Jongejan, 1999; Guglielmone et al., 2006). Additional factors associated with the emergence or re-emergence of vector-borne diseases include global warming (and resultant climate change), increased outdoor recreation, global travel, urbanization, encroachment of human development on natural environments, deforestation, and habitat fragmentation, which together promote greater contact between ticks, wildlife, humans, and domestic animals (Beugnet and Chalvet-Monfray, 2013; Dantas-Torres, 2015).

The major zoonoses whose causative agents are transmitted by ticks are rickettsioses, borrelioses, ehrlichiosis, and babesiosis. Rickettsioses are mainly associated with ticks of the genera *Amblyomma, Dermacentor, Ixodes*, and *Rhipicephalus*, borrelioses to *Ixodes* and *Ornithodoros*, and ehrlichiosis and babesiosis mostly to *Rhipicephalus* (Barros-Battesti et al., 2006). These diseases and other zoonotic tick-borne illnesses, such as those of viral origin, characterized by encephalitis and hemorrhagic fevers, are the major cause of host morbidity and mortality (Jongejan and Uilenberg, 2004; Dantas-Torres et al., 2012b). In the following sections, the main tick-borne diseases of humans and other animals are summarized.

Anaplasmosis

Anaplasmosis is a disease caused by gram-negative bacteria of the order Rickettsiales, family Anaplasmataceae, and genus *Anaplasma* (Dumler et al., 2001).

Bovine anaplasmosis occurs in tropical, subtropical, and temperate regions of the world, and is caused by the intraerythrocytic rickettsia *Anaplasma marginale*, a member of the ehrlichial genogroup II (Dumler et al., 2001); *A. marginale* is transmitted biologically by ixodid ticks, by hematophagous insects, and mechanically by needles contaminated with blood of infected animals.

After inoculation of a suitable bovine host, and after an incubation period of 20 to 40 days, there is an increase in rickettsemia, resulting in anemia, weight loss, abortion, and death (Richey, 1981). The disease can have serious consequences, especially when susceptible animals are introduced into endemic areas. In this case, mortality may exceed 50%, causing serious problems to genetic breeding programs, based on the importation of animals from disease-free areas (Machado, 1995).

Combining tick control and vaccination results in the most effective measure against this disease (Palmer, 1989). Immunized cattle may develop persistent field infections, acting as reservoirs of *Anaplasma marginale* helping to maintain the pathogen circulation in endemic areas.

The most important species in dogs is *Anaplasma platys*, which mainly infects platelets and causes infectious canine cyclic thrombocytopenia (Ferreira et al., 2007). It is generally found in coinfections with *Babesia* and *Ehrlichia*, and

