

Alberto A. Guglielmone
Richard G. Robbins

Hard Ticks (Acari: Ixodida: Ixodidae) Parasitizing Humans

A Global Overview



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This work is dedicated to the memory of
Natalia Aleksandrovna FILIPPOVA
(1930–2018)

for her pioneering contributions to our knowledge of the tick fauna of Russia and neighboring countries. Natalia Filippova's meticulous studies of tick taxonomy and ecology were of inestimable value to her contemporaries and are certain to be appreciated by generations of tick researchers as yet unborn.

(Photo courtesy of Alexey Khalin)

Preface

The hard tick family Ixodidae currently comprises 729 species worldwide, but information on the species that feed on humans is scattered and often difficult to access. We have undertaken the task of compiling such information for each species of ixodid tick that we consider valid, believing that our summary will prove to be a valuable reference for the many people interested in ticks as organisms and also for specialists in tick-borne diseases. Data for all species treated here were gleaned from a search of the world literature that concluded on 31 March 2018.

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Methodology

The family Ixodidae is traditionally divided into two groups: Prostriata (ticks in which the anal groove curves anterior to the anus), and Metastrata (ticks in which the anal groove, when present, curves posterior to the anus). The Prostriata consists exclusively of the 253 species in the genus *Ixodes*, while the Metastrata comprises 476 taxa in 14 genera as follows: *Amblyomma* (238 species), *Anomalohimalaya* (3), *Bothriocroton* (7), *Compluriscutula* (fossil, 1 species), *Cornupalpatum* (fossil, 1 species), *Cosmiomma* (1), *Dermacentor* (40), *Haemaphysalis* (166), *Hyalomma* (27), *Margaropus* (3), *Nosomma* (2), *Rhipicentor* (2) and *Rhipicephalus* (85).

Our analysis of the human-biting ticks in these genera is presented in three chapters. The first and main chapter lists each valid species of Prostriata or Metastrata found on humans, with brief introductory comments on the genera included in this part of the study. The accompanying zoogeographic distribution of each species includes countries or territories where it is found along with the species' principal hosts. In most cases this information is followed by paragraphs describing the frequency of human infestation and the tick stages found on humans, together with the countries (or widely recognized territories), localities and reported administrative divisions where the species has been observed on humans, with comments when appropriate. For several species, a note is added in a separate paragraph providing explanatory taxonomic information. Zoogeographic regions are based on Cox & Moore (2005), as defined in Guglielmone *et al.* (2014), for the Afrotropical, Australasian, Nearctic, Neotropical, Oriental and Palearctic Zoogeographic Regions, with any exceptions to this distributional pattern provided under the corresponding tick species. Hosts are based on Guglielmone *et al.* (2014) with several modifications due to information obtained after the publication of that study. The second chapter includes valid species that have been reported as parasites of people but that in fact have either not been found on humans or are of uncertain status as human parasites. The third chapter lists hard tick species collected from humans under names currently considered invalid according to Guglielmone & Nava (2014) and Guglielmone *et al.* (2015).

The most common ixodid life cycle is the three-host cycle (larvae, nymphs and adult ticks feed on a different vertebrate individual of the same or different species), but a few species have a two-host cycle (larvae and nymphs feed on the same individual host and adults on another host) or a one-host cycle (larvae, nymphs and adult ticks feed successively on the same individual host). In this work, species with a one-host or two-host life cycle are specifically noted.

Each tick taxon is broadly classified as very rare (one to three ticks found on humans), rare (four to ten ticks), sporadic (11 to 100 ticks), frequent (101 to 1000) or very frequent (more than 1000 specimens), indications of the degree of human parasitism reported in the literature. This information should not be viewed statistically because data on the frequency with which a given tick species has been recovered from humans in relation to all infestations by that species are available for very few taxa. Nonetheless, it is safe to assume that tick species classified as “frequent” or “very frequent” often bite humans, which itself is epidemiologically relevant. Conversely, tick species classified as “sporadic,” “rare” or “very rare” may either be epidemiologically insignificant or in need of additional investigation, a condition that appears to be increasingly the case in those parts of the world where novel tick-borne disease agents are being described. We also provide a general comparison of our information on hard tick infestation of humans with that of Estrada-Peña & Jongejan (1999), an exercise that may reflect evolving changes in host-parasite relationships over the years spanned by these reviews.

Finally, tables are presented that show the proportions of hard ticks from the genera constituting the family Ixodidae found on people in the different zoogeographic regions, countries and territories of the world.

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Introduction

Ticks of the family Ixodidae (Acari: Ixodida), commonly known as hard ticks, occur worldwide and are obligate blood-feeding ectoparasites of all classes of terrestrial vertebrates. Ixodids may cause dermatoses, anemia and even paralysis of their hosts, but their chief importance lies in their capacity to transmit a wide range of pathogens (viruses, bacteria, protozoa, nematodes) to infested hosts. There are currently 729 generally recognized ixodid species (Guglielmone *et al.* 2015), although none are specific to humans. Nevertheless, people are frequently attacked by hard ticks, mostly as a consequence of outdoor activities in rural or recreational areas, but also in urban green spaces, such as parks and vacant lots, which are becoming increasingly important as sites of human exposure to ticks and consequent acquisition of tick-borne pathogens (Akimov & Nebogatkin 2016, Uspensky 2016, Noden *et al.* 2017).

From a public health perspective, knowledge of the species of Ixodidae found attached to humans worldwide can assist in recognizing those species that are demonstrated or potential vectors of disease-causing agents. Although the species of ticks that parasitize humans have long attracted the attention of researchers, few globally comprehensive studies of these species have been conducted. The two most recent reviews are those of Estrada-Peña & Jongejan (1999), who discussed tick species feeding on humans with special reference to pathogen transmission, and Guglielmone *et al.* (2014), who simply listed 267 species found on humans based on examination of the literature.

Tick-borne pathogens of humans are now a major focus of biomedical research worldwide, but their vectors are seldom discussed in any depth because most authors lack the expertise to correctly identify ticks to species and thereby link them to the voluminous literature on tick-transmitted pathogenic (or potentially pathogenic) agents. It is hoped that the current compilation will prove valuable to such investigators because accurate tick identification and knowledge of tick distribution are crucial factors in epidemiological analyses. Additionally, the rise of molecular genetic methods has led to increases in the number of recognized tick species, either through reinstatement of formerly suppressed taxa or the revelation that some widely distributed “species” actually represent groups of morphologically cryptic species

(Nava *et al.* 2014a, Lado *et al.* 2016). Thus, at a taxonomic level, a complex picture is emerging of tick-host relationships and tick distribution – both critical factors in studies of ticks in relation to disease.

Here we present a list of species of Ixodidae found feeding on humans, with special emphasis on their geographical distribution, principal hosts, and tick life history stages associated with human parasitism. Particularly before 1950, the literature contains several accounts of ticks found on humans in which the tick species involved are now considered to have been incorrectly identified. For example, *Ixodes ricinus* (Linnaeus), *Amblyomma cajennense* (Fabricius) and *Hyalomma aegyptium* (Linnaeus) are valid species, but for decades they were also catch-all names; therefore, it has been necessary to ignore many human tick bite records published under these and other names. Additionally, records of species that cannot currently be determined to species based on available knowledge, *e.g.*, *Rhipicephalus sanguineus* (Latreille), are included as *R. sanguineus sensu lato*. It needs also to be emphasized that the role of nymphs and, especially, larvae in pathogen transmission is often underestimated because in many cases of human parasitism, these stages were not or could not be identified to the species level. As well, there exist some doubtful cases in which valid tick species were reported as feeding on people or, inversely, invalid species names were published in papers on human parasitism.

This work is intended to be a global survey of hard tick parasitism of humans, but it is important to bear in mind that we have been unable to examine every paper on such a vast subject, either because some publications have proved inaccessible or because translations are often unclear or uncertain. Our presentation is therefore biased toward Indo-European languages and the Western peer-reviewed scientific literature, but even in this case we have been unable to examine all papers containing data on ixodids as parasites of humans. It is also important to stress that this survey is based solely on a critical review of the literature, not on personal examination of particular tick specimens, whose future status may change with advances in our knowledge of tick systematics, host relationships and distribution. However, even with these caveats, we trust that the information presented here will prove helpful to those engaged in the daunting task of elucidating the dynamics of tick-transmitted disease agents.

