Biology of *Ixodiphagus* spp. and Geographic Distribution

Subjects: Parasitology

Contributor: Rafael Antonio Nascimento Ramos , Lucia Oliveira de Macedo , Marcos Antônio Bezerra-Santos , Gílcia Aparecida de Carvalho , Guilherme Gomes Verocai , Domenico Otranto

Species within the genus *Ixodiphagus* (Hymenoptera: Encyrtidae) are natural parasitoid wasps of ticks (Acari: Ixodida), which were first described more than a century ago, in *Haemaphysalis leporispalustris* from Texas, United States (USA).

Ixodiphagus hookeri | biological control | ixodid | argasid

1. Introduction

Species within the genus *Ixodiphagus* (Hymenoptera: Encyrtidae) are natural parasitoid wasps of ticks (Acari: Ixodida) [1], which were first described more than a century ago, in *Haemaphysalis leporispalustris* from Texas, United States (USA) [2]. The etymology of the genus name *Ixodiphagus* (from Greek ixod = tick and phage = eater) alludes to its parasitoid behavior. After its first description, other species of “tick eaters” within this genus were formally described worldwide [3][4][5][6].

Currently, at least ten species of these parasitoids are considered valid, namely *Ixodiphagus texanus* Howard, 1907; *Ixodiphagus hookeri* Howard, 1908; *Ixodiphagus mysorensis* Mani, 1941; *Ixodiphagus hirtus* Nikolskava, 1950; *Ixodiphagus theilerae* Fielder, 1953; *Ixodiphagus biroi* Erdos, 1956; *Ixodiphagus sagarensis* Geevarghese, 1977; *Ixodiphagus taiaroaensis* Heath and Cane, 2010; *Ixodiphagus sureshani* Hayat and Islam, 2011; and *Ixodiphagus aethes* Hayat and Veenakumari, 2015. These insects are small, generally measuring less than 1 cm in length, blackish in color, and exhibiting the typical appearance of members of the superfamily Chalcidoidea, and display similar biological and ecological features [7].

Despite being known for over a century, many knowledge gaps remain about the biology of these parasitoid wasps, with most information limited to *I. hookeri* [5][8]. The life cycle of these wasps starts when gravid females lay eggs inside the tick’s body. After an incubation period, the larvae hatch and feed on the internal content of the tick [7]. Approximately 30–57 days after oviposition, new adult male and female wasps emerge from the dead tick, mating and continuing their life cycle [9]. Based on this life cycle, the use of *Ixodiphagus* spp. as an agent for biological control of ticks has inspired the interest of the scientific community [10]. In addition, populations of *I. hookeri* may have different developmental times, parasitism rates, and host preferences according to the geographical area of occurrence [10], which may explain the failure, or the limited efficacy, of these wasps in the control of ticks in field studies [11][12].

2. Biology of *Ixodiphagus* spp. and Geographic Distribution

Information on the biology of *Ixodiphagus* species is insufficient and mainly limited to experimental studies [10]. The entire life cycle ranges from 28 to 70 days, and starts when female wasps lay eggs into ticks through the penetration of their ovipositor into the tick's body (**Figure 1**). After hatching, larvae (**Figure 2**) develop inside the tick. While no information is available about the pupal stage, adult wasps emerge from their tick hosts through a hole at the posterior end, with mating occurring soon after the emergence [9]. There have been no studies assessing the number of *Ixodiphagus* eggs released by females in natural conditions. However, based on experimental studies, it is estimated that during the entire life span, *I. hookeri* and *I. texanus* lay about 120 and 200 eggs, respectively [13][14].

