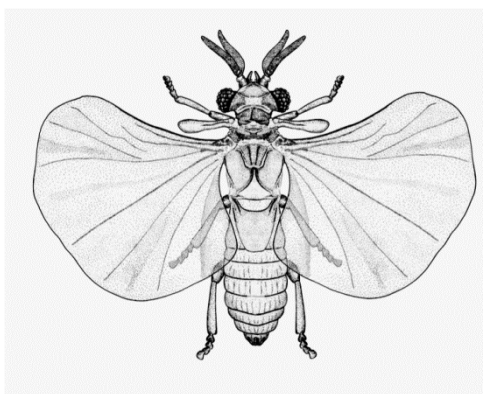


[Versión española](#)



CLASS INSECTA

## Order Strepsiptera

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### 1. Short group definition and main diagnostic characters

Strepsiptera are entomophagous parasitoids with free-living adult males and endoparasitic females (except in the family Mengerillidae). The hosts of this group are referred in the bibliography as “stylopized”; the two more frequently parasitized insect order are Homoptera and Hymenoptera.

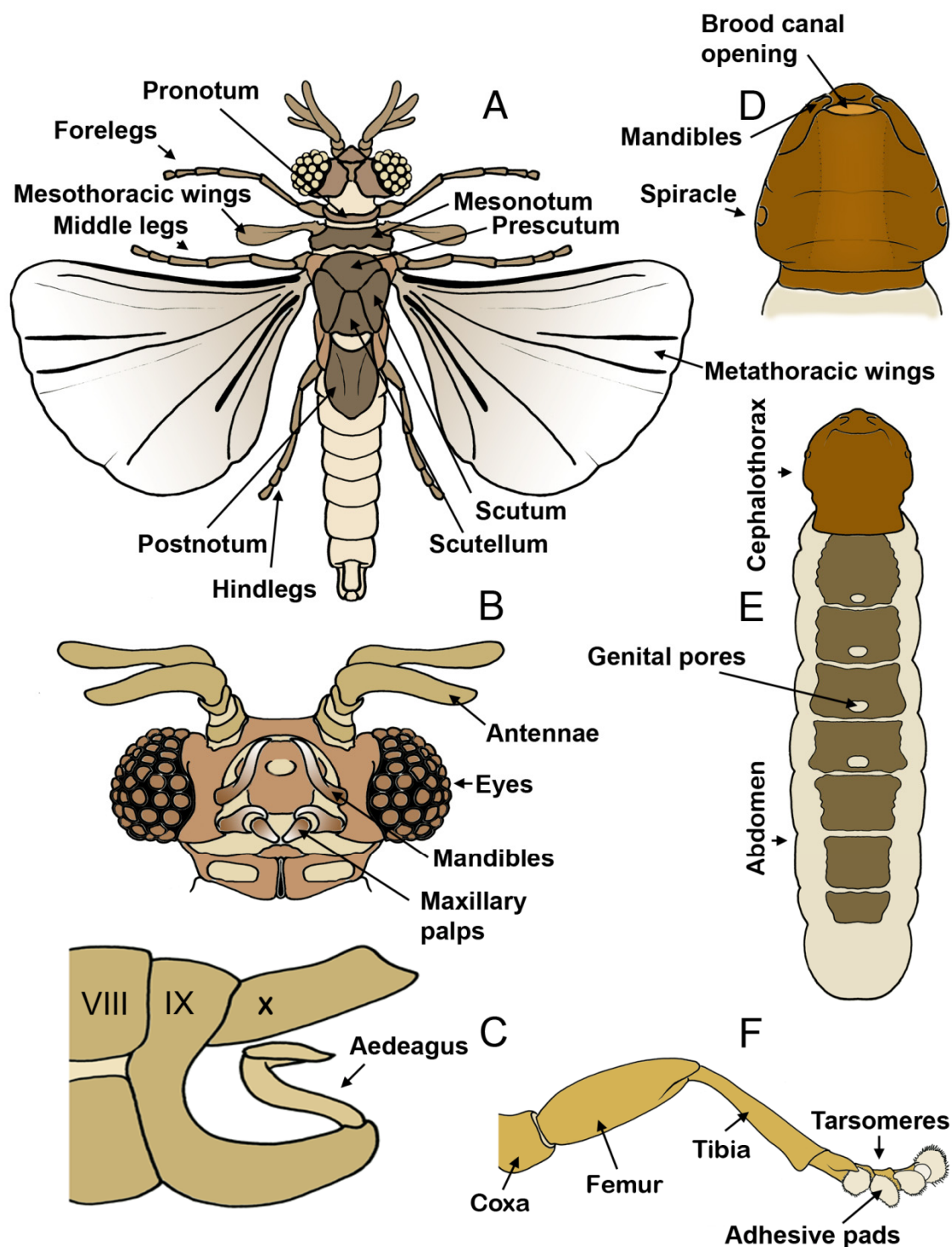
The males have large raspberry-like eyes, flabellate antennae, shortened forewings resembling dipteran halteres and large hind wings (Fig. 2A and 2C). The females are neotenic and endoparasitic in the suborder Stylopodia. The endoparasitic females are divided into two regions: a sacciform body, which is endoparasitic in the host and an extruded cephalothorax (Fig. 4). In the extant family Mengerillidae both males and females (Fig. 2A and 2B) emerge from the host to pupate externally, and the neotenic females of this family are, as the males, free living (Kinzelbach, 1971, 1978; Kathirithamby, 1989, 2009).