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Chapter 1

Tick Species Found Feeding on Humans



A total of 283 tick species have been found feeding on humans, 69 Prostriata (27% of all prostriate ticks) and 214 Metastriata (45% of all metastriate ticks).

Prostriata

Genus *Ixodes*: Guglielmone & Nava (2014) listed 244 species for the genus *Ixodes*, but this number has since increased to 253 with the description of *Ixodes ariadnae* Hornok, *Ixodes bocatorensis* Apanaskevich and Bermúdez, *Ixodes collaris* Hornok, *Ixodes inopinatus* Estrada-Peña, Petney and Nava, *Ixodes laridis* Heath and Palma, *Ixodes microgaei* Apanaskevich, Soarimalala and Goodman, *Ixodes woyliei* Ash, Elliot, Godfrey, Burmej, Abdad, Northover, Wayne, Morris, Clode, Lymbery and Thompson, *Ixodes kandingensis* Guo, Sun, Xu and Durden, and *Ixodes goliath* Apanaskevich and Lemon (Guglielmone *et al.* 2015). Species of *Ixodes* are found in all zoogeographic regions of the world, including areas close to the poles. The greatest number of *Ixodes* species is found in the Afrotropical Region, followed by the Palearctic and Neotropical Regions. A recent test of the identities of ixodid ticks of medical and veterinary importance that are broadly distributed in the western Palearctic yielded a misidentification rate of 17% for the genus *Ixodes* (Estrada-Peña *et al.* 2017b).

1. ***Ixodes acuminatus*** Neumann: a Palearctic species found in Belgium, France, Germany, Great Britain, Italy, Hungary, Portugal, Spain (Petney *et al.* 2015) and Turkey (Kar *et al.* 2017). Usual hosts for all parasitic stages of *I. acuminatus* are rodents (Cricetidae, Muridae), but these stages have also been found on mammals of several orders. Additionally, adults and nymphs have been collected from passeriform birds (Turdidae), while adult ticks alone have been found on galliform birds (Phasianidae), and immature stages have been recovered from accipitriform (Accipitridae) and passeriform (Sylviidae),

Troglodytidae) birds (Guglielmone *et al.* 2014, Norte *et al.* 2015, Diakou *et al.* 2016, Llopis *et al.* 2017).

Ixodes acuminatus is a sporadic parasite of humans. It was not included in the Estrada-Peña & Jongejan (1999) list of ticks found on people. Females, males and nymphs of *I. acuminatus* have been found on people, but most cases of human parasitism have been due to females.

France: Aubry *et al.* (2016) collected two *I. acuminatus* from humans but provided no further data.

Italy: Manilla (1998) reported a nymph on a person, but the collection locality was not given; Otranto *et al.* (2014) found two *I. acuminatus* on people in the Apulia and/or Basilicata Regions, but tick stages were not provided.

Turkey: Kar *et al.* (2017) collected 39 females and four males during a six-year study in Istanbul Province.

Undetermined northwest European countries: Hillyard (1996) stated that *I. acuminatus* rarely attacks people in northwestern Europe but provided no information on localities or the tick stages involved.

Note: there is debate as to whether *Ixodes redikorzevi* Olenov is a synonym of *I. acuminatus* (Kolonin 2009, Estrada-Peña *et al.* 2017a); both names are treated as provisionally valid here, following Guglielmone & Nava (2014), Guglielmone *et al.* (2014, 2015) and Petney *et al.* (2015).

2. ***Ixodes acutitarsus* (Karsch):** an Oriental and Palearctic species found in China, India, Japan, Myanmar, Nepal, Taiwan and Thailand (Kolonin 2009); according to Clifford *et al.* (1975), an Indonesian record of this tick in Santos Dias (1961a) requires confirmation. Adults of *I. acutitarsus* are usually found on artiodactyl mammals (Bovidae), while larvae are commonly collected from rodents (Muridae, Sciuridae) with some records from other hosts, including birds; nymphs have been found on rodents (Cricetidae, Muridae, Sciuridae).

Ixodes acutitarsus is a frequent parasite of humans, but it was not included in the Estrada-Peña & Jongejan (1999) list of ticks found on people. Reports of *I. acutitarsus* biting people have implicated larvae, male and female ticks, but the majority of cases have involved female ticks.

China: Teng & Jiang (1991) listed this species as a parasite of humans, under the name *Ixodes gigas* Warburton. Nuttall (1916) reported a male tick found on a human in the Salween Valley, Tibet Autonomous Region; this record was also included in Keirans (1985).

Japan: Yamaguti *et al.* (1971) reported three cases of human infestation in Osaka, Saitama, and Wakayama Prefectures; two of these cases were due to female ticks, but the tick stage involved in the third case is unknown. Takada *et al.* (1978) recorded 76 females of *I. acutitarsus* parasitizing people in Aomori, and Yamaguti & Takada (1981) found a female on a person in Kanagawa. Yamamoto *et al.* (1997) found a female of this tick plus two females of *Ixodes monospinosus* Saito on a person infested along the border of Oita and Miyazaki Prefectures, while Yamauchi *et al.* (2010a) described six cases of human infestation with females of *I. acutitarsus* in Toyama. Okino *et al.* (2010a) summarized 12 cases in which this tick was found on humans in Fukuoka, Kagoshima,

Nagasaki, Shimane, Tokyo and Toyama Prefectures, but the tick stages involved were not provided. Woo *et al.* (1990) confirmed that human parasitism by *I. acutitarsus* in Japan had amounted to 44 cases by the year 1990.

India: Sharif (1938) stated that *I. acutitarsus* occasionally attacks humans in the eastern Himalayas, while Hoogstraal (1970a) listed one male and one female tick from persons in Darjeeling in West Bengal State, a record also included in Keirans (1985).

Myanmar: Schulze (1939a) reported five male and six female ticks from a person infested on Mount Victoria, Chin State; Nuttall (1916) listed a female tick from a human at Hpimaw, Kachin State, a record that is also included in Hoogstraal (1970a) and Keirans (1985).

Nepal: Hoogstraal (1970a, 1971) listed about ten females and one male of *I. acutitarsus* parasitizing people in Baitidi, Baglung, Chitwan, Ilam, Jumla, Kaski, Kathmandu, Makwanpur, Ramechhap, Rasuwa and Solukhumbu Districts; later, Clifford *et al.* (1975) recorded one larva, 52 males and more than 100 females from people, thereby adding Nuwakot, Sankhuwasabha and Sindhupalchowk Districts to the above list. Daniel (1979) found two female ticks at Bunkin village, Sankhuwasabha District.

Taiwan: Maa & Kuo (1966) listed *I. acutitarsus* as a parasite of humans but provided no further information. Tsai *et al.* (2012) reported an adult of *I. acutitarsus* on a person in Kaohsiung, while Chao & Shih (2012) found eight female ticks on humans in Chiayi, Hsinchu, Hualien, Kaohsiung, Nantou and Taitung Counties.

Thailand: Tanskul *et al.* (1983) found adults of this tick on people in Chiang Mai Province.

3. *Ixodes angustus* Neumann: this species is one of two *Ixodes* found in the Nearctic and Palearctic Zoogeographic Regions; the other is *Ixodes signatus* Birula, a tick that has never been reported from humans. *Ixodes angustus* is found in Canada and the USA (Nearctic), and Russia and Japan (Palearctic) (Kolonin 2009). Yamaguti *et al.* (1971) included Argentina in the range of *I. angustus* but this is incorrect (see note below). Usual hosts for larvae, nymphs and adults of *I. angustus* are rodents (Muridae) and soricomorphs (Soricidae), but the range of hosts of this tick is broad, including mammals of several orders, with occasional records from birds.

Ixodes angustus is a sporadic parasite of humans. It was listed as a tick rarely found on people in the review of Estrada-Peña & Jongejan (1999). The great majority of cases of human parasitism by *I. angustus* have been caused by female ticks and the remainder by nymphs.

