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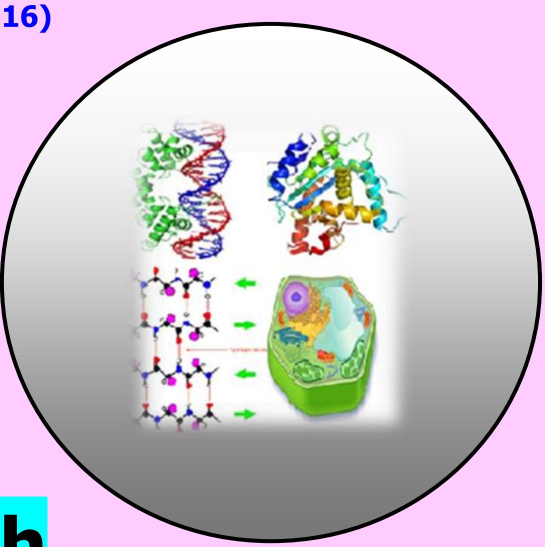

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REVIEW ARTICLE
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Review of Twisted winged Parasitoids (Insecta: Strepsiptera)

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ABSTRACT

Strepsiptera comprise a group of unusual, obligate endoparasitoid. Every aspect of their morphology, life history, genetics, and hostparasitoid relationship is unusual. They have one of the smallest insect genomes, although the size of the entire 18S ribosomal DNA sequence is among the biggest, containing a number of totally unique expansion segments. Till now 639 species have been described globally. Prior to this study only 28 species are known from India. The last species of this weird order described in 2000 from India by Kathirithamby and Ponnamma. Strepsiptera castrate their hosts and death of the host is a direct and/or indirect consequence of parasitization. Some of the hosts are economic pests. For example, Nilaparvata lugens Stål (Hemiptera: Delphacidae) which spread virus diseases and cause 'hopper burn' in rice in South and South East Asia. Strepsiptera being found over a wide geographical range. Studies of different families of Strepsiptera are in progress to untangle cryptic species, their host associations and sexual selection. Infestation of strepsipteran parasitoid causes changes in the morphology and physiology of the host that make their host infertile.

Keywords: Endoparasitoid, Neotenic, Castrate and Expansion Segments.

INTRODUCTION

Strepsiptera (Greek *strepsi*, "twisted",*pteron*, "wing") comprise a group of unusual, obligate endoparasitoid that most entomologists might have heard or read about but very few have actually seen live (Proffitt, 2005). Every aspect of their morphology, life history, genetics, and hostparasitoid relationship is unusual. They maintain one of the most bizarre and complex life cycles of any organism, and they have one of the smallest insect genomes (Johnston et al., 2004), although the size of the entire *18S* ribosomal DNA sequence is among the biggest, containing a number of totally unique expansion segments (Gillespie et al., 2005).

One of the numerous complex features of Strepsiptera is their extreme sexual dimorphism, whereby the adult male and female share no external morphological characters

(Kathirithamby, 1989).Free living and flying males have twisted hind wings, while their fore wings are reduced to club–like appendages. Usually endoparasitoid and wingless females are known to colonize members of seven insect orders. Males of the Strepsiptera have wings, legs, eyes, and antennae, and superficially look like flies, though their mouthparts cannot be used for feeding. Many of their mouthparts are modified into sensory structures. Adult males are very short–lived, usually surviving less than five hours, and do not feed. Females, in all families except the Mengenillidae, are not known to leave their hosts and are neotenic in form, lacking wings, legs and eyes. Virgin females release a pheromone which the males use to locate them. Homoptera and Hymenoptera are the two commonest hosts of Strepsiptera (Kathirithamby, 1988).Some of the hosts are economic pests. For example, *Nilaparvata lugens* Stål and *Sogatella furcifera* Horvath (Homoptera: Delphacidae) which spread virus diseases and cause 'hopper burn' in rice in South and South East Asia. The other host species that are known to attack are Thysanura, Blattodea, Mantodea, Orthoptera, and Diptera (Kathirithamby, 1989).

