Twisted Winged Endoparasitoids

An Enigma for Entomologists

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Strepsiptera are parasitoids exhibiting a unique degree of sexual dimorphism. The males are free-living, whereas the females are typically maggot-like and neotenic, living within the body of the host insects. First instar larvae of both sexes, however, are free-living and motile, seeking fresh hosts to parasitize. Strepsipterans are known to affect hosts in thirty five families belonging to six orders of Class Insecta. Parasitization by strepsipterans is also known as stylopization, and can grossly affect morphological characters and physiological activities of the hosts, often even causing sterility in the host. So far 585 species of strepsipterans, in 41 genera, have been recorded from around the world, including 21 Indian species.

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Strepsiptera are an order of enigmatic insects that are small, little studied endoparasitoids (parasitic insects living completely within, rather than on, their hosts) possessing a unique combination of specialized or reduced characters which sometimes elude even the most experienced pair of eyes. Parasitization by strepsipterans (stylopization) induces changes in the morphology and physiology of the hosts, resulting in deformations of structures and even the reversal of sex. These changes can sometimes be so dramatic that parasitized and unparasitized individuals of the same species have been classified as belonging to different species. The phylogenetic placement of these insects has been proven to be remarkably difficult to resolve. However, the discovery of a fossil strepsipteran, *Mengea tertiara*, in the Baltic amber, critical evaluation of the morphology, and application of molecular systematics have resolved a long standing debate that existed for almost 200 years! Today, Strepsiptera are thought to be close to the order Diptera (flies), though earlier they were though to be closely related to Coleoptera (beetles).

Keywords
Strepsiptera, entomophagous, triungulin, stylopization, parasitoid.

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History

In 1793, Peter Rossi first described a strepsipteran specimen, *Xenos vesparum*, parasitic in the wasp *Polistes gallica*. A few years later, in 1802, Kirby described another strepsipteran species *Stylops melittae,* a parasite in *Andrena nigroaenea*, but he could not associate it with *X. vesparum* until 1813 when he proposed the new order Strepsiptera after its twisted wings in order to incorporate the above two genera. The first record of a strepsipteran species from India, *Halictophagus membraciphaga*, was by Subramanian in 1927, from a membracid bug in Mysore.

Geographical Distribution

Scientists have now recorded 585 species of Strepsiptera worldwide, belonging to 41 genera distributed into nine families. The largest number of species are reported from the Australian realm, followed by the Orient (*Table* 1), including 21 species in 8 genera from the Indian subcontinent.

Table 1. World-wide distribution of Strepsiptera.

Realms	Number of Species
Australian	169
Oriental	112
Afrotropical	94
Nearctic	64
Neotropical	73
Palaearctic	73

Hosts

Strepsiptera parasitize a wide spectrum of hosts belonging to six orders of insects, with the most common host species being from the orders Hymenoptera (bees, wasps and ants) and Hemiptera (bugs) (*Table* 2). All the strepsipteran species are not host specific and the specificity sometimes extends to a genus or even a family.

Life Cycle

Adult male strepsipterans are typically short lived, dark brown or black, measuring 1.5-6 mm in length (*Figure* 1). The males are easily recognized by their conspicuous flabellate antennae, small club shaped fore wings 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,

Orders	**Hosts**
	Families
Hymenoptera	Andrenidae, Colletidae, Dictyopharidae, Formicidae, Halictidae Mutillidae, Sphecidae and Vespidae.
Hemiptera	Cercopidae, Cicadellidae, Coreidae, Cydnidae, Delphacidae, Dictyopharidae, Eurybrachyidae, Ricaniidae, Flatidae, Fulgoridae, Issidae, Lygaeidae Membracidae, Pentatomidae Psyllidae, Ricaniidae Scutelleridae and Tettigometridae.
Orthoptera	Gryllidae, Gryllotalpidae, Tettigoniidae and Tridactylidae
Diptera	Platysomatidae and Tephritidae
Dictyoptera	Blattidae and Mantidae
Thysanura	Lepismatidae

Table 2. Hosts of Strepsiptera.

legs and external genitalia (*Figure* 2). The cephalothorax, comprising of fused head, pro-thorax and mesothorax, protrudes through the arthroidal membrane of the host, leaving the abdomen of the female within the host.