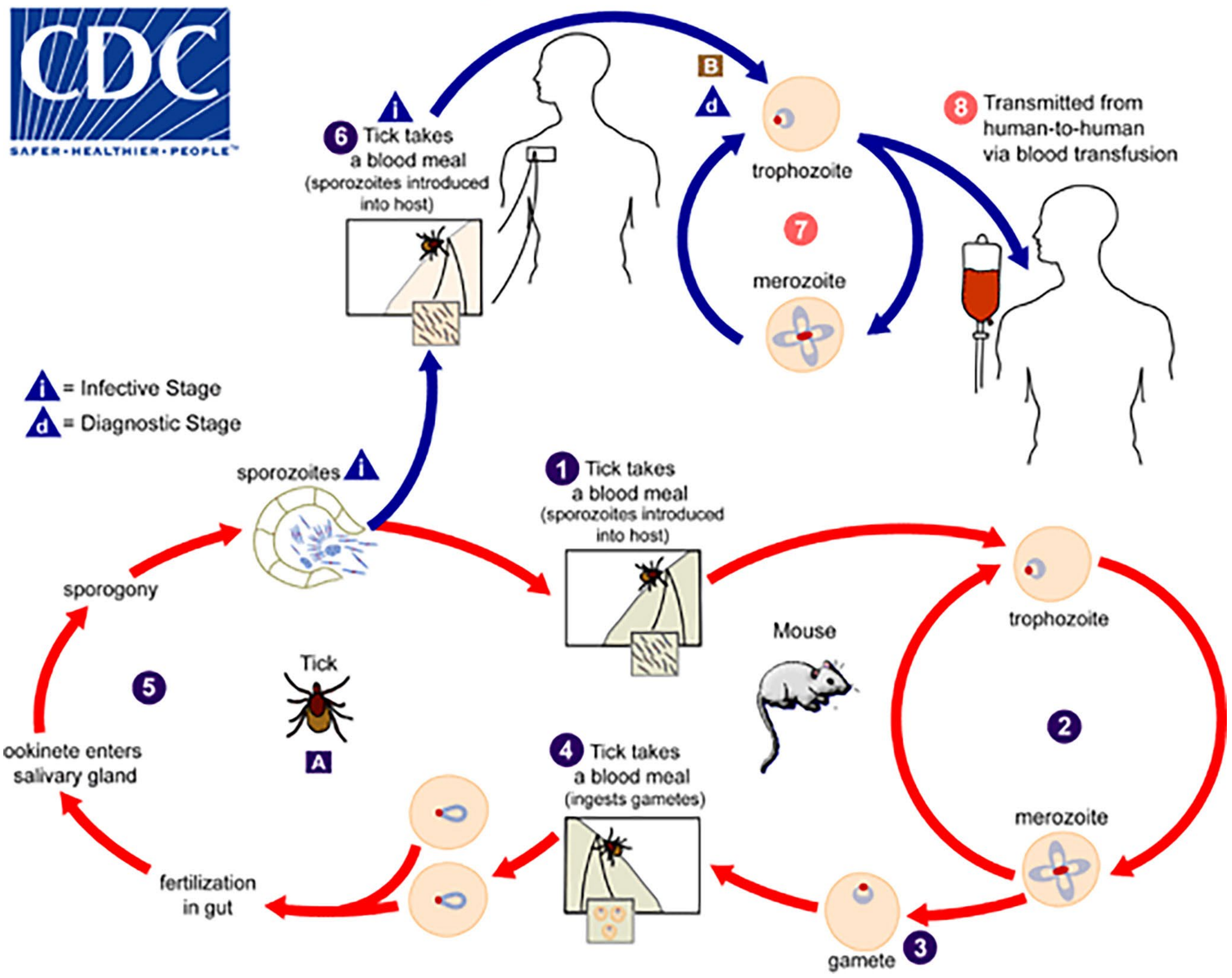

Figure 13. Babesiosis life cycle. Babesiosis is caused by apicomplexan parasites of the genus, *Babesia*. While more than 100 species have been reported, only a few have been identified as causing human infections, including *B*. *microti*, *B*. *divergens*, *B*. *duncani*, and a currently unnamed strain designated MO-1. — The *Babesia microti* life cycle involves 2 hosts, which includes a rodent, primarily the white-footed mouse, *Peromyscus leucopus*, and a tick in the genus *Ixodes*. During a blood meal, a *Babesia*-infected tick introduces sporozoites into the mouse host (1). Sporozoites enter erythrocytes and undergo asexual reproduction (budding) (2). In the blood, some parasites differentiate into male and female gametes although these cannot be distinguished at the light microscope level (3). The definitive host is the tick. Once ingested by an appropriate tick (4), gametes unite and undergo a sporogonic cycle resulting in sporozoites (5). Transovarial transmission (also known as vertical, or hereditary, transmission) has been documented for “large” *Babesia* spp. but not for the “small” babesiae, such as *B*. *microti* (A). — Humans enter the cycle when bitten by infected ticks. During a blood meal, a *Babesia*-infected tick introduces sporozoites into the human host (6). Sporozoites enter erythrocytes (B) and undergo asexual replication (budding) (7). Multiplication of the blood stage parasites is responsible for the clinical manifestations of the disease. Humans are, for all practical purposes, dead-end hosts and there is probably little, if any, subsequent transmission that occurs from ticks feeding on infected persons. However, human to human transmission is well recognized to occur through blood transfusions (8).

Rhipicephalus sanguineus sensu lato is suspected to be a vector, though its role remains unproven (Dantas-Torres, 2008; Ribeiro et al., 2017). This pathogen is widespread on several continents but has a predilection for tropical and subtropical regions (Ferreira et al., 2007).