History

Since the description of the first strepsipteran, *Xenos vesparum*, by Rossi in 1793, their phylogenetic position has been debated (Kristensen, 1981) and is still not resolved (Huelsenbeck, 2001). Most of the described species comprise free–living adult males. A few years later, in 1802, Kirby described another strepsipteran species *Stylops melittae,* a parasite in *Andrena nigroaenea*. In 1836, the Royal Entomological Society of London adopted *Stylops kirbii* as its seal for a letter signed by the President and members to Rev. William Kirby when he had presented a cabinet containing his entire insect collection. The seal thus adopted was appropriate, as Kirby was the founding President of the Society and also proposed the erection of the order Strepsiptera. The word "stylops" first crept into the literature as a common name for the group when Kirby (Kirby, 1813) referred to *Xenos* as "styloid," and Westwood (Pohl and Kinzelbach, 1995) referred to hosts that were parasitized by *Stylops* as "stylopized."The first record of a strepsipteran species from India, *Halictophagus membraciphaga,* was by Subramanian in 1927, from a membracid bug in Mysore.

Geographical Distribution

Approximately 639 species are known to exist in the globe including 28 species in 13 genera under 6 families from India subcontinent. The largest numbers of species are reported from the Australian realm, followed by the Oriental region.

Biology

Adult male Strepsipterans are typically short lived, dark brown or black, measuring 2–7 mm in length. The males are easily recognized by their conspicuous flabellate antennae, small club shaped forewings called pseudohalteres, and large fan shaped hind wings with no cross veins. The copulatory organ or aedaegus is small and pointed. Adult females are larviform (resemble larvae, rather than typical adult insects), measuring 2 – 6.2 mm in length, and lack antennae, mouthparts, eyes, wings, legs and external genitalia. The cephalothorax, comprising of fused head, prothorax and mesothorax, protrudes through the arthroidal membrane of the host, leaving the abdomen of the female within the host.