Last molecular studies confirm the sister group relationships of Strepsiptera with Coleoptera. Both lineages split from a common ancestor during the Permian (Wiegmann *et al.*, 2009; Misof *et al.*, 2014). Unfortunately, the fossil record of this group is restricted to only a few specimens preserved in amber. The oldest example comes from the Cretaceous Burma amber (100 my) (Grimaldi *et al.*, 2005; Kathirithamby & Engel, 2014).

#### 1.1. Morphology

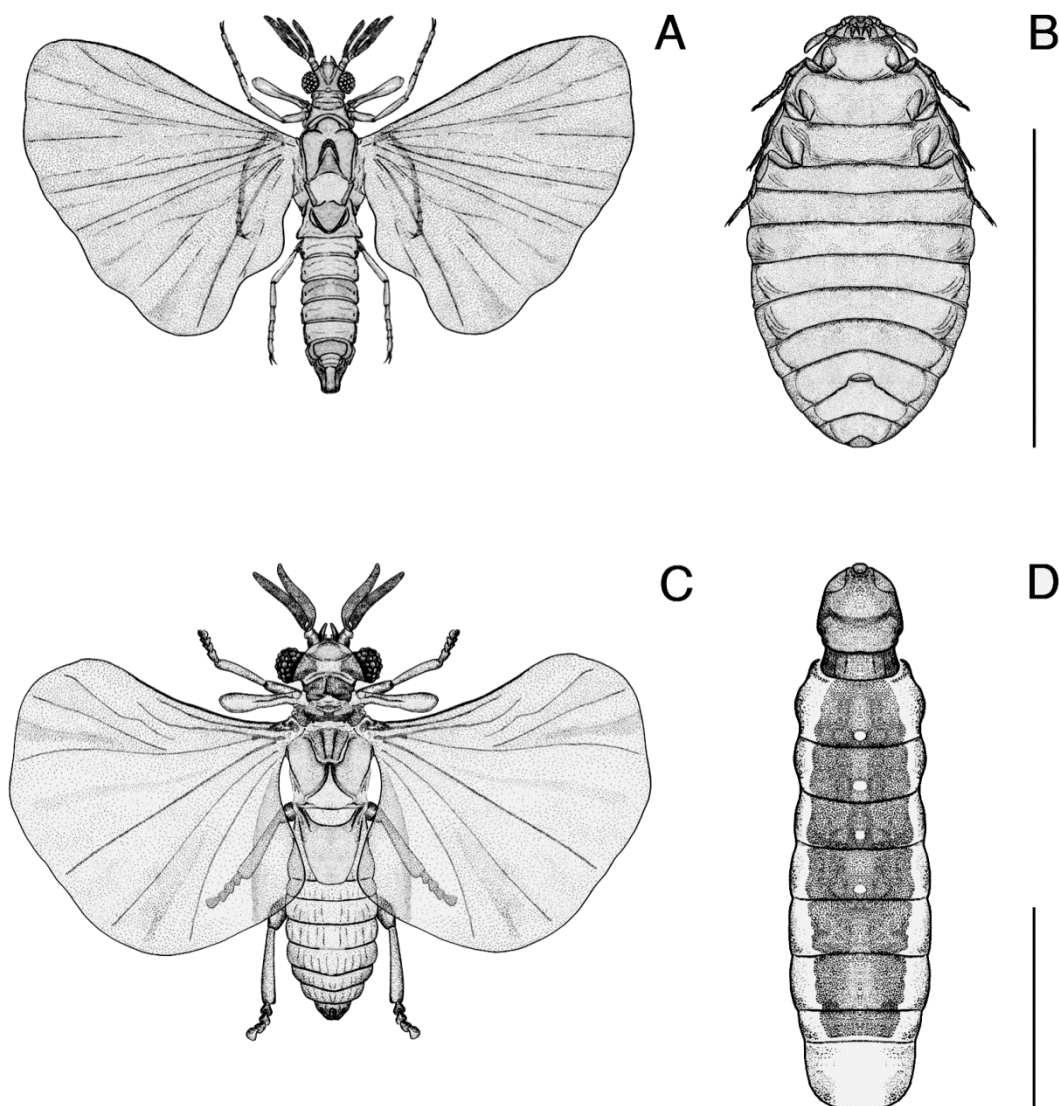
Sexes are clearly dimorphic. The adult males are free living and has conspicuous flabellate **antennae** and **eyes** with 15-150 individual eyelets (Fig. 1B) separated by cuticle or setae. The **mandibles** are blade-like which are absent in the family Corioxenidae, and **maxillae** are 2 segmented. The **prothorax** is short and the **mesothorax** bears the reduced forewings (Kathirithamby, 1989; Pix *et al.*, 1993). The **metathorax**, is sometimes ten times larger than rest of the thorax, and bears a pair of large **hind wing** with reduced venation, and has asynchronous-type flight muscles (Smith & Kathirithamby, 1984). In the **legs**, the trochanter is fused with the **femur**, in the fore- and mid-legs **tarsi** may be 2-5 segmented, which frequently bear **adhesive pads**. There are ten abdominal segments, of which the ninth bears the **aedeagus** with no parameres, and the tenth segment dorsally covers the aedeagus (Fig. 1C).

