# 1

# Order Strepsiptera

## 1.1 Introduction

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Strepsiptera are an unusual, indeed extraordinary, group of sexually dimorphic, entomophagous parasitoids. Adult male strepsipterans look frightening, grotesque and bizarre and conjure up an image of a creature that hails from ‘outer space’ (Proffitt 2005) (Figure 1.1a–c; cover). The title of this book is taken from Fiona Proffitt’s article in *Science*, and I have expressed my thanks in dedicating this book to her memory.

Strepsiptera are one of the least species-rich among insect parasitoids, with 14 families, and their hosts include 7 orders and 36 families of Insecta (Figure 1.2) (Table 1.1 and 1.2). It is now over 220 years since the discovery of the first strepsipteran species, but we are still ignorant on many aspects of their unusual life cycle. Partly because of their small size and fragile nature, they are one of the most difficult of insect groups to locate and collect. Until the advent of molecular techniques, many of the morphological features of Strepsiptera seemed akin to *Just So Stories* (Kipling 1902) (sensu Ffrench-Constant 2014). The case of the monarch butterfly, *Danaus plexippus*, comes to mind, which long remained a puzzle for biologists until Zhan et al. (2014), using genomes of 101 specimens, were able to explain some of the features of its unusual migration and coloration patterns. That scenario is quite similar now to the unravelling of the puzzle concerning Strepsiptera. These are exciting times for research on Strepsiptera, since, using molecular tools, we are beginning to understand and explain the basis of their natural history, morphology and evolution. Even tattooists are beginning to include Strepsiptera in their design (Figure 1.3).

Strepsiptera are the only parasitoids that have adapted to varied and diverse hosts and exhibit one of the largest host ranges of any insect parasitoid group. Unlike most other parasitoids, Strepsiptera stylopise hosts with ametabolous, hemimetabolous and holometabolous development – Zygentoma (Lepismatidae); Blattodea (Blattidae, Ectobiidae); Diptera (Platystomatidae, Tephritidae); Mantodea (Mantidae); Orthoptera (Gryllidae, Mogoplistidae, Tettigoniidae, Tridactylidae, Trigonidiidae); Hemiptera (Aphrophoridae, Blissidae, Cercopidae, Cicadellidae, Coreidae, Cydnidae, Delphacidae, Derbidae, Dictyopharidae, Eurybrachidae, Flatidae, Lygaeidae, Membracidae, Pentatomidae, Psyllidae, Scutelleridae, Tettigometridae, Tropoduchidae); Hymenoptera (Formicidae, Andrenidae, Colletidae, Halictidae, Melittidae, Sphecidae, Vespidae)

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Companion website: www.wiley.com/go/kathirithamby/strepsiptera1e

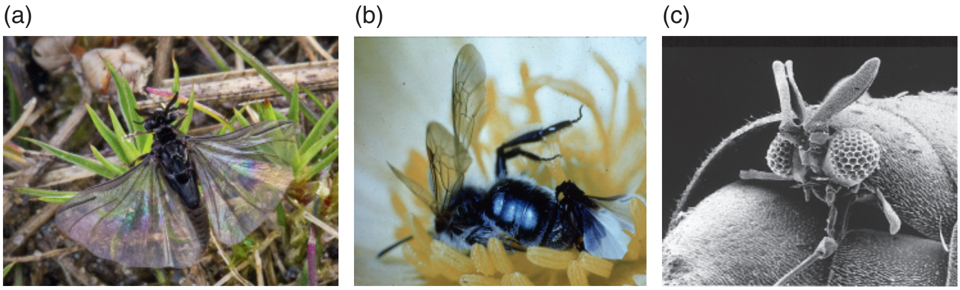

**Figure 1.1** (a) Male *Stylops* sp. in the field (length of male = 5 mm). *Source:* Courtesy: H. Henderickx. (b) Male *Stylops pacificus* mating with female endoparasitic in *Andrena complexa* (length of male = 3 mm). *Source:* Courtesy: E.S. Ross. Kathirithamby (1998a). (c) SEM of adult male *Pseudoxenos* sp. emerging from *Odynerus bicolor* (Hymenoptera) (×50). *Source:* Kathirithamby (1989)/ John Wiley & Sons.

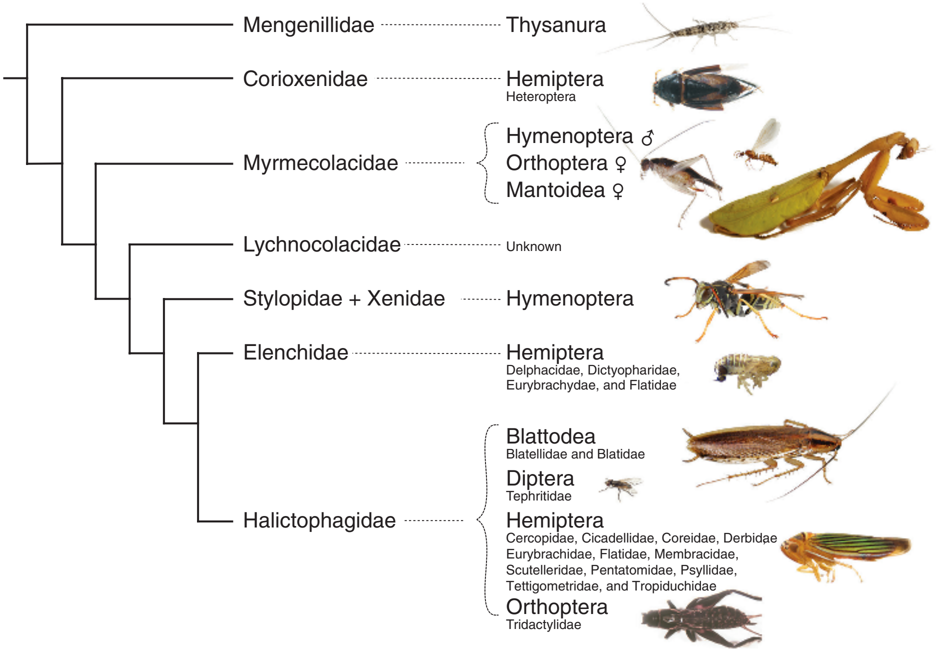

**Figure 1.2** Representations of host preferences (excluding Bahiaxenidae) mapped onto a cladogram derived from a molecular phylogenetic analysis of the major lineages (not to scale). *Source:* Photos by McMahon and Kathirithamby.

