

Host-Parasitoid Associations in Strepsiptera

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Key Words

entomophagous parasitoid, sexual dimorphism, macrynobionts,
heterotrophic heteronomy, cryptic species

Abstract

Strepsiptera are obligate endoparasitoids that exhibit extreme sexual dimorphism and parasitize seven orders and 33 families of Insecta. The adult males and the first instar larvae in the Mengenillidia and Stylopodia are free-living, whereas the adult females in Mengenillidia are free-living but in the suborder Stylopodia they remain endoparasitic in the host. Parasitism occurs at the host larval/nymphal stage and continues in a mobile host until that host's adult stage. The life of the host is lengthened to allow the male strepsipteran to complete maturation and the viviparous female to release the first instar larvae when the next generation of the host's larvae/nymphs has been produced. The ability of strepsipterans to parasitize a wide range of hosts, in spite of being endoparasitoids, is perhaps due to their unique immune avoidance system. Aspects of virulence, heterotrophic heteronomy in the family Myrmecolacidae, cryptic species, genomics, immune response, and behavior of styloped hosts are discussed in this chapter.

Neotenic: adult retaining juvenile physical characteristics well into maturity

Styloped: parasitized by Strepsiptera

Campodeiform larva: active, predatory larva with well-developed sense organs, legs, and cerci

Triungulin larva: first instar free-living larva capable of dispersal

INTRODUCTION

The organization and habits of the tiny Stylops are as much proper subjects of investigation, of wonder and admiration, to the right-thinking mind, as are those of the Leviathan of the deep, or of the Elephant of the forest; while their very diminutiveness and isolation, like all microscopic analyses of organism, or singleness of action, tend greatly to facilitate our investigation of principles, and lead us more easily to understand those on which structure is formed, and function and instinct unfolded.
George Newport (104)

Strepsiptera (Greek *strepsi*, “twisted”; *pteron*, “wing”) comprise a group of unusual, obligate endoparasitoids that most entomologists might have heard or read about but very few have actually seen live (116). Every aspect of their morphology, life history, genetics, and host-parasitoid 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 (48), although the size of the entire 18S ribosomal DNA sequence is among the biggest, containing a number of totally unique expansion segments (23).

One of the numerous complex features of Strepsiptera is their extreme sexual dimorphism, whereby the adult male and female share no external morphological characters and the females are neotenic (52). Since the description of the first strepsipteran, *Xenos vesparum*, by Rossi in 1793 (117), their phylogenetic position has been debated [the “Strepsiptera problem” sensu Kristensen (86)] and is still not resolved (39). Most of the described species comprise free-living adult males (52, 54, 55, 77–79).

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. There have been doubts as to why an obscure

parasite should be on the seal, but it was argued that, although obscure, Strepsiptera are indeed unique among insects and thus an appropriate emblem (49, 92).

The word “stylops” first crept into the literature as a common name for the group when Kirby (84) referred to *Xenos* as “styloid,” and Westwood (133) referred to hosts that were parasitized by *Stylops* as “styloped.”

LIFE CYCLE

In the family Mengenillidae, the male and female emerge to pupate externally and are free-living as adults. In the suborder Stylopida, the male remains endoparasitic at the pupal stage and is free-living as an adult, whereas the female remains endoparasitic, even as an adult (52, 77) (**Figure 1**).

First Instar Larva

The first instar is a campodeiform larva (80–300 μm) (**Figure 2a**) (**Supplemental Video 1**; follow the **Supplemental Material link** from the Annual Reviews home page at <http://www.annualreviews.org>), and larvae of Strepsiptera and select families within Coleoptera, Meloidae (blister beetles), and Rhipiphoridae (wedge-shaped beetles) are often referred to as triungulin larvae (meaning three-clawed). The only similarity among the larvae of these groups is that they are the free-living and host-seeking stage. Tarsi in Strepsiptera are either (a) disc-like pulvilli on the first two pairs of legs and slender tarsi on the last, or (b) a spine-like pretarsus on all three pairs of legs, with an absence of claws (52, 110, 111). The first instars were initially thought to be parasites of Strepsiptera until Westwood (134) observed them emerging from a female strepsipteran of the genus *Xenos* (Stylopidae).

The ninth and tenth abdominal segments bear a pair of long bristles; those on the tenth segment have a swelling at the base, which is a reservoir for a sticky secretion (12), the function of which is unknown. In the free-living female Mengenillidae, the first instars

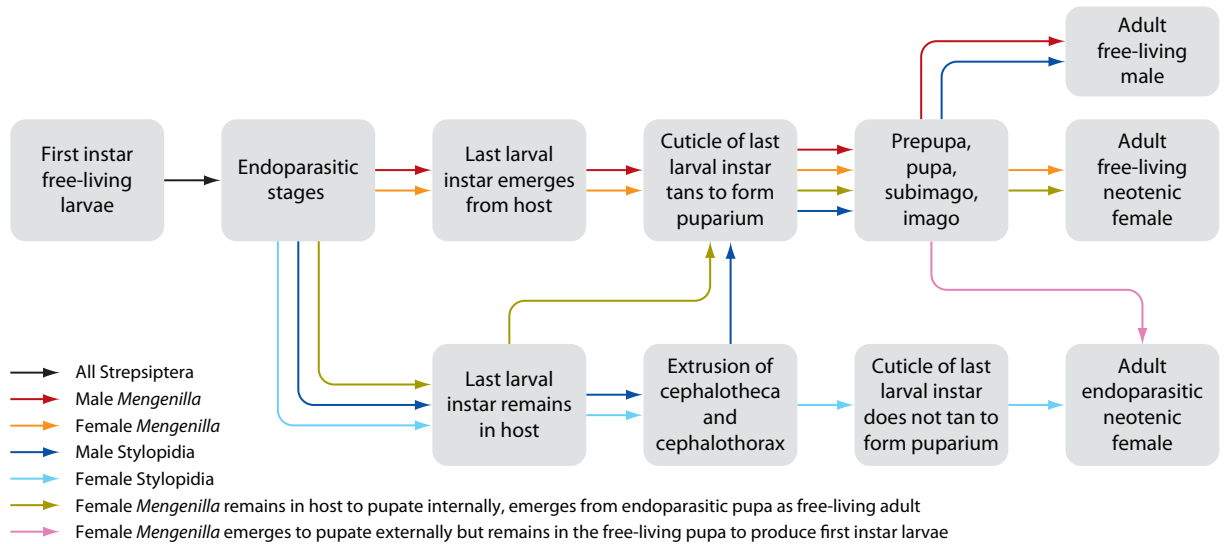


Figure 1

A schematic representation of *Mengenilla*: Male and female emerge to pupate externally; and Stylopidia: the male pupa is endoparasitic, the male adult is free living, and the neotenic female is endoparasitic. Two innovations in some *Mengenilla*: The last larval instar larva of the female remains in the host to pupate and emerges as a free-living adult; or the neotenic female remains in the free-living puparium and produces first instar larvae (52, 122).

emerge via the genital opening; in the endoparasitic female Stylopidia emergence is via the brood canal opening in the cephalothorax (**Supplemental Video 2**).

The first instars live for a short time, because physical conditions, such as relative humidity, have a profound effect on their longevity (33). The first instars of *Corioxenos antestiae* Blair, a parasitoid of a pest of coffee, *Antestia lineaticollis* Stål (Heteroptera), in Tanzania, have been observed to jump onto strips of black and orange paper, which are their preferred colors and are also the colors of nymphal *A. lineaticollis* (85).