The females of the suborder Stylopodia are devoid of all adult characteristics and except for the extruded **cephalothorax** (Fig. 1D), are totally endoparasitic. The cephalothorax is composed by the head and thorax and it is separated by a constriction from the **abdomen** (Fig. 1F). The cephalothorax lacks antennae and eyes, with only simple vestiges of mouth parts. However, the **mandibles** are always present during extrusion. A **brood canal opening** is present in the cephalothorax which is used during mating for insertion of sperm, as well as for the emergence of the planidia I instar larvae. The brood canal opening leads to the brood canal which has **genital ducts** (varying in number depending on the family) leading into the haemolymph where the free-floating oocytes are situated. The cephalothorax also bears a pair of **spiracles**. Some members of the suborder Stylopodia are found in the Iberian Peninsula and the Macaronesian isles.



**Figure 1.** External morphological characters of the order Strepsiptera. **A:** Adult male, dorsal view; **B:** Head of male in ventral view; **C:** Last abdominal segments and aedeagus in lateral view; **D:** Female cephalothorax in the suborder Stylopida, ventral view; **E:** General aspect of a female in the suborder Stylopida, ventral view; **F:** Middle leg of an adult male showing the apparent lack of trochanter.

Members of the basal family Megenillidae (Fig. 2A and 2B) are free-living as pupae and the neotenic females have a distinct head with eyes, antennae and mouth parts as well as three pairs of legs in the thorax, but are wing-less (Fig. 2B). On the ventral part of the abdomen is a birth opening. Members of the family Megenillidae are found throughout southern Europe, including the Iberian Peninsula and Canary islands.