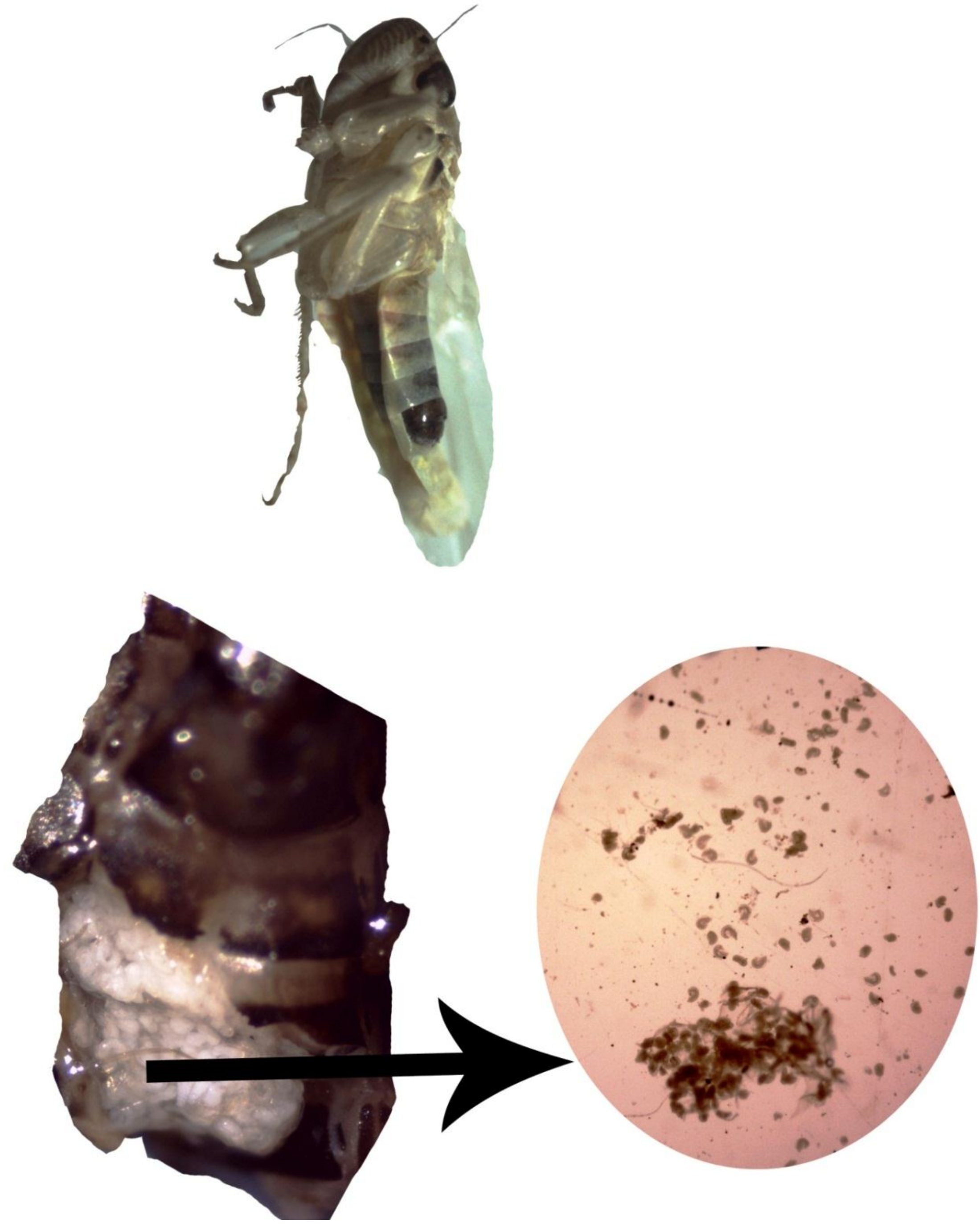

Figure 1. Emergence of first instar larvae (triungulin) from host body (*Cofana spectra*) Endoparasitic larval stages.

The female's anterior region protrudes out of the host body and the male mates by rupturing the female's brood canal opening, which lies between the head and prothorax. Sperm passes through the opening in a process termed hypodermic insemination (Resh and Cardé, 2003). The offspring consume their mother from the inside in a process known as haemocelous viviparity. Each female thus produces many thousands of first instar larvae (triungulin) that emerge from the brood opening on the head, which protrudes outside the host body.

These larvae have legs (which lack a trochanter), and actively search out new hosts (Borror and Johnson, 1989). The larvae are very active, as they only have a limited amount of time to find a host before they exhaust their food reserves. Once inside the host, they undergo hyper metamorphosis and become a less–mobile, legless larval form (second instar larva). They induce the host to produce a bag–like structure inside which they feed and grow. This structure, made from host tissue, protects them from the immune defenses of the host. Larvae go through two more successive instars, and in each moult there is separation of the older cuticle ("apolysis without ecdysis"), leading to multiple layers being formed around the larvae (Kathirithamby et al., 2003). Male larvae produce pupae after the last moult, but females directly become neotenic (Kathirithamby, 2000).

First instar larva

They are the host–seek stage of the strepsipteran and emerge live from the viviparous female mother to seek and parasitize new hosts. They have a sclerotized external cuticle with highly serrated ventral regions of the head, thorax and abdomen which is made up of microtrichia with serrated edges with fringes which is presumably used to clinging to hosts before entry. Serrated edges are also present on the intercoxal sternites (Pohl and Beutel, 2004). The head has a pair of antennae, mandibles and labrum. The legs are slender with single–jointed tarsi without claws which are ventrally modified as adhesive pads. The tarsi of the pro– and mesothorax are similar but that of the metathorax are different. The abdomen has a pair or two of long cerci which are used for jumping.

The 1st instar larva i.e. triungulin are active and in many species, capable of jumping for distances of 2 or 3 cm using the caudal setae (present on 9th abdominal segment). They normally enter the host via the abdominal cuticle. The entry is gained through a combination of enzymatic (e.g. chitinase) and physical activity. A fluid is secreted from the mouth of the triungulin and appears to partially dissolve the host's cuticle and enter into the host body. Within the host body, the larvae soon moult to 2nd stage, a more grub like form.

It was observed that the first instar larva exuded a considerable quantity of fluid from its mouth and became immersed in this exudation. This fluid hardened after 3 or 4 min on the outside, while at the same time it effected the softening of the cuticle of the host. When the cuticle of the host larva breaks, the first instar larva sinks into the host tissue. Soon after this it molts to the second instar.