Dispersal of the first instars to parasitize exopterygote hosts can be minimal, as the host adults and nymphs often live in the same habitat. To parasitize endopterygote hosts, however, the first instars have to disperse to nests where the host larvae are located. Stylopized solitary *Andrena* bees curve and drag their abdomens across stamens, thus picking up pollen, while releasing first instar larvae of *Stylops pacificus* Bohart onto the flowers, which are later taken to the nest by another foraging *Andrena* (91). Phoresy was also observed in the nonsocial

Pseudoxenos iwatai Esaki (Hymenoptera) (97) and was hypothesized for *Xenos vesparum* Rossi (41). An unusual form of phoresy was observed in the hymenopteran *Andrena complexa* Viereck (Hymenoptera) parasitized by *S. pacificus*: First instars were taken along with the nectar into the honey stomach of the bee and regurgitated onto the pollen ball in the nest (91). First instars have been reported in pollen loads of *Apis mellifera* L. (Hymenoptera) from the Italian Alps, although this species of bee is not stylopized (120). The prevalence of *X. vesparum* reached high levels in some nests of the paper wasp, *Polistes dominulus* (Christ) (Hymenoptera), which indicated that phoresy, assumed in nest-making Hymenoptera, might not be the only mechanism whereby the first instars are transported to the nest. It was observed that, in the spring, *P. dominulus* parasitized by gravid female *X. vesparum* were found close to temporarily undefended nests. A high parasite load in these nests suggests that stylopized wasps move near nests and release the first instar larvae directly onto the nests (41). The first instars in the family Myrmecolacidae, in which the males and

Cephalothorax: extruded and externally visible anterior region of the female strepsipteran

Phoresy: a form of transport whereby small insects use the bodies of larger ones

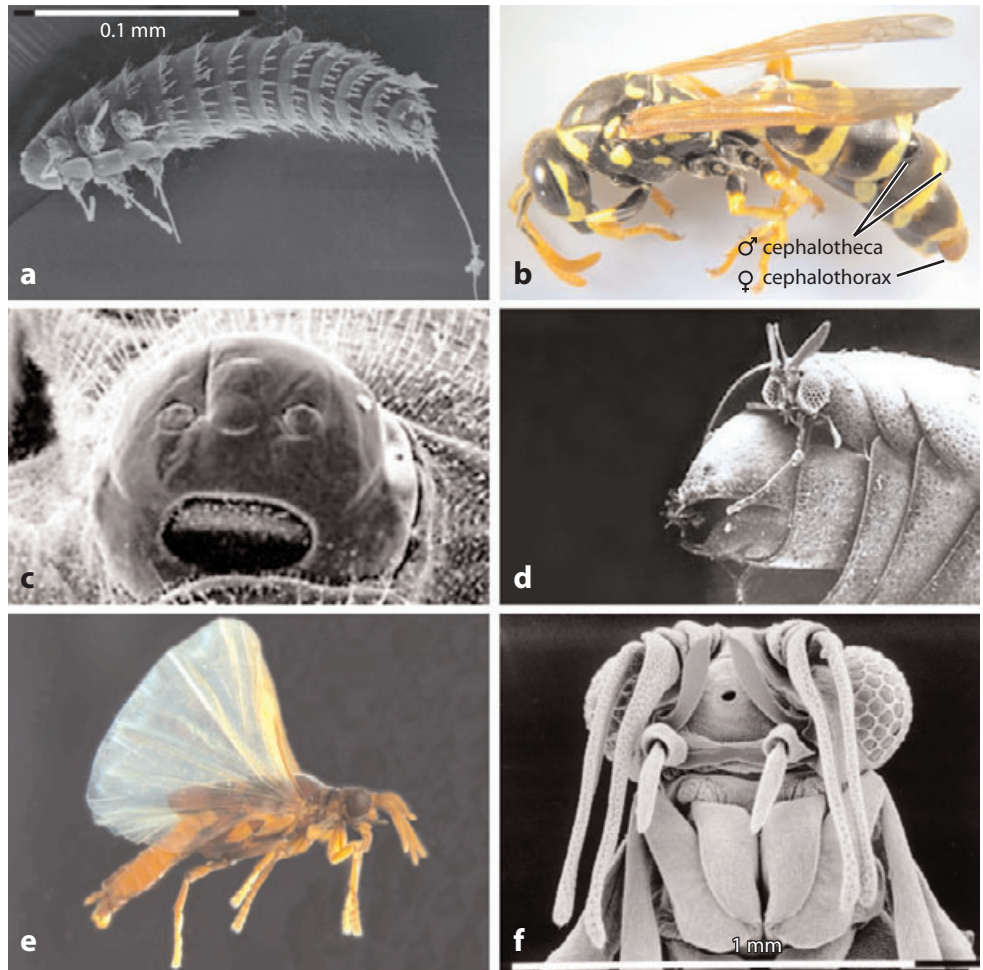


Figure 2

(a) Scanning electron micrograph (SEM) of first instar larva of *Stylops* sp., a parasite of *Andrena* sp. (Hymenoptera) from Japan. (b) *Polistes dominulus* (Christ) with two extruded male pupae and one female cephalothorax (total length of *Polistes* = 15.4 mm). (c) SEM of female cephalothorax of *Dipterophagus daci* Drew & Allwood, a parasite of *Dacus* (Diptera: Tephritidae) from Australia x85. (d) Adult male *Pseudoxenos* sp. emerging from *Odynerus bicolor* Saussure (Hymenoptera) x25. (e) Male *Xenos vesparum* Rossi (length of male = 3.5 mm). (f) SEM of male *X. vesparum* Rossi frontal view.

Hypermetamorphosis:

process by which a larva goes through several successive instars, each with different form and habit

females parasitize different hosts (64, 105), have been said to show morphological sexual dimorphism (38, 75, 93, 136), but this is yet to be empirically demonstrated. Entry into the host is usually via any part of the body in exopterygote nymphs or endopterygote larvae, but in orthopteran hosts, entry has also been observed via the tarsi (58). Most first instar larvae parasitize the larval/nymphal stages of the host, but

parasitization of the eggs of hosts has also been reported (41, 91, 97).

Endoparasitic Larva

On entering the host, the first instar undergoes hypermetamorphosis and molts to an apodous second instar. There are three endoparasitic larval stages that undergo apolysis without

ecdysis (**Supplemental Video 3**). The sexes are distinguishable from the third larval instar onward, when males have prolegs (57, 72) (**Supplemental Video 4**). A gut is present during the endoparasitic larval stages (28, 57), and ultrastructural analysis of *X. vesparum* fed on an isotopically labeled diet confirms the finding that the midgut is the site for synthesis of digestive enzymes and for nutrient uptake (28).

The ovary anlage does not develop ovarioles during the first and second larval stages but does lose the outer envelope. The synchronous development of the germ cells, together with fission, allows the multiplication of the germ cells from 10–12 in the gonad anlage in the first instar to 1500 eggs in neotenic female *Elenchus tenuicornis* (Kirby) (4, 5). The follicles then reach a development stage similar to polytrophic meroistic ovaries (4, 5, 27, 61).

At the end of the fourth instar, both male and female Mengenillidae emerge to pupate externally (although there are some exceptions) (122) (**Figure 1**). In Stylopodia, the head and anterior thoracic regions of both sexes extrude through the host cuticle (**Figure 2b**). The last instar cuticle of the male sclerotizes to form a puparium, and the female becomes a neotenic adult without an obvious pupal instar (57) (**Figure 1, Figure 2b,c**).