Canada: human parasitism by *I. angustus* was recorded in British Columbia by Gregson (1956), who found one female on a person at Burnaby and another at Mission, while Spencer (1963) recovered three female ticks from humans at White Rock, Vancouver and North Surrey.

Russia: Pomerantzev (1950) apparently found adults of *I. angustus* on humans on islands situated in the Far Eastern District, and Serdjukova (1956) also listed this tick as found on people there. Nonetheless, Filippova (1977) did

not list *I. angustus* as a parasite of humans in the former USSR, and we therefore consider these Russian records of human parasitism provisionally valid.

USA: Bishopp & Trembley (1945) listed three females of *I. angustus* collected from humans, but collection localities were not provided. Chamberlin (1937) confirmed that this tick had been found on humans at several localities in western Oregon, although tick stages were not provided, while Cooley (1946) found three female ticks on people, one in Newport, Oregon, and the other two ticks at Elma, Grays Harbor County, and Clark County in Washington State. Additional records for Washington State are in Damrow *et al.* (1989), who found a female tick on a child from Redmond, and Merten & Durden (2000), who listed 15 females of *I. angustus* collected from people. Walker *et al.* (1998) found two specimens of this tick on persons during a 12-year study in Michigan, although tick stages were not provided. Merten & Durden (2000) recorded a female and a nymph from humans in Alaska; later, Durden *et al.* (2016) added a female and a nymph recovered from humans at Cordova and Gustavus.

Note: there are several erroneous records of *I. angustus* for the Neotropical Region, as discussed in Guglielmone & Nava (2014) and Guglielmone *et al.* (2003a, 2014).

4. ***Ixodes apronophorus*** Schulze: a Palearctic species found in Austria, Belarus, Czech Republic, Denmark, Estonia, France, Germany, Great Britain, Hungary, Kazakhstan, Kyrgyzstan, Latvia, Moldova, Poland, Romania, Russia, Slovakia, Switzerland and Ukraine (Koloinin 2009), Netherlands (Jaenson *et al.* 1994) and China (Guo *et al.* 2016). Most records for all parasitic stages of *I. apronophorus* have been reported from rodents (Cricetidae), but larvae, nymphs and adult ticks have also been collected from rodents (Myocastoridae) and soricomorphs (Soricidae); adults alone have been collected from carnivores (Canidae), lagomorphs (Leporidae), rodents (Castoridae) and passeriform birds (Muscicapidae), while immature stages have been recovered from artiodactyls (Suidae), rodents (Muridae), squamates (Viperidae) and passeriforms (Fringillidae) (Guglielmone *et al.* 2014, Andersson *et al.* 2018a).

Ixodes apronophorus is a very rare parasite of humans. Ravdonikas *et al.* (1968) stated that *I. apronophorus* does not bite people, and it was not included in the Estrada-Peña & Jongejan (1999) list of ticks found on humans.

Russia: Fedorov (1968) reported human parasitism by one adult of *I. apronophorus* in the Omsk Region of Western Siberia.

5. ***Ixodes asanumai*** Kitaoka: Guglielmone *et al.* (2014) listed this tick as a Palearctic species, but *I. asanumai* has also been found in the southern islands of Japan, which are in the Oriental Region (Takano *et al.* 2014). *Ixodes asanumai* is known only from Japan (Koloinin 2009). All parasitic stages of *I. asanumai* are usually found on squamate hosts (Lacertidae), but there are some records of nymphs collected from squamate (Scincidae) and avian hosts (Passeriformes), and adult ticks collected from dogs (Guglielmone *et al.* 2014, Takano *et al.* 2014).

Ixodes asanumai is a very rare parasite of humans. It was not included in the Estrada-Peña & Jongejan (1999) list of ticks found on people. The only record

of human parasitism by *I. asanumai* is from the Palearctic Zoogeographic Region.

Japan: a single record of an *I. asanumai* female found on a human in Saitama Prefecture is listed in the review by Okino *et al.* (2010b).

6. *Ixodes australiensis* Neumann: an Australasian species known only from Australia (Kolonin 2009). All parasitic stages of *I. australiensis* have been found on diprotodontian mammals (Potoroidae); adult ticks have been recovered from artiodactyls (Bovidae, Suidae), carnivores (Canidae), dasyuromorphs (Dasyuridae) and diprotodontians (Macropodidae); unknown stages have been collected from diprotodontians (Phalangeridae) and peramelemorphs (Peramelidae) (Guglielmone *et al.* 2014, Ash *et al.* 2017). The larva of *I. australiensis* remains undescribed.

Ixodes australiensis is a very rare parasite of humans.

Australia: Raby *et al.* (2016) removed one specimen of *I. australiensis* from a human infested at Bibbulmun Track, Western Australia, but the tick stage found was not provided, and Kwak (2018) removed a male tick from a human infested near Denmark, also in Western Australia.

7. *Ixodes baergi* Cooley & Kohls: a Nearctic species known only from the USA (Kolonin 2009). All parasitic stages of *I. baergi* feed on passeriform birds (Hirundinidae).

Ixodes baergi is a very rare parasite of humans. It was not included in the Estrada-Peña & Jongejan (1999) list of ticks found on people.

USA: one record of *I. baergi* feeding on a person resulted from a 12-year study in Ogemaw County, Michigan, by Walker *et al.* (1998), but the tick stage was not provided.

8. *Ixodes banksi* Bishopp: a Nearctic species found in Canada and the USA (Lindquist *et al.* 2016). Usual hosts for adults and nymphs of *I. banksi* are rodents (Castoridae), but these stages have also been found on rodents (Cricetidae) and carnivores (Mustelidae); the natural hosts for the larva of this tick remain unknown.

Ixodes banksi is a rare parasite of humans. It was not included in the Estrada-Peña & Jongejan (1999) list of ticks found on people. With one exception, the stages of *I. banksi* found on people remain unknown.

USA: Durden & Keirans (1996) confirmed that a few specimens of *I. banksi* have been found on humans, although tick stages and collection localities were not provided. Walker *et al.* (1998) recorded one *I. banksi* from a human during a 12-year study in Michigan, but, again, the tick stage found was not given. Merten & Durden (2000) listed one male collected from a person in New York State.

9. *Ixodes boliviensis* Neumann: a Neotropical species found in Bolivia, Colombia, Costa Rica, Guatemala, Honduras, Mexico, Panama (Guglielmone *et al.* 2003a), Belize (Redell & Veni 1996) and Nicaragua (Bermúdez *et al.* 2015). Males and females of *I. boliviensis* have been found on mammals of several orders and occasionally on galliform birds (Phasianidae); a few nymphs have been taken from artiodactyls (Bovidae, Cervidae), carnivores (Canidae) and

galliform birds (Cracidae), while larvae have been collected from carnivores (Procyonidae).

Ixodes boliviensis is a rare parasite of humans. It was not included in the Estrada-Peña & Jongejan (1999) list of ticks found on people. Only adults of *I. boliviensis* have been identified as causing human parasitism, and in such cases female ticks outnumbered males.

Belize: Reddell & Veni (1996) found a female of *I. boliviensis* on a human who was exploring the Cebada Cave, Cayo District.

Mexico: Neumann (1906) reported a female tick collected from a child at Atoyac, Guerrero State, a specimen that was subsequently used to describe *Ixodes bicornis* Neumann, a synonym of *I. boliviensis*, while Guzmán-Cornejo *et al.* (2007) reported a female tick from a human at Cerro El Vigía, Chiapas State.

Panama: Cooley & Kohls (1945) listed a male of *I. boliviensis*, under the name *I. bicornis*, from a person at Boquete, Chiriquí Province, and Fairchild *et al.* (1966) added a female tick found on a human, but the collection locality was not provided.

10. ***Ixodes brunneus*** Koch: a Nearctic and Neotropical species, but most records are of Nearctic origin in the USA (see note below). This species is a parasite of birds, and males, females, nymphs and larvae commonly feed on passeriforms (several families), but *I. brunneus* has also been found on galliforms (Odontophoridae, Phasianidae), piciforms (Ramphastidae), strigiforms (Strigidae) and columbiforms (Columbidae).

