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Bibliographic abstract on parasitoids of the Order Strepsipterans (Insecta: Strepsiptera): A review

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Abstract

The objective of this study was to conduct a bibliographic summary of the parasitoids of the order strepsipterans. The mini review consists of a literature search on strepsipterans (Order: Strepsiptera). The research was conducted in studies related to the quantitative aspects of the Family, Genus and Species (taxonomic groups) and in conceptual aspects such as: neoteny, cryptic species, endoparasitic larva and parasitism. A literature search was conducted containing articles published from 1978 to 2021. The mini review was conducted in Goiânia, Goiás, from August to September 2021, through the Online Scientific Library (Scielo) and internet.

Keywords: Strepsipterans; Neoteny; Cryptic species; Endoparasitic larva

1. Introduction

The Order Strepsiptera is an order of tiny insects, with cosmopolitan distribution, consisting of nine extant families and about 600 described species. 1793 (in the description of the species *Xenos vesparum* Rossius, 1793 (Strepsiptera: Bahiaxenidae) (Figure 1) and are defined as entomophagous endoparasites, attacking insect species from 34 families distributed in seven orders, with the orders Homoptera and Hymenoptera being the most sought after with one family (Mengenillidae) attacking insects Apterygota (Thysanura) [1,2].

Aim

The aim of this study was to conduct a bibliographic summary of the parasitoids of the order strepsipterans.

2. Methods

The research was conducted in studies related to the quantitative aspects of the Family, Genus and Species (taxonomic groups) and also in conceptual aspects such as: neoteny, cryptic species, endoparasitic larva and parasitism. A literature search was conducted containing articles published from 1978 to 2021. The mini review was conducted in Goiânia, Goiás, from August to September 2021, through the Online Scientific Library (Scielo) and internet.

3. Concepts

Development: Holometabola complete metamorphosis (egg, larva, pupa, and adult). Strepsiptera exhibit hypermetamorphic development: first instars (planidia) are free-living and highly mobile. They locate and enter the body of a host. Subsequent instars are legless, grub-like internal parasites (Figure 1) [3].

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Distribution: Uncommon. Larvae and adult females are internal parasites of other insects. Approximately 5 family and 110 species in North America and 9 family and 530 species worldwide [3].

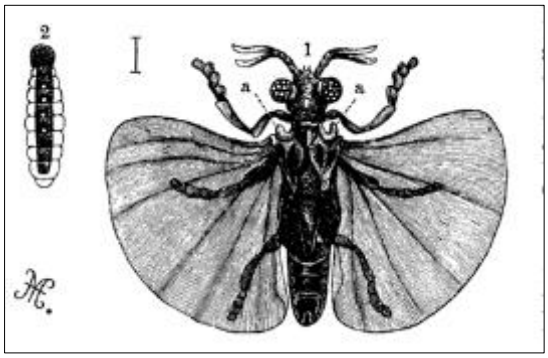

Figure 1 Male *Xenos peckii* Kirby 1813 i in her winged insect stage (1) and female *Xenos vesparum* Rossius, 1793 (Strepsiptera: Bahiaxenidae) in her neotenic stage (2); Source: https://en.wikipedia.org/wiki/Xenos_vesparum

The striking feature of this group of insects is the presence of forewings reduced to dumbbells, in adult males, and the larviform shape of adult females (neotenia) demonstrating a marked sexual dimorphism. Strepsiptera have two more families Bahiaxenidae and Mengenillidae [4,5].

3.1. Male

The adult male is free-living and winged with compound and spherical eyes, presenting a smaller number of relatively large ommatidia, very uncommon among living insects. Mouthparts are degenerate. The antennas are flabeled, conspicuous, with long processes in some segments. The prothorax and mesothorax are short, with the second having the first pair of wings reduced. The metathorax is sometimes ten times larger than the rest of the thorax and has a pair of large hindwings with little venation. They are short-lived, five to six hours as adults, and their only mission, in the emergence of the host, is to find and fertilize a female; located, by its pheromone, usually in bees or other insects (male size: 1 to 7 millimeters) (Figure 2) [5,6].