There are a total of four larval stages (Kathirithamby et al., 1984) although previous estimates have been from one to seven instars (Nassonow, 1910, Kirkpatrick, 1937, Waloff, 1981). On entering into the host the 1st instar moult to an apodous 2nd instar. The sexes are indistinguishable at this stage. A mouth and a gut are evident in the endoparasitic larval stages (Kathirithamby, 2000). Males at the 3rd instar possess three pairs of prolegs and a bulbous head, and the female has a rounded anterior region with a tapering abdomen. In the fourth instar larva the bulbous head is similar to that of third instar and on extrusion through the host cuticle. The head and prothoracic segment of the female which forms the cephalothorax is distinct from that of the male. The female cephalothorax extrudes through the host cuticle and becomes sclerotized. The process of apolysis is unique. The increase in size between the first instar and final instar larva is presumably attained by the stretching and/or extension of the initial convolution. The maintenance of the superseding exuvium is presumably a defensive role against host encapsulation (Tothill, 1922, Rosenberg, 1934).

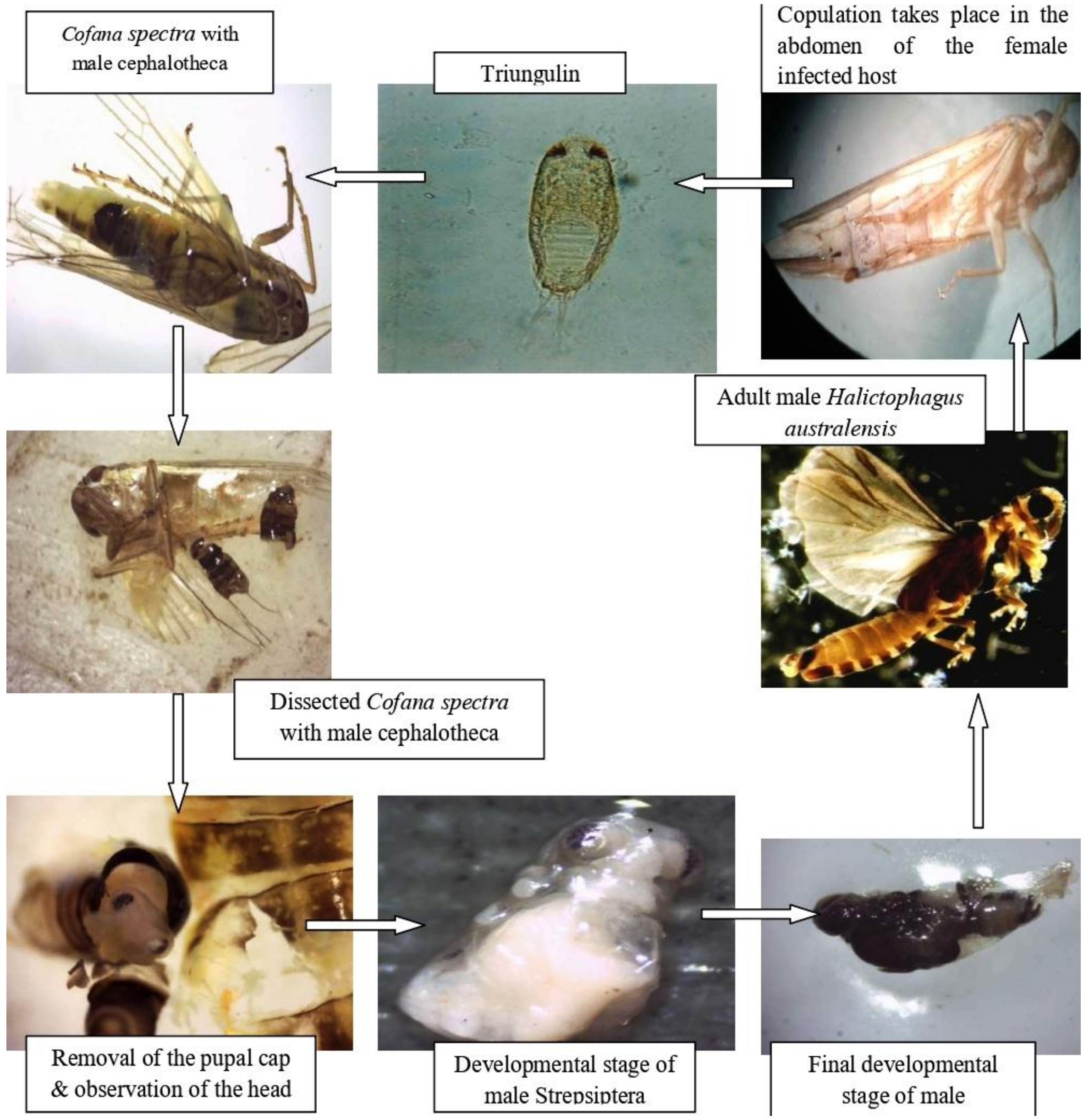

Figure 2. Life cycle of Strepsipteran parasitoid (*Halictophagus australensis*).