Male Pupa

The male and female puparia in Mengenillidae are free-living and mobile (122). In Stylopodia, the male in the endoparasitic puparium undergoes several molts: (*a*) to a prepupa, in which the prefrontal nervous system is built up, the complex eyes (already evident in the larval instars) are further developed, and the wings grow in size; (*b*) to a pupa, in which the wings and genital appendages reach their full size; (*c*) to a subimago, in which the wings are still in their sheath; and finally (*d*) to an imago. The imago, unlike in other insects, sheds the three previous cuticles (prepupal, pupal, and subimaginal) to the base of the puparium (76). When free of the cuticles, and while still within the puparium, the wings are fully inflated, the flight

muscles are developed (123), and maturation of the sperm takes place (9). In Mengenillidae, the adult male emerges via the anterior of the free-living puparium (122). In Stylopodia, a structure analogous to the ptilinum aids the removal of the cap of the male puparium neatly along the ecdysial line of weakness (51, 69) (**Figure 2d**). On emergence, the adult male sheds the meconium and begins flight almost immediately, in search of a female (**Supplemental Video 5**).

Adult Male

The adult male, 1.5 to 6 mm in length, lives for about 3–6 hours and has an unusual suite of characters: large, unique, raspberry-like eyes, branched antennae, highly modified forewings, and large hindwings (**Figure 2e,f**). Kirby (84) 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: There are fewer but larger convex lenses and each eye is a self-contained eyelet with a retina with photoreceptors surrounded by a pigmented cup akin to those of long-extinct trilobites (6). Histochemical studies by Buschbeck et al. (7) suggest that the size and shape of rhabdoms and the slow flicker-fusion frequency of strepsipteran eyes have evolved from nocturnal ancestors, such as the family Mengenillidae. Behavioral analysis by Pix et al. (109) indicates that, for optomotor response to moving patterns, the resolution is limited to an ommatidial sampling array. The posterior foregut is a balloon gut, a wide air-filled, balloon-like structure (2).

The mesothoracic forewings consist of a dorso-ventrally flattened stalk with a distal club (129), and resemble the dipteran metathoracic halteres. Just distal to the forewing articulation, on the dorsal and ventral side, are two sets of campaniform sensilla with a thick nerve bundle that runs from these sensilla to the thoracic ganglion (108, 129). As with halteres in flies, these sensilla sense forces by the moving forewings and send impulses to control head and abdominal movements (108). The metathorax is large and bears the indirect flight muscles

Apolysis: freeing of the epidermal cells from the old exoskeleton

Ecdysis: shedding of the cuticular remnants of the previous instar

Balloon gut: transformation of the digestive tract into an air-filled balloon-like structure

and the large hindwings (123). The aedeagus is hook-like, except for some species and subspecies in the genus *Caenocholax*.

Males of *X. vesparum* were attracted to virgin females when placed near aggregations (44). Glands on the cephalothorax (13, 36, 90, 103) suggest that the male might be attracted to the female by pheromones. On finding a female, the male Mengenillidae transfers its sperm into any part of the body of a free-living female, except the head (122) or, in the case of the endoparasitic female Stylopodia, into the brood canal opening (52, 57).

Neotenic Female

Except for the putatively basal Mengenillidae, in which adult females are wingless and free-living (122), all female strepsipterans (which range in size from 2.5 mm to 3.6 cm) are neotenic and remain permanently endoparasitic in the host (**Figure 1, Figure 2c**). Only

the cephalothorax is visible externally; the rest of the cylindrical body stays within the host and is devoid of all adult insect characters (**Figure 3a,b**). In neotenic females that have overwintered, the gut is degenerate and filled with hemolymph (28). The mechanism of nutrient uptake in the females may vary with the biology of the host they parasitize: There is no fat body in the female *Stichotrema dallatorreanum* Hofeneder from Papua New Guinea (57), whereas it is present in *X. vesparum* from Italy, which overwinters in its host (28).

The neotenic female is a viviparous reproductive machine, producing 1000 to 750,000 free-living first instar larvae by hemocoelous ovovivipary. The brood canal opening and brood canal serve for both the entry of sperm and the emergence of the first instar larvae (52, 57) (**Supplemental Video 2**). There is reduction in vitellogenesis, which results in small eggs, and reduction in chorionogenesis, since embryogenesis is within the mother

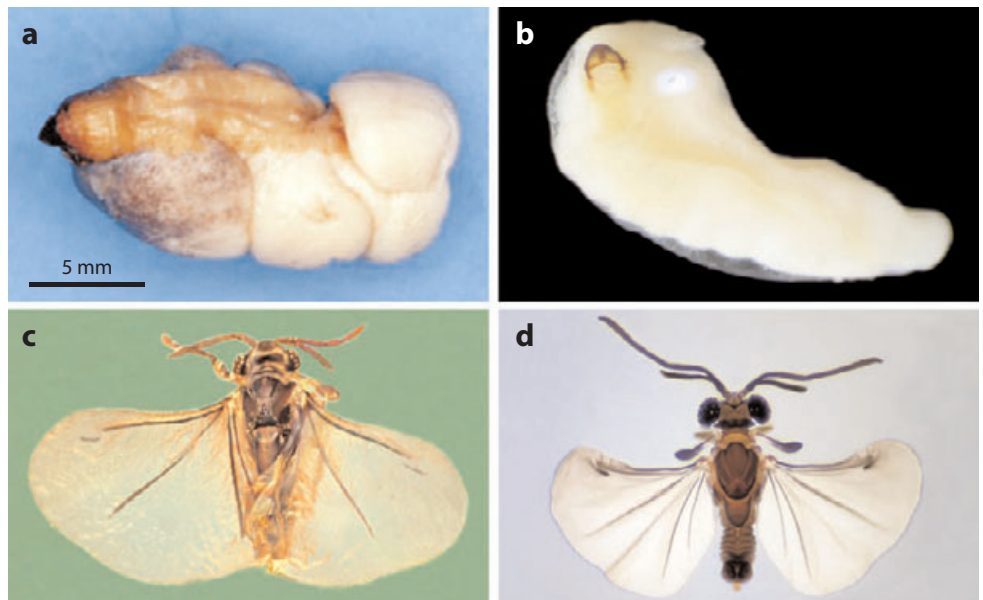


Figure 3

(a) Female *Stichotrema dallatorreanum* Hofeneder, a parasitoid of *Segestidae novaeguineae* (Brancsik) (Orthoptera), from Papua New Guinea. (b) Female *Caenocholax fenyesi* sensu lato parasitic in a cricket from Tapachula, Mexico (total length = 4 mm). (c) *Caenocholax groehni* Kathirithamby & Henderickx from Baltic amber (total length = 1.35 mm). (d) Male *C. fenyesi* sensu lato from Tapachula, Mexico (total length = 0.92 mm).

(4, 5). The development of the first instars is nonsynchronous and emergence takes place over a period of time. When one gently blows at the cephalothorax, a large batch of first instars emerges within a few minutes (**Supplemental Video 6**). A host, especially one parasitized by a female strepsipteran, lives much longer than an unstyloped host. Host death occurs only after all the first instars have emerged from the female, at which point the next generation of host larvae/nymphs is present to enable the emerging first instars to seek new hosts. Extended life on the part of the host is more pronounced in female strepsipterans that overwinter in their hosts (**Supplemental Figure 1**).