Ixodes brunneus is a very rare parasite of humans. It was not included in the Estrada-Peña & Jongejan (1999) list of ticks found on people. Goddard (2008) stated that *I. brunneus* does not bite humans, but we consider the following records from the Nearctic Zoogeographic Region valid.

USA: Williams *et al.* (1999) reported *I. brunneus* on people in South Carolina, but the tick stage was not given, while Merten & Durden (2000) recorded a female tick from a person, also in South Carolina; the latter authors were probably referring to the specimen found by Williams *et al.* (1999) because the same database was accessed for both studies.

Note: reports of *I. brunneus* from localities outside the Western Hemisphere are probably based on misidentifications (Guglielmone *et al.* 2014). Keirans & Brewster (1981) stated that other than one *bona fide* record of *I. brunneus* from Venezuela, all valid records of this species originated from localities in the Nearctic Region. Fairchild *et al.* (1966) noted that *I. brunneus* collected in Panama differ somewhat morphologically from USA specimens. See also notes under *I. frontalis* and *I. pacificus*.

11. ***Ixodes canisuga*** Johnston: a Palearctic species found in Bosnia and Herzegovina, Croatia, Denmark, France, Germany, Great Britain, Hungary, Ireland, Latvia, Lithuania, Poland, Portugal, Romania, Serbia, Spain, Sweden and Switzerland (Jaenson *et al.* 1994, Petney *et al.* 2012, Hornok *et al.* 2017), but also present in Belgium (Fain 1990) and Italy (Manilla 1985). All parasitic stages of *I. canisuga* are usually found on carnivorous mammals (Canidae),

with some records from several other orders of mammals; immature stages have also been collected on passeriform (several families) and strigiform (Strigidae) birds.

Ixodes canisuga is a very rare parasite of humans. It was not included in the Estrada-Peña & Jongejan (1999) and Guglielmone *et al.* (2014) lists of ticks found on people.

Great Britain: there is a record of *I. canisuga* feeding on a person in McGarry *et al.* (2001), but the tick stage was not provided. This record is treated as provisionally valid here.

Note: Kolonin (2009) regards *I. canisuga* as a synonym of *Ixodes crenulatus* Koch, but both species are treated as valid here.

12. ***Ixodes cavipalpus*** Nuttall and Warburton: an Afrotropical species found in Angola, Burundi, Cameroon, Democratic Republic of Congo, Kenya, Malawi, Mozambique, South Africa, South Sudan, Tanzania, Uganda, Zambia and Zimbabwe (adapted from Kolonin 2009). Adults of *I. cavipalpus* are usually found on artiodactyls (Bovidae), with some additional records from a variety of mammals representing several orders; nymphs and larvae of this species have also been recovered from Bovidae. The nymph of *I. cavipalpus* remains undescribed.

Ixodes cavipalpus is a very rare parasite of humans. In the review of Estrada-Peña & Jongejan (1999), this species was categorized as rarely found on people. Schwetz (1927a) stated that larvae of *I. cavipalpus*, under the name *Ixodes rubicundus limbatus* Neumann, attacked people in the Democratic Republic of Congo, but this statement requires confirmation and this country is excluded from the list below.

Angola: Nuttall & Warburton (1911) recorded a male tick feeding on a person in Benguela Province; this record was later repeated by other workers (*e.g.*, Hoogstraal 1956, Santos Dias 1956a, Keirans 1985).

Zambia: Estrada-Peña & Jongejan (1999) listed *I. cavipalpus* as causing human parasitism but provided no further information.

Undetermined African countries: Theiler (1962) listed two records of adults of *I. cavipalpus* from humans in Africa, but collection localities were not provided. One of them is probably the above record of Nuttall & Warburton (1911).

13. ***Ixodes columnae*** Takada and Fujita: a Palearctic species known only from Japan (Kolonin 2009) and, if confirmed, from Taiwan (Kuo *et al.* 2017). All parasitic stages of *I. columnae* have been found on rodents (Sciuridae), while immature stages have also been collected from galliform (Phasianidae), pici-form (Picidae) and passeriform (several families) birds, as well as rodents (Cricetidae, Muridae).

Ixodes columnae is a very rare parasite of humans. It was not included in the Estrada-Peña & Jongejan (1999) list of ticks found on people.

Japan: there is a single record of a larva of this tick feeding on a human at Yonezawa, Yamagata Prefecture, in Takada & Fujita (1992).

14. ***Ixodes confusus*** Roberts: an Australasian species known from Australia and Papua New Guinea (Kolonin 2009). *Bona fide* host records for adults of

I. confusus include artiodactyl mammals (Bovidae), perissodactyls (Equidae) and diprotodontians (Macropodidae). The larva and nymph of this tick remain unknown.

Ixodes confusus is a very rare parasite of humans. It was not included in the Estrada-Peña & Jongejan (1999) list of ticks found on people.

Australia: there is a single record of a female of *I. confusus* feeding on a human in northern Queensland (Roberts 1960).

15. ***Ixodes cookei*** Packard: mainly a Nearctic species of medical importance that is found in Canada, Mexico and the USA, with a few additional records from the Neotropical portion of Mexico (Guzmán-Cornejo *et al.* 2007, Lindquist *et al.* 2016). All parasitic stages of *I. cookei* feed chiefly on small to medium-sized mammals of several orders; immature stages have occasionally been found on passeriform (Emberizidae, Turdidae) and strigiform (Strigidae) birds.

Ixodes cookei is a very frequent parasite of humans. In the review of Estrada-Peña & Jongejan (1999) it was listed as a tick that readily attacks people. No cases of human parasitism by *I. cookei* have been recorded for the Neotropical Region. Females, nymphs and larvae of *I. cookei* have been found on people in the Nearctic, where the most common stage causing human parasitism is the nymph.

Canada: there are several records for Quebec, where Twinn (1942) found a nymph on a child at “Aulmer” (Aylmer?), Bequaert (1945) listed nymphal infestation of a person, Bishopp & Trembley (1945) reported that one of 11 lots of *I. cookei* from humans was from this province, and Gasmi *et al.* (2016) stated that 874 ticks (19% of the total) feeding on people from 2008 to 2014 in Quebec were *I. cookei*, although tick stages were not provided. There are also several studies for the Province of Ontario, where Bequaert (1945) listed a female tick from a person, while MacNay (1950) reported human parasitism at Lucknow and Ottawa in Ontario Province, but tick stages were not provided. Scholten (1977) found 12 females, 16 nymphs and one larva of *I. cookei* on people during a ten-year study in the same province. Barker *et al.* (1993) also found this tick on persons in Ontario, where, later, Nelder *et al.* (2014) recovered 838 specimens of *I. cookei* from people (5.8% of the total collected from humans) during a five-year study, but tick stages recovered were not provided in either of these studies. Scott *et al.* (2017b) found one nymph on a person at Kenora, again in Ontario. Additionally, Gregson (1956) reported four cases of human infestation by two females, one nymph and one *I. cookei* of unknown stage at localities in Ontario, Quebec and New Brunswick.

Patterson *et al.* (2017) collected ten *I. cookei* from people during a two-year study in New Brunswick and Nova Scotia, along with 14 *I. scapularis* and 17 alleged crosses from both tick species. Tick stages found in this study were not provided but figures included in the paper show only female ticks, and morphological parameters used for tick identification appear to be restricted to females.

USA: Merten & Durden (2000) stated that *I. cookei* is one of the eight principal human-biting ticks in this country; these authors recorded *I. cookei* on

humans (11 nymphs, five females and two larvae) in Connecticut, Kansas, Maine, New Hampshire, New York, Pennsylvania, Texas and Vermont. However, there are a number of other studies that demonstrate the importance of *I. cookei* as a parasite of humans. The first record of *I. cookei* on a human was from New York (Fitch 1872) under the name *Ixodes cruciarius* Fitch; other records from people in New York State include two specimens of unknown stages (Cooley & Kolhs 1938) and one larva and two nymphs in Campbell *et al.* (1994). Hamilton (1934) described four cases of human parasitism under the name *Ixodes hexagenia cookei*, a *lapsus* for *Ixodes hexagonus cookei* Packard, but tick stages and localities were not provided. Later, Bequaert (1945) found a few nymphs and adult ticks on people in New Hampshire, New York and Massachusetts; Bishopp & Trembley (1945) recorded ten lots (females and nymphs) of this tick from people, eight for the New England states and two for Pennsylvania; and Cooley & Kohls (1945) found an adult tick on a human at Brattleboro, Vermont, while Eads *et al.* (1956) found a female and a nymph of this tick on humans in Texas.