Pupal stage

In most Strepsiptera the male extrudes and pupates, and the neotenic female extrudes and becomes mature in adult hosts. Host nymph stylopized by male puparia eventually die, but this is due to fungal growth of the gaping empty male puparia that is left after the emergence of the free–living adult male.

The metamorphosis of the male takes place in two stages within the puparium (the pupal stage and preadult stage). During the preadult stage (the cuticle of the pupa is shed and is therefore not a pharate adult) the cuticle hardens (tans), the sperm matures, the wings expand and the flight muscles are developed (Kathirithamby, 2009). The male emerges as a free–living adult by breaking the cephalotheca along the line of weakness (Kathirithamby, 1983, Kathirithamby et al., 1990).

The only task a free living adult male performs on emergence from the puparium is to excrete its waste products of pupal metabolism. It then takes flight immediately in order to seek and fertilize a female: the adult male has a very short life span (~2– 4 h). Unlike most other insects the metamorphosis to a free living adult male in Strepsiptera therefore occurs within the puparium, during the preadult stage.

Neotenic female

The female Strepsiptera, on extrusion the anterior region, forms the cephalothorax and becomes a neotenic female without undergoing a pupal instar and the posterior region remains within the host. The cephalothorax has a brood canal opening which leads to brood canal. In the brood canal there are varying numbers of genital tubes which lead into the haemocoel where the oocytes are situated.

The male inserts the sperm in the brood canal opening, which travel down the brood canal, and via the genital tubes enter the body cavity. The oocytes are then fertilized after which the numerous embryos develop within the viviparous female. The first instar larvae leave the female via the genital tubes, up the brood canal and out to the open via the brood canal opening (Kathirithamby, 2000).

Adult free–living male

The adult male, 2 to 7 mm in length, lives for about 2–4 hours and has an unusual suite of characters: large, unique, raspberry like eyes, branched antennae, highly modified forewings, and large hind wings. Kirby (1813) describes the eyes, as the “most striking peculiarity” possessing “an appearance of diamonds set in jet or ebony.” The eyes break all rules of compound eye design: The posterior foregut is a balloon like structure (Beutel and Pohl, 2006). The mesothoracic forewings consist of a dorso-ventrally flattened stalk with a distal club (Ulrich, 1930), and resemble the dipteran metathoracic halteres. The metathorax is large and bears the indirect flight muscles and the large hind wings (Smith and Kathirithamby, 1984). The aedeagus is hook–like, except for some species.

Effects of stylopization

Effects of stylopization were studied earlier on Hymenoptera. The most significant changes due to stylopization is that male *Andrena* sp tends to resemble normal females and the pollen collection basket is reduced in females and males display a marked development. The interchange of characters in stylopised bees have been referred to as “intersexes” (Salt, 1927). Like bees stylopised Delphacidae (Hemiptera) were also thought to be “intersexes” and “intermediate” forms (Otakeet al., 1976). Stylopization or parasitism is known to cause many noticeable morphological, behavioral, dispersal and physiological changes in the insect hosts, even leading to the formation of intersexes by modification of the genitalia.

The consequences of stylopization include changes in antennae, wings, pilosity, facial colouration, pollen collecting apparatus, metasomal shapes, and digestive tract length. Stylopization can also impair ovarian egg development, and cause reduction of egg number, gonadal weight, primary, secondary and tertiary sexual characters, vitality and fertility of the host. Stylopized host insects often become less active and may become incapable of establishing nests in the case of some Hymenoptera. Dispersal of the parasitoids occurs mostly through the hosts including the macropterous Hemiptera.

Some species of Strepsiptera are not absolutely host–specific. The genus *Halictophagus* parasitizes hosts from the families Fulgoridae, Cicadellidae, Membracidae and Cercopidae (Homoptera), while the closely related genus *Tridactylophagus* parasitizes only Gryllidae (Orthoptera). Riek (1970) says the host specificity is high in Hymenoptera while it is not so in Homoptera. For example, *Pseudoxenos* parasitizes eight species of wasps belonging to the genera *Odynerus* and *Paralastor*, but it is only common in two or three of them.