Figure 2 Male of a Strepsiptera; showing the structures (dumbbells) that are its front wings, just below the forelegs. The middle legs are under the extremely developed hindwings and are not illustrated; Source: https://www.passeidireto.com/disciplina/entomologia/? type=6&materialid=6036

3.2. Female

The female never has wings. In parasitic species it lacks legs, eyes, or antennae, with its head and chest fused together. It does not leave its host, spending all its life in its pupal envelope. The entire abdominal cavity of the adult female is filled with developing embryos. In its presence, the color and shape of the host's abdomen can be altered, and the host often becomes sterile. In species of the Mengenillidae family, they leave the host at the end of their last larval instar to

pupate externally and, after hatching, they are free-living and vermiform in appearance; with the presence of all other adult male characteristics such as eyes, mouthparts, antennae, legs and a ventral genital opening (female size: 2mm to 3cm) (Figures 3, 4, 5 and 6) [5,6,7,8].

Figure 3 The Female of a Strepsiptera is, in most cases, a neotenic endoparasite of the abdomen of insects of the orders Homoptera (with the female indicated by the letter "a" at the end of the abdomen); Source: https://pt.wikipedia.org/wiki/Strepsiptera#cite_ref-encyclo_6-6

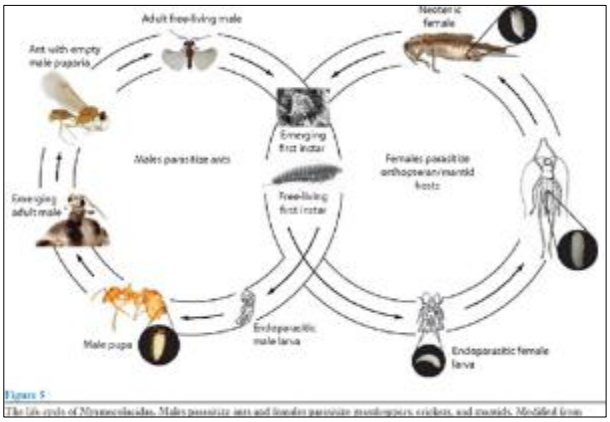

Figure 4 Host-parasitoid associations in Strepsiptera. Life cycle of a Strepsiptera; Source: https://www.semanticscholar.org/paper/Host-parasitoid-associations-in-Strepsiptera.-Kathirithamby/ba2e9f69ad43fafff96e52de3dc647b092055b7f/figure/5

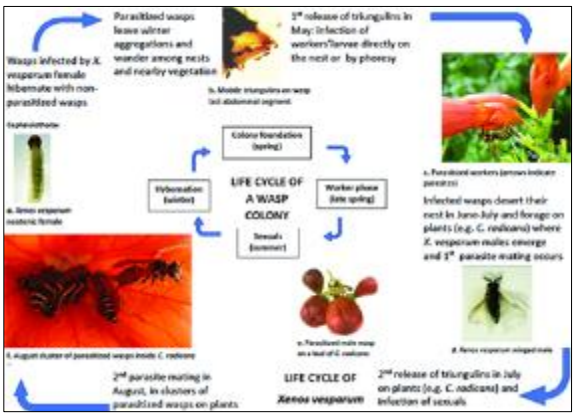

Figure 5 The life cycle of the strepsipteran *Xenos vesparum* Rossius, 1793 (Strepsiptera: Bahiaxenidae) in parallel with the lifecycle of its primary host, the paper wasp *Polistes dominula* (Christ, 1791) (Hymenoptera: Vespidae). a) female. An *X. vesparum* extragenital canal opens in the cephalothorax of the female, where both mating and larval escape occur. b) Triungulins escaping from female canal. c) Parasitized workers on *Campsis radicans* L. (Bignoniaceae). Note the distortion of wasp abdomen due to parasites (arrows). d) *X. vesparum* male. Observe the striking sexual dimorphism of

the parasite. e) A parasitized P. dominula male. f) Aggregation of parasitized wasps; Source: Photos by Laura Beani. https://doi.org/10.1371/journal.pone.0205201.g001