Magnarelli & Anderson (1989) found four *I. cookei* (presumably nymphs) on persons in Connecticut, while Hall *et al.* (1991) reported one female, two larvae and 33 nymphs of *I. cookei* collected from people at several localities in West Virginia. The preponderance of nymphs of this species on humans was also reported by Smith *et al.* (1992) in Maine, where 24 larvae, 27 adults and 179 nymphs were recovered from people, while four nymphs were collected from humans at three localities in North Carolina by Harrison *et al.* (1997). Snetsinger (1968) stated that *I. cookei* has been found on people in Pennsylvania, while Walker *et al.* (1998), in a 12-year Michigan study, and Rand *et al.* (2007), after an 18-year study in Maine (USA), observed that 5.6% and 12.2%, respectively, of ticks feeding on people were *I. cookei*, but tick stages were not provided in any of these three studies. Lubelczyck *et al.* (2010) recorded *I. cookei* on people in Vermont, but again tick stages were not given.

16. ***Ixodes cornuatus*** Roberts: an Australasian species known only from Australia (Kolonin 2009). All parasitic stages of *I. cornuatus* have been found on carnivorous mammals (Canidae) and rodents (Muridae). Adult ticks have been collected from Felidae and struthioniform birds (Casuariidae), and a combination of adult and immature stages have been taken from peramelemorphs (Peramelidae) and several families of diprotodontians; immature stages have also been found on passeriform birds (Cracticidae, Acanthizidae) (Barker *et al.* 2014, Guglielmone *et al.* 2014, Kwak & Madden 2017). Wait *et al.* (2017) stated that Tasmanian records of *Ixodes holocyclus* Neumann are, in fact, *I. cornuatus* Roberts.

Ixodes cornuatus is a sporadic parasite of humans. It was not included in the Estrada-Peña & Jongejan (1999) list of ticks found on people. With the exception of a female tick (see below), there is no information about the life stages that have caused human parasitism.

Australia: three records exist of *I. cornuatus* feeding on humans in this country. One is in Roberts (1970), but the tick stage and collection locality were

not provided; another is in Tibballs & Cooper (1986), who found a female of *I. cornuatus* feeding on a child, but the locality is uncertain; and a third is in Graves *et al.* (1993), who found a large number of *I. cornuatus* (39 specimens, probably adults) on six humans at Gippsland in Victoria State.

Note: Barker & Walker (2014) stressed the difficulties involved in morphologically separating *I. cornuatus* and *I. holocyclus*.

17. ***Ixodes crenulatus*** Koch: a Palearctic species whose identification is difficult (see note below) and that is generally considered to occur from Eastern Europe through Russia, the Central Asian countries, and China. All parasitic stages of *I. crenulatus* are usually found on rodents (several families), carnivores (Canidae, Felidae, Mustelidae) and lagomorphs (Leporidae), with several records from mammals of other orders; nymphs and larvae have also been collected from birds of several orders.

Ixodes crenulatus is a very rare parasite of humans. It was not included in the Estrada-Peña & Jongejan (1999) list of ticks found on people. Siuda (1995) and Nowak-Chmura & Siuda (2012) listed humans as hosts for this species in their analyses of the tick fauna of Poland and state that human parasitism has been detected outside Poland.

Russia: Fedorov (1968) reported two adult ticks from humans in the Omsk and Novosibirsk Regions, Western Siberia, while Filippova (1977) stated that humans can be attacked if they enter biotopes infested with this tick.

Note: *Ixodes crenulatus* has been confused with several species (Guglielmone & Nava 2014). Černý (1969a) proposed that this name be declared invalid, and Emel'yanova (1979) suggested that *I. crenulatus* represents a species complex, while Filippova & Panova (2000) described morphotypes of this species. Probably more than one species is represented under the name *I. crenulatus*.

18. ***Ixodes cumulatimpunctatus*** Schulze: an Afrotropical species found in Cameroon, Central African Republic, Congo, Democratic Republic of Congo, Equatorial Guinea, Gabon, Ivory Coast, Kenya, Malawi, Rwanda, Senegal, Sierra Leone, Tanzania, Uganda, and Zimbabwe (adapted from Morel 2003). All parasitic stages of *I. cumulatimpunctatus* have been collected from a variety of mammals of several orders, but no obvious preference for a particular host has been discerned. Adult ticks and nymphs have been recovered from cuculiform (Cuculidae) birds, nymphs from galliforms (Phasianidae), and larvae from galliform (Numididae) and passeriform (Turdidae) birds.

Ixodes cumulatimpunctatus is a rare parasite of humans. It was not included in the Estrada-Peña & Jongejan (1999) list of ticks found on people. Guglielmone *et al.* (2014) stated, erroneously, that *I. cumulatimpunctatus* has not been found on humans, based on Aeschlimann (1967), who noted that a female of this species found on a human in the Ivory Coast was not attached, but overlooked records on this tick on people under the name *Ixodes pseudorasus* Arthur and Burrow, a synonym of *I. cumulatimpunctatus*. The female of *I. cumulatimpunctatus* appears to be the usual tick stage causing human parasitism.

Ivory Coast: Morel (1963) reported *I. cumulatimpunctatus* on a human in the Ivory Coast, but later (Morel 2003) stated that the tick was not attached. Nevertheless, Cordellier (1984) found one case of human infestation with *I. cumulatimpunctatus* (presumably an adult tick), although the collection locality was not provided.

Rwanda: Elbl & Anastos (1966a, under the name *I. pseudorasus*) found a female tick on a human at Mount Bigugu, Western Province.

Tanzania: Nishida (1988, also using the name *I. pseudorasus*) stated that this tick infested humans at Mahale National Park in the Kigoma Region, but tick stages were not provided.

Zimbabwe: Arthur & Burrow (1957, using the name *I. pseudorasus*), found three female ticks on persons at Mount Selinda in Manicaland Province.

19. ***Ixodes dentatus*** Marx: a Nearctic species found in Canada, the USA (Lindquist *et al.* 2016) and Mexico (Guzmán-Cornejo *et al.* 2007). All parasitic stages of *I. dentatus* are usually found on lagomorphs (Leporidae), but adult ticks have also been collected from carnivores (Procyonidae), while larvae and nymphs have been found on artiodactyls (Bovidae), didelphimorphs (Didelphidae), rodents (Cricetidae, Sciuridae, Muridae) and passeriform birds (several families).

Ixodes dentatus is a sporadic parasite of humans. In Estrada-Peña & Jongejan (1999) it was categorized as rarely found on people. The great majority of cases of human parasitism by *I. dentatus* have been caused by nymphs, and just one case is known to have been due to larval infestation.

Canada: in Ontario, Nelder *et al.* (2014) found a single tick on a human over a five-year period, but the tick stage was not provided.

USA: Merten & Durden (2000), in their state-by-state survey of ticks recovered from humans, listed four nymphs of *I. dentatus* for Maine, Michigan and West Virginia. Additionally, Collins *et al.* (1949) found *I. dentatus* on people on Long Island, New York, but tick stages found were not provided, while Sollers (1955) reported a nymph from a person in Washington, D.C. Hall *et al.* (1991) recorded five nymphs on people at four localities in West Virginia, and Walker *et al.* (1992) found a nymph on a person in Berrien County, Michigan. Anderson *et al.* (1996) recorded a nymph from a person in Connecticut, while Harrison *et al.* (1997) reported a larva and a nymph collected from a child at Black Mountain, North Carolina, and Armstrong *et al.* (2001) found that 0.5% of 1,556 ticks recovered from persons in Maryland were nymphs of *I. dentatus*. Keirans & Lacombe (1998) found a nymph feeding on a child at Morrill in Maine. Walker *et al.* (1998) listed nine specimens of this tick collected from people during a 12-year study in Michigan, but it is uncertain whether all the specimens were attached, and Rand *et al.* (2007) reported three *I. dentatus* from persons after an 18-year study in Maine, although tick stages were not provided in either of these studies.