HOSTS

Strepsiptera are cosmopolitan in distribution and parasitize seven orders of Insecta (**Supplemental Tables 1, 2, and 3**). As obligate endoparasitoids, they need to interact with the immune system of a live host (like koinobionts). Despite this, they have an extraordinarily wide host range relative to species richness, whereas koinobionts generally have a narrow host range (1, 126, 127). Although Strepsiptera are the least species rich of all parasitoids, they parasitize seven orders of Insecta (**Supplemental Table 3**). Parasitoids of Hymenoptera, whose species richness is over a hundred times that of Strepsiptera, parasitize hosts from 19 orders; parasitoids of Coleoptera comprise six times more species than Strepsiptera, but parasitize 8 orders of insects; and parasitoids of Diptera (which parasitize several phyla other than Insecta) parasitize 22 orders of Insecta.

In an attempt to reconstruct ancestral hosts, extant host preferences were mapped onto the molecular phylogeny of the major lineages of Strepsiptera. **Figure 4** gives the pattern of host associations across the seven extant families (101). These new data suggest that the family Callipharixenidae is a subfamily of Halictophagidae, and *Dipterophagus* is a genus within Halictophagidae. Xenidae (parasitoids of Vespoidea and Sphecoidea) and Stylopidae (parasitoids of Apoidea) are separate families.

PARASITE OR PARASITOID?

A parasitoid develops and feeds on a single host (perhaps for one or two of its life stages) and, as a direct or indirect consequence of development, eventually kills the host (18, 89). When the host survives until the completion of the entire life cycle of the parasitoid, but is castrated (as in Strepsiptera), the definition is less clear-cut. Kuris (89) concluded that parasitic castrators cause another form of death—reproductive death. Castrators were therefore classed by Kuris as parasitoids. Eggleton & Belshaw (16) and Eggleton & Gaston (18) rejected Kuris's definition of parasitoids: Their view was that parasitized hosts are only sterilized but continue to compete for resources with conspecifics and could also still be attacked by parasitoids.

Strepsiptera castrate their hosts, and host death is a direct and/or indirect consequence of parasitization. However, one of the key features of Strepsiptera is that immediate host death is not an inevitable consequence of successful parasitization. In fact, a vital criterion of successful parasitization in Strepsiptera is host survival (including mobility). After parasitization of the larval/nymphal stage, the host metamorphoses through to the adult stage, except in some male Elenchidae (50) and some female Mengenillidae (122). As a consequence of parasitization, host death does eventually occur, but only after the emergence of the free-living male from the endoparasitic puparium (creating a gaping hole that inevitably gets infected by fungi), or after the first instar larvae have emerged from the female (leaving the host abdomen a shell, with an atrophied digestive system). The host may outlive the strepsipteran (the castrator), but this may be by only a few hours or days, and (most importantly) the host does not recover its reproductive capacity. Because host death is delayed until the emergence of the strepsipteran, biologists have not been aware of such consequences as reproductive death and have considered Strepsiptera similar to parasites. Strepsiptera parasitize, develop, and obtain nutrients from a single host, thereby castrating and

Koinobionts:

parasitoids that permit the host to grow and metamorphose beyond the stage at which it is attacked, and the host is then consumed after maturation of the parasitoid

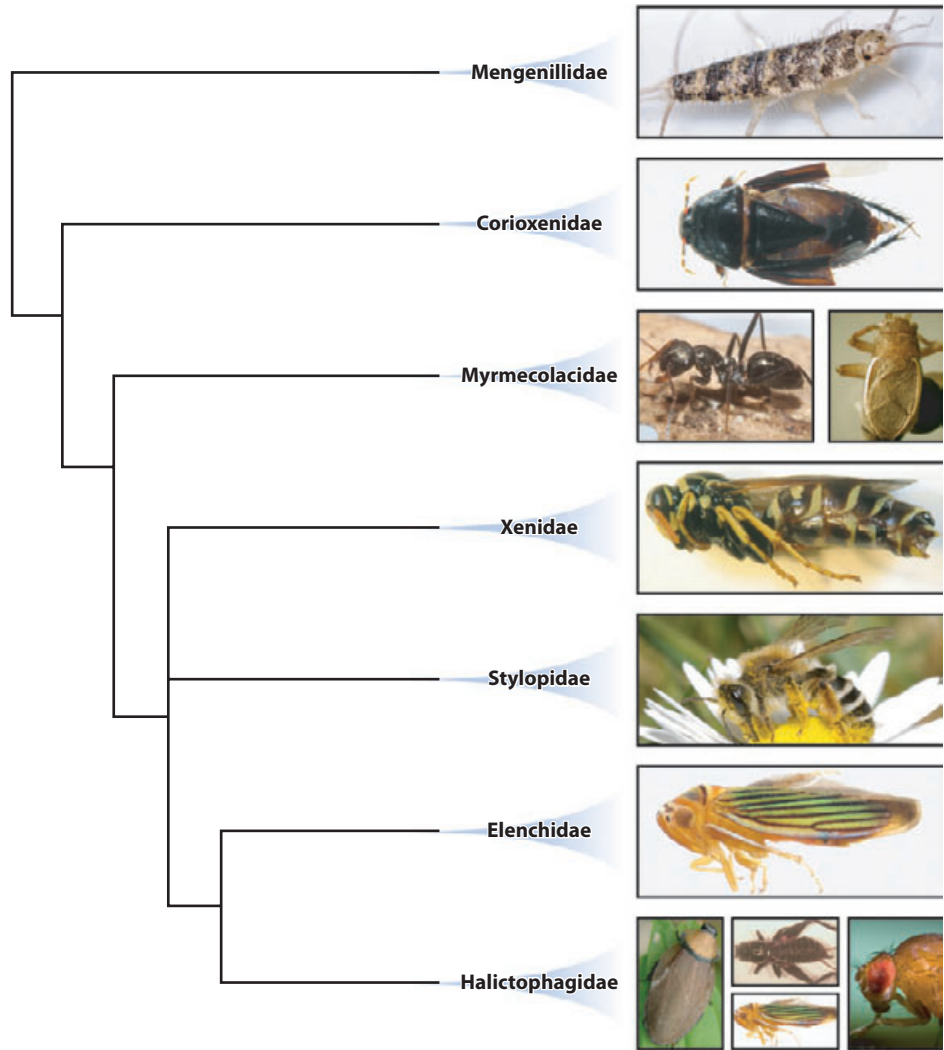


Figure 4

Representation of host preference in Strepsiptera mapped onto a cladogram derived from a molecular phylogenetic analysis of the major lineages (adapted from Reference 101). (Photos by A. Anker, J. Hallmén, A. Gould, J. Kathirithamby, and N. Vereecken.) Not to scale.

eventually killing it: They are therefore to be considered parasitoids.

Trichotomous Hypothesis of Insect Parasitoids

Strepsiptera defy, in all aspects of their biology and life history, the general characteristics of the dichotomous hypothesis concern-

ing parasitoids (1, 21, 24, 29). The differences between koinobionts, idiobionts, and strepsipterans are summarized in **Table 1**. Although Strepsiptera are similar to koinobionts in many respects, they also differ from them in many ways.