(Kinzelbach 1971; Kathirithamby 1989, 2009, 2018, 2025a, b) (Figure 1.2). Hosts parasitised by Strepsiptera are said to be ‘stylopised’, a term initially used by Westwood (1836) to refer to bees parasitised by *Stylops* (see Chapter 2).

There are about 603 species of Strepsiptera described so far, and the first list of the World was in the Catalogue of Life (14th October 2011), which is updated yearly (http://rameau.snv.jussieu.fr/cgi-bin/strepsiptera.pl) (Kathirithamby 2025a). In 2021, the World

**Table 1.1** Hierarchical classification of Strepsiptera.

- Order Strepsiptera Kirby
- *Incertae sedis*
  - Family †Protoxenidae Pohl et al. 2005
  - Family †Phthanoxenidae Engel and Huang 2016 (in Engel et al. 2016)
    - †Phthanoxenos Engle and Huang 2016 (in Engel et al. 2016)
    - †Kinzelbachilla Pohl and Beutel 2016
    - †Heterobathmilla Pohl and Beutel 2021 (in Pohl et al. 2021)
  - Family †Cretostylopidae Kathirithamby and Engel 2014
  - Family †Mengeidae Pierce 1908 (+2 fossil species)
  - Family Bahiaxenidae Bravo et al. 2009
- Suborder Mengenillidia Kinzelbach 1969a
  - Infraorder Mengenilliformia Kinzelbach 1969a
    - Family Mengenillidae Hofeneder 1910
- Suborder Stylopidia Kinzelbach 1969a
    - Family Corioxenidae Kinzelbach 1970 (+1 fossil species)
  - Infraorder Stylopiformia Pohl and Beutel 2005
    - Family Myrmecolacidae Saunders 1872 (+27 fossil species)
    - Family Lychnocolacidae Kathirithamby and Engel 2014 (+1 fossil species)
    - Family Bohartillidae Kinzelbach 1969b (+3 fossil species)
    - Family Stylopidae Kirby 1813 (+1 fossil species)
    - Family Xenidae Saunders 1872
    - Family Elenchidae Perkins 1905 (+3 fossil species)
    - Family Halictophagidae Perkins 1905

† Extinct taxa.
*Source:* After Kathirithamby and Engle (2014) and Kathirithamby (2018).

**Table 1.2** Number of phyla and orders of parasitised taxa.

| | | **Hosts** | |
|---|---|---|---|
| **Taxon** | **No. of species** | **No. of phyla** | **No. of orders** |
| Diptera | 16 | 5 | 22 |
| Hymenoptera | 67,750 | 1 | 19 |
| Coleoptera | 3,619 | 1 | 8 |
| Strepsiptera | 603 | 1 | 7 |

*Source:* After Kathirithamby (1989, 2009).

**Figure 1.3** A tattoo of *Halictophagus serratus*. *Source:* Courtesy of V. Block.

Register of Marine Species (WoRMS) included non-marine species such as Strepsiptera of the World (https://strepsiptera.aphia.org) (Kathirithamby 2025b). However, the described species represent only a small proportion of the total number of Strepsiptera, and if cryptic species, as studied in Myrmecolacidae by Hayward et al. (2011), are present at a similar level in other Strepsiptera genera, the order-wide estimates of diversity may be underestimated.

The rarity of an encounter with a strepsipteran in the field might also reflect the small number of keen Strepsiptera collectors, unlike with colourful, showy beetles and butterflies, which are generally more attractive and popular among both amateur and serious collectors. Hopefully, the numbers of dedicated Strepsiptera collectors will soon improve.

Another interesting aspect of Strepsiptera is that they exhibit two examples of polyphenism: (i) free-larval planidia moult to endoparasitic larval instars (hypermetamorphosis) and (ii) females of derived families have lost the adult stage and are neotenic (Erezyilmaz 2024, Chafino et al. 2018).

On account of their brief existence (*c.* three to six hours), very few people have actually seen live, adult free-living, male strepsipterans (Video 1.1). A male with outstretched wings in the field is an even rarer phenomenon, but was recorded by Hans Henderickx (Figure 1.1a). Moreover, it is near impossible to encounter a male emerging from its host in the field, as the process is very rapid. Nonetheless, a male *Stylops* sp. emerging from the bee *Andrena vaga*, in Mol, Belgium, was photographed by Hans Henderickx. My gratitude to Hans Henderickx is expressed in the dedication of this book to his memory. It is also rare to have seen live, free-living planidia, due to their microscopic size (Video 6.1). The first image of mating in Strepsiptera was of a male *Stylops pacificus* inseminating a female endoparasitic in the bee

*Andrena complexa* (Figure 1.1b), taken by Edward S. Ross in the 1950s in California – a sight to behold. A video clip of mating in *Xenos peckii* by Hrabar et al. (2014) is enchanting (see Section 11.5) (Figure 11.4) (Video 11.1).

