

THE TWISTED - WINGED PARASITOID OF AUCHENORRHYNCHA

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ABSTRACT

Homoptera - Auchenorrhyncha and Hymenoptera are the two commonest hosts of Strepsiptera. The two families of Strepsiptera (the Halictophagidae and Elenchidae) that parasitize Auchenorrhyncha are discussed. The host - parasitoid relationship of Auchenorrhyncha and Strepsiptera is outlined.

KEY WORDS

Strepsiptera, stylopisation, Halictophagidae, Elenchidae, host-parasitoid relationship.

INTRODUCTION

Strepsiptera are entomophagous parasitoids of cosmopolitan distribution. They exhibit sexual dimorphism in the form of an adult male which is free-living and a neotenic female which is permanently endoparasitic in the host (except in the family Mengenillidae when the female is also free-living). Strepsiptera parasitize seven orders of Insecta; the largest sub-order parasitized is Homoptera (Auchenorrhyncha) (table 1).

LIFE HISTORY

The first instar larva is one of the two free-living stages of Strepsiptera (except in the family Mengenillidae). This is the active host seeking stage of the parasitoid, to be contrasted with the subsequent larval stages which are endoparasitic. Sexual dimorphism is said to be present only in the family Myrmecolacidae, where the male parasitizes a different host order to the female, but this needs to be proved experimentally.

The first instar larva parasitizes second to fourth instar nymphs of Auchenorrhyncha. On entering the nymphal host it moults to an apodous second larva and remains endoparasitic until the fourth larval stage.

Table 1 - The known hosts of Strepsiptera

Family of Strepsiptera	Host		Family
	Order	Suborder/Superfamily	
Mengenidae	Fossil		Lepismatidae
Mengenillidae	Thysanura	Zygentoma	Lygaeidae
Corioxenidae	Hemiptera	Heteroptera	Scutelleridae
			Cydnidae
			Pentatomidae
Halictophagidae	Orthoptera	Caelifera	Tridactylidae
			Gryllidae
	Blattodea	Blattodae	Blattidae
	Hemiptera	Homoptera	Tettigometridae
			Delphacidae
			Fulgoridae
			Eurybrachyidae
			Issidae
			Flatidae
			Dictyopharidae
			Cercopidae
			Cicadellidae
			Membracidae
		-Heteroptera	Coreidae
			Pentatomidae
			Tephritidae
Calliphorixenidae	Diptera	Brachycera	
Bohartillidae	Unknown		Mutillidae (?)
Elenchidae	Hymenoptera		Delphacidae
	Hemiptera	Homoptera	Fulgoridae
			Eurybrachyidae
			Issidae
			Ricanidae
			Flatidae
			Dictyopharidae
Myrmecolacidae	Diptera	Cyclorrhapha	Platystomatidae
	Hymenoptera	Apocrita	Formicidae(M)
	Orthoptera	Ensifera	Tettigoniidae
			Gryllidae(F)
			Gryllotalpidae
Stylopidae	Mantodea		Mantidae(F)
	Hymenoptera	Apocrita	Vespidae
			Sphecidae
			Masaridae
			Andrenidae
			Halictidae
			Colletidae
			Eumenidae

M = Male  
F =Female

In all the families (except the Mengenillidae) at the end of the fourth larval instar the male extrudes its head and prothorax and pupates while the female extrudes the head, pro- and mesothorax, and becomes a neotenic female. In the Mengenillidae, at the end of the last instar, the male and female larvae emerge from the host to pupate externally.

At the end of pupation the male emerges from the puparium as a free-living adult while the female remains endoparasitic in the host. The females of Mengenillidae are free-living, like the males.

#### TAXONOMY

Kinzelbach (1978) divided the order into two suborders (Mengenillidia and Stylopidia) and nine families. The known hosts of the families of Strepsiptera are given in table 1.