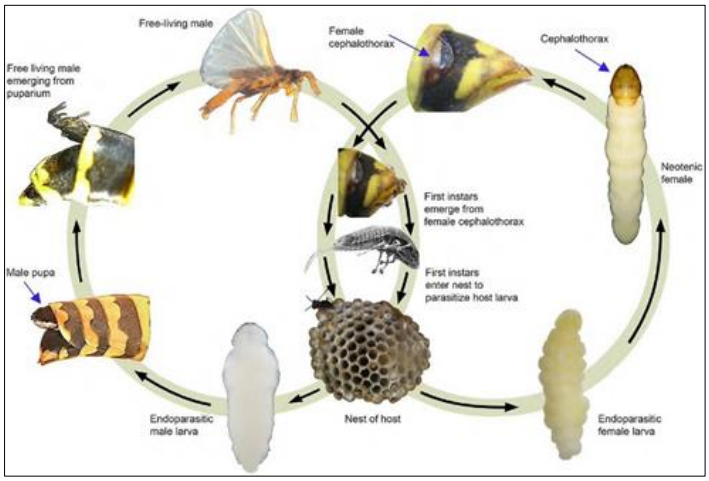

Figure 6 He knew about parasitoid wasps, but not about wasp parasites. In this case *Xenos vesparum* Rossius, 1793 (Strepsiptera: Bahiaxenidae), which spends its entire life cycle attached to the abdomen of its host; Source: https://twitter.com/eltoniio/status/1175979478117470208

Neoteny - When a non-terminal star develops reproductive characteristics of the adult, including the ability to locate a sexual partner, copulate and deposit eggs (or larvae) of a conventional manner, we call neoteny. It occurs in all the members of the Strepsiptera order (Figures 7 and 8) [9,10].

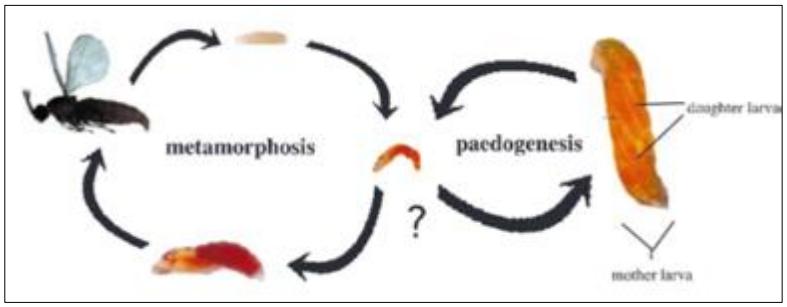

Figure 7 Life cycle of *Mimocalothyrza speyeri* Hintz 1919 (Coleoptera: Cerambycidae). The switch between metamorphosis (left) and paedogenesis (right) seems to be environmental, specifically triggered by bad food; Source Image credit: Hodin & Rididiford, 2000

Figure 8 (Neotenic Female) example: *Mimocalothyrza speyeri* Hintz, 1919 (Coleoptera: Cerambycidae); Source: https://collectionneurdinsectes.com/product/mimocalothyrza-speyeri/

3.2.1. Cryptic species

The cryptic term species is applied to taxonomic units whose components are confused with other different species when "traditional" characters, mainly morphological, are used. Its recognition is not evident and depends on comparisons based on molecular biology (Figure 9) [9,10,11].

Figure 9 Cryptic species (Example); Source: chrome-extension://efaidnbmnnnibpcajpcglclefindmkaj/viewer.html

3.2.2. Endoparasitic Larva

On entering the host, the first instar undergoes hypermetamorphosis and molts to an apodous second instar. Three endoparasitic larval stages undergo apolysis without 230 ecdysis. The sexes are distinguishable from the third larval instar onward, when males have prolegs [9,10,11].

3.3. Neotenic Female

Except for the putatively basal Mengenillidae, in which adult females are wingless and freeliving, all female strepsipterans (which range in size from 2.5 mm to 3.6 cm) are neotenic and remain permanently endoparasitic in the host. Only the cephalothorax is visible externally; the rest of the cylindrical body stays within the host and is devoid of all adult insect characters. In neotenic females that have overwintered, the gut is degenerate and filled with hemolymph (Figure 10) [11].