Most of the world's major museums have small collections of Strepsiptera, one of the largest of these being the Australian National Insect Collection, Entomology Division, at CSIRO, Canberra. This collection was started through the interest and enthusiasm of the late Edgar Riek, who made copious notes on the group, including their mating behaviour (see Section 11.5). Furthermore, Strepsiptera and stylopised hosts have lain unstudied in collections due to their fragile nature. But now, with digitised on-line collections from natural history museums through open-access biodiversity databases and non-destructive DNA techniques, it is possible to study this material. Museomics (Raxworthy and Smith 2021), a study of DNA sequences obtained from preserved museum material and their hosts, which includes ancient DNA (aDNA), historical (hDNA) and enviromental DNA (eDNA), will give a better understanding of the evolutionary history of Strepsiptera. Next-generation sequencing methods applied to the preserved Strepsiptera will no doubt

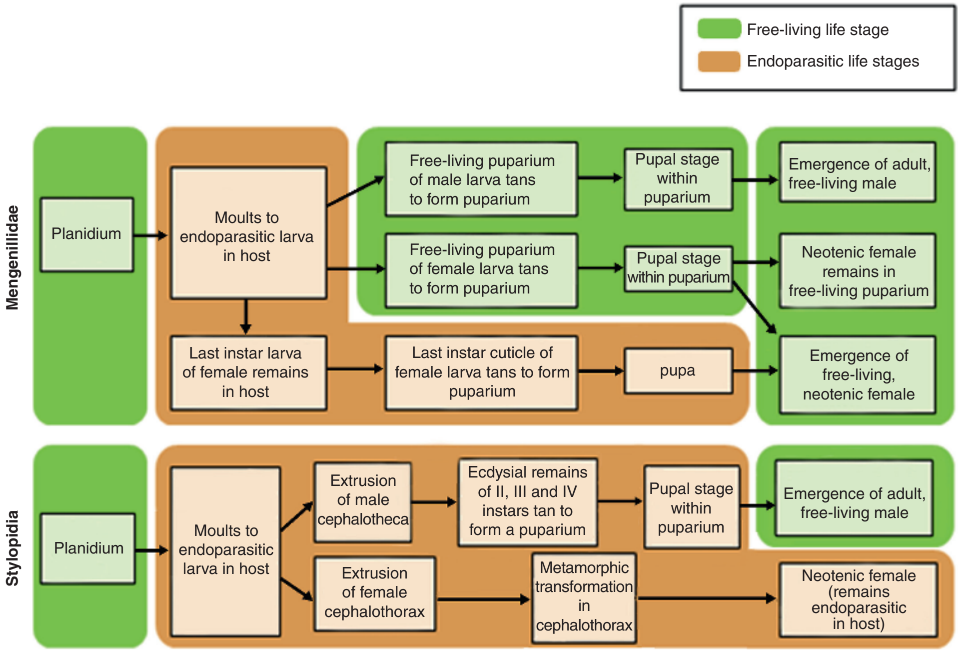

**Figure 1.4** A schematic representation of the life history in Strepsiptera: (i) male and female Mengenillidae generally emerge to pupate externally from the host and are free-living as adults; (ii) males of Stylopidia pupate as endoparasites with an extruded cephalotheca and emerge as free-living adults; females remain permanently endoparasitic and neotenic with an extruded cephalothorax, becoming sexually reproductive without undergoing a pupal instar, with metamorphic transformation occurring only in the cephalothorax. Two innovations occur in Mengenillidae: when some neotenic females remain in the free-living puparium to produce planidia; and the last larval instar may remain in the host to undergo a pupal instar and then emerges from the host as a free-living, sexually reproductive, neotenic female.
*Source:* Kathirithamby, Hrabar and Delgado.

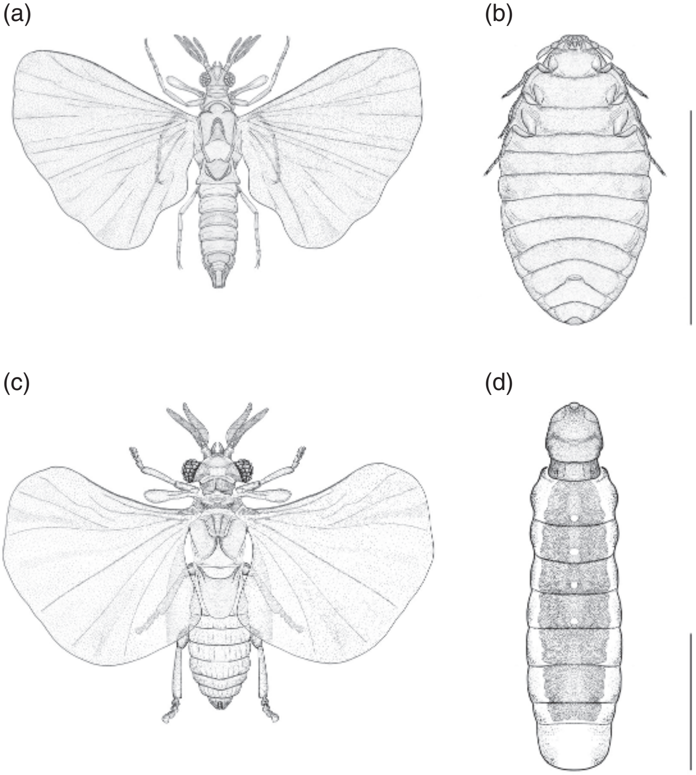

**Figure 1.5** *Eoxenos laboulbenei*: (a) free-living male; (b) partially neotenic, free-living female; *Xenos vesparum*: (c) free-living male; (d) neotenic, endoparasitic female (scale a–c = 3 mm). *Source:* Kathirithamby et al. (2015a)/with permission of S.E.A..

provide exciting data on the Strepsiptera-host relationships. The strepsipteran life cycle is markedly different between the suborders Mengenillidia (a more ancestral lineage) and Stylopidia (a recent suborder) (Figures 1.4 and 1.5). The family Mengenillidae (and possibly Mengeidae) have primitive characters and depend on the host for their interaction with the external environment only during the endoparasitic larval stages. Endoparasitic male and female Mengenillidae emerge from the host to form a free-living puparium from which males emerge as free-living adults, and females emerge as neotenic, and are wingless (some females remain in the puparium) (Kathirithamby 1989, 2009, 2018) (Figures 1.4 and 1.5) (see Section 13.4). In Stylopidia, after the endoparasitic larval stages, the males form an endoparasitic puparium, albeit with an extruded cephalotheca (Figure 1.5a), and emerge as free-living adults (cover photo; Figures 1.1a, c, 1.4c and 9.1a, b) (Video 1.1), leaving a gaping hole (Figure 19.5d), resulting in the death of the host. Female Stylopidia remain as obligate endoparasites, except for an extruded cephalothorax at the neotenic stage (Figure 1.6a–d) (Kinzelbach 1971; Kathirithamby 2009, 2018), and do not have a pupal instar (Erezyilmaz et al. 2014; Chafino et al. 2018) (see Section 1.4) (Figure 1.7) (Section 10.4).