Parasitism in Strepsiptera has no similarity to parasitism in any other insect parasitoid group and exhibits several biological

Idiobionts:

parasitoids that paralyze/kill host and do not allow it to grow and metamorphose

Table 1 Comparison of koinobionts, idiobionts (1, 21, 24, 106, 126, 127), and strepsipterans (not in order of importance)

Koinobionts	Idiobionts	Strepsipterans
Endoparasitoids (plus a few ectoparasitoids)	Ectoparasitoids or endoparasitoids of sessile hosts	Obligate endoparasitoids
Development of host for one or two stages after parasitization	Parasitism prevents host development	Host development continues, including metamorphosis after parasitization
Egg, larval, or pupal parasitoids	Egg, larval, pupal, or adult parasitoids	Larval/nymphal (sometimes egg) parasitoids
Parasitism restricted to one or two stages of host	Parasitism restricted to one or two stages of host	Parasitism continues in all host stages for life-history completion
Parasitize exposed hosts, which normally have shorter developmental time	Parasitize concealed hosts (pupae/eggs), which normally have longer developmental time	Parasitize both concealed and exposed hosts, in which there is a longer developmental time in females and a shorter time in males
Narrow host range	Wide host range from varied habitats	Very wide host range from varied habitats
Hosts of similar size range	Hosts of varied sizes	Hosts of a wide range of sizes (3–110 mm)
Host consumed after development of parasite	Hosts paralyzed and consumed soon after parasitization	Live host of larval-pupal-adult/nymphal-adult stages (sometimes egg) required for life cycle completion; host castrated and then dies
Only temporarily paralyzed after parasitization	Permanently paralyzed after parasitization	Not paralyzed after parasitization
Host continues to be mobile after parasitization	Host becomes immobile after parasitization due to paralysis	Host continues to be mobile until emergence of the free-living male and the first instar from the female
Higher fecundities	Lower fecundities	Fecundity always high—production of several hundred to 750,000 first instar larvae

innovations that are adaptations to a unique parasitoid life style. Strepsiptera parasitize and persist in 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) (**Supplemental Figure 1**). Female strepsipterans 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. Idiobionts, by contrast, parasitize older hosts and have lower fecundities (100). As in Ichneumonidae (20), the first instar larvae of strepsipterans enter earlier stages of hosts. Strepsiptera, like koinobionts, delay their development until the host is at the pupal stage (42). In koinobionts, this delay results in larger females, which seek many more hosts in which to lay their eggs. Strepsipteran females are of varied sizes, neotenic, and viviparous,

but they are highly fecund, producing numerous first instars. Host entry in Strepsiptera is performed exclusively by first instar larvae, as in two coleopteran and in three hymenopteran families.

These numerous differences between strepsipterans, koinobionts, and idiobionts suggest a trichotomous hypothesis concerning insect parasitoids, and the term *macrynobionts* (*macryno*, “lengthen”; *bionts*, “life”), referring to lengthening the life of the host by Strepsiptera, is proposed for the inclusion of Strepsiptera within this framework. Previous reviews of insect parasitoids have not taken into account the full breadth of the complex life history of Strepsiptera.

Predicted Origin of a Parasitoid System

Eggleton & Belshaw (16) conclude for the following reasons that Strepsiptera were originally parasitoids but have evolved to become

Macrynobionts: parasitoids that extend the life of their hosts to complete their own life cycle, after which the castrated host dies

parasites: (a) A late developmental stage of Strepsiptera does not leave the host, and (b) the host location is not carried out by an adult female. In the putative basal family Mengenillidae, the males and females emerge to pupate externally (with some exceptions) and the host is thus killed, which would place Mengenillidae among parasitoids. In the derived suborder Stylopodia, reproductive death occurs first (by way of castration and/or evisceration), and host death follows completion of the strepsipteran life cycle: after the emergence of the adult male, or after the release of the first instar larvae by the female. Members of the suborder Stylopodia (like the Mengenillidae) are therefore also parasitoids.

Transition of the free-living adult females in *Mengenilla* to endoparasitism in Stylopodia is already evident in some *Mengenilla* that exhibit two different pathways from the usual life cycle (in which the male and female emerge to pupate externally and are free-living as adults). (a) Some endoparasitic last instar larvae of female *Mengenilla* form a puparium within the host rather than emerging to pupate externally. The pupal development proceeds endoparasitically, and the adult females emerge as free-living neotenic adults. (b) Some female *Mengenilla* emerge to pupate externally but remain within the puparium even when they become neotenic adults. Although they were not seen to be inseminated, they proceeded to produce first instar larvae (122) (**Figure 1**).

Moreover, free-living puparia of *Mengenilla* are heavily parasitized by two hymenopteran species: Chalcidoidea parasitoids *Idiomacromerus gregarious* (Silvestri) and *Hockeria mengenillarum* (Silvestri) (122). Total endoparasitism of the females and the existence of the endoparasitic pupal stage of the male might have arisen due to selection pressure of parasitism on the free-living pupa.

FOSSIL HISTORY

Strepsiptera from Burmese Cretaceous (100 MYO), Canadian (75 MYO), Eocene Baltic (42–45 MYO), and Miocene Dominican am-

bers (25 MYO) and from Eocene brown coal have provided new insights into the early evolution of the order (26, 63, 65, 80–83, 87, 88, 96, 102, 112–114, 128). These findings suggest a greater diversity of primitive strepsipterans from middle Eocene Baltic amber and middle Cretaceous Burmese amber. The Eocene was probably the transitional period between primitive and modern Strepsiptera, as both extinct and recent families are known from the Baltic and Dominican ambers (25, 26).

Fossil records of Strepsiptera have shown punctuated change in extinct species (26, 112), and taxa similar to recent species. The extinct genera *Protoxenos* (the most primitive strepsipteran from the Eocene Baltic amber) and *Cretostylops* (from the Cretaceous Burmese amber) have some striking features not found in any other known strepsipteran. The eye facets are small and not separated by microtrichia, which are extinct in the genus *Mengea* (from the Baltic amber) and all other recent strepsipterans. The mandibles in *Protoxenos* and *Cretostylops* are remarkable in that they are broad and triangle-shaped with a generalized chewing structure unlike that of recent taxa, which have small blade-like mandibles. *Protoxenos* and *Cretostylops* have eight antennal segments, whereas all other known strepsipterans have a maximum of seven. The abdominal tergites are large and sclerotized in these two extinct genera, compared with the reduced tergites in the other strepsipterans (25, 112). *Protoxenos* and *Cretostylops* are thus highly modified and do not show ordinal relationships, but they do exhibit the general morphology of early strepsipterans. Meso-American and Neotropical taxa have been discovered from Dominican amber (63, 83). From Baltic amber, *Caenocholax groebni* Kathirithamby & Henderickx (65) similar to extant *Caenocholax* was described (**Figure 3c,d**). The discovery of this fossil offers a possible explanation of the biogeography of the *Caenocholax fenyesei* species complex, which at present has an East Asian, southern Nearctic, and Neotropical distribution (65): The ancestors were widespread during the globally tropical/subtropical Eocene.

First instar larvae from Eocene Brown coal and from Canadian amber have been described (26, 82). A few fossil strepsipterans are associated with their hosts: A *Camponotus* ant (Formicidae) with two puparia was found in Middle Eocene oil slate of “Messel” (96); a *Prionomyrmex* ant (Prionomyrmecinae) with an extruded parasite (tentatively described as a myrmecolacid female cephalothorax) was found in Baltic amber (114); and a female halicid *Augochloropsis* sp. (Hymenoptera) with an empty male puparium and two stylopized planthoppers (Hemiptera) were found in Dominican amber. One planthopper had first instars that were presumably emerging from a female (misidentified as a male), and the other was an achilid adult parasitized by a male pupa, and an empty male puparium (115).