Anaplasma phagocytophilum is incriminated as the causal agent of the human granulocytic anaplasmosis (HGA) in the Northern Hemisphere, tick-borne fever in cattle and sheep in Europe, and equine and canine granulocytic anaplasmosis in the United States (Woldehiwet, 2010; André, 2018).

Babesiosis

Babesiosis is caused by tick-transmitted intraerythrocytic protozoa of the order Piroplasmida, family Babesiidae, and genus *Babesia* (see Figure 13). *Babesia* protozoa are one of the most common blood parasites in the world and they have a wide host range, including mammals and bird species (Schnittger et al., 2012). Hard ticks are the known vectors of these protozoa, such as *Rhipicephalus sanguineus* sensu lato that transmits *B. vogeli* (Gray et al., 2010; René et al., 2012; Silva et al., 2012).

The disease can occur in subclinical, acute, hyperacute, or chronic forms, ranging from mild clinical signs to fatal disease. Severity of illness depends on many factors, such as *Babesia* species and immunocompetence of the patient (Schetters et al., 1997; Gray et al., 2010; Yabsley and Shock, 2013).

Bovine babesiosis (BB) is a tick-borne disease of cattle caused by protozoan parasites of the genus *Babesia* (phylum Apicomplexa, order Piroplasmida). The principal species of *Babesia* that cause BB are: *Babesia bovis, B. bigemina*, and *B. divergens.* Other species that can infect cattle include *B. major, B. ovata, B. occultans,* and *B. jakimovi. Rhipicephalus* tick species are most commonly involved in the transmission of this disease, generally in tropical and subtropical countries (WOAH, 2021).

Canine babesiosis may be caused by several species of *Babesia*, which are usually classified as small and large *Babesia*. Small *Babesia* species include *B. gibsoni*, *B. conradae*, and *B. microti*-like (also referred to *Theileria annae* and *B. vulpes*, but these are nomina nuda, meaning that the scientific names are used but without the necessary accompanying scientific description), whereas large *Babesia* species include *B. canis*, *B. vogeli*, *B. rossi*, and an unclassified species ("*Babesia* sp. Coco") found in dogs in North Carolina, United States (Citard et al., 1995; Schetters et al., 1997; Köster et al., 2015; Solano-Gallego et al., 2016). *Babesia gibsoni* is transmitted by *Haemaphysalis longicornis* Neumann, 1901 in Asia and possibly by blood exchange during dog fights. *Babesia canis* is transmitted by *Dermacentor reticulatus* in Europe, *B. vogeli* is transmitted by *R. sanguineus* sensu lato in tropical and subtropical regions, and *B. rossi* is transmitted by *H. elliptica* (Koch, 1844) in southern Africa (Uilenberg et al., 1989; Sasaki et al., 2007; Köster et al., 2015). The vectors of *B. conradae* and *B. microti*-like remain unknown.

Ehrlichiosis

Ehrlichiosis is a disease caused by several species of obligate intracellular gram-negative bacteria of the genus *Ehrlichia* that infect humans and other animals in different parts of the world (Dumler et al., 2001).

Human ehrlichiosis is caused by *Ehrlichia chaffeensis* (human monocytic ehrlichiosis), *E. ewingii* (human granulocytic ehrlichiosis), or *E. muris eauclairensis* (undetermined ehrlichiosis) (Dantas-Torres et al., 2012b; Pritt et al., 2017). *Ehrlichia chaffeensis* is the most common causative agent of human ehrlichiosis in the United States. It is maintained in a cycle that involves the white-tailed deer (*Odocoileus virginianus*) and the lone star tick *Amblyomma americanum* (Linnaeus, 1758), which play a role as primary reservoir and vector, respectively (Skotarczak, 2003; Yabsley, 2010). Even though white-tailed deer seem to be the main host for *E. chaffeensis*, serological and molecular evidence of infection by this agent has been reported in wild carnivores (André, 2018). *Amblyomma americanum* also transmits *E. ewingii*, while the vector of *E. muris eauclairensis* is *Ixodes scapularis* Say, 1821.