In 1872 Saunders divided the Strepsiptera into two groups - the Hymenopterobiae parasitic in Hymenoptera and the Homopterobiae parasitic in Homoptera. Homopterobiae contained Colacina Westwood (1877) parasitic in a leafhopper from Borneo. Dale in Curtis (1832) and Curtis (1831) described Halictophagus and Elenchus respectively. Both genera were thought to be parasites of Hymenoptera until Perkins (1905, 1918) and Saunders (1892) confirmed that they were parasites of Homoptera. Perkins (1905) erected the two families Halictophagidae and Elenchidae to incorporate the Australian species he described. The Australian species he examined were so close to Halictophagus figured by Westwood that he described one species under this genus and erected another subgenus for the others. Perkins was not sure if Halictophagus was actually bred from the bee Halictus or if this was purely speculative. In (1918) he writes that Hymenopterists have said Halictophagus to be parasites of Halictus. He points out that this name was an unfortunate creation of Curtis who probably at Dale's suggestion and on the feeblest kind of evidence imaginable conjectured that Halictus was the host. Halictophagidae and Elenchidae are the only two families of Strepsiptera that parasitize Auchenorrhyncha.

#### Halictophagidae:

There are five subfamilies in this family (Kathirithamby, in press):- Dipterophaginae, Tridactylophaginae, Coriophaginae, Blat-tophaginae and Halictophaginae.

Halictophaginae - This is a cosmopolitan family and parasitizes Homoptera- Auchenorrhyncha. There are two genera Halictophagus and Stenocranophilus. Table 2 gives the families of Auchenorrhyncha parasitized by Halictophagus and Stenocranophilus and table 3 the genera of Australian Auchenorrhyncha hosts of Halictophagus.

#### Elenchidae

There is one subfamily - Elenchinae, and four genera in this family. Protelencholax is found in the Dominican Amber, Elencholax is recorded from the Philippines, Deinelenchus is recorded from Australia, New Guinea and Africa, and Elenchus is cosmopolitan.

Table 2 - Auchenorrhyncha hosts of Halictophagidae and Elenchidae.

Host	Strepsiptera	
	Halictophagidae	Elenchidae
Issidae	<u>Halictophagus</u>	-
Tettigometridae	"	-
Cercopidae	"	-
Membracidae	"	-
Cicadellidae	"	-
Flatidae	"	<u>Deinelenchus</u>
Fulgoridae	"	"
Eurybrachidae	"	"
Ricaniidae	-	"
Dictyopharidae	-	"
Delphacidae	<u>Stenocranophilus</u>	<u>Elenchus</u>
	<u>Halictophagus</u>	

Table 3 - Genera of Australian Auchenorrhyncha hosts of Halictophagidae and Elenchidae.

Host	<u>Halictophagus</u>	<u>Deinelenchus</u>	<u>Elenchus</u>
<u>Platybrachys</u> (Eurybrachidae)	"	"	-
<u>Dardus</u> "	"	"	-
<u>Colar</u> (Flatidae)	"	"	-
<u>Siphanta</u> "	-	"	-
<u>Sephena</u> "	-	"	-
<u>Euryphantia</u> "	-	"	-
<u>Dascalina</u> "	-	"	-
<u>Hasta</u> (Dictyopharidae)	-	"	-
<u>Eutettix</u> (Cicadellidae)	"	-	-
<u>Macrosteles</u> "	"	-	-
<u>Phrynophyes</u> "	"	-	-
<u>Deltocephalus</u> "	"	-	-
<u>Putoniessa</u> "	"	-	-
<u>Cicadella</u> "	"	-	-
<u>Tartessus</u> "	"	-	-
<u>Acanthacus</u> (Membracidae)	"	-	-
<u>Toya</u> (Delphacidae)	-	-	"
<u>Sogatella</u> "	-	-	"
<u>Liburnia</u> " (Perkins 1905)	-	-	"
<u>Haedeodelphax</u> " "	-	-	"

Perkins (1905) described Deinelenchus under the family Elenchidae. Table 2 gives the families of Auchenorrhyncha that are parasitized by Deinelenchus and Elenchus and table 3 the genera of

Australian Auchenorrhyncha that are parasitized by Deinelenchus and Elenchus

Kinzelbach (1978) synonymised all the Palaearctic species of Elenchus as Elenchus tenuicornis (Kirby). About sixty-six delphacids have been recorded as parasitized by this species. Waloff and Jervis (1987) list forty-two species from the Palaearctic region that are parasitized by this species.