AVIRULENCE AND VIRULENCE

Strepsiptera are highly virulent parasitoids and castrate their hosts (3, 52, 56, 98, 118, 124, 125), an event that occurs prior to host death and without noticeable external effects. In the long-horned grasshopper *Segestidae novaeuguineae* (Orthoptera: Tettigoniidae), a pest of oil palm in Papua New Guinea, parasitization by *Stichotrema dallarreaenum* causes the eggs to develop a bulbous protrusion (56, 71). In *Bembicinus* sp. (Hymenoptera: Sphecidae), parasitized by *Paraxenos nagatomii* Kifune, egg development is likewise damaged (98).

Whereas Strepsiptera are highly virulent to their adult hosts, they are avirulent to their larval hosts. After the strepsipteran enters the larval host and molts to a second instar, it commences a lag phase, which continues until the later pupal stages of the host, when development of the parasitoid begins (42). The controlled rate of growth of the strepsipteran larva may explain why virulence effects are limited to the adult host. This lag phase is thought to reduce any negative impact on the host during its early developmental phase, reducing host stress and deformities in the early stages (42). Strepsipterans are the only parasitoids that lengthen

host life span to allow for parasitoid life cycle completion, especially in hosts parasitized by female Strepsiptera (**Supplemental Figure 1**). Hughes & Kathirithamby’s (42) study was the first to demonstrate that a parasitoid develops more slowly during the early stages of a social insect host, in which the immature stages are in concealed nests, similar to the slower development observed in hosts that occupy galls and roots compared with parasites of hosts in exposed habitats (32). Such periods of slow growth have been recorded by Salt (119) and Godfray (24), but in most other examples of parasitoids, the purpose of the lag phase is to allow for host growth—the same host that is later consumed by the parasitoid.

Another aspect of the avirulent phase of strepsipterans is that, during the endoparasitic stages, the molting cycle comprises apolysis without ecdysis (72). This unique form of molting limits growth in size, but the hormonal interactions allow for other physiological processes, such as the development of oocytes (4, 5, 61).

The study of the evolution of virulence has focused on host mobility, reduction of which has a negative effect on a parasite dependent on the mobility of the host (19). Strepsiptera depend almost entirely on their hosts for dispersal, and such activity has been documented: Stylopized winged ants and hemipterans have been found in traps (52, 74), and stylopized wasps parasitized by neotenic female Strepsiptera have been found near undefended nests (41). Host mobility is critical for strepsipterans parasitizing endopterygote hosts, as host larvae (such as ants, bees, and wasps) are located in nests. Horizontal transmission of Strepsiptera to hosts does not take place in or on the nest: Hosts parasitized by male and female Strepsiptera abandon the nest and copulation takes place outside the nest; the strepsipteran first instar larvae are then taken to the nest in order to parasitize the host larvae within the cells. Strepsiptera, although virulent to their hosts in many ways, do not compromise the mobility of their hosts.

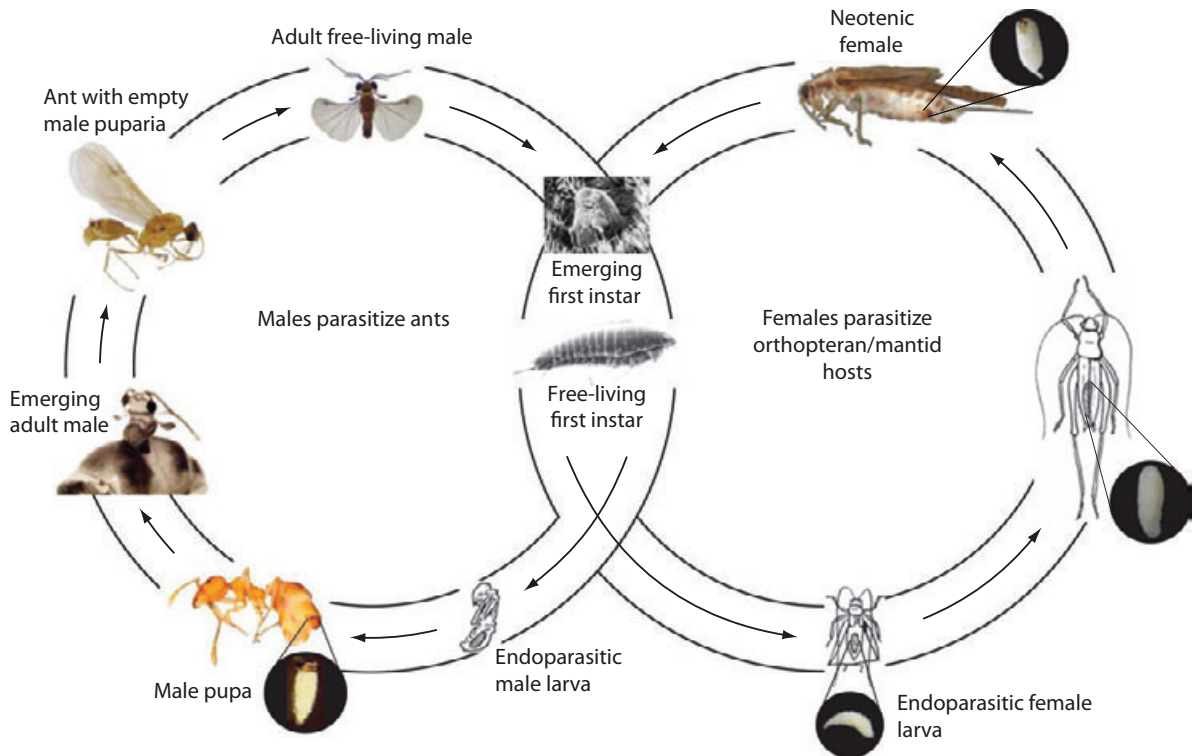


Figure 5

The life cycle of Myrmecolacidae. Males parasitize ants and females parasitize grasshoppers, crickets, and mantids. Modified from Reference 93. Not to scale.

HETEROTROPHIC HETERONOMY

An extraordinary phenomenon occurs in Myrmecolacidae, whereby the males and females parasitize hosts belonging not only to different species but to different orders of insects (53, 64, 105) (**Figure 5**). This complex and extreme form of behavior, heterotrophic heteronomy, *sensu* Walter (132), is a less common and often overlooked type of polymorphism (46). It is found in only two lineages of animals: the hymenopteran subfamily Coccophaginae (Aphelinidae) (46, 132) and the strepsipteran family Myrmecolacidae (53). In Aphelinidae, the mother seeks the host to lay the egg of the appropriate sex, and she is efficient because the hymenopteran haplodiploid system enables her to control the sex of the egg (46). In Myrmecolacidae, host-seeking is performed by the first

instar larvae and may be less efficient; the females are therefore highly fecund and produce several thousand progeny.

In Myrmecolacidae, the males develop as primary parasites in ants (Formicidae: Hymenoptera), and the females develop as primary parasites in grasshoppers, crickets, and mantids (Orthoptera: Tettigoniidae, Gryllidae; Mantidae) (52, 53, 64, 67, 68, 105) (**Figure 5**). Heterotrophic heteronomy in Myrmecolacidae was first discovered by Ogloblin (105), when the first instar exuviae in the mantid *Acanthiotespis maculatus* (Sussure) and in the ant *Camponotus punctulatus* Mayr, and those in a cricket and in an ant (*Pheidole* sp.), were found to be similar. Of the 109 species of extant Myrmecolacidae so far described, only 10 are of females, and because females are obligate endoparasites, the host records for all 10 species are known

Heterotrophic heteronomy: process by which male parasitoids have hosts different from those of female parasitoids

(35, 36, 60, 68, 73, 75, 95, 105). The rest of the Myrmecolacidae are free-living males that have been caught in traps, except for 10 that were collected as endoparasitic pupae in single ant hosts or from nests of ants. Six subfamilies of Formicidae, Dolichoderinae, Ecitoninae, Formicinae, Myrmicinae, Ponerinae, and Pseudomyrmecinae (11, 37, 45, 53, 60, 66–68, 94, 105, 135), have so far been found to be parasitized by male Myrmecolacidae. Kathirithamby & Hamilton (64) call this intriguing phenomenon of the elusive females of Myrmecolacidae—whereby only about 10% of females are known—an evolutionary scandal.