Canine monocytic ehrlichiosis (CME) is a life-threatening disease in dogs that requires rapid and accurate diagnosis in order to initiate appropriate therapy (Skotarczak, 2003). *Ehrlichia canis*, the agent of CME, infects monocytes and macrophages of domestic dogs and wild carnivores (Stich et al., 2008). *Rhipicephalus sanguineus* sensu lato and *Dermacentor variabilis* (Say, 1821) are the recognized vectors for *E. canis* (Johnson et al., 1998; Dantas-Torres, 2008). The disease is described around the world, but CME appears to be particularly prevalent in tropical regions where it is principally vectored by *R. sanguineus* sensu lato (Cicuttin et al., 2015). In South America, the occurrence of CME in tropical regions is related to the difference in vector competence. Populations of *R. sanguineus* sensu lato belonging to the tropical lineage are highly competent vectors of *E. canis*, while South American populations of *R. sanguineus* sensu stricto (= temperate lineage) are incompetent vectors of *E. canis*, which partly explains the scarcity or absence of CME in colder regions of South America (Nava et al., 2012; Moraes-Filho et al., 2015).

Lyme disease (or Lyme borreliosis)

Lyme borreliosis (LB) is the most frequent tick-borne disease in the Northern Hemisphere. The disease is caused by spirochetes of the *Borrelia burgdorferi* sensu lato complex, which are transmitted by several tick species of the genus *Ixodes* (Gray et al, 2002; Rauter and Hartung, 2005). LB is recognized as the most commonly reported arthropod-borne disease in North America and Europe, accounting for thousands of new cases yearly in both regions (Piesman and Eisen, 2008; Marques, 2010; CDC, 2017).

In most cases, the tick must be attached to its mammalian host for 36 to 48 hours or more before the bacteria can be transmitted. Typical symptoms include fever, headache, fatigue, and a characteristic skin rash called erythema migrans (CDC, 2017). The complications of untreated LB in humans can be severe and disabling (Dennis and Hayes, 2002).

Rickettsioses

Tick-borne rickettsioses are caused by intracellular bacteria belonging to the spotted fever group (SFG) of the genus *Rickettsia* and are among the oldest known vector-borne diseases of humans. The importance of the recognized rickettsial pathogens has increased in the past several years. Several species of tick-borne rickettsiae that were considered nonpathogenic for decades are now associated with human infections, such as *R. slovaca, R. aeschlimannii, R. massiliae, R. monacensis*, and *R. parkeri*. New species of *Rickettsia* of undetermined pathogenicity continue to be detected in or isolated from ticks around the world (Labruna et al., 2011; Parola et al., 2013).

Ticks can be reservoirs and vectors for most species of *Rickettsia*. Bacteria remain in tick populations by transovarial and transstadial transmission. However, some rickettsiae may also be deleterious to ticks, such as *R. rickettsii* (Labruna, 2009).

Vertical transmission of rickettsial agents in arthropods helps to maintain the infection in nature, but for some species of rickettsiae, a life cycle including infected arthropods and 1 or more amplifying hosts is required to guarantee survival of the bacteria (Davoust et al., 2010). Humans are only occasional hosts for ticks and, thus, play no role in maintaining these bacteria in nature (Socolovschi et al., 2009).

Rickettsia rickettsii is the most pathogenic *Rickettsia* species, and the disease caused by this agent is generally called Rocky Mountain spotted fever (RMSF), because it was first reported in the Rocky Mountain region of the United States (CDC, 2006). In Brazil, the disease is Brazilian spotted fever and has a high fatality rate (Oliveira et al., 2016). Despite the availability of accurate diagnostic tools and efficacious therapy, RMSF continues to be a life-threatening disease, with high lethality rate in several endemic geographic foci. The disease has been shown to have a complex ecology with participation of different vertebrate animals and tick species (CDC, 2006).

Several tick species have been implicated as vectors of *Rickettsia rickettsii* accordingly to different geographic areas. While *Dermacentor andersoni* Stiles, 1908 and *D. variablilis* are the main vectors in the United States, ticks of the *Amblyomma cajennense* (Fabricius, 1787) species complex, such as *A. cajennense* sensu stricto and *A. sculptum* (Berlese, 1888), have been implicated as the most important vectors in South America, mainly in Brazil (Labruna et al., 2017). Moreover, *R. sanguineus* sensu lato has been implicated as a vector in Mexico and the United States (Dantas-Torres, 2007).