The life cycle of these insects is fascinating due to hypermetamorphosis, a term used to describe metamorphoses wherein one of the larval instars is very different morphologically from

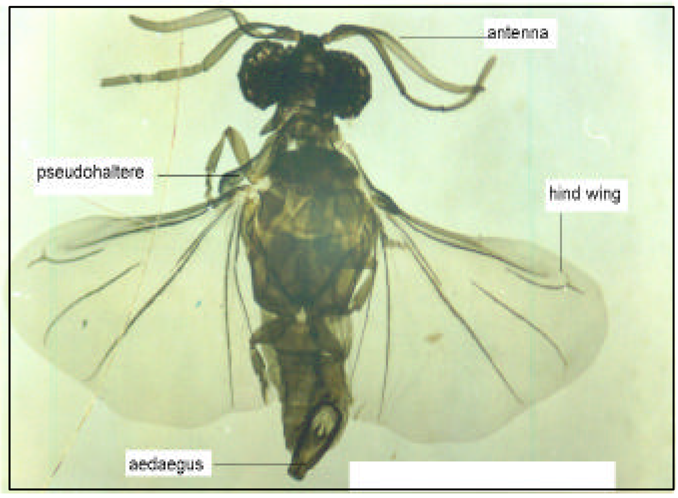

Figure 1. Adult male of H. australensis Perkins.

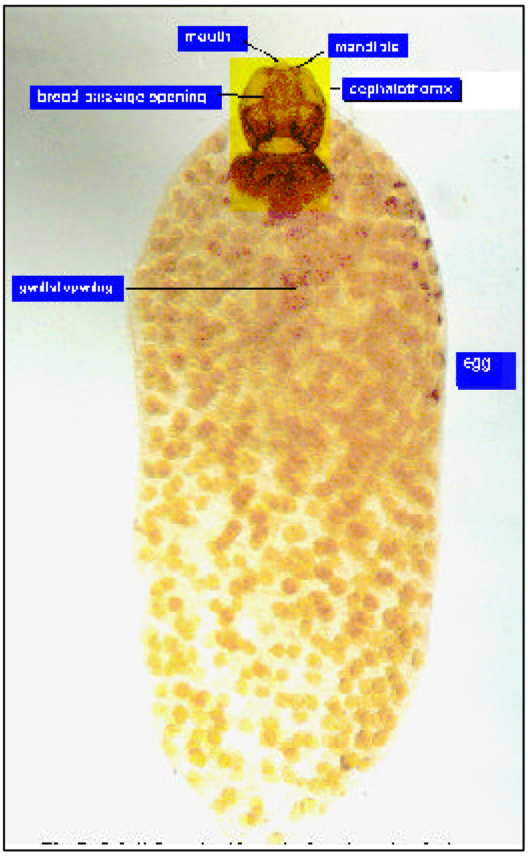

Figure 2. Adult female of H. australensis Perkins.

others. Here, we illustrate this phenomenon with the life cycle of an Indian strepsipteran *Halictophagus austra-lensis* (*Figure* 3). The virgin female tucks inside the host and releases pheromones in order to attract the very short lived free-living males. The male inseminates the female through a brood passage in the female's cephalothorax which protrudes outside the host. The tiny first instar larva (0.08 - 0.30 mm), also called a triungulin, develops viviparously and emerges through the genital opening of the female. The head bears antennae, mandible and the labium, and the larva has three pairs of thoracic legs, with a pair of caudal setae on the ninth abdominal segment, which are thought to assist in jumping (*Figure* 4). Thoracic and abdominal sternites are highly serrated which enables the triungulin larvae to cling to the host or to the vegetation before reaching a suitable host. Triungulins are the free living and host seeking (dispersing) stage of the parasite. As soon as the larva comes in contact with a host, it penetrates into the body by softening the cuticle, probably with the help of an enzyme, and encapsulates itself with the host tissue for evading the hosts' immune system. The next moult leads to a legless larval instar, more like a typical maggot, followed by four sexually different instars. The larvae within the host feed by filtering the host's hemolymph. On reaching the last larval instar, the anterior part of male extrudes dorsally, and the female ventrally, (*Figure* 5), except in the family Mengenillidae in which females are not larviform, and both sexes leave the host at the last larval instar before pupation. The male larval cuticle tans to form the puparium in which the male ecloses to an imago (*Figure* 6) and emerges by breaking the cap of puparium (cephalotheca). The female dwells in the haemocoel and extrudes its cephalothorax from the host. Parthenogenesis has also been reported in a few cases.