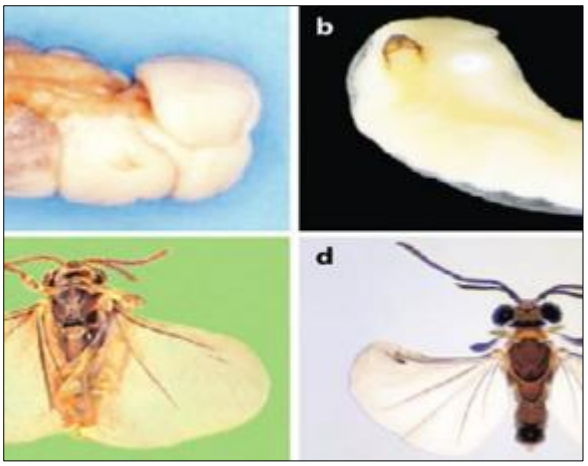

Figure 10 (a) Female *Stichotrema dallatorreanum* Hofeneder, 1910 (Strepsiptera: Myrmecolacidae), a parasitoid of *Segestidae novaeguineae* (Brancsik, 1874) (Orthoptera: Tettigoniidae), from Papua New Guinea. (b) Female *Caenocholax fenyesi* Pierce, 1909 (Strepsiptera: Myrmecolacidae) lato sensu parasitic in a cricket from Tapachula, Mexico (total length = 4 mm). (c) *Caenocholax groehni* Kathirithamby & Henderickx, 2008 (Strepsiptera: Myrmecolacidae) from Baltic amber (total length = 1.35 mm). (d) Male *C. fenyesi* lato sensu from Tapachula, Mexico (total length = 0.92 mm)

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, 1910 (Strepsiptera: Myrmecolacidae) Hofeneder from Papua New Guinea whereas it is present in *Xenos vesparum* Rossius, 1793 (Strepsiptera: Bahiaxenidae) from Italy, which overwinters in its host. 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 (Figure 11) [11].

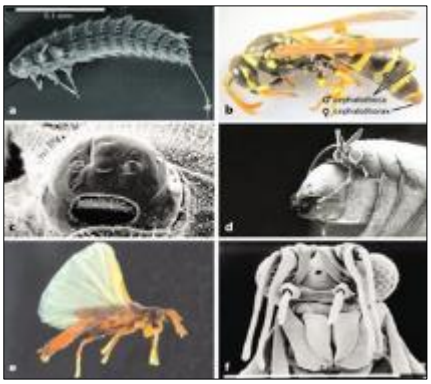

Figure 11 (a) Scanning electron micrograph (SEM) of first instar larva of *Stylops* sp., a parasite of *Andrena* sp. (Hymenoptera) from Japan. (b) *Polistes dominulus* (Christ) with two extruded male pupae and one female cephalothorax (total length of *Polistes* = 15.4 mm). (c) SEM of female cephalothorax 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* frontal view

4. Studies performed

4.1. Study 1

4.1.1. Parasitism by Strepsipterans

Among the bees collected on *Hydrangea serrata* (Thunb, 1830) (Hydrangeaceae) and *Aruncus dioicus* (Walter, 1930) (Rosaceae) flowers, *Lasioglossum apristum* (Vachal, 1903) (Hymenoptera: Halictidae) was the most collected parasitized species (12.3%, 117 of 953 *L. apristum* individuals were parasitized, all by *Halictoxenos borealis* (Kifune, Hirashima & Maeta, 1982) (Strepsiptera, Stylopide) (Figures 12 and 13). The number of species and individuals of all bees collected in the 2010 and 2011 sampling, as well as their parasitic strepsipterans, all collected *L. apristum* bees and their *H. borealis* parasites were female. Eight bees were parasitized by two strepsipterans and one bee was parasitized by three strepsipterans. None of the parasitized bees collected from *H. serrata* had developed ovaries (N = 105) and they were likely infertile. All of the strepsipterans were mature females and contained first-instar larvae in their cephalothorax. The plant species (105 parasitized, 695 unparasitized from *H. serrata* and 12 parasitized, 141 unparasitized from *A. dioicus* (X-squared = 2.8547, DF = 1, P= 0.091) [12].