20. ***Ixodes eichhorni*** Nuttall: an Australasian and Oriental species in Guglielmone *et al.* (2014) but also found on remote Pacific islands (Kolonin 2009). *Ixodes eichhorni* is a poorly known tick whose females have been found on galliform

(Phasianidae) and passeriform (Turdidae) birds, while nymphs have been collected on coraciiform birds (Alcedinidae). The male and larva of this species remain unknown.

Ixodes eichhorni is a very rare parasite of humans. It was not included in the Estrada-Peña & Jongejan (1999) list of ticks found on people. The only record of human parasitism by *I. eichhorni* is from the Australasian Zoogeographic Region.

Papua New Guinea: a female tick collected from a person on Umboi Island is included in the original description of *I. eichhorni* by Nuttall (1916) and is the lectotype for this species, as explained in Keirans (1985). Other references concerning human parasitism by this species (e.g., Hoogstraal 1982) seem to be reiterations of the Nuttall record.

21. ***Ixodes feicialis*** Warburton and Nuttall: an Australasian species known from Australia (Kolonin 2009) and, perhaps, Papua New Guinea (Owen 2011). Adults and nymphs of *I. feicialis* are found on dasyuromorphs (Dasyuridae, Myrmecobiidae), peramelemorphs (Peramelidae) and diprotodonts (Potoroidae), but all parasitic stages have been collected from rodents (Muridae); adult ticks have also been recovered from carnivores (Felidae). Additionally, there are several records of *I. feicialis* from wild and domestic mammals, but tick stages found on these hosts have not been reported.

Ixodes feicialis is a very rare parasite of humans. It was not included in the Estrada-Peña & Jongejan (1999) list of ticks found on people.

Australia: the only report of this tick from people is in Domrow & Derrick (1965), who found one specimen of *I. feicialis* on a person at Mount Tamborine, Queensland, but the tick stage was not provided.

22. ***Ixodes festai*** Tonelli Rondelli: a Palearctic species found in France, Libya, Morocco, Tunisia (Kolonin 2009), Switzerland (Papadopoulos *et al.* 2001) and Italy (Estrada-Peña *et al.* 2017a), with a few European records, i.e., Hungary (Hornok *et al.* 2016a), outside this range from migratory birds. The morphological identification of *I. festai* is difficult, as discussed in Guglielmone *et al.* (2014, 2015) and Estrada-Peña *et al.* (2017a), among others. The confusion surrounding this species is underscored by the fact that Camicas *et al.* (1998) state that all parasitic stages of *I. festai* have been described, whereas Pérez-Aid (2007) maintains that the larva and nymph are still unknown. We agree with the latter author. Guglielmone *et al.* (2014) recognized galliform and passeriform birds as hosts for adult ticks, with an odd record from a carnivorous mammal.

Chisu *et al.* (2017, 2018) listed humans as hosts of *I. festai* in Sardinia, Italy. Chisu *et al.* (2017) gave a rather confused description of the ticks found on humans and hedgehogs, but Chisu *et al.* (2018) clearly stated that they found one nymph (a questionable record in light of the above paragraph), one male and three females of *I. festai*, of which, three specimens were collected from two persons, with the obvious implication that at least two adult ticks had fed on humans. This record is treated here as provisionally valid, given the difficulties involved in identifying this species, and that the two reported hosts (human and hedgehog) are unusual for *I. festai*.

23. *Ixodes frontalis* (Panzer): a Palearctic species found in Belgium, Croatia, Cyprus, Czech Republic, Denmark, France, Georgia, Germany, Great Britain, Hungary, Italy, Malta, Moldova, Netherlands, Norway, Poland, Portugal, Russia, Serbia, Slovakia, Spain, Sweden, Switzerland, Turkey and Ukraine (Krčmar 2012, Petney *et al.* 2012, Bona & Stanko 2013, Pflieger *et al.* 2017, Pfäffle *et al.* 2017a) and allegedly in China (Guo *et al.* 2016). There are records of *I. frontalis* from other countries, especially in northern Africa (*i.e.*, Hoogstraal & Kaiser 1961), based on collections from migrant birds, but these records are not discussed here. See also the notes below. All parasitic stages of *I. frontalis* are usually found on passeriform birds (Turdidae), but they have also been collected from birds of several orders, with some odd records of adult ticks from carnivores (Mustelidae).

Ixodes frontalis is a very rare parasite of humans. It was not included in the Estrada-Peña & Jongejan (1999) list of ticks found on people. Kar *et al.* (2017) found 37 females and four males of *I. frontalis* in Turkey, but we believe that these records require confirmation.

France: there is a single record of a female tick attached to a person at Pailhès Ariège Department in the Occitanie Region, as discussed in Gilot *et al.* (1997).

Great Britain: Cull *et al.* (2018) reported two females collected from people but collection localities were not provided.

Notes: Heylen *et al.* (2012) determined that the first Finlandian record of *I. frontalis* (two nymphs) by Laakkonen *et al.* (2009) was in error; in fact, the specimens were *I. ricinus*. Thereafter, Laakkonen *et al.* (2012) recognized the difficulties involved in the morphological identification of *Ixodes* nymphs. Wilson (1970) recorded nymphs and larvae of *I. frontalis* in the Philippines, but his diagnosis was tentative because this species is similar to *Ixodes turdus* from Japan and Korea; additionally, both species are similar to *I. brunneus* (Nearctic, Neotropical), and all three species are usually parasites of birds, rarely biting humans. These two examples clearly demonstrate the problems attending morphological identification of ticks of this group. Hornok *et al.* (2016a) presented molecular evidence indicating that more than one taxon may be included under the name *I. frontalis*. See also *I. brunneus*.

24. *Ixodes gibbosus* Nuttall: a Palearctic species found in Albania, Bulgaria, Croatia, Cyprus, Greece, Israel, Italy, Macedonia, Palestine, Serbia and Turkey (adapted from Kolonin 2009). Usual hosts for adults of *I. gibbosus* are artiodactyl mammals (Bovidae), but they have also been collected from mammals of several orders and rarely from birds. Immature stages have been collected from Bovidae, perissodactyls (Equidae) and passeriform birds (Turdidae).

Ixodes gibbosus is a sporadic parasite of humans. It was not included in the Estrada-Peña & Jongejan (1999) list of ticks recorded from humans. Females and nymphs of *I. gibbosus* have been found on people, but most cases of human parasitism have been due to females.

Greece: Saratsiotis (1970) listed nymphs of *I. gibbosus* from humans but collection localities were not provided. Papa *et al.* (2011) recorded six female

ticks (1.1% of all ticks collected from people) in northeastern Greece, Eastern Macedonia and Thrace Region.

Turkey: Kar *et al.* (2017) collected 25 females during a six-year study in Istanbul Province.

25. ***Ixodes granulatus*** Supino: an Australasian, Oriental and Palearctic species found in Cambodia, China, India, Indonesia, Japan, Laos, Malaysia, Myanmar, Nepal, Philippines, Singapore, South Korea, Taiwan, Thailand and Vietnam (Robbins 2005, Paperna 2006, Kolonin 2009). All parasitic stages of *I. granulatus* have been found on mammals of several orders, while only adult ticks have been recovered from squamates (Scincidae) and passeriform birds (Timaliidae, Turdidae); immature stages have also been collected from passeriforms (Emberizidae, Sylviidae) (Guglielmone *et al.* 2014, Kuo *et al.* 2017).

Ixodes granulatus is a rare parasite of humans. It was not included in the Estrada-Peña & Jongejan (1999) list of ticks found on people. There is no record of this tick feeding on humans in the Australasian Zoogeographic Region. Human parasitism by *I. granulatus* appears to be confined to adult ticks, but only females have been clearly identified as biting humans.

Malaysia: Audy *et al.* (1960) found a female tick on a person, but the collection locality was not provided.

South Korea: Yun *et al.* (2014) collected 261 ticks from humans in a period of six months, but only one female of *I. granulatus* was found on a person and the collection locality was not given.

Thailand: Tanskul *et al.* (1983) stated that adults of *I. granulatus* have been found on people, but collection localities were not provided.