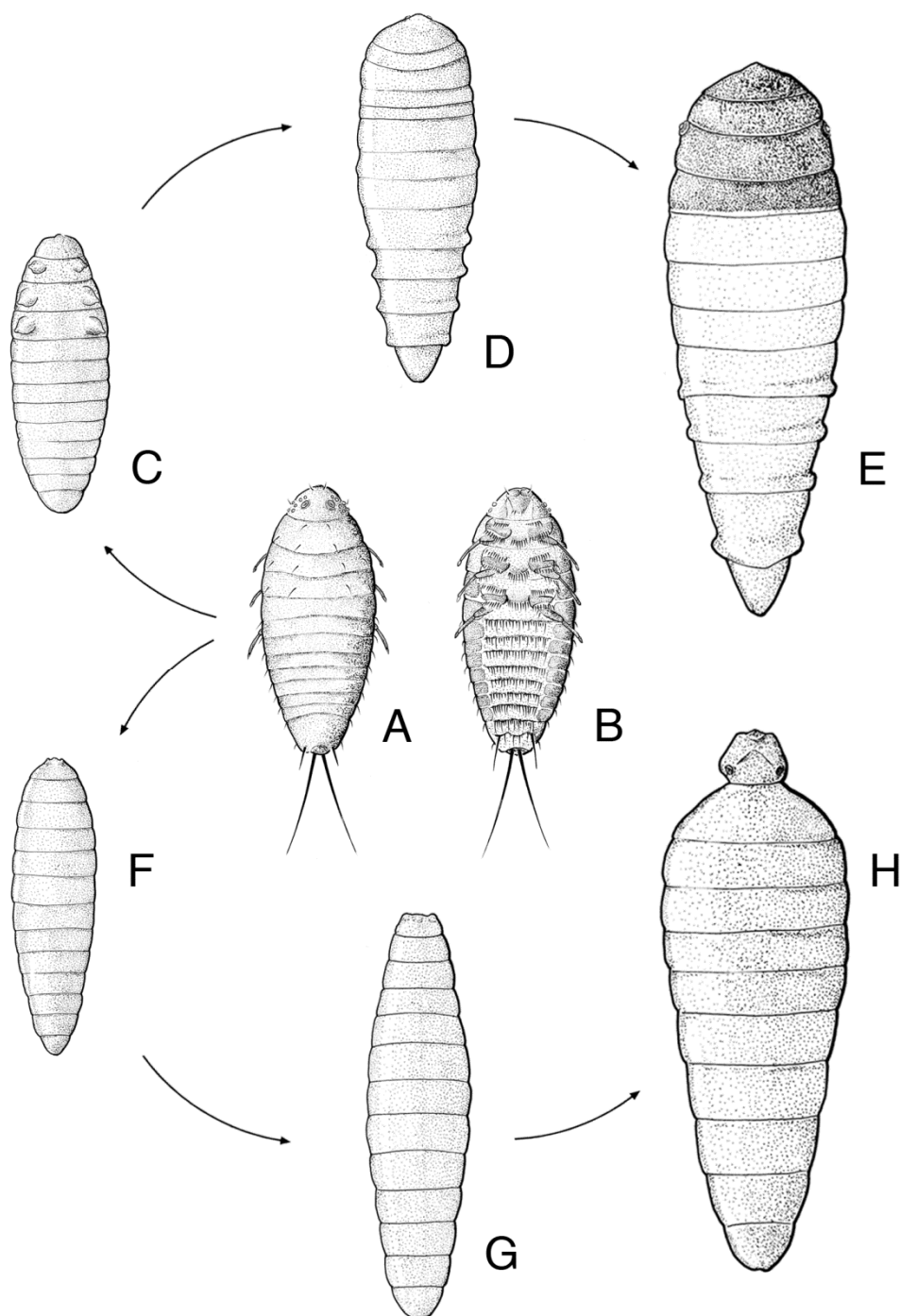


**Figure 2.** Mengenillidia and Stylopidia. **A:** Dorsal view of the male of *Eoxenos laboulbenei*. **B:** Ventral view of a female of *Eoxenos laboulbenei*. **C:** Dorsal view of a male of *Xenos vesparum*. **D:** Ventral view of a female of *Xenos vesparum*. Scales (top for A to C and below for D): 3 mm.

## 1.2. Lyfe cycle

The planidia I instar larvae are the free-living and host-seeking stage with highly serrated ventral region, presumably to cling to hosts (Fig. 3A and 3B). Due to external resemblance to the planidia I instar larvae of Meloidae they are frequently referred as triangulins. On entering into the host the planidia I instar larva moults to an apodous II instar (Fig. 3C and 3F) and the sexes are distinguishable from the II or III instar onwards (Fig. 3D and 3G). At the late IV instar the bulbous head of both the male (Fig. 3E) and female develops mandibles which are used during extrusion through the host cuticle. On extrusion, the head region of the male Stylopidia sclerotizes to form the cap of the puparium (cephalotheca) and the anterior region of the female on extrusion forms the cephalothorax (Fig. 3H) with a brood canal opening. The male Stylopidia pupates in a living host and emerges as a free-living adult by breaking the cap of the puparium (cephalotheca). The viviparous female continues to remain endoparasitic and after fertilization by the male, and the embryos develop within the body cavity (vivipary). The life cycle of *Xenos vesparum* (Rossi) is shown in figure 4.