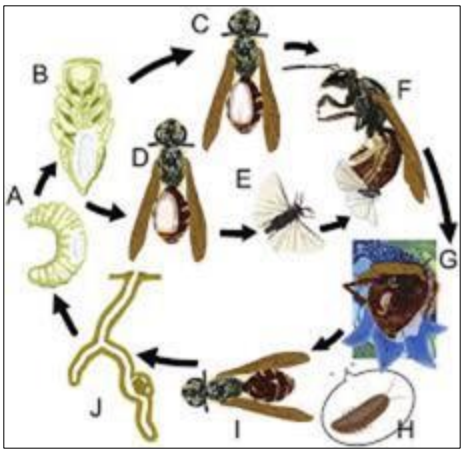

Figure 12 Life history of the strepsipteran *Halictoxenos borealis* (Kifune, Hirashima & Maeta, 1982) (Strepsiptera, Stylopide). (A and B) The endoparasitic larva grows in the host's abdomen. (C) The mature female extrudes her cephalothorax in the interstice between tergites IV and V. (D). The maturing male pupates within the host's abdomen. (E) The adult male emerges from the host. (F) The winged free-living male copulates with an endoparasitic adult female.

(G and H) First-instar larvae are released onto a flower. J) and (I First-instar larvae attach themselves to a bee and are carried to its nest, where they parasitize the bee's offspring

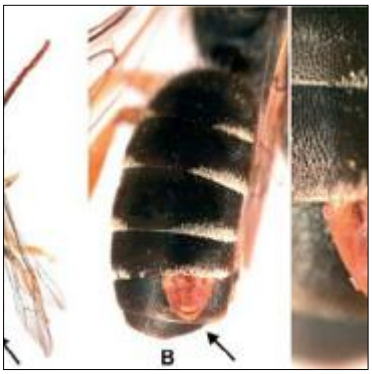

Figure 13 *Halictus simplex* Blüthgen, 1923 (Hymenoptera: Halictidae) parasitized by *Halictoxenos tumulorum* Perkins, 1918 (Strepsiptera: Stylopidae). Arrows point at the female cephalothorax extruding exterior of host. A – dorsal view of the host. B – detail of the host abdomen, in dorso-lateral view. C – detail of the cephalothorax of *H. tumulorum*

4.2. Study 2

4.2.1. Manipulation of host bee behavior by strepsipteran parasites

The behavior of parasitized and non-parasitized bees in *Hydrangea serrata* (Thumb., 1830) (Hydrangeaceae) inflorescences was observed both directly and indirectly in contrast, parasitized bees walked over inflorescences and folded their abdomens downwards and pressed them against the flowers without collecting pollen. Time sequences of eight bee individuals (three non-parasitized and five parasitized) confirmed that the behavior of bees in flowers differed between non-parasitized and parasitized bees. Non-parasitized bees exhibited behavioral units in the order of 1-23, while the parasitized bees exhibited behavioral units it was 1-2-4, as a reminder, (3) it is collecting pollen and (4) it is bending the abdomen down and pressing the dorsal abdomen against the flower only non-parasitized bees collected pollen, and only parasitized bees exhibited behavioral unity 4 [13].

4.3. Study 3

This is believed to be mediated by chemical cues released by virgin females. Here, we report the first identification and synthesis of a female-produced strepsipteran sex pheromone, (3*R*,5*R*,9*R*)-3,5,9-trimethyldodecanal, from *Stylops melittae* Kirby, 1802 (Strepsiptera: Stylopidae), a species parasitizing andrenid bees. We found this highly EAD-active compound to be present in cephalothoraxes of and released from unmated females, and synthetic samples proved to be extremely attractive when offered in the field during the swarming period of the males. The structural features of this new natural compound may further support the re-establishment of the Strepsiptera (Figure 14) [13].