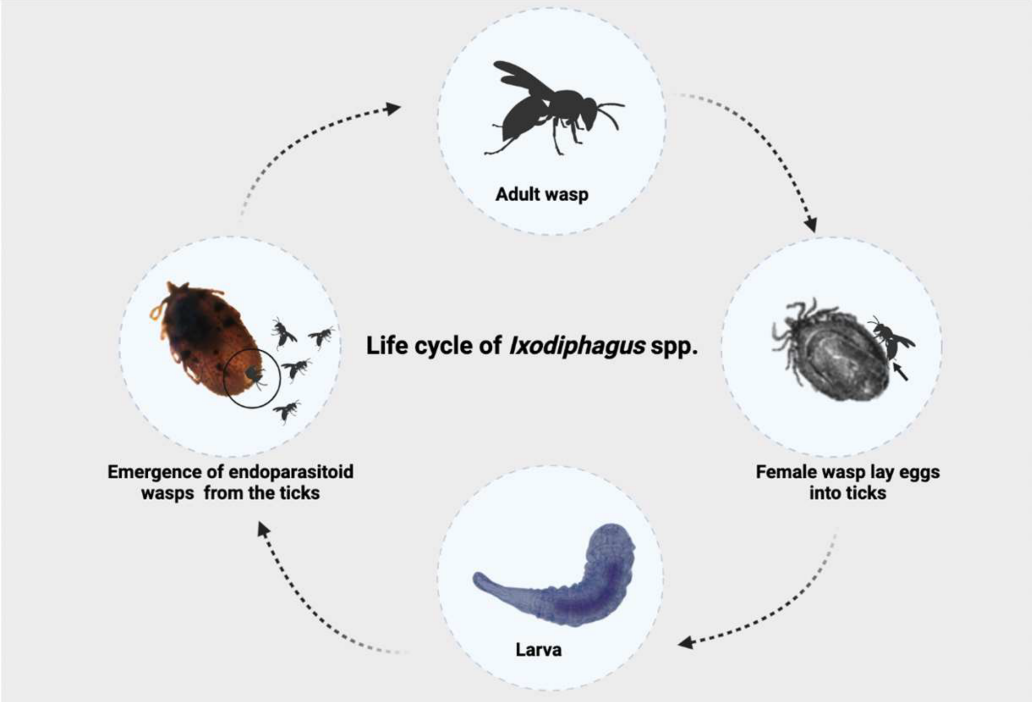

Figure 1. Life cycle of *Ixodiphagus* spp.

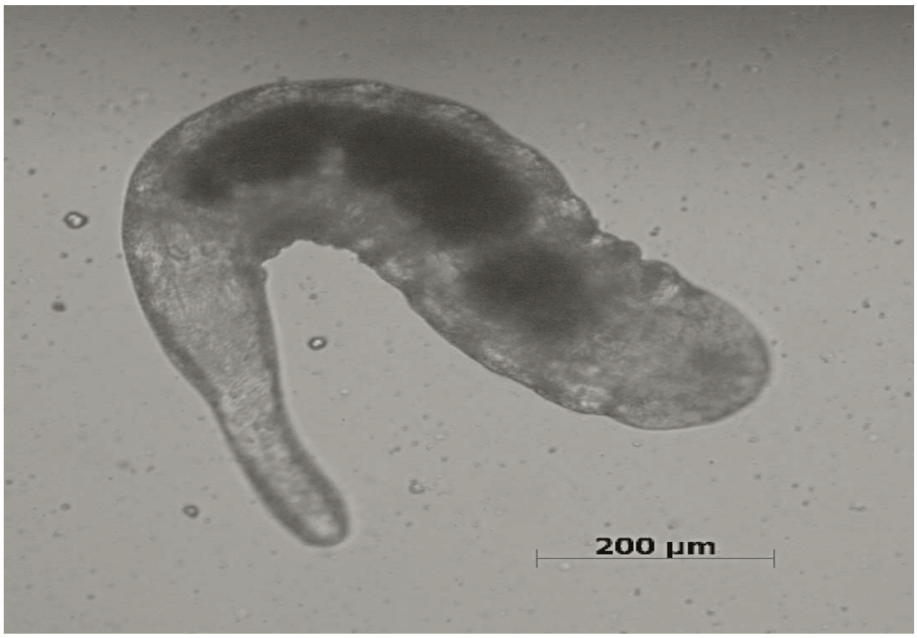

Figure 2. *Ixodiphagus* sp. larva in a *Rhipicephalus sanguineus* s.l. tick (Scale bar = 200 µm).