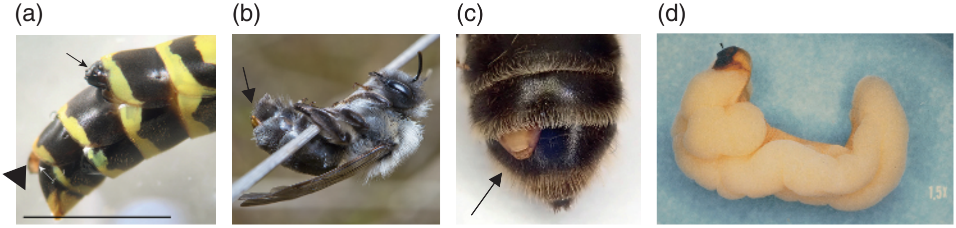

**Figure 1.6** (a) *Polistes dominula* stylopised by male cephalotheca (arrow) and female cephalothorax of *Xenos vesparum* (arrowhead) (Florence, Italy) (scale bar = 5 mm). *Source:* Kathirithamby et al. (2015b)/Oxford University Press. (b) *Andrena* sp. stylopised by cephalothorax of endoparasitic, neotenic female *Stylops* sp. (arrow) (Belgium) (length = 13 mm). *Source:* Courtesy of H. Henderickx. (c) *Andrena carantonica* stylopised by cephalothorax of endoparasitic neotenic female *Stylops atterrimus* (arrow) (Wytham Woods, Oxford) (×4). *Source:* Courtesy of L. Crowley. (d) Endoparasitic, neotenic female *Stichotrema asahinai* (arrow head = cephalothorax) which stylopises *Mecopoda elongata* (Tettigoniidae) (Yona, Kunigami-son, Okinawa Pref., Okinawa Is. Japan) (×1.5). *Source:* Courtesy of Y. Maeta.

Host specificity is an interesting phenomenon, since stylopisation by the free-living planidia means (as is the case with hymenopteran hosts) that they would encounter numerous hosts while waiting on flowers. One would expect them therefore to be generalist, but this is not so in some Stylopidae and Xenidae, and all female Myrmecolacidae. Is there some mechanism for planidia to 'select' the right host in the phoretic process?

The host and the parasitoid form a complex system (Thompson 1990), which has been termed an 'extended phenotype' (Dawkins 1982). Laciny (2021) rightly points out that, although the role of parasitised hosts has been mentioned in the context of the 'extended phenotype' (Dawkins 1982; Hughes 2013; Geffre et al. 2017), not only parasites but also symbionts, pathogens and microbes form a network of interactions in a 'parasitogenic phenotype'. Presently, the application of metagenomics would provide a powerful approach to revealing the diverse communities within Strepsiptera and their hosts.

For instance, Tang et al. (2015) analysed four DNA transposons of the strepsipteran *Mengenilla moldrzyki*, which, through a homology-based strategy, were also identified in other insects, freshwater planaria, hydrozoans and bats. Of these, only the alfalfa leaf-cutting bee *Megachile rotundata* is recorded as a host of Strepsiptera (Tang et al. 2015). The phylogenetic distribution of these transposons showed extremely high sequence identities (>87%). Phylogenies and comparisons of transposons versus orthologous gene identities demonstrated that these transposons have transferred into their hosts by independent horizontal transfers (HTs) (Tang et al. 2015). That stylopisation by Strepsiptera facilitates an exchanging of the genetic material with their hosts, and that predation (by bats) of a large quantity of insects might increase bats' exposure to horizontal transfer, is speculated by Tang et al. (2015).

Rickettsia-like microorganisms have been reported in strepsipteran species by electron microscopy (Kathirithamby 1998b) and by PCR (Noda et al. 2001), indicating that *Wolbachia* may be common in Strepsiptera (see Section 20.8). Interestingly, 50% of insects and other Arthropods are said to be infected by common endosymbiont *Wolbachia* (Hilgenboecker et al. 2008; Kaur et al. 2021).