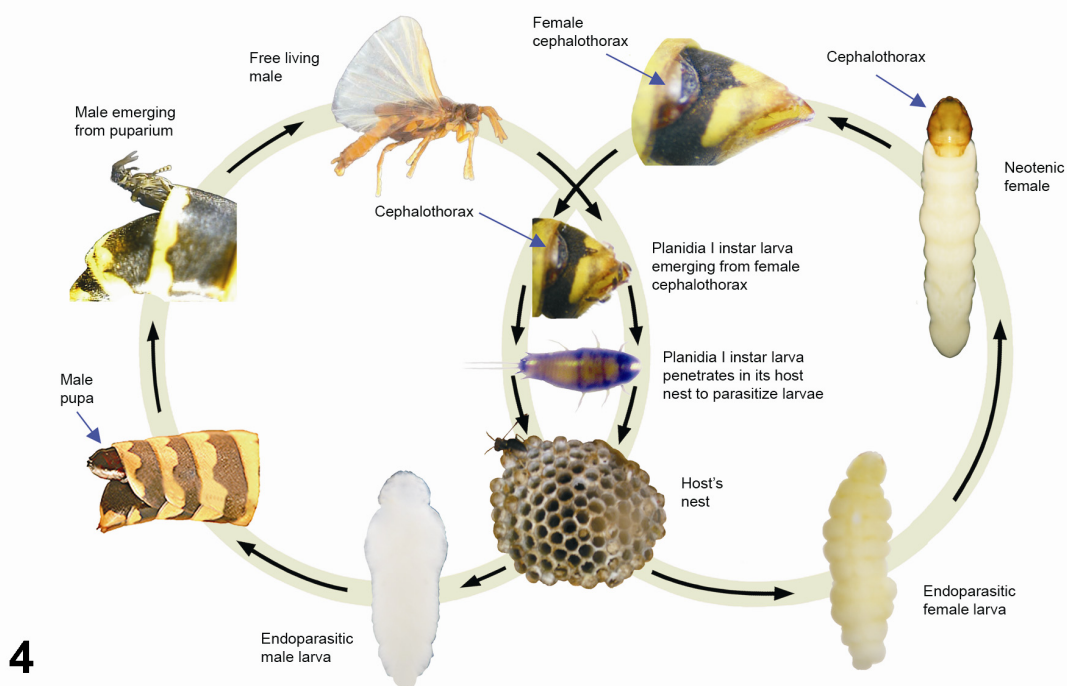
In the family Mengenillidae at the end of the IV instar both males and females emerge from the host to pupate externally (see Fig. 5). The free-living puparium of the male and female have mouth parts, legs and abdominal segments. The adult free-living male and the free-living neotenic female emerge from the free-living puparia.



**Figure 3.** General view of the different larval stages of the suborder Stylopodia based on species of *Halictophagus* (redrawn from Luna de Carvalho & Kogan (1991), with scales and some errors omitted). **A:** planidia I instar larva, dorsal view. **B:** planidia I instar larva, ventral view. **C:** II instar larva, male in ventral view. **D:** III instar larva III, male ventral view. **E:** IV instar larva, male dorsal view showing cephalotheca. **F:** II instar larva, female ventral view. **G:** III instar larva, female dorsal view. **H:** IV instar larva, female ventral view showing the cephalothorax.

### 1.3. Biology

There are only two free-living stages in Strepsiptera Stylopodia: the adult male and the planidia I instar larva. The planidia I instars emerge live from the viviparous female and are the host-seeking stage (Fig. 4). The females of the extant Mengenillidia are free-living as adults, and both the males and females emerge to pupate externally. On entry into the host they moult to a II instar apodous larva (Kinzelbach 1971; Kathirithamby, 1989, 2009). Planidia I instar larvae of the family Stylopidae have also been reported to parasitize eggs of endopterygote hosts (Linsley & MacSwain, 1957; Maeta *et al.*, 2001; Hughes *et al.*, 2003), and those of *Stichotrema dallatorreanum* Hofeneder in Papua New Guinea have been observed to enter the host via the tarsi (Kathirithamby, 2001).



4



5

A



B

**Figure 4.** Life cycle of *Xenos vesparum*. **Figure 5. A:** Puparium of a female of *Eoxenos laboulbenei* parasitized by larvae of the chalcid *Idiomacromerus gregarious*. **B:** Same puparium after wasp eclosion showing the opening used during hatching in the dorsal region.