Information about the preference for certain tick developmental stage remains unclear. For instance, some researchers reported that larvae of *Ixodiphagus* are mostly detected in tick nymphs and adults when the latter are engorged, suggesting that parasitism is likely to occur in blood-fed ticks rather than in unfed ones [15]. However, an experimental study demonstrated that unfed nymphs of *I. ricinus* were more parasitized than other stages [10]. This observation was later confirmed with the finding of *I. hookeri* DNA in unfed *I. ricinus* nymphs collected from the environment [3]. Furthermore, it has been demonstrated that unfed ticks can be collected from vegetation, and after feeding them on laboratory animals (e.g., mice) the parasitoids emerge [16]. In their searching for ticks, *Ixodiphagus* spp. females may be driven by chemical attractants produced by vertebrate animals hosting ticks [10], as well as by tick feces [17]. In fact, some experiments have demonstrated that *I. hookeri* females appear to be attracted by odors produced by the haircoat of roe deer (*Capreolus capreolus*) and wild boar (*Sus scrofa*) [10] but not from those of mice, cattle, and rabbits [10]. This mechanism of attraction is crucial for facilitating the encounter of *Ixodiphagus* spp. with their preferred tick species [8], increasing the chances of completion of their lifecycle. Despite this observation, this is most likely not the general scenario in nature. It is believed that in most cases, hosts are attractive for ticks, in which eggs of the parasitoids are already present. The development of wasp larvae is directly dependent on nutrients contained in the engorged blood meal of the ticks; hence it is unlikely that *Ixodiphagus* larvae could develop in unfed ticks due to the depletion of nutrients [18]. This translates into a correlation between the occurrence of *Ixodiphagus* larvae, tick density, and infestation rate in vertebrate hosts [8][19]. For example, in *I. scapularis* nymphs the infestation of wasp parasitoids occurred only in individuals parasitizing white-tailed deer (*Odocoileus virginianus*) in the northeastern USA, and in areas with deer population density of 13–20 animals per km^2 or higher [19]. In addition, no association was observed between the occurrence of wasps and *I. ricinus* infesting rodents in northern Europe [8], suggesting that the species of vertebrate host is crucial for the behavior of *Ixodiphagus* spp.. Despite the lack of an association between wasps and ticks of rodents, it is known that in laboratory conditions parasitoids develop and emerge from ticks that feed on mice. The dynamic of *Ixodiphagus*

has been poorly assessed in field conditions. Based on the few studies conducted so far, adults fly for a short period of time. In Germany, adult wasps were found during 3–5 weeks, in late summer/early fall [10]. This seasonal activity overlaps with a high density and feeding activity of *I. ricinus* immature stages in the same area, which incidentally occurs when vertebrate hosts are also more abundant. For example, it has been demonstrated that wasps from ticks fed before July have a shorter developmental time compared with those from ticks engorged later on [10]. This finding is similar to those previously observed in field conditions in Texas (USA), where wasps required a development time of 25 and 33 days for ticks fed in May and September, respectively [9].

In southern Italy, the majority of ticks that tested positive for *I. hookeri* (i.e., 92%) were collected during fall–winter (from October to March) [3], when *I. ricinus* peaked [20]. Overall, the detection in ticks is related to developmental time of *Ixodiphagus* and to the synchronization with tick development [10]. Curiously, non-embryonated eggs of *I. hookeri* are able to survive over winter inside unfed nymphs of *I. ricinus* [21] and *I. scapularis* [6][15]. From a biological perspective, this characteristic allows wasp populations to survive through different seasons in spite of unfavorable climate conditions (e.g., extreme cold).

The molecular detection of *Wolbachia* endosymbionts in *I. hookeri* [22] suggests that it could be the reason for the presence of *Wolbachia pipientis* in *I. ricinus* [23], with a role in their parthenogenesis (i.e., development from unfertilized eggs). This is demonstrated in other hymenopteran species (e.g., *Encarsia pergandiella*) [24]. Despite the suggested parthenogenesis for *Ixodiphagus* [14], the potential involvement of *Wolbachia* has never been demonstrated. Recently, the assessment of the microbiota in *I. ricinus* in high-throughput sequencing revealed the presence of a wide plethora of microorganisms, including *I. hookeri* and *Wolbachia* [25]. These multiple interactions among microorganisms in *I. ricinus* may affect a wasp population, influencing differences in its biology observed in different tick populations worldwide [10][26][27]. *Ixodiphagus* spp. have been widely reported in various species of ixodid ticks, with a broad distribution across all five inhabited continents [4][28][29], but more commonly reported from Europe and the US [3][6][19]. In fact, several hard tick species within the genera *Amblyomma*, *Dermacentor*, *Haemaphysalis*, *Hyalomma*, *Ixodes*, and *Rhipicephalus*, in various life stages, have been found parasitized by *Ixodiphagus* wasps (**Table 1**). So far, the only argasid soft tick found parasitized by an *Ixodiphagus* species (*I. mysorensis*) was *Ornithodoros* sp. [30].

Table 1. Distribution of *Ixodiphagus* spp. parasitizing different tick species in the world.