Rickettsia parkeri is another SFG rickettsia recognized as a human pathogen, with several confirmed cases in the United States. The first confirmed human infection with *R. parkeri* was reported in the United States in 2004, more than 60 years after this bacterium was first isolated in that country, from the Gulf Coast tick *Amblyomma maculatum* Koch, 1844 (Paddock et al., 2004). *Rickettsia parkeri* rickettsiosis can be difficult to distinguish from RMSF and other spotted fevers, especially during the early stages. A retrospective study provided serological evidence that a number of cases previously diagnosed as RMSF in the United States were actually caused by *R. parkeri,* suggesting that both rickettsioses have been misidentified in that country. This disease is characteristically less severe than RMSF and almost always associated with an inoculation eschar (an ulcerated, necrotic lesion) at the site of tick attachment (Paddock et al., 2004).

Several other SFG rickettsia (for example, *Rickettsia conorii*) are important human pathogens and may also infect and cause disease in animals, such as dogs, in Europe and elsewhere in the world. Comprehensive information about other rickettsiae infection humans can be found elsewhere (Dantas-Torres et al., 2012a; Parola et al., 2013; Portillo et al., 2015).

Epidemiological Tick Control and Preventative Measures

Human behavior (for example, sitting on logs, gathering wood, leaning against trees, and walking) might increase the risk of exposure to ticks (Lane et al., 2004). For instance, people visiting forested areas might be exposed to hard ticks whereas people entering tick-infested caves and encountering rodent burrows might be exposed to soft ticks.

Strategies to reduce populations of vector ticks through area-wide application of acaricides and control of tick habitats (for example, clearing leaf litter and brush) have been effective in small-scale trials. Community-based, integrated, tick-management strategies may prove to be an effective public health response to reduce the incidence of tick-borne infections. However, limiting exposure to ticks is currently the most effective method of prevention (Dantas-Torres, 2007; Pinter et al., 2011).

Whenever possible, areas that are likely to be infected with ticks should be avoided, particularly in the seasons in which larvae and nymphs feed and can be found in abundance. Ticks are commonly found in humid and shady environments, especially grassy or litter areas with low-lying vegetation.

From a practical perspective, it is unreasonable to assume that a person can eliminate all activities that may result in tick exposure. Therefore, measures should be aimed at personal protection (Dantas-Torres, 2007; Piesman and Eisen, 2008; CDC, 2006; 2017). The following measures are recommended:

- When walking through forested areas or with shrubby vegetation, avoid places potentially infested by ticks, and if possible, walk in the center of trails.
- Wear long-sleeved shirts and long trousers (not shorts) and tuck pant bottoms into tops of socks or boots. Wear light colored clothing which makes it easier to find crawling ticks.
- Check often for ticks especially after leaving forested areas. Common sites of attachment include the groin, the underarms, the nape of the neck, around the waist, and behind the knee.
- Examine children more often, paying special attention to the head, neck, and ears. Teach them to avoid tall grass and low brush.
- Do not let pets roam freely in these areas, and if they are allowed to go to these spots, check them daily, especially if allowed indoors. Free-roaming pets may carry ticks of all life stages and can be infected with tick-borne diseases. This is rather important for companion animals living in close contact with humans.
- To remove attached ticks, use fine-tipped tweezers or shield your fingers with a tissue, paper towel, or rubber gloves. Avoid removing ticks with bare hands.
- Grasp the tick with the tweezers as close as possible to the surface of the skin, turn it gently, and from time to time pull upward with steady, even pressure.
- Do not squeeze, crush, or puncture the body of the tick because its fluids (saliva, body fluids, gut contents) may contain infectious organisms.
- Save the tick for identification and potentially test for pathogens. This may help your doctor make an accurate diagnosis if you become sick.

Supplemental Materials

Supplemental documents are available online including keys for the identification of tick families and genera, and a list of extant species described chronologically from 1758 to October 2019.

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