Larval endoparasitic strepsipterans undergo an unusual means of moulting whereby apolysis is not followed by ecdysis (Kathirithamby *et al.* 1984). At the end of the IV instar the male extrudes the anterior region (cephalotheca, see Fig. 3E) through the host cuticle and begins to pupate, and the female extrudes the cephalothorax and becomes a neotenic female, without a pupal instar (Erezyilmaz *et al.*, 2014).

At the end of the pupal instar the adult free-living male emerges from the puparium and seeks a female within its very short life (c.5-6 hours). After insemination, via the brood canal opening of the female, the male dies almost immediately. The viviparous female is highly fecund and produces numerous planidia I instar larvae (3,000-750,000) which emerge via the brood canal opening to seek new hosts.

#### 1.4. Natural History

Female *Eoxenos laboulbenei* de Peyerimhoff are parasitized by some hymenopteran Chalcidoidea (Fig. 5): *Idiomacromerus gregarious* (Silvestri) and *Hockeria mungenillarum* (Silvestri). *Idiomacromerus gregarious*, first reported by Silvestri (1943), was recently found by Delgado *et al.* (2014). The thysanuran hosts of *Eoxenos* are myrmecophilous and stylopized Thysanura have been found to live among ants (Kathirithamby, Delgado & Collantes unpub.). The mechanism of stylopization by planidia I instar larvae and the behavior of the thysanuran hosts before the emergence of the male and female strepsipteran is still unknown. Ants, silverfish, strepsipterans and the chalcid parasitoid form a multitrophic food web which might be an indication of the manner in which invertebrates have adapted to the arid conditions in the Iberian Peninsula.

### 1.5. Distribution

The order has a worldwide distribution although is more diverse in the tropics. Many species are present in the terrestrial habitats of the Iberian Peninsula and Macaronesian islands. The males are only relatively frequently found are rarely collected by the entomologists, which causes the false impression of being a rare group in many ecosystems and regions.

### 1.6. Scientific interest and applied importance

Strepsiptera are an enigmatic group with amazing morphological traits and natural history which is of special interest for entomology. However, the extreme difficulty of collecting material makes this group as one of the least known among insects. As for the hosts of this order, is worthy to point out that stylopization frequently changes their morphology and behavior. An example of is when the external genitalia in stylopized Delphacidae parasitized by *Elenchus* (Elenchidae) becomes extremely reduced and are sometimes absent (Lindberg, 1939; Kathirithamby, 1978). As such stylopized delphacids have been thought to be intersexes. *Javesella dubia* (F.) (Delphacidae) is a serious pest of cereals, especially oats in Europe, including Spain, and is parasitized by *Elenchus tenuicornis* (Elenchidae) which acts as a biocontrol measure (Raatikainen, 1967).

## 2. Systematics

Strepsiptera is a monophyletic group. Kinzelbach (1971, 1978) divided the order in two suborders: Mengenillidia and Stylopodia, and into 13 families (including fossils) based on a cladistic approach using adult characters (mainly males). Mengenillidia and Stylopodia are sister groups (McMahon *et al.*, 2011). The first molecular phylogeny of Strepsiptera combined with morphological data (McMahon *et al.*, 2011) confirmed the monophyletic nature of the order as well as of some other clades as Stylopodia and Stylopiformia. Similar data were pointed out in previous works based exclusively on morphological characters (Kathirithamby, 1989, 2009; Kinzelbach, 1978; Pohl & Beutel, 2005).

The clade Stylopiformia is characterized by some tarsal modifications and reduction in number of tarsomeres, loss of larval legs in males (Fig. 3) and presence of cephalothorax in females. The analysis of McMahon *et al.* (2011) also suggest that Xenidae (that parasitize Vespidae and Sphecidae) and Stylopidae (that parasitize Halictidae, Andrenidae y Colletidae) are separate lineages, presently considered as families.

The suborder Mengenillidia is represented in the Iberian Peninsula by a few species. Mengenillidia is distinct from the Stylopodia in that the males and females emerge to pupate externally from the host and the adult females are free-living like the males. In the Stylopodia the neotenic female remains endoparasitic, except for the extruded cephalothorax, and the males remain endoparasitic during the pupal stage.