Host - Parasitoid Relationship.

I. Morphological.

Some styloped Auchenorrhyncha show definite morphological changes as outlined in Kathirithamby (1977, 1978, 1979, 1981, 1982, 1985, in press). It is interesting to note that the dramatic changes (eg. the total absence) in the secondary and tertiary sexual characters occur only in the family Delphacidae. In all the other families the sexual characters (except for the primary - internal sexual organs which are lost/extremely reduced due to the physical presence of the parasitoid) remain near - normal (eg. they range from remaining normal to slight reduction in length of the ovipositors/aedeagus) when styloped. Like crucean parasitic castrators Strepsiptera cause reproductive "death" in their host. But this is however simultaneously accompanied by prolonged life (Kathirithamby, 1978), as in some parasitic castrators (Kuris, 1974).

II. Behavioural.

The only obvious behavioural change that occurs in styloped Homoptera is the possible loss of the power of flight in adults parasitized by the extruded neotenic female Strepsiptera. No hosts with neotenic females were found in light traps in Malaysia. Raatikainen (1967) stated that styloped Javesella begin flying a few days after the emergence of the planthopper and that flight ends about two weeks before the emergence of E. tenuicornis.

III. Dispersal.

This is achieved by two ways in the Strepsiptera:- active dispersal by the free-living first instar larva, and passive dispersal (Waloff and Jervis, 1987) by the styloped hosts.

Active dispersal:- nymphs and adults of most Homoptera live in the same habitat. Strepsiptera parasitizing such groups therefore "directly" parasitize their hosts. In Oxford E. tenuicornis parasitizing Javesella dubia (Kirschbaum) the 2nd / 3rd instar nymphs are found in the same habitat as the adult hosts. When the 1st instar larvae of E. tenuicornis emerge from the neotenic female they sit on the vegetation and await a new host.

Some Auchenorrhyncha hosts live in temporary habitats such as Nilaparvata lugens (Stål) in Malaysia. 1st instar larvae of Elenchus sp. were found sitting on N. lugens and this was attributed to phoresy (Kathirithamby 1982, 1985). The macropterous N. lugens find a site with mature or "hopper burn" rice to be unsuitable and consequently migrate to freshly planted fields. Dispersal of the 1st instar Elenchus larvae which emerge from neotenic female adults at a site away from their future host nymphs is therefore conveniently provided by

the migrating N. lugens. In this instance the 1st instar larvae of Elenchus reach their hosts through a "carrier".

Passive dispersal - Raatikainen (1967, 1972) Waloff (1973) and Kathirithamby (1985) found macropterous delphacids with male pupae and endoparasitic larvae in aerial nets, aerial suction traps and light traps. Passive dispersal is therefore achieved by the macropterous Delphacidae hosts of Strepsiptera.

#### IV. Extrusion of the Neotenic Female of Strepsiptera.

In J. dubia parasitized by E. tenuicornis, N. lugens and Sogatella furcifera Horvath parasitized by Elenchus, and Toya drope (Kirk.) and Sogetella kolophon (Kirk.) parasitized by Elenchus varleyi Kathirithamby, the neotenic female always extruded in adult hosts. Hassan (1939), Lindberg (1939, 1949), Williams (1957) and Raatikainen (1967) also recorded the extrusion of neotenic female Strepsiptera exclusively from adult hosts. In all the other Auchenorrhyncha families studied, the neotenic females were also found in adult hosts. Prolonged life is marked in styloped adults. The neotenic adult female Elenchus keeps the host alive until such time that the viviparous 1st instar larvae developing in it emerge to parasitize the 2nd generation J. dubia nymphs.

#### V. Extrusion of the Male Strepsiptera.

In Delphacidae there is a variation in the stage of the host from which the male extrudes. Table 4 gives details of some of the records of the stage of the host from which the male E. tenuicornis extrudes.