Vietnam: Grokhovskaya & Nguyen Huan Hoe (1968) reported that *I. granulatus* has been found on humans in Vietnam, but no tick stages or collection localities were provided.

Note: Lah *et al.* (2016) found important molecular differences within populations of *I. granulatus* from Malaysia and even greater divergences when such populations were compared with samples from China and Japan, but these authors do not question the monospecificity of this tick species. Nonetheless, their results appear to indicate that more than one species is included under the name *I. granulatus*.

26. ***Ixodes hexagonus*** Leach: a Palearctic species found in Austria, Belgium, Bosnia and Herzegovina, Bulgaria, Croatia, Czech Republic, Denmark, France, Germany, Great Britain, Greece, Hungary, Iceland, Ireland, Italy, Luxembourg, Macedonia, Netherlands, Norway, Poland, Portugal, Romania, Russia, Serbia, Slovakia, Slovenia, Spain, Sweden, Switzerland and Ukraine (Burridge 2011) and Turkey (Bursali *et al.* 2012). All parasitic stages of *I. hexagonus* are usually found on erinaceomorphs (Erinaceidae), but they have also been collected from mammals of various orders. Additionally, adult ticks have been collected from galliform (Phasianidae) and passeriform (Turdidae) birds, whereas immature stages have been recovered from passeriform (several families) and strigiform birds (Strigidae).

Ixodes hexagonus is a frequent parasite of humans. It was classified as a relatively common tick found on people in Estrada-Peña & Jongejan (1999). All parasitic stages of *I. hexagonus* have been found feeding on humans, but most cases have involved nymphs and females.

Belgium: Fain (1990) found a female tick on a person in Amberes.

France: Garin & Bujadoux (1922) presented a questionable record of human parasitism by *I. hexagonus* (tick stage unknown), treated as valid in Roman *et al.* (1973). Gilot & Marjolet (1982) found two cases of human parasitism by female ticks in Isère Department, while Aubry *et al.* (2016) collected another two specimens of *I. hexagonus* from people but provided no further data.

Germany: Liebisch & Walter (1986) found four nymphs attached to humans out of a total of 2,195 *I. hexagonus* specimens collected from all hosts, while Liebisch & Liebisch (1996) recovered 10 adults, 20 nymphs and one larva representing 1% of all ticks collected from humans over a three-year study, but collection localities were not provided in either of these studies. Liebisch *et al.* (1998) collected 11 *I. hexagonus* during a two-year study in Lower Saxony, and Maiwald *et al.* (1998) reported two *I. hexagonus* parasitizing humans in the Heidelberg area of Baden-Württemberg State, but tick stages were not provided in either of these studies. Faulde *et al.* (2014) recovered five nymphs (0.7% of all ticks collected from humans) during a one-year study in northwestern Germany. Waindok *et al.* (2017) recovered six adults and four nymphs during a two-year study in Greater Hannover, Lower Saxony State.

Great Britain: Nuttall & Warburton (1911) listed a female tick recovered from a person at Caxton in Cambridgeshire, a record repeated in Keirans (1985). Arthur (1947) described two cases of human parasitism by female ticks in Surrey and Glamorgan Counties, and Arthur (1953) listed 35 females, 13 nymphs, two males and one larva of *I. hexagonus* found on people in London and its surroundings. Carter (1955) described a case of human infestation with a female of *I. hexagonus* but the collection locality was not provided. Martyn (1988) presented 50 records from humans (apparently repeating records in Arthur 1947, 1953), but tick stages and collection localities were not provided. McGarry *et al.* (2001) described two additional instances of human parasitism, but no further information was provided, while Jameson & Medlock (2011) listed two females of *I. hexagonus* from humans over a five-year study but, again, collection localities were not given. Cull *et al.* (2018) reported 26 females, 18 nymphs and two larvae collected from people without giving the localities where they were found.

Ireland: Martyn (1988) reported 50 cases of human parasitism by *I. hexagonus* in the British Isles, but it is unclear whether any of them occurred in Ireland. Therefore, reports of human parasitism by *I. hexagonus* in Ireland should be considered provisionally valid.

Italy: Manilla (1985) listed a female tick recovered from a human at San Demetrio in the Abruzzo Region, while Sanogo *et al.* (2003) found one *I.*

hexagonus on a person in Belluno Province in the Veneto Region, but the tick stage was not provided.

Netherlands: Nijhof *et al.* (2007) and Lenssen *et al.* (2011) each reported a case of human parasitism by *I. hexagonus*, one by an adult tick and the other by an unstated tick stage; collection localities were not provided.

Poland: Siuda (1995) and Nowak-Chmura & Siuda (2012) stated that *I. hexagonus* has been found on people, but tick stages and collection localities were not provided in either of these studies.

Turkey: Bursali *et al.* (2011) found three females and two males of *I. hexagonus* on people in Amasya Province, representing 0.3% of all ticks recovered from humans. Kar *et al.* (2017) collected one female over a six-year study in Istanbul Province.

Undetermined northwest European countries: Hillyard (1996) stated that *I. hexagonus* is a frequent parasite of people at unspecified localities in north-western Europe, but he mentions records from London and its surroundings, as Arthur (1953) did earlier, based on Browning & Shaw (1944), cited as Browning (1944); however, these authors did not report *I. hexagonus* from people apart from a general statement that “it has been taken from man.”

Note: Guglielmone *et al.* (2014) stated that there are several erroneous records of *I. hexagonus* from localities in the Nearctic, Neotropical and Oriental Zoogeographic Regions.

27. ***Ixodes holocyclus*** Neumann: an Australasian species of medical and veterinary importance known only from Australia (Kolonin 2009). All parasitic stages have been found on mammals of various orders, but no obvious preference for a particular host has been discerned. All stages have also been collected from passeriform birds (Cracticidae); adult ticks alone have been taken from passeriforms (Corvidae) and psittaciforms (Psittacidae); larvae alone have been found on cuculiforms (Cuculidae) and passeriforms (Acanthizidae). There are numerous species of tetrapods listed as hosts of *I. holocyclus* in Roberts (1960, 1970) and Barker & Walker (2014), but tick stages are not provided. Wait *et al.* (2017) stated that Tasmanian records of *I. holocyclus* are, in fact, *Ixodes cornuatus* Roberts.

Ixodes holocyclus is a frequent parasite of humans. In the review of Estrada-Peña & Jongejans (1999), it was listed as causing tick paralysis in Australia. All parasitic stages of *I. holocyclus* have been found on humans, but most specimens have been female ticks.

Australia: Roberts (1960, 1970) listed humans as hosts for *I. holocyclus* but provided neither tick stages found on people nor collection localities. Nuttall (1916) reported four cases of persons attacked by females of *I. holocyclus* at Underbrook, Illawara Region, and Sydney in New South Wales, while Grattan-Smith *et al.* (1997) reported three humans infested with *I. holocyclus* (presumably female ticks), also in New South Wales. Roberts (1934a) reported this tick from people in Queensland but tick stages were not provided. However, Andrew *et al.* (1946) found a larva on a person at Atherthon Tableland in northern Queensland, and Domrow & Derrick (1965) collected 92 females, five males,

16 nymphs and 16 larvae of this tick from humans over a period of 14 years in southeastern Queensland, while Sutherst & Moorhouse (1972) found a female tick on a person at Mount Tamborine, also in southeastern Queensland. Mayne *et al.* (2014) described another case of human parasitism by a nymph of *I. holocyclus* in Queensland. Jackson *et al.* (2000) reported six cases of human infestation with *I. holocyclus* at six localities in Victoria State; one case was due to a female and two male ticks, another was caused by females, and the tick stages involved in the other cases were not mentioned. Gofton *et al.* (2015) collected 167 females, 49 males and 63 nymphs of this species from people during three years of research in southeastern Queensland and the eastern part of New South Wales; and Teong *et al.* (2015) found one larva of *I. holocyclus* on a child in Sydney, New South Wales. Pek *et al.* (2016) found a female tick on a human infested in Sydney, New South Wales, that was detected upon arrival in Singapore. Miller (2002) collected 41 females and three males of *I. holocyclus* from a person, but the collection locality was not provided.