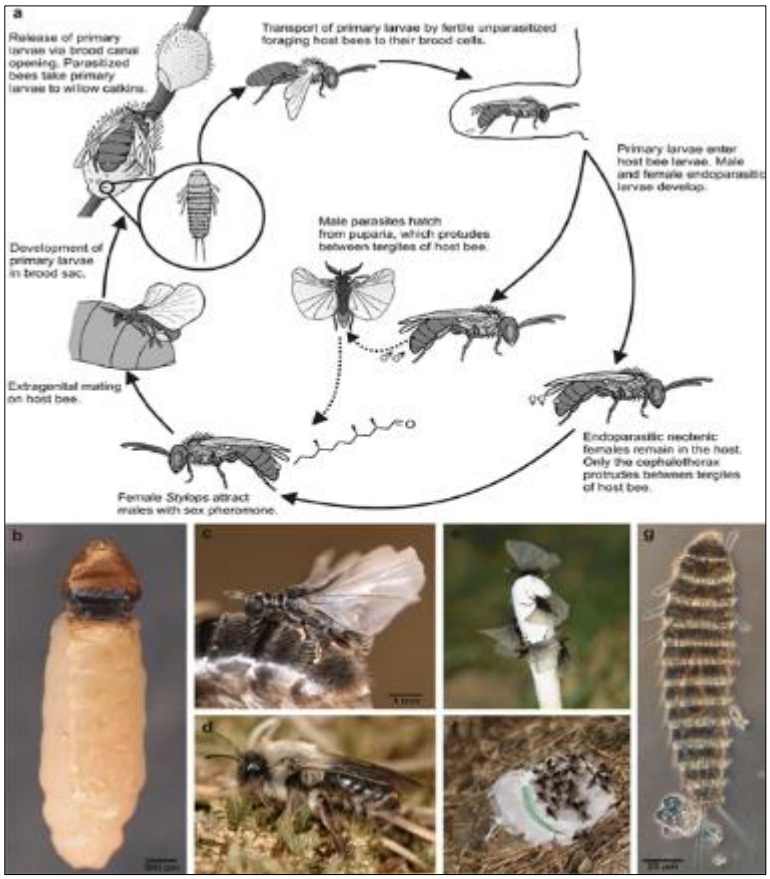

Figure 14 *Stylops melittae* Kirby, 1802 (Strepsiptera: Stylopidae); Source: https://link.springer.com/article/10.1007/s10886-012-0215-6

4.4. Study 4

4.4.1. Bahiaxenidae Family

Bahiaxenos relictus Bravo, Pohl, Silva-Neto & Beutel, 2009 (Strepsiptera: Bahiaxenidae) is the sole member of the family Bahiaxenidae, a type of winged insect. It was only discovered and described in 2009 from relictual sand dunes associated with the São Francisco River in Bahia, Brazil. It is the most basal living member of the order Strepsiptera, so is the sister taxon to the remaining extant species. It is known from only a single male specimen, and its biology is unknown (Figure 15) [14].

Figure 15 *Bahiaxenos relictus* Bravo, Pohl, Silva-Neto & Beutel, 2009 (Strepsiptera: Bahiaxenidae); Source: https://www.researchgate.net/figure/Figura-1-Bahiaxenos-relictus-Bravo-Pohl-Silva-Neto-Beutel-foto-do-especime-tipo_fig1_292155290

4.5. Study 5

4.5.1. Mengenillidae Family

All species within this group are obligate endoparasites of insects and, except in Mengenillidae, only the first instar larvae (host-seeking stage) and the adult males (which live just long enough to seek and fertilize a female are free-living. Males and females of this order exhibit an extreme form of sexual dimorphism. Hosts include apterygote insects, Polyneoptera, Hemiptera, and seven orders (34 families) of holometabolous hexapods, namely Zygentoma, Blattodea, Mantodea, Orthoptera, Hemiptera, Diptera and aculeate Hymenoptera [15,16,17].

The Mengenillidae represent the second branch and form the sister taxon to the remaining Strepsiptera, a group known as Stylopidia. Mengenillidae parasitize *Zygentoma*, and in contrast to the other strepsipteran species, both male and female larvae emerge to pupate externally and are free-living as adults [16,17].

There is only one valid species in the genus *Eoxenos*. *Eoxenos laboulbenei* Peyerimhoff, 1919 has been recorded from Algeria, the Canary Islands and the Iberian Peninsula, France, Italy including Sardinia and Sicily, Libya, and Greece [18].

The known hosts are *Tricholepsima aurea* (Dufour), *Neoasterolepisma crassipes* (Escherich), *Neoasterolepisma* wasmanni (Moniez) and *Neoasterolepisma pallida* Molero, Gaju and Bach (Zygentoma) [18].

The genus *Mengenilla* is restricted to Palearctic, Afrotropical, Australian and Oriental regions. *Mengenilla chobauti* Hofeneder, 1910 and *Mengenilla parvula* Silvestri, 1941 occur in the Mediterranean region. *Mengenilla chobauti* has been recorded from North Africa, Spain, Portugal, Crete, Malta, and Italy including Sicily and Sardinia and has the widest distribution of all described Mengenilla species. *Mengenilla parvula* Silvestri, 1941. is found only in Sicily. The known hosts of *Mengenilla* are *Ctenolepisma* (Figures 16, 17, 18, 19, 20, 21 and 22). [19,20, 21,22].