Heterotrophic heteronomy, together with extreme sexual dimorphism, makes it impossible to match males and females phenotypically, and only molecular tools can confirm conspecifics. Male *C. fenyasi* sensu lato from Veracruz, Mexico, discovered in 1909 (107) (the host of which was then unknown), was only matched to its conspecific female parasitic in a cricket, *Macroanaxipha macilenta* (Saussure) (Gryllidae), from the same site 94 years later. This was the first study to match unambiguously a female myrmecolacid to a male parasitic in an ant (*Dolichoderus bispinosus* Olivier, Dolichoderinae): The pair was named *Caenocholax fenyasi waloffi* Kathirithamby & Johnston (68). Recently, male *C. fenyasi* sensu lato from Tapachula, Mexico, which are morphologically similar to, but genetically divergent from, male *C. f. waloffi*, have been matched to females parasitic in a cricket from the same area (Figure 3b,c). Like the free-living males, the female *C. f. waloffi* from Veracruz and female *C. fenyasi* sensu lato from Tapachula are morphologically similar (60).

A female parasitic in a mantid, *Stagmatoptera* sp., from Manaus, Brazil, was matched by molecular characterization with a male parasitic in a primitive ant, *Pachycondyla verena* (Forel), and *P. apicalis* (Latrielle) (Ponerinae) from French Guyana. This is the first record of a female *Myrmecolax* and also the first record of a male strepsipteran parasitic in the primitive ant subfamily Ponerinae (60). There are two other records of stylopized mantids, *A. macula-*

tus (Saussure) from Argentina (105) and *Sphodromantis lineola pinguis* La Greca from Angola (95).

CRYPTIC SPECIES

Male *C. fenyasi* sensu lato are morphologically similar over a large geographic range (southern United States, through Central America to South America) but are genetically divergent (34, 65, 67, 68) (Figure 3c,d). A cryptic species in Strepsiptera was discovered when the male *C. f. waloffi* parasitic in the ant *D. bispinosus* and its conspecific female parasitic in the cricket *M. macilenta* from Veracruz, Mexico, were compared (by molecular characterization) with the morphologically similar male parasitic in the red imported fire ant, *Solenopsis invicta* Buren (Formicidae), from Bee Creek and Lick Creek, Texas. Expansion segment D2 of the 28S ribosomal rRNA and 7 of the 11 variable regions of the 18S rRNA gene region were 13.9% and 14.0% divergent, respectively (62, 68). The high molecular divergence within morphologically similar males from distant populations (Veracruz and Texas) argues that these individuals are from different subspecies: They were named *C. f. waloffi* and *C. f. texensis*, respectively (68). A previous study of *COI* and *18S* rDNA found an average divergence between strepsipteran species to be 16.1% (18.1% corrected) (30). A study of the *COI* of *C. fenyasi* sensu lato from seven different sites in the southern United States and Central and South America indicates seven clades with 7% to 15% divergence between them, suggesting the existence of cryptic species (34).

The variation within the gene regions was characterized using models of arthropod (22) and strepsipteran (23) rRNA secondary structure intended to characterize populations and aid alignment between species. Individuals compared within each site (Veracruz and Texas) were nearly identical, confirming that the variation observed was interpopulation, and not intrapopulation, polymorphism. The intrapopulation variation was zero in *C. fenyasi* (62). The myrmecolacid species studied by Halbert et al.

(30) also showed low (but not zero) intrapopulation variation, and, in the study of *C. fenyasi* sensu lato from seven sites in the United States and Central and South America, the diversity was low but haplotypes were not always identical within clades (34). Founder events, bottlenecks, and isolation of small effective size in myrmecolacid populations were proposed as contributing factors to explain the low intrapopulation variation (62), and although a criticism of the two earlier studies might be that the sample sizes were small, the new study from a wider geographical range and larger sample size of *C. fenyasi* sensu lato confirms this hypothesis (34).

A study of five nests of *X. vesparum* (Stylopidae) in Tuscany, Italy, from fairly close geographical range showed a distribution of 12 different haplotypes with infections reaching 50% to 70%. The low haplotype diversity in some nests was thought to be the result of the direct release of first instars by a stylopized wasp that stayed near a nest, while the intracolony diversity was thought to be due to phoresy (130). Parasitization in the fire ant *S. invicta* by the myrmecolacid *C. f. texensis*, however, reached only 1% to 1.5% in some nests (10). As the studies on myrmecolacids have shown low intrapopulation variation, it can perhaps be maintained that the mechanism of transfer of first instars to nests of wasps is different from the transfer of first instars to nests of ants (which would be by a stylopized orthopteran or mantid). This difference might be due to the unique biology of Myrmecolacidae, i.e., heterotrophic heteronomy, and the sex determination mechanism.

Cryptic species might exist outside the family Myrmecolacidae as well. Morphologically similar males of other families (e.g., Elenchidae, Myrmecolacidae, and Corioxenidae) have been recorded from several hosts and from different locations.

GENOMICS

The complete mtDNA sequences from *X. vesparum* (8), and the partial sequences of an addi-

tional 238 strepsipteran protein-coding genes from *S. dallatorreanum*, are available with associated homologous gene name and gene ontology for 170 of the coding sequences. Partial sequences are also available for 66 transposable elements and for an additional 418 reads (oligos) that to date produced no significant matches with existing sequences in the genome databases NCBI and UniProt. Included in the latter are 16 simple sequence repeats (microsatellite loci) useful for genetic mapping and population genetic studies (47). As has been true of all aspects of strepsipteran biology, these additional sequences are likely to hold surprises associated with the small genome and unique biology of the family Myrmecolacidae.

IMMUNE RESPONSE

Parasites and hosts have been in a continuous arms race with each other (15). Strepsiptera, as endoparasitoids, have to deal directly with the host immune system, but, surprisingly, exhibit a wide host range. Strepsiptera parasitize hosts at the larval/nymphal stage, but they flourish until the hosts (which inexplicably live longer than unstylopized hosts) are adults. Until recently, the mechanism by which Strepsiptera avoid the immune system of the host has been a mystery. Even more mysterious is that (*a*) in the family Myrmecolacidae, the males and females parasitize different hosts that probably have different immune systems; and (*b*) there seems to be no interference from the host when the first instar larvae enter and penetrate the host (41) and when the male and female Stylopidae extrude through the host cuticle.

Insect parasitoids have evolved several active and passive mechanisms to evade the host immune response (127). A unique mechanism of immune avoidance not seen in other taxa before was described by Kathirithamby et al. (70). The first instar larva of *S. dallatorreanum*, on entry into the host, manipulates and detaches the epidermal layer from the endocuticle. It then wraps itself with host epidermis and suspends itself from the epidermis into the hemocoel 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. The autonomous growth capacity of the epidermal cells explains the ability of the bag to grow from an initial length (of 100 to 300 μm) that surrounds the first instar larva to a bag that measures 1.8 mm to 3.9 cm on the surface of the neotenic female. Comparisons of the nuclear 28S rRNA (D2) and mitochondrial 12S gene fragments of the host tissue and bag showed no differences, but the larval and bag sequences were significantly different. 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 (70).