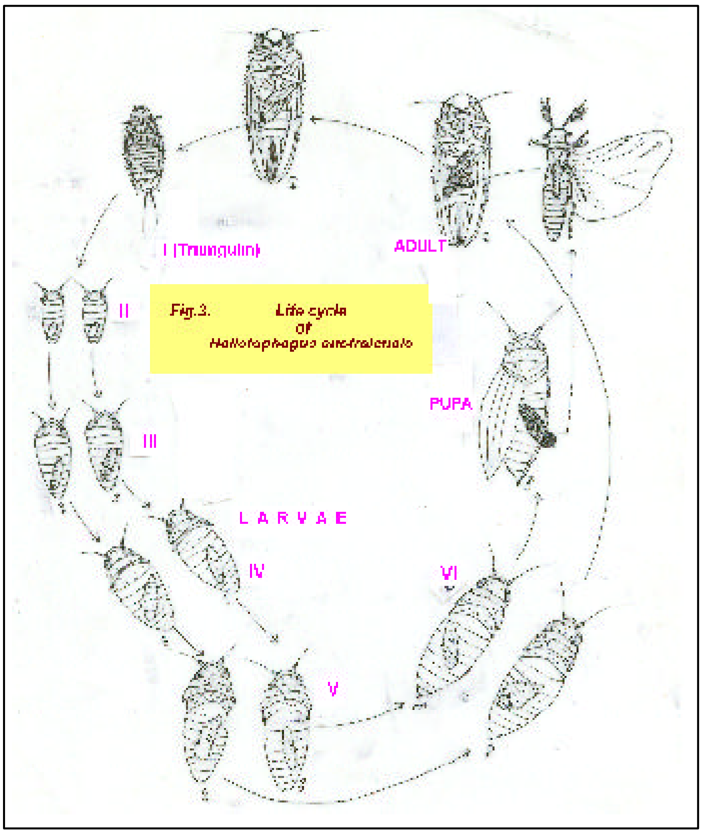

Figure 3. Life cycle of Halictophagus australensis.

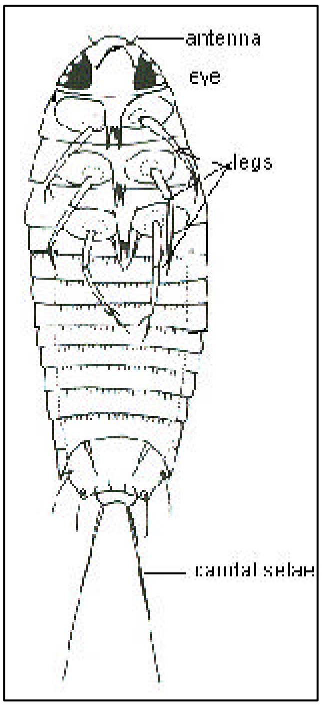

Figure 4. Triungulin (first instar larva).

Effects of Parasitism on Host

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

Figure 5. Showing position of parasitoids on the host abdomen. Male cephalotheca on the dorsal and female on the ventral side.

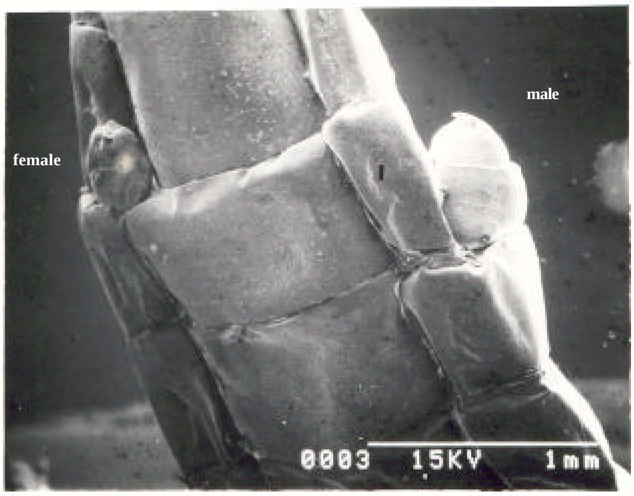

Figure 6. Male pupa of H. australensis Perkins.

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. Several species of Strepsiptera are not absolutely host-specific and parasitise several genera and species of hosts. In some cases male and female hosts may differ. For example, in some members of family Myrmecolacidae, the female invades orthopteran insects while the male parasitizes hymenopterans.

Use as Biocontrol Agents

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 10% to 65% depending on several factors including seasons and locations. Strepsiptera have the potential to be effective bio-control 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 enignatic 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 bio-control agents.

Suggested Reading

[1] J Kathirithamby, *Systematic Entomology*, Vol. 14, pp.41-92, 1989.

[2] R Kinzelbach, *American Entomologist*, pp.292-303, 1990.

[3] A Rokas, J Kathirithamby and P W H Holland, *Insect Molecular Biology*, Vol.8, No. 4, pp 527-530, 1999.

[4] P K Chaudhuri and A Mazumdar, *Mitteilungen aus dem Museum fur Naturkunde in Berlin - Deutsche Entomologische Zeitschrift*, Wiley-VCH, Vol.47, No. 2, pp.203-215, 2000.

[5] A Mazumdar and P K Chaudhuri, *Proceedings of the Zoological Society*, Calcutta, (accepted for publication in 2004).

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