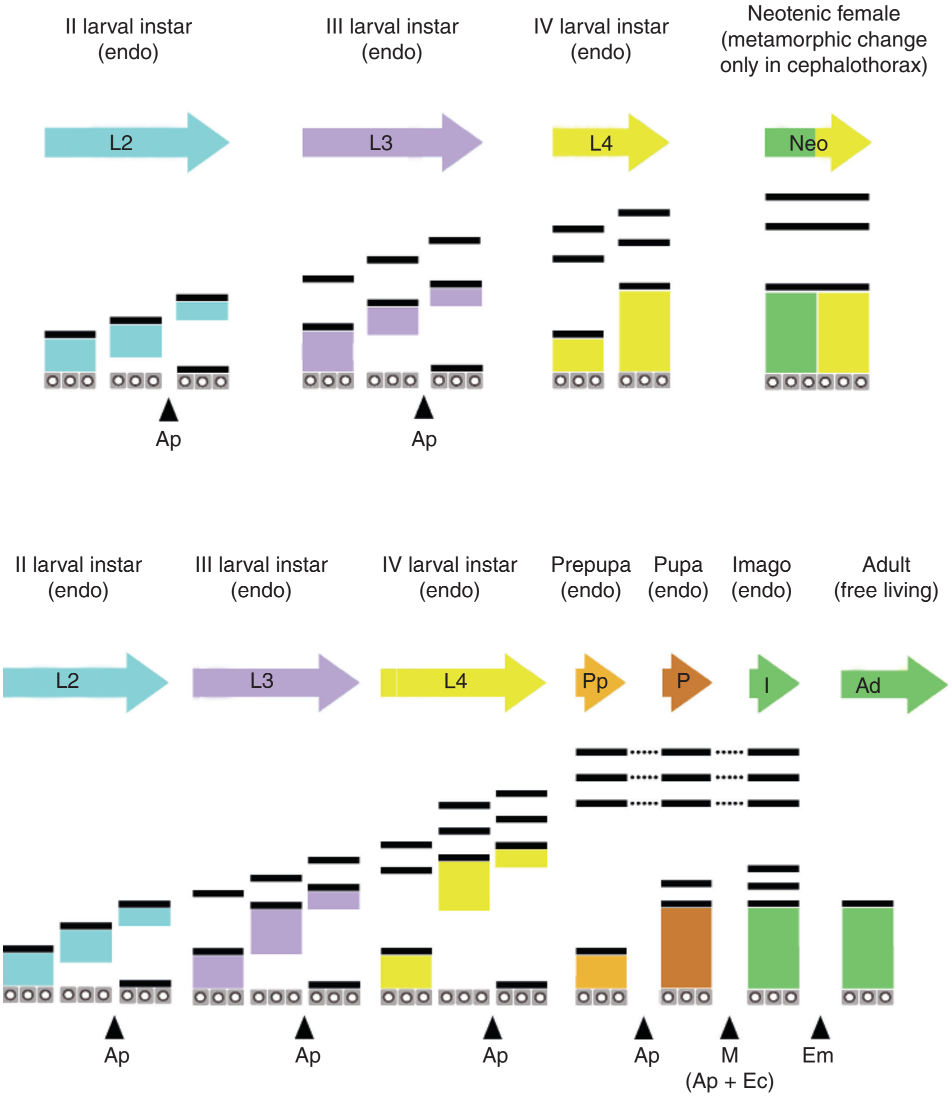

**Figure 1.7** Schematic representation of metamorphosis in Strepsiptera (Stylopidia) during endoparasitic larval development: of second instar larva to neotenic female); and second instar larva to adult, free-living male. Arrows: life history stages. II = second instar (L2); III = third instar instar (L3); IV = fourth instar (L4); Pp = prepupa; P = pupa; I = imago; Ad = adult male, Neo = neotenic female after metamorphic transformation; blue box = second instar larva; purple box = third instar larva; yellow box = fourth instar larva; green box = adult; black arrow heads: Ap = apolysis – detachment of the old cuticle from the underlying epidermis; Ec = ecdysis – the shedding of the old cuticle; Ap+Ec = apolysis followed by ecdysis; Em = emergence from puparium; M = moult when epicuticles of prepupa and pupa are shed within the puparium. Three main parts of each cuticle from outside to inside are represented with black boxes. Epicuticle = single black line on epidermal cell; pre-ecdysial cuticle = epicuticle after ecdysis; post-ecdysial cuticle = epicuticle retained by endoparasitic larva and neotenic female. Epidermal cells are shown as squares with round nuclei. *Source:* After Charles (2010). Kathirithamby, courtesy drawn by: J. A. Delgado.

The whole genome sequence of seven field-caught Dacini fruit-fly species which were presumed to be *Wolbachia*-positive was examined by Towett-Kirui et al. (2021). However, unexpectedly, they also found the complete mitogenomes of the strepsipteran *Dipterophagus daci*. Previous to this study, concealed endoparasitic stages of strepsipteran led to the incorrect assignment of *Wolbachia* co-infections to tephritid species. Towett-Kirui et al. (2021) confirmed that *Wolbachia* not only infects *D. daci*, but also occurs in stylopised fruit-fly tissues.

Towett-Kirui et al. (2023) were the first, by high-throughput 16S rRNA gene amplicon sequence, to characterise the bacterial communities of the strepsipteran *D. daci* and seven of its tephritid fruit fly host species: a study that revealed the effects of concealed stages of stylopisation on host bacterial communities. Towett-Kirui et al. (2021, 2023) showed that Strepsiptera, like all multicellular animals and plants, are not individuals, and have to be considered as holobionts (Rosenberg and Zilber-Rosenberg 2016): a host with its own microbes and viruses. Therefore, the holobiont and hologenome concept of the endoparasite Strepsiptera is more complex than that of a free-living insect: it consists not only of the strepsipteran and its microbes, but the host and its microbes as well. A holobiont strepsipteran endoparasite (and its microbes) and the host (and its microbes) need to be included in studies, to convey an overall picture of the role microbes might play in the strepsipteran host–parasitoid relationship (Zilber-Rosenberg and Rosenberg 2008). How widespread is the endosymbiont *Wolbachia* in other species of Strepsiptera, whether there is any horizontal gene transfer to its host, and if host fitness is affected, would be interesting subjects for future studies.

Souto-Vilarós et al. (2024), when monitoring data from the Arthropod Program of the Smithsonian Tropical Research Institute (STRI) on Barro Colorado Island (BCI), Panama, detected 4402 species through metabarcoding of bulk insect samples obtained by automatic light-trapping. Although the light traps are mainly used for collecting nocturnal insects, their analyses also detected several flightless species, which, they hypothesise, were probably hitchhiking on the bodies of other insects. In their subsection 'Unknown Guests' they record that DNA from a *Myrmecolax* (Myrmecolacidae) was recovered, which was either an adult free-living male, a juvenile male stylopised in an ant, or an endoparasitic female 'from within one of its potential hosts'. Possibly, the *Myrmecolax* was either endoparasitic in an orthopteran or mantid (in which case it would have been a female) or could have been a free-living male (such have been found in light traps) (see Chapter 2, Collections). This study indicates that in future studies the application of metabarcoding of large samples could unravel such 'unknown guests'. However, Daniel Souto-Vilarós (personal communication) cautions against the use of metabarcoding, as 'there is no physical record of the 'insect soup' as there is nothing else to show for this little critter!' But at least metabarcoding shows us the location of these elusive 'critters'.

Doherty and Matthews (2022) suggest the need for a multidisciplinary approach to elucidating the fundamental nature of host manipulation and behavioural regulation. Like many parasites/parasitoids, Strepsiptera modify the behaviour of their hosts to enhance their mating, avoid predation, and release planidia at appropriate sites for transmission and stylopisation of new hosts. Furthermore, Strepsiptera are macrynobionts and extend the life of the host, with the continued development of the host insect, to the adult stage (except in some Delphacidae), and host mortality occurring after completion of the strepsipteran life cycle. To discover whether the above changes in a stylopised host are the parasite's adoptive strategy, or a side effect of stylopisation, requires studies on the molecular level of the phenotype and its ecological consequences (Hughes 2013; Thomas et al. 2005).