Figure 16 *Mengenilla moldrzyki* sp. n. ♂ A Head frontal view B Head, thorax and anterior part of abdomen, dorsal view;Source:https://www.researchgate.net/publication/227180088_A_new_species_of_Mengenilla_Insecta_Strepsiptera_from-unisia

Figure 17 *Mengenilla moldrzyki* sp. n. ♀, lateral view; Source: https://en.wikipedia.org/wiki/Mengenillidae#/media/File:Mengenilla_moldrzyki.jpg

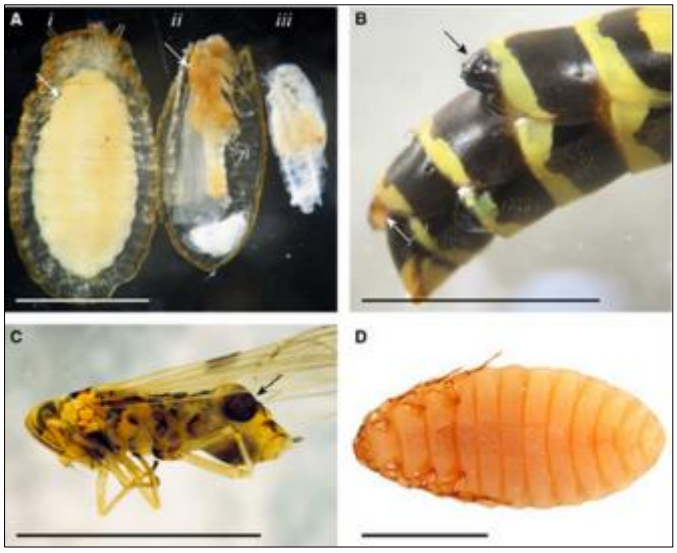

Figure 18 A, *Mengenilla* sp.: (i) Neotenic female (arrow) enclosed in a puparium. (ii) Adult male (arrow) emerging from a puparium with shed pupal and prepupal cuticles at the base of the puparium. (iii) Shed cuticle of male prepupa (taken out of the puparium). B, paper wasp *Polistes dominula* (Christ, 1791) (Hymenoptera: Vespidae) parasitized by male *Xenos vesparum* Rossius, 1793 (Strepsiptera: Xenidae), male cephalotheca (black arrow), female cephalothorax (white arrow). C, planthopper *Sogatella furcifera* (Horváth, 1899) (Hemiptera: Delphacidae) parasitized by *Elenchus japonicus* Esaki & Hashimoto, 1931 (Strepsiptera, Elenchidae), male cephalotheca (black arrow). D, *Eoxenos laboulbenei* Peyerimhoff, 1919 (Strepsiptera: Mengenillidae) neotenic female, ventral view; Source: https://www.researchgate.net/figure/A-Mengenilla-sp-i-Neotenic-female-arrow-enclosed-in-a-puparium-ii-Adult-male_fig10_278037889