Five families (Mengenillidae, Xenidae, Stylopidae, Lychnocolacidae and Elenchidae) and 41 species are represented in the Iberian Peninsula (Table I, pag. 7 ►). In Spain 35 species have been reported, 17 in Portugal, eight in the Canary islands, two in Madeira and one in Azores.

## 3. Diversity of Strepsiptera in the area of study

### 3.1. Mengenillidae

This small family shows the more plesiomorphic traits (both morphological and biological) among the extant Strepsiptera, namely the absence of adhesive pads in the male tarsomeres, free-living females and the use of apterygote insects as host. *Eoxenos laboulbenei* (Luna de Carvalho, 1953, 1960, 1985; Delgado *et al.*, 2014; del Río *et al.*, 2014) has been collected in the mainland Iberian Peninsula as well as in the Balearic and Canary Islands. *Mengenilla chobauti* Hofeneder (Luna de Carvalho, 1953, 1985; Kathirithamby, Delgado & Collantes, unpubl.) has been collected in the Iberian Peninsula and Canary Islands. Both species might belong to a group of cryptic species which are currently studied (Kathirithamby, Delgado & Collantes, unpubl.). A recently discovered undescribed species of *Mengenilla* in the Balearic Islands (del Río *et al.*, 2014) might belong to this group of cryptic species. Known hosts of *Eoxenos* and *Mengenilla* are species of the order Thysanura.

### 3.2 Elenchidae

This family is of worldwide distribution, including the Palaearctic Region. *Elenchus tenuicornis* (Luna de Carvalho, 1990) has been collected in Cabo Verde and Canary islands (Luna de Carvalho, 1985) and in Azores (Borges *et al.*, 2010). *E. tenuicornis* parasitizes several hemipterans of the family Delphacidae (Homoptera) (Lindberg, 1960).

Table I. Families, genera and species of Strepsiptera from the Iberian Peninsula and Macaronesian isles.

	SP.	Portugal	España	Madeira	Canarias	Azores
<b>Suborden Mengenillidia</b>	<b>2</b>	<b>2</b>	<b>2</b>	<b>–</b>	<b>2</b>	<b>–</b>
Mengenillidae	2	2	2	–	2	–
<i>Eoxenos laboulbenei</i>		•	•	–	•	–
<i>Mengenilla chobauti</i>		•	•	–	•	–
<b>Suborden Stylopida</b>	<b>39</b>	<b>14</b>	<b>33</b>	<b>2</b>	<b>6</b>	<b>1</b>
Elenchidae	1	–	–	1	1	1
<i>Elenchus tenuicornis</i>		–	–	•	•	•
Lychnocolacidae	1	–	1	–	–	–
<i>Lychnocolax hispanicus</i>		–	•	–	–	–
Stylopidae	31	10	28	–	4	–
<i>Halictoxenos spencei</i>		–	•	–	•	–
<i>Halictoxenos tumulorum</i>		•	•	–	•	–
<i>Hylechthrus rubi</i>		•	•	–	–	–
<i>Stylops andrenaphilus</i>		–	•	–	–	–
<i>Stylops borcherti</i>		–	•	–	–	–
<i>Stylops dinizi</i>		–	•	–	–	–
<i>Stylops dominiquei</i>		•	•	–	–	–
<i>Stylops duriensis</i>		•	•	–	–	–
<i>Stylops esteponensis</i>		–	•	–	–	–
<i>Stylops flavipedis</i>		•	–	–	–	–
<i>Stylops giganteus</i>		–	•	–	–	–
<i>Stylops gwynanai</i>		–	•	–	–	–
<i>Stylops ibericus</i>		•	•	–	–	–
<i>Stylops kinzelbachi</i>		–	•	–	–	–
<i>Stylops liliputanus</i>		–	•	–	–	–
<i>Stylops lusohispanicus</i>		•	•	–	–	–
<i>Stylops madrilensis</i>		–	•	–	–	–
<i>Stylops melittai</i>		•	–	–	–	–
<i>Stylops moniliaphagus</i>		–	•	–	–	–
<i>Stylops nassanowi</i>		•	•	–	–	–
<i>Stylops nitidiusculai</i>		–	•	–	–	–
<i>Stylops obsoletus</i>		–	•	–	–	–
<i>Stylops paracuellus</i>		–	•	–	–	–
<i>Stylops pasteelsi</i>		–	•	–	–	–
<i>Stylops praecocis</i>		–	•	–	–	–
<i>Stylops risleri</i>		–	–	–	•	–
<i>Stylops salamancanus</i>		–	•	–	–	–
<i>Stylops spencei</i>		–	•	–	–	–
<i>Stylops spretus</i>		–	•	–	•	–
<i>Stylops thwaitei</i>		•	•	–	–	–
<i>Stylops warnckeii</i>		–	•	–	–	–
Xenidae	6	4	4	1	1	0
<i>Paraxenos sphecedarum</i>		•	•	–	–	–
<i>Pseudoxenos atlanticus</i>		–	–	•	–	–
<i>Pseudoxenos heydeni</i>		–	–	–	•	–
<i>Pseudoxenos schaumii</i>		•	–	–	–	–
<i>Pseudoxenos seyrigi</i>		–	•	–	–	–
<i>Xenos vesparum</i>		•	•	–	–	–
<b>Total</b>	<b>41</b>	<b>16</b>	<b>35</b>	<b>2</b>	<b>8</b>	<b>1</b>