A strepsipteran synchronises its life cycle to the respective larval/pupal or nymphal stages of the host life cycle, and undergoes diapause (if required), with the host stage. A stylopised host (strepsiptogenic phenotype), depending on its life cycle and cast (as in wasps and bees), undergoes changes in colouration, castration, behaviour, and depletion of fat reserves, which are discussed in the relevant chapters.

Strepsiptera have co-evolved with their hosts: a Red Queen model, named after a character from Lewis Carroll's *Alice Through the Looking Glass*, who needs to run constantly to maintain her position (Carroll 1872). In the theory of evolution, a successful parasite adapts to the common host genotypes. However, studies on Red Queen co-evolution have concentrated on the host, while the co-evolving parasite/parasitoid has largely remained unknown.

## 1.2 Are Strepsiptera Parasites or Parasitoids?

The term 'parasitoid' was used by Reuter (1913) to describe organisms that have a life cycle intermediate between that of a parasite, which does not kill its host, and a predator, which does. Parasitoidism is a specialised strategy of carnivory parasitoids, i.e. carnivores that complete their entire life cycle, feeding on just one individual prey item, i.e. the host (Godfray 1994; Blaimer et al. 2023). A parasitoid develops and feeds either on, or inside, another arthropod prey host (perhaps for one or two life stages), extracting nourishment, completing its life cycle in a single host, and as a direct result of that development, kills the host (Vinson and Iwantsch 1980a, b; Waage and Greathead 1986; Gould and Bolton 1988; Eggleton and Gaston 1990; Godfray 1994; Quicke 1997; Brodeur and Boivin 2004; Pennacchio and Strand 2006; Kathirithamby 2009; Barber and Dingemanse 2010). Strepsipteran parasitoids also manipulate their hosts to move to specific habitats where the planidia emerge to stylopise immature stages of the host, thus providing food and shelter and continuation of life cycle.

As a direct result of parasitisation, parasitoids may sterilise the host (Kuris 1974; Kathirithamby 2009). Castrators have been considered functionally similar to parasitoids, since they cause 'reproductive death' (Kuris 1974; Kathirithamby 2009). But this definition was rejected by Eggleton and Belshaw (1992, 1993) and Eggleton and Gaston (1990), who argued that sterilisation may be equivalent to killing. They further argued that hosts, if sterilised, may still continue to compete for resources with conspecifics, and may still be attacked by parasitoids, in which case they should not be considered parasitoids. The biology, host information and physiological interactions of parasitoids and parasites are little-known outside Hymenoptera (Eggleton and Belshaw 1993; Blaimer et al. 2023).

Strepsiptera develop and feed as endoparasites in the same host throughout their larval life stages and do not feed on the host's internal tissues. A live stylopised host continues to metamorphose to an adult host (except in stylopised brachypterous Delphacidae). As a direct consequence of development of a strepsipteran, the host (in most instances) is eventually sterilised. Death of the host occurs in: (i) Mengenillidae after the male and female emerge to pupate externally from the host, (ii) Stylopidia after the emergence of the free-living male, or when the free-living planidia have emerged from the endoparasitic, neotenic female. The host, after the emergence of the strepsipteran, is a shell with an atrophied digestive system and (in most cases) a lost/reduced reproductive system. Occasionally, however, planidia do emerge from a recently dead host that was stylopised by a female strepsipteran (Kathirithamby, personal observation). Only juvenile hosts that are stylopised can be re-stylopised by conspecifics, as seen in superparasitism, and by other parasitoids, as in multiparasitism. Adult stylopised hosts, however, are not re-stylopised, since it is too late in the host's life cycle for reinfection (Hughes 2003). Most crucial of all is the fact that the majority of sterilised hosts do not recover their reproductive potential. However, biologists have considered Strepsiptera to be parasites, unaware that the death of a stylopised host is due to stylopisation.

Strepsiptera are considered to be parasitoids because: (i) stylopisation of a host occurs at the egg/larval/nymphal instar, until host eclosion: this constitutes a synchronisation of life cycle of Strepsiptera with that of its host, but parasites do *not* synchronise their life cycle with that of their hosts; (ii) a stylopised host is mobile until the emergence of the strepsipteran, which is a vital criterion for Strepsiptera dispersal and insemination: mobility of a host is not a requirement for a parasite, and (iii) a stylopised host does *not* recover from stylopisation and dies only after the emergence of the Strepsiptera: a parasite allows the host to survive after infection (Godfray 1994), and the host *would* recover. Therefore, the term 'parasitoid' applies to Strepsiptera that live in a single host until completion of life cycle, resulting in the eventual death of the host.

## 1.3 Trichotomous Hypothesis of Insect Parasitoids

The variation in life histories observed in parasitoids is classified into two developmental modes: (i) idiobiont parasitoids halt host development, and (ii) koinobiont parasitoids enable the host to continue development (Haeselbarth 1979; Askew and Shaw 1986; Gould and Bolton 1988; Godfray 1994; Quicke 1997; Mayhew and Blackburn 1999; Pennacchio and Strand 2006) (Table 1.3). Idiobionts permanently paralyse their hosts and arrest their development by injecting venoms (or other biochemical factors), prior to oviposition (Vinson and Iwantsch 1980a, b; Strand 1986), which may destroy vital host organs (Führer and Kilincer 1972). Most idiobionts attack exposed hosts, while a few are endoparasitic, parasitising sessile hosts such as eggs and pupae (Gould and Bolton 1988). But some have larvae that are ectoparasitic males and endoparasitic females, e.g. aphelinids (Flanders 1959).