Additionally, Yajima *et al.* (1998), Watanabe *et al.* (1999), Miyamoto *et al.* (2000) and Sowa *et al.* (2001) listed one case each of people infested with *I. holocyclus*, while Okino *et al.* (2007) listed seven cases of human infestation with females of this species, all from travelers that had returned to Japan from Australia. Heath & Hardwick (2011) related the interception of 31 cases of persons infested with *I. holocyclus* in Australia and detected upon arrival in New Zealand, although, with the exception of one case of larval infestation that occurred in New South Wales, tick stages found on these people were not provided. See note under *I. cornuatus*.

Note: Jackson *et al.* (2000) stated that electrophoretic information suggests that more than one species is included under the name *I. holocyclus*.

28. *Ixodes kashmiricus* Pomerantzev: an Oriental and Palearctic species found in China, India, Kyrgyzstan and Pakistan (Koloinin 2009). Adults of *I. kashmiricus* have been found on artiodactyl mammals (Bovidae) and carnivores (Canidae), while nymphs have been collected from rodents (Muridae), with an odd record from squamates (Agamidae). Hosts of the larva are unknown.

Ixodes kashmiricus is a rare parasite of humans. It was not included in the Estrada-Peña & Jongejans (1999) list of ticks found on people. Guglielmone *et al.* (2014), based on Hoogstraal (1970a), stated that *I. kashmiricus* has been found on humans, but the latter author noted that ticks had been found on clothing. Human parasitism by *I. kashmiricus* has been recorded only in the Oriental Zoogeographic Region. The limited records of this tick feeding on people have been ascribed to females and nymphs, but available information is insufficient to determine which tick stage is the principal parasite of humans.

India: Miranpuri & Naithani (1978) and Koloinin (2009) stated that this species has been found on persons in this country but provided no further information. Sharma (1993) reported a female and three nymphs of *I. kashmiricus* from humans at “Gragian-sauzian” in Jammu and Kashmir State, but on page 258 he states that two specimens were crawling on people.

29. *Ixodes kazakstani* Olenov and Sorokoumov: a Palearctic species found in Kazakhstan and Kyrgyzstan (Kolonin 2009); however, Yu *et al.* (1997) reported this tick from China, and this statement was accepted as valid by Chen *et al.* (2010). Morel (2003) suggests that *I. kazakstani* is established in Tajikistan, and Lyashko (1973) stated that this tick is also established in Turkmenistan. All parasitic stages of *I. kazakstani* are usually found on lagomorphs (Leporidae) and galliform birds (Phasianidae); adult ticks have also been collected from artiodactyls (Bovidae) and carnivores (Canidae), and larvae and nymphs from rodents (Cricetidae, Dipodidae, Muridae) (Guglielmone *et al.* 2014, Kovalev *et al.* 2018).

Ixodes kazakstani is a very rare parasite of humans. It was not included in the Estrada-Peña & Jongejan (1999) list of ticks found on people.

Kyrgyzstan: Lyashko (1973) reported *I. kazakstani* (presumably adult ticks) from persons in Talas Province. This record is repeated in Filippova (1977).

30. *Ixodes kingi* Bishopp: a Nearctic species found in Canada and the USA (Lindquist *et al.* 2016). All parasitic stages of *I. kingi* usually feed on carnivorous mammals (several families) and rodents (several families); there are also a few records from lagomorphs (Leporidae, Ochotonidae).

Ixodes kingi is a rare parasite of humans. It was not included in the Estrada-Peña & Jongejan (1999) list of ticks found on people. The few cases of human parasitism have been caused by females and nymphs.

USA: Merten & Durden (2000) found three nymphs and a female of *I. kingi* on humans in Kansas, New Mexico and Nebraska. Cortinas & Spomer (2014) listed one *I. kingi* (stage unknown) from a person in Nebraska, but this seems to be a repetition of the record in Merten & Durden (2000).

31. *Ixodes kohlsi* Arthur: an Australasian species known only from Australia (Kolonin 2009). All parasitic stages of *I. kohlsi* are usually found on spheonisciforms (Spheniscidae); adult ticks have also been collected from suliforms (Phalacrocoracidae) and procellariiforms (Procellariidae).

Ixodes kohlsi is a very rare parasite of humans. It was not included in the Estrada-Peña & Jongejan (1999) list of ticks found on people.

Australia: Roberts (1960) reported a nymph of *I. kohlsi* attached to a human on Tollgates Island, New South Wales State, a record repeated in Heath & Palma (2017).

32. *Ixodes laguri* Olenov: a Palearctic species found in Armenia, Azerbaijan, Bulgaria, Czech Republic, Georgia, Hungary, Kazakhstan, Moldova, Mongolia, Romania, Russia, Slovakia, Turkey, Turkmenistan and Ukraine (Kolonin 2009). Although Austria, Belarus, Estonia, Latvia, Lithuania, and Uzbekistan are included within the range of *I. laguri* by Mihalca & D'Amico (2017), using the authors' bibliography, we were unable to confirm the presence of *I. laguri* in all these countries. Most records of larvae, nymphs and adults are from rodents (Sciuridae), but all parasitic stages of *I. laguri* have been found on lagomorphs (Ochotonidae), rodents (several families) and soricomorphs (Soricidae); adult ticks alone have been collected from erinaceomorphs (Erinaceidae); adult ticks and nymphs have been detected on carnivores (Mustelidae) and rodents

(Dipodidae, Gliridae); and larvae alone have been recorded from carnivores (Canidae) (Ushakova & Busalaeva 1962, Guglielmone *et al.* 2014, Tsapko 2017).

Ixodes laguri is a sporadic parasite of humans. It was not included in the Estrada-Peña & Jongejan (1999) list of ticks found on people. Females, larvae and nymphs parasitize humans, but female ticks appear to be the most common feeding stage.

Russia: Fedorov (1968) found an adult tick on a human in the Omsk Region of Western Siberia, while Filippova (1977) mentioned that larvae and nymphs have been found on persons.

Turkey: Bursali *et al.* (2010) reported human parasitism by adults of *I. laguri* in Tokat Province, while Bursali *et al.* (2011) claimed that 17 females of *I. laguri* had been found on people in the five districts of Amasya Province that were sampled, representing 0.9% of all adult ticks found on people there. Keskin *et al.* (2015) listed a female feeding on a person in Mecitozu District of Corum Province.

Note: *Ixodes laguri* is divided into four subspecies in Filippova (1977), indicating that more than one species may be included under this name (Guglielmone *et al.* 2014).

33. ***Ixodes marxi*** Banks: a Nearctic species found in Canada and the USA (Lindquist *et al.* 2016). All parasitic stages of *I. marxi* are usually found on rodents (Sciuridae), but different stages of this tick have been found on mammals of several orders, with some odd records from passeriform birds (unknown family).

Ixodes marxi is a frequent parasite of humans. It was not included in the Estrada-Peña & Jongejan (1999) list of ticks found on people. Most records of human parasitism by *I. marxi* below do not include the tick stages collected, although a few of them mention females and nymphs.

Canada: Lindquist *et al.* (2016) stated that there are numerous records of this tick from humans in this country but provided no further information. Nelder *et al.* (2014) found 102 specimens of *I. marxi* (0.7% of the total collected from humans) during a five-year study in Ontario, but tick stages were not provided. Gasmi *et al.* (2016) reported that during a seven-year study in Quebec, less than 1% of the ticks removed from people were *I. marxi*, and, again, tick stages were not given.

USA: Merten & Durden (2000), in their state-by-state survey of ticks found on humans, reported two females of *I. marxi* on persons in Ohio and Vermont, while Smith *et al.* (1992) found 15 nymphs and five adult ticks on people in Maine. Snetsinger (1968) stated that *I. marxi* had been recovered from persons in Pennsylvania, Walker *et al.* (1998) found 17 *I. marxi* (0.9% of the total from humans) over a 12-year study in Michigan, and Rand *et al.* (2007) found 141 *I. marxi* on persons (1.1% of the total) during an 18-year study in Maine, but tick stages were not provided in any of these three studies. Lubelczyk *et al.* (2010) reported tick bites of people by *I. marxi* in Maine but, again, tick stages were not given.