It is clear that in delphacids that are mainly brachypterous (as in J. dubia in Oxford) the male strepsipteron pupa always extrudes and the free-living adult male always emerges from Vth instar nymphs. In delphacids that are mainly macropterous the male extrudes and emerges from adult hosts (table 4). The macropterous delphacids are the agents of dispersal of the strepsipteron male.

When the male pupa extrudes from Vth instar nymphal hosts the styloped nymphs do not moult to become adults although they live far longer than unstyloped nymphs. The ecdysial cleavage line develops within a few days of the moulting of the Vth instar unstyloped nymphs but Vth instar nymphs styloped by male Elenchus never develop this line (although they moult normally from the 1st to the Vth instar). Transmission electron micrograph sections of various ages of Vth instar nymphs styloped by male Elenchus showed no indication of any moulting cycle in these nymphs, whereas Vth instar nymphs styloped by female Elenchus showed indications of a moulting cycle, as did unstyloped nymphs. When the adult male strepsipteron emerged from the puparium, the host nymph (which is merely a shell containing the puparium) eventually dies.

In all other Auchenorrhyncha families the male pupa extruded and the adult male emerged from adult hosts.

VI. Superparasitism.

Often there is one strepsipteron parasitoid to one host, but sometimes there are more than one, with any combination of sexes. Halictophagidae is more prone to superparasitism than Elenchidae. Superparasitism in E. varleyi in Australia did not cause any more morphological damage to the host than a single parasitism (Kathirithamby, in press). If there are males and females, the males will emerge first, leaving a gaping hole in the abdomen of the host. The host is eventually killed along with the female strepsipteron, within a matter of hours or a day. The hole left by the emerged male gets infected by fungus within this time.

Table 4 - The stage of the host from which the adult male E. tenuicornis emerges.

Species	Investigator	Remarks
<u>Javesella pellucida</u>	Lindberg 1949 Waloff (unpub)  Raatikainen 1967	100% emerged from adults. (1986-70) - 31 stylipised specimens only 1 nymphal host had male pupa (3%). 1957-58 - all males emerged from adult hosts 1959 - many nymphal hosts had pupa. Rough estimate: 10% of males emerged from nymphal hosts.
<u>Javesella dubia</u>	Kathirithamby (unpub)	1975-87 - only 2 males from adult hosts.
<u>Chlorina unicolor</u> and <u>samaradula</u>	Lindberg 1939	Over 200 specimens: only 1 male emerged from an adult host.
<u>Dicantropis hamata</u>	Lindberg 1949	8% emerged from adult hosts.
<u>Xanthodelphax flaveolus</u>	Lindberg 1949	93% from adult hosts.
<u>Calligozona propinqua</u>	Lindberg 1960	1953 - 6 emerged from adults, 16 from brac. & 13 from adult hosts.

## VII. Multiparasitism

The first record of multiparasitism of two strepsipteron parasitoids was a unique specimen from Australia Platybrachus (Eurybrachyidae) parasitized by both Halictophagus tryoni (Perkins) and Deinelenchus australiensis Perkins (Kathirithamby, in press). A single host species is parasitized by a single strepsipteron species, but in this instance two species from two different families are involved. Although Flatidae, Eurybrachyidae, Dictyopharidae and Delphacidae are parasitized by both Halictophagidae and Elenchidae, the above is the only host recorded so far as parasitized by the two families simultaneously.

There have been records of multiparasitism of parasitoids belonging to different orders of Insecta of which one is a strepsipteron. Heikinheimo (1957) and Raatikainen (1967) found Javesella pellucida (F.) simultaneously parasitized by Dicondylus bicolor (Holiday in Curtis) (Dryinidae) and E.tenuicornis. Abdul - Nour (1971) recorded Gonatopas sepsoides Westwood (Dryinidae) and Halictophagus languedoci Abdul-Nour in leafhoppers.

Clearly mixed-species infections occur in low frequencies in Strepsiptera, as in other parasitoids and parasitic castrators of crustacea.

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