Most koinobionts are endoparasitoids, but a few are ectoparasitoids (e.g. some Ichneumonidae and Eulophidae) (Gould and Bolton 1988). Furthermore, koinobionts do not paralyse their hosts, or do so only transiently (Wharton 1984; Shaw 1994), thus allowing the hosts to develop, move and occasionally reproduce. Desneux et al. (2009) suggest that this transient paralysis of the host by koinobiont parasitoids may be an ancestral trait. Endoparasitoids, which are mainly koinobionts, have a more intimate and prolonged relationship with the host, not only physically, by occupying the internal body cavity, but, more importantly, physiologically (Gould and Bolton 1988; Godfray 1994; Quicke 1997; Pennacchio and Strand 2006; Henry et al. 2008; Desneux et al. 2012). Hence, to avoid host resistance and immunity, parasitoids have developed sophisticated physiological and molecular adaptations (Pennacchio and Strand 2006).

**Table 1.3** Comparison of koinobionts, idiobionts, (not in order of importance).

| Koinbiont | Idiobiont | Strepsiptera |
|---|---|---|
| 1) Endoparasites (a few ectoparasites) | Ectoparasites or endoparasites of sessile hosts | Obligate larval endoparasites |
| 2) Development of host for one or two stages after parasitisation | Parasitism prevents host development | Host development continues, including metamorphosis |
| 3) Egg, larval or pupal parasitoids | Egg, larval, pupal or adult parasitoids | Larval or nymphal (sometimes egg) parasitoids |
| 4) Parasitism restricted to one or two stages of host | Parasitism restricted to one or two stages of host | Parasitism continues through all host stages, which is required for life history completion |
| 5) Parasitise exposed hosts, which normally have shorter developmental time | Parasitise concealed hosts (pupae or eggs), which normally have longer developmental time | Parasitise both concealed and exposed hosts, with longer developmental time in females and shorter in males |
| 6) Narrow host range | Wide host range from varied habitats | Wide host range from varied habitats |
| 7) Hosts of similar size range | Hosts of varied sizes | Hosts of a wide range (3–40 mm). |
| 8) Host consumed after development of parasite | Hosts paralysed and consumed soon after parasitisation | Live larval-pupal-adult or nymphal-adult stages (sometimes egg) of host required for life-cycle completion, after which the adult host dies |
| 9) Only temporarily paralysed after parasitisation | Permanently paralysed after parasitisation | Not paralysed after parasitisation |
| 10) Host continues to be mobile after parasitisation | Host becomes immobile after parasitisation due to paralysis | Host continues to be mobile until emergence of the free-living male and the live planidia from endoparasitic female |
| 11) Higher fecundities | Lower fecundities | Fecundity always high (production of several hundred planidia) |

*Source:* After Kathirithamby (2009)/with permission of Annual Reviews.

Most parasitoids have only a small host range (Godfray 1994; Quicke 1997), since a large and variable host range might result in resistance from the host, leading to mortality (Hawkins et al. 1997; Kraaijeveld and Godfray 1999). However, idiobionts have a large host range and kill the host upon parasitisation, thus eliminating any possibility of immune response by the host. Whereas koinobionts, which are endoparasitoids, generally tend to have a narrow host range and interact with live hosts, albeit for only a small fraction of their life history (Askew and Shaw 1986; Strand 1986; Gould and Bolton 1988; Strand and

Peach 1995). Furthermore, koinobionts have evolved to become more specialised in their adaptation to host responses and parasitise early host stages found in exposed habitats that have a less efficient defence against attack (Gould and Bolton 1988).

The foraging behaviour of idiobionts and koinobionts might have given rise to the two types of developmental modes: koinobionts favour foraging hosts, while idiobionts have a broader host range (Gould and Bolton 1988; Shaw 1994).

Parasitoids' life histories, classified by the mode of their development, are not the only factors attributed to dichotomous hypotheses, and factors such as fecundity may also play a part (Mayhew and Blackburn 1999). Koinobionts usually suspend their development at first instar larval stage, while the host continues to feed and grow. They also avoid feeding on the vital organs of the host (Gould and Bolton 1988; Godfray 1994) and only begin destructive feeding when the host is at a specific larval instar, or size, enabling sufficient resources for growth and to complete development (Hagen 1964; Harvey et al. 1994). Furthermore, endoparasitic koinobionts encounter different larval instars of hosts, and may develop rapidly in smaller hosts (resulting in reduced size), or have a lag phase with longer development time in larger hosts (resulting in bigger size). Development time and size depend on host-feeding ecology (exposed or concealed) and are likely correlated to mortality risks (Harvey and Strand 2002). Developmental changes of the solitary and/or gregarious endoparasitic koinobionts, e.g. prevention of pupation, or enabling the host to moult to a prepupal stage instead of the pupal instar, are due to changes in host endocrine physiology (Beckage and Gelman 2004). According to Pennacchio and Strand (2006), arrested development, or inhibition of metamorphosis, is an indirect consequence of the redirection of nutritional resources of the host for the metabolic advantage of the developing parasitoid.

In Strepsiptera, mobility to locate, recognise, enter and stylopise the egg/larva/nymph of the host is the task of the free-living planidia. In most other insect parasitoids, the free-living adult female displays the above-mentioned complex behavioural features for host location and parasitisation (Kuris 1974; Godfray 1994 Quicke 1997; Pennacchio and Strand 2006). Strepsiptera could be considered as endoparasitic koinobionts, whose hosts continue to develop after stylopisation in a live host. However, unlike koinobionts, Strepsiptera are parasitic in their hosts for almost their *entire* life history. This developmental strategy allows a stylopised host to metamorphose to an adult (except in Homoptera Delphacidae) (Hughes and Kathirithamby 2005), thus enabling a strepsipteran to live in the same host until completion of its life cycle – the only parasitoids recorded so to do. Furthermore, a stylopised host is not paralysed, killed or consumed, since the strepsipteran is dependent on a live host for diapause, dispersal and life cycle completion (Kathirithamby 2009).

Unlike other parasitoids, Strepsiptera parasitise several orders of Insecta (Kathirithamby 2009, 2018) (Figure 1.2). Although the fitness of juvenile stages of the stylopised host is not affected (Hughes and Kathirithamby 2005), stylopised adult hosts may have changes in colour, the pollen collecting apparatus, undeveloped external and internal genitalia, disruption in the juvenile hormone secreting corpora allata. They may also exhibit unusual behaviour.