Superparasitisation, Hyperparasitisation and Multiparasitisation

Usually one Strepsiptera can parasitise to one host, but every so often more than one with any amalgamation of sexes. If two males or more than any combination of sex are present in the host and the male will emerge first leaving an empty puparium which gets fungal infected and kills the host along with the remaining one.

Strepsiptera have been found to be parasitized by Hymenoptera (Silvestri, 1943) and Nematoda (Dollfus and Theodories, 1950, Kinzelbach, 1971).

On the otherhand sometime two species of Strepsiptera from two different families parasitizes a single host species. One unique specimen from Australia, *Platybrachus* (Eurybrachyidae), is parasitized by both *Halictophagus tryoni* (Perkins) and *Deinelenchus australiensis* (Kathirithamby, 1989).

Macrynobiont Hypothesis

Strepsiptera confront, in all aspects of their biology and life history. The differences between koinobionts, idiobionts, and strepsipteran are quite different. Parasitization by Strepsiptera has no resemblance with the mode of parasitization by any other insect parasitoid group and exhibits several biological. Strepsiptera parasitize and stick with a mobile host until life cycle completion. Strepsiptera can lengthen the life span of their host for as long as it takes them to mature (in the case of the male) or to produce progeny (in the case of the viviparous female). Female strepsipteran have higher than average fecundity (comparable to koinobionts), involving smaller eggs with less yolk, because embryonic development takes place in the hemolymph of an endoparasitic (except in the Mengenillidae) viviparous mother. These numerous dissimilarity of strepsipteran suggest a new term macrynobionts (*macryno,* “lengthen”; *bionts*, “life”), referring to lengthening the life of the host by Strepsiptera.

Immune response

Strepsiptera have to treaty directly with the host immune system, but, astonishingly, exhibit a wide host range. Strepsiptera parasitize hosts at the larval/nymphal stage, but they flourish until the hosts become adults. Even more strange is that some of the Strepsipteran family like Myrmecolacidae, the males and females parasitize different hosts that probably have different immune systems. Insect parasitoids have evolved several active and passive mechanisms to evade the host immune response (Strand and Peach, 1995). A unique mechanism of immune escaping not seen in other taxa before was described by Kathirithamby et al. 2003. The first instar larva of *S. dallatorreanum,* on entry into the host, manipulates and detaches them epidermal layer from the endocuticle. It then wraps itself with host epidermis and suspends itself from the epidermis into the haemocoel and molts to an apodous second instar within the epidermal bag.

The stalk that suspends the second instar pinches off from the contiguous epidermal monolayer and moves deeper into the host body cavity. The basal lamina is in direct contact with the host hemolymph, enabling secretion and withdrawal of materials from the host. This confirmed that the bag is host derived and that *S. dallatorreanum* masquerades as self in the host–derived epidermal bag and remains unnoticed by the host (Kathirithamby et al, 2003).

DISCUSSION

While Strepsiptera are endoparasites, they have a wide host range relative to their own species richness, and need a mobile host for completion of their life cycle. One key feature is that, when parasitized by Strepsiptera, the host's life cycle is lengthened. Some subtle underlying aspects of the host/parasitoid biology designed to advance host development and minimize damage include the way in which Strepsiptera are avirulent during the early stages of host development and have a unique immune avoidance system. Strepsiptera are reported to exert some sort of control over the population level of insect pests, many of which are of economic importance. The rate of parasitism fluctuates from 2 % to 65%depending on several factors including seasons and locations. Strepsiptera have the potential to be effective biocontrol agents but their effectiveness remains low due to their its poor searching ability. Numerous questions about genetics, sex determining mechanisms, host location, physiology and alteration of host physiology in this enigmatic order of insects still remain unanswered. Perhaps, once more is known about the basic biology of these insects, it may be possible to use them more effectively as biocontrol agents. Such a venture is already in place in Papua New Guinea where the female strepsipteran *Stichotrema dallatorreanum* Hofeneder is being used as a biocontrol agent for the long-horned grasshopper that severely defoliates oil palm (Kathirithamby et al, 1998).

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