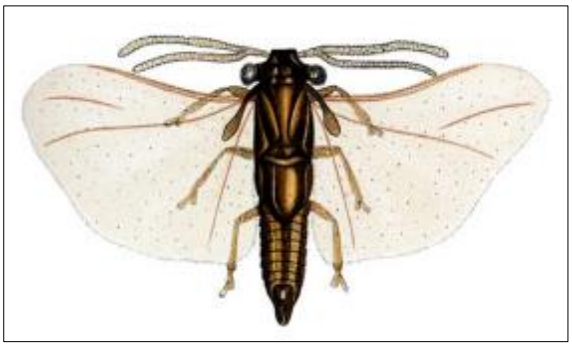

Figure 19 Elenchus; Source: http://tolweb.org/Elenchus/66597

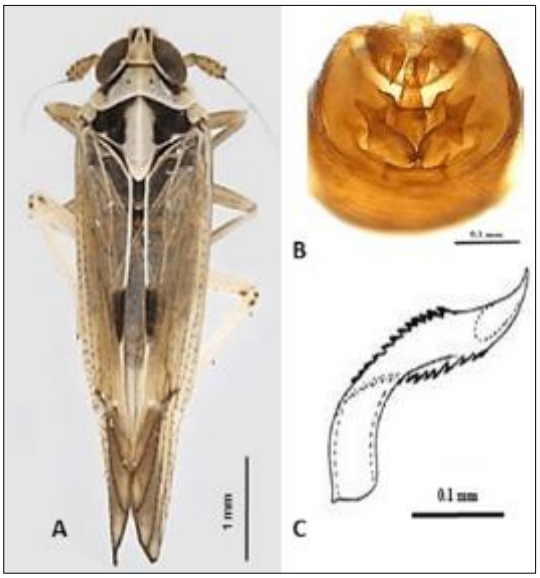

Figure 20 *Sogatella furcifera* (Horvath), (A) habitus dorsal view (originals); (B) genital segments (Bartlett, 2020); (C) aedeagus (Asche and Wilson, 1990). *Sogatella vibix* (Haupt) Distribution: Palearctic, Ethiopian, and Oriental regions; Australia and the Western Pacific (Asche and Wilson, 1990); Source: esearchgate.net/figure/Sogatella-furcifera-Horvath-A-habitus-dorsal-view-originals-B-genital-segments_fig3_344191526

Figure 21 *Xenos vesparum* Rossius, 1793 (Strepsiptera: Xenidae), a parasitic insect, escapes from a paper wasp; Source: piegel.de/consent-a-?targetUrl=https%3A%2F%2Fwww.spiegel.de%2Fwissenschaft%2Ffremdgesteuerte-wespen-a-80f94213-

Figure 22 *Eoxenos laboulbenei* Peyerimhoff, 1919 (Strepsiptera: Mengenillidae)

4.6. Study 6

4.6.1. Xenos Vesparum Rossius, 1793 (Strepsiptera: Xenidae)

Xenos vesparum is a species of parasitic insect of the genus Strepsiptera which are endoparasites of paper wasps in the genus *Polistes* (most commonly *Polistes dominula* (Christ, 1791) (Hymenoptera: Vespidae) which was first described in 1793. Like other members of this family, *X. vesparum* exhibits a peculiar style characteristic of life and demonstrates extensive sexual dimorphism.

4.6.2. Host manipulation

Worker wasps infected with *X. vesparum* seem to have their behavior modified because they act as if they were future queens and stop working, leaving the nest before future founders and uninfected males do and form aggregations outside the nest. When future uninfected queens leave the nest to go to these mating sites, this provides an area where infected and uninfected wasps mix, and is often where the release of infective larvae occurs. As the parasite does not change the male wasp's behavior, it is a "dead end" for the female *X. vesparum*, as male wasps do not join these large aggregations and provide little opportunity for the parasite to receive a mate (Figure 23).

Figure 23 *Polystes* sp. parasitized by three parasites *Xenos vesparum* Rossius, 1793 (Strepsiptera: Xenidae); Source: https://stringfixer.com/pt/Xenos_vesparum

In addition, the male wasp dies before winter, eliminating the chance for the larvae to spread into hibernating aggregates. However, if infected with a male parasite, the male wasp is not a "dead end" because the free-living male parasite can emerge and fly to a suitable mate within mating aggregations. This may explain the recorded preference of *X. vesparum* larvae for infecting female wasps.

A trend observed in paper wasps infected with this parasite is that they appear to exhibit a strong preference for gathering in trumpet bushes (*Campsis radicans* (L.) Seem ex Bureau 1867 (Bignoniaceae). This indicates a likely case of co-evolution between parasite and host, as wasps are manipulated to prefer trumpet bushes that provide shelter and

excellent nutrition for the wasp, increasing its chance of survival and, by extension, also increasing the parasite's chances.

In addition, the preference for a specific type of plant allows fora greater chance of the parasite to spread because many forage wasps are athered in one location, providing a vector so that the released infective larvae reach the nest and infect the young wasps [23, 24].

5. Conclusion

The striking feature of this group of insects is the presence of forewings reduced to dumbbells, in adult males, and the larviform shape of adult females (neotenia) demonstrating a marked sexual dimorphism. Strepsiptera have two more families Bahiaxenidae and Mengenillidae.

Compliance with ethical standards

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Disclosure of conflict of interest

No conflict of interest statement.

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