Idiobionts that parasitise older hosts have lower fecundities (Mayhew and Blackburn 1999). As in Ichneumonidae (Gould 1988), Strepsiptera stylopise early host stages (eggs/larvae/nymphs), and, like koinobionts, delay their endoparasitic development until the prepupal instar, or after the host has become an adult (Hughes and Kathirithamby 2005).

In koinobionts, delay in their development results in larger females, which seek more hosts to lay their eggs. In Strepsiptera, after entry by planidia of *Xenos vesparum*, although there is minimal growth during the endoparasitic larval stages (Hughes and Kathirithamby 2005), the reproductive system of the strepsipteran continues to develop. Only at the host prepupal stage has growth in the body length of *X. vesparum* been observed (Hughes and Kathirithamby 2005). Neotenic females are of varied sizes, depending on size of host, and are highly fecund, producing thousands of planidia. That Strepsiptera have higher fecundity is due to smaller eggs containing less yolk (Büning 1998).

Stylopisation by Strepsiptera exhibits no similarity to parasitism by any other insect parasitoid group and displays several biological innovations. Due to the numerous differences between idiobionts, koinobionts and Strepsiptera, a trichotomous hypothesis of development was suggested: macrynobionts (*macryno*-lengthen, *bionts*-living creatures) were introduced to incorporate the unusual mode of life history, mainly their ability to lengthen the life cycle of the host to complete their own (Kathirithamby 2009). This phenomenon is seen particularly in hosts stylopised by female Strepsiptera, as the free-living planidia emerge during the period when the next generation of host egg/larvae/nymphs are available for stylopisation (Kathirithamby 2009).

## 1.4 Metamorphosis

Metamorphosis is a crucial process in insect evolution (Belles 2020) and is a particularly interesting phenomenon in the sexually dimorphic Strepsiptera. There have been several misidentifications of the ecdysial remains of the endoparasitic female Stylopidia (see Section 7.2) (see Table 1.4). It should be emphasised that both morphological and molecular studies were necessary to settle this controversy (Erezyilmaz et al. 2014; Chafino et al. 2018).

The expression of all isoforms of *Broad complex* (*Br-C*), during the transition from larvae to pupae in males, and from larvae to reproductively competent, neotenic females, shows elevated levels. However, the zinc finger isoforms *Z1*, *Z3* and *Z4* show elevated levels only in the last (fourth) instar larva in the males, and not in females. This shows the reason explaining the absence of a pupal instar in endoparasitic females as *Br-C* codes for transcription factor that specifies the pupal stage. This study showed that, since the *Br-C* expression does not increase beyond the fourth instar larva, this stage in the female does not transform to a pupa (Erezyilmaz et al. 2014). This above interpretation is *not* ambiguous, as was stated by Löwe et al. (2016). Molecular studies also revealed that, while an increase of adult specifier *E93* expression is observed in the pupal and adult stages of the male, there are persistent low levels of *E93* expression in the female (Chafino et al. 2018) (see Section 10.4). However, there is an increase of *E93* expression in the late fourth instar larva of the female, where *Br-C* expression tends to be upregulated in the cephalothoracic

**Table 1.4** Terminology and references for description of the neotenic female Stylopidia. Left column: terminology hitherto used. Right column: terminology in light of molecular studies.

| Terminology in previous publications | Correct terminology |
|---|---|
| Adult/adult female/adult cuticle/pharate adult/puparium: (Lauterbach 1954; Kinzelbach 1971; Löwe et al. 2016; Beani 2005; Pohl and Beutel 2005, 2008; Richter et al. 2017; Straka et al. 2015a; Tröger et al. 2020) | Neotenic female |
| Puparium/middle layer that of the pupal exuvium/pupal cuticle: (Lauterbach 1954; Richter et al. 2017; Kinzelbach 1971; Pohl and Beutel 2005, 2008; Peinert et al. 2016; Löwe et al. 2016; Tröger et al. 2019, 2020; Straka et al. 2014, 2015b). | Fourth instar larva |
| Exuvium of the secondary larva (puparium)/second- and third instar larva/second larval stage/secondary/tertiary larva: (Lauterbach 1954; Löwe et al. 2016; Kinzelbach 1971; Pohl and Beutel 2005; Beani 2005; Richter et al. 2017; Tröger et al. 2020; Benda et al. 2022). | Epicuticles |

*Source:* J. Kathirithamby.

region, compared with the abdominal region (Chafino et al. 2018). Interestingly, the female, in spite of being larviform, undergoes a metamorphic transformation in the cephalothoracic region. The persistent low expression of *Br-C* and *E93* in the abdominal region of the female explains why metamorphosis does not proceed in that region. Hence, the females of Stylopidia, unlike the males, which follow typical complete metamorphosis, undergo a metamorphic change. This change occurs only in the extruded cephalothorax, for development of: (i) the pheromone glands for the attraction of the male; and (ii) a brood canal opening for insemination and emergence of the viviparous planidia (Figures 1.5d and 1.6c) (see Section 10.4).

In previous studies, the cuticular layers of the neotenic female Stylopidia were labelled without carefully monitoring the life cycle (see Section 10.5). Due to this misidentifications of the cuticular layers associated in female Stylopidia have occurred. For example, Tröger et al. (2020) provide a summary of the postembryonic development in Mengenillidae and Stylopidia, but the developmental stages are incorrectly represented. Furthermore, Weingardt et al. (2023) summarily state that there is only one ‘secondary larva’ in Stylopidia. However, Strepsiptera have three endoparasitic larval instars which undergo apolysis without ecdysis (Kathirithamby et al. 1984). The ecdysial remains in postembryonic development and the neotenic female are discussed in different contexts throughout this book. To avoid repetition in the following chapters, the previous and current terminologies are summarised in Table 1.4, and a schematic representation of metamorphosis in Strepsiptera is provided in Figure 1.7.

As external and internal morphologies of Strepsiptera have been studied extensively, I shall focus on the host–parasitoid relationships, which has been my main interest in this group.

**Video 1.1** Live adult male *Xenos vesparum*. *Source:* Kathirithamby (2009)/Annual Reviews.

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