Hughes et al. (41) made the initial observation that the exuvium of the first instar larva of *X. vesparum* is encapsulated, and that this encapsulation by the host is not always successful, because the second instar continues to develop. They also noted that the entry hole made by the first instar does not melanize, implying that there is suppression of the host's normal melanization response to injury. Puncturing the cuticle of the host with an inanimate object did, however, lead to melanization (42).

The first instar of *X. vesparum* enters the host and passes to the epidermal layer (which completely surrounds the larva) and then crosses the integumental layer and reaches the hemocoel. The first instar then molts to the second instar after 48 hours, and the second instar moves away from the exuvium, which becomes encapsulated but not melanized (99). No critical details, however, are given by Manfredini et al. (99) of how, and when, the epidermal layer surrounding the first instar larva is broken or, more importantly, of the events that follow. The delayed encapsulation of the exuvium of the first instar might be relevant to precisely when and where in the host initial molting occurs.

Vertebrates, invertebrates, and, to some extent, plants employ both constitutive and induced responses upon exposure to parasites. A within-host model, based on the insect immune system, to study why both responses are maintained, showed that parasite growth rates use a combination of both of these responses (31). Strepsiptera are avirulent during the early larval and pupal stages of their hosts (42), and this slow growth might be one of the major contributing factors that explain why hosts are susceptible to parasitization by Strepsiptera.

It is unclear whether there is a common mechanism that permits Strepsiptera to overcome the immune responses of such a diverse array of hosts, or whether separate adaptations have evolved to fit different groups/orders of hosts that they parasitize. Until this mechanism is understood, the intriguing question remains as to what adaptations enable male and female Myrmecolacidae to parasitize dimorphic hosts.

BEHAVIOR OF STYLOPIZED WASPS AND ANTS

W.D. Hamilton first noticed (in August 1998) aggregations of *Polistes dominulus* that were too early for hibernation; members of these aggregations were found to be highly parasitized by *X. vesparum* (59). The aggregations that occur in the summer are indeed composed of stylopized female *P. dominulus*. These females deserted the colony just before the extrusion of the male cephalotheca and female cephalothorax. Nest desertion and summer aggregation by stylopized castrated wasps at leks were thought to be an adaptive parasite manipulation of host behavior to facilitate parasite mating (44). The desertion, just before the extrusion of the cephalotheca and cephalothorax, was probably intended to reduce the attacks by nestmates. This is aberrant behavior, the existence of which was predicted by W.D. Hamilton (personal communication) and is the first example of the occurrence of stylopized *P. dominulus* in extranidal aggregations (43, 44).

A number of studies have recorded parasitized individuals that leave the colony, in most

Cephalotheca:
extruded and
externally visible
anterior region of the
male strepsipteran
pupa

cases to facilitate life-history completion (40). However, stylopization in Formicidae seems to impose an effect on their hosts opposite to that seen in the paper wasp. Ants form the largest number of invertebrates in many habitats, yet to date there are only two records of wandering stylopized ants (105, 135). When ants are stylopized, they may “change their nocturnal habits, acquiring positive phototropism, but evidently lose their social instincts, abandoning their nests and rambling singly, often climbing high on grass and bushes” (105). Kathirithamby & Hamilton (64) observed that the reason many more stylopized ants (like stylopized bees, wasps, and Hemiptera) have not been found may be because stylopized ants remain in the nest: Although many myrmecologists did examine nests, the insects went unnoticed, as the extruded cephalotheca is cryptic and hidden between the tergites or sternites, and the cephalotheca is the same color as the ant cuticle, which makes it incredibly difficult to detect, even to the experienced eye (59). Pupation in males lasts a long time, and during this period stylopized ants may remain in the nest, because all parasitized ants obtained from nests so far have been found with extruded cephalotheca. Only when the male strepsipteran is ready to emerge does the ant come out of the nest and climb a tall stem of grass. The change in behavior of stylopized ants is exactly the opposite of that seen in the stylopized paper wasp *P. dominulus*.

Dapporto et al. (14) compared the cuticular hydrocarbon composition of aggregations of prehibernating stylopized and unstylopized *Polistes* wasps and found that there was only a slight difference between them, which might help stylopized wasps to remain unnoticed in autumnal clusters and in nests in the spring

(when stylopized wasps remain near nests). The very slight modification between the stylopized and unstylopized wasps in the cuticular hydrocarbon composition might also be due to some physiological facts (14).

CONCLUSIONS

This review examines some of the bizarre aspects of Strepsiptera in the context of their unique endoparasitic life history. Ecological and morphological innovations of strepsipterans, koinobionts, and idiobionts are discussed, and a trichotomous classification hypothesis of parasitoids is proposed, as Strepsiptera, although in some ways similar to koinobionts, differ from them in many ways. 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; the term macrynobionts is suggested for the insects that produce this process. 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. I discuss the bizarre phenomenon of heterotrophic heteronomy in the family Myrmecolacidae, where the males parasitize ants and females parasitize grasshoppers, crickets, and mantids. Molecular studies have revealed that cryptic speciation might be common in Strepsiptera. Endopterygote hosts stylopized by Strepsiptera exhibit a change in behavior, and the difference in behavior of stylopized wasps is contrasted with that of stylopized ants.

SUMMARY POINTS

1. Strepsiptera are unusual entomophagous parasitoids that exhibit extreme sexual dimorphism and have free-living males and endoparasitic females, except in the family Menganillidae, in which the females are free-living.

2. As endoparasites, Strepsiptera have to cope with the host immune system, notwithstanding their wide range of hosts relative to their own species richness.
3. Hosts are stylopized at the larval/nymphal stage, and they remain alive and mobile until the adult stage. The life of a stylopized host is lengthened so that the strepsipteran male can reach maturity and the viviparous female can release the first instar larvae after the next generation of larvae/nymphs of the host is present. The emerging first instars can thus seek and parasitize the new generation of hosts.
4. Strepsiptera have unique features that distinguish them from koinobionts and idiobionts, and a trichotomous classification of insect parasitoids is proposed, with Strepsiptera classified as macrynobionts, which refers to their lengthening of the host life cycle.
5. Early stages of Strepsiptera show slow growth during the larval and early pupal stages of the hosts; this may reduce host stress during early development, as survival of a mobile host (with lengthened life) is critical for completion of the strepsipteran life cycle.
6. Males and females in the family Myrmecolacidae parasitize hosts not only from different species, but also from different orders of insects (i.e., heterotrophic heteronomy).
7. Only molecular characterization can unambiguously match the sexually dimorphic male and female Myrmecolacidae.
8. Molecular studies are revealing that cryptic species in *Caenocholax fenyesi* sensu lato occur over a large geographic range; a phenomenon that might be common in other strepsipterans.

FUTURE ISSUES

1. Sequencing of a strepsipteran genome will provide opportunities for detailed studies of the complex and extraordinary host/parasitoid relationships, particularly in the family Myrmecolacidae, where males and females parasitize different hosts—a phenomenon seen only in one other insect subfamily and in no other form of life.
2. The morphologically diverse male and female Myrmecolacidae are model organisms for the study and understanding of host/parasitoid adaptations and of speciation in sexes that have disparate hosts.

DISCLOSURE STATEMENT

The author is not aware of any biases that might be perceived as affecting the objectivity of this review.

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endoreduplication in
one of the smallest
genome sizes in
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