Parasitoid	Tick	Tick Life Stage	Country	Reference
I. texanus	*H. leporispalustris*	Nymph	United States	[2]
I. hookeri	*R. sanguineus*	Nymph	United States	[31]
I. hookeri	*R. sanguineus*, *D. marginatus*	Nymph	United States	[9]
I. hookeri	*I. ricinus*	Nymph	France	[32]
I. hookeri	*H. concinna, D. reticulatus, D. venustus,*	NA	France	[33]

Parasitoid	Tick	Tick Life Stage	Country	Reference
	R. sanguineus			
I. hookeri	*R. sanguineus*	Nymph	Brazil	[34]
I. hookeri	*R. sanguineus*	NA	India	[35]
I. hookeri	*D. nitens*	NA	United States	[36]
I. hookeri	*D. variabilis*	NA	United States	[11]
I. hookeri	*H. aegyptium*	NA	South Africa	[37]
I. hookeri	*R. sanguineus*	Nymph	Nigeria	[38]
I. hookeri	*I. cookei*	Nymph	United States	[39]
I. hookeri	*R. sanguineus*	NA	United States	[40]
I. texanus	*H. leporispalustris*	Nymph	United States	[41]
I. hookeri	*R. sanguineus*	Nymph	United States	[42]
I. mysorensis	*Ornithodorus* sp.	NA	India	[30]
I. texanus	*I. persulcatus*	Nymph	Russia	[43]
I. hookeri	*I. ricinus*	Nymph	Czech Republic/Slovakia (Czechoslovakia)	[44]
I. hookeri	*R. sanguineus*	Nymph	Kenya	[45]
I. hookeri	*R. sanguineus*	Nymph	Africa	[46]
Ixodiphagus sp.	*H. bancrofti, H. bremneri, I. holocyclus, I. tasmani*	NA	Australia	[47]
I. hookeri	*R. sanguineus*	NA	Indonesia	[48]
I. hookeri	*R. sanguineus*	Nymph	Malaysia	[49]
I. texanus	*H. leporispalustris*	Larva, Nymph	Canada	[50]
I. hookeri	*I. dammini*	Nymph	United States	[51]
I. hookeri	*H. punctata*	Nymph	Spain	[52]
I. hookeri	*A. variegatum*	Nymph	Kenya	[53]
I. hookeri	*I. ricinus*	NA	France	[54]

Parasitoid	Tick	Tick Life Stage	Country	Reference
I. texanus	*I. dammini*	Nymph	United States	[55]
I. hookeri	*R. sanguineus*	Nymph	Mexico	[56]
I. hookeri	*I. scapularis*	Nymph	United States	[57]
I. hookeri	*I. scapularis*	Nymph	United States	[15]
I. hookeri	*A. variegatum*	Nymph	Kenya	[58]
I. hookeri	*I. scapularis*	Nymph	United States	[19]
I. hookeri	*R. sanguineus*	Nymph	Venezuela	[59]
I. hookeri	*A. variegatum*	Nymph	Kenya	[27]
I.hookeri	*H. concinna*	Nymph	Slovakia	[16]
I. taiaroaensis	*I. uriae, I. eudyptidis*	Larva, Nymph	New Zealand	[60]
I. hookeri	*I. ricinus*	Nymph	Germany	[10]
I. hookeri	*I. ricinus*	Nymph	Netherlands	[22]
I. hookeri, I. texanus	*R. sanguineus, Amblyomma* sp.	Nymph	Brazil	[61]
I. hookeri	*I. ricinus*	Nymph	France	[22]
I. hookeri, I. texanus	*R. sanguineus*	Nymph	Panama	[62]
I. hookeri	*I. ricinus*	Nymph, Adult	Italy	[3]
I. hookeri	*I. ricinus*	Nymph	Slovakia	[63]
Ixodiphagus sp.	*R. sanguineus*	Nymph, Adult	Brazil	[4]
I. hookeri	*I. ricinus*	Nymph	Finland	[5]
I. hookeri	*R. sanguineus*	Nymph	United States	[64]
I. hookeri	*R. microplus*, *I. persulcatus*, *D. silvarum*, *H. concinna*	Adult	Côte d'Ivoire, Senegal, Russia	[29]
I. hookeri	*I. ricinus*	Larva,	Netherlands	[8]

Parasitoid	Tick	Tick Life Stage	Country	Reference
		Nymph		
I. hookeri	*I. ricinus*, *H. concinna*	Nymph	Slovakia	[1]
I. hookeri	*I. ricinus*	Nymph	France	[25]
I. hookeri	*I. ricinus*	Nymph	United Kingdom	[65]
I. hookeri	*A. nodosum*	Nymph, Adult	Brazil	[66]
I. hookeri	*I. ricinus*	Nymph	Hungary	[6]

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