### 3.3. Lychnocolacidae

The genus *Lychnocolax* was historically placed as a genus in the family Myrmecolacidae (Kinzelbach, 1971; Kathirithamby, 1989), but a molecular phylogenetic analysis placed it as a different family and sister to Stylopidae, Xenidae, Elenchidae and Halictophagidae (McMahon *et al.*, 2011). Like Myrmecolacidae, Lychnocolacidae is found in Circum-Tropical, Australian, Oriental and Afrotropical Regions but not in the Palaearctic, although one species was found in light traps in Zaragoza province. It was described as a new species *Lychnocolax hispanicus* (Kathirithamby & Kifune, 1991), and might have been blown in by the winds from North Africa.

### 3.4. Stylopidae

Is the most speciose family of the order and with a wide distribution, only absent in Australia. All its members are parasites of Hymenoptera in the families Halictidae, Andrenidae, Colletidae and Sphecidae. Males of Stylopidae are easily distinguished by the 6-segmented antennae. In the Iberian Peninsula two

species of *Halictoxenos* (Kinzelbach, 1978), one of *Hylechthrus* (Luna de Carvalho, 1953) and 28 species in the genus *Stylops* (Luna de Carvalho, 1960, 1974, 1985) have been described. In the Canary Islands two species of *Stylops*, one of them endemic of this archipelago (Luna de Carvalho, 1985), and the two species of *Halictoxenos* have been described.

### 3.5. Xenidae

It is one of the most diverse families of Strepsiptera and has a worldwide distribution. Members of this family parasitize the order Hymenoptera, mainly the social Vespidae, solitary Sphecidae and wasps of the families Eumenidae and Crabronidae. Males of Xenidae have 4-segmented antennae. *Xenos vesparum* is a common species in the Palaearctic Region (Luna de Carvalho, 1953; Kathirithamby, Delgado & Collantes, unpubl.). Four species of *Pseudoxenos* (Monod, 1925; Luna de Carvalho, 1953, 1960) have been described from the Iberian Peninsula.

## 4. Main information resources

Information about Iberian Strepsiptera is scarce and dispersed in articles and works, which are difficult to trace. Here we offer some resources that can be useful for the identification of the species cited in the Iberian Peninsula and the Macaronesian islands.

### 4.1. General resources related with terminology, taxonomy and identification of Strepsiptera

As for the information published in Spanish we can only cite the chapter devoted to this order in the entomology book by Imms (Richards & Davies, 1984). There is no published handbook or guide of this group for the Central-Europe fauna however, the whole of the European fauna has been treated in the work by Kinzelbach (1978), which is the best source of information, even today, for this group. In relation to the Iberian fauna the works by Abdul-Nour (1969), Bolívar (1926) and, especially, the articles by Luna de Carvalho (1950a, 1950b, 1953, 1960, 1969 and 1974), are relevant. With respect to the Macaronesian fauna works studies by Kinzelbach (1967) and Luna de Carvalho (1985) are relevant. General information can be obtained in Jeannel (1951), Kathirithamby (1989), Luna de Carvalho & Kogan (1991) and Pohl & Beutel (2008).

### 4.2. Keys of the families, genera and species

Two studies are fundamental for the identification to the species level: Kinzelbach (1978) and Luna de Carvalho (1974).

### 4.3. Páginas web interesantes

- Kathirithamby, J. 2002. Strepsiptera. Twisted-wing parasites. The Tree of Life Web Project. <http://tolweb.org/tree?group=Strepsiptera>.
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