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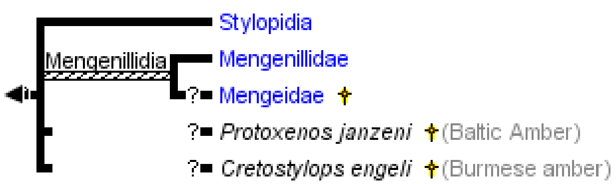
Jeyaraney Kathirithamby



Relationships after Kinzelbach 1978.

Containing group: Endopterygota

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Strepsiptera

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Strepsiptera are obligate parasites of insects, with hosts ranging across 7 orders and 34 families. The name of the group is derived from the Greek words for twisted (*streptos*) and wing (*pteron*) and refers to the peculiar twisted wing of the male's hind-wings while in flight. Representatives of the suborder Mengenillidia generally show more primitive characteristics (fig. 1). The Mengenillidae parasitize Thysanura (Lepismatidae), the only known order in the sub-class Apterygota to be attacked by strepsipterans, while Mengeidae are known only from fossil males from Baltic amber. We have very little information about their life history, therefore.

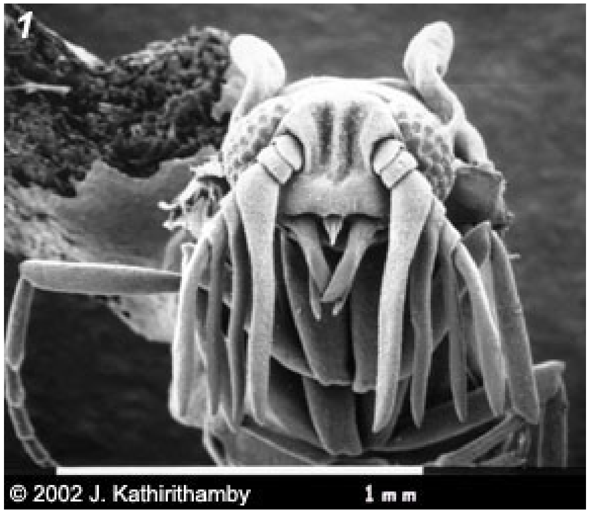


Figure 1. Adult male: *Mengenilla* sp. (Mengenillidae) (Northern Territory, Australia). Copyright © 2002 J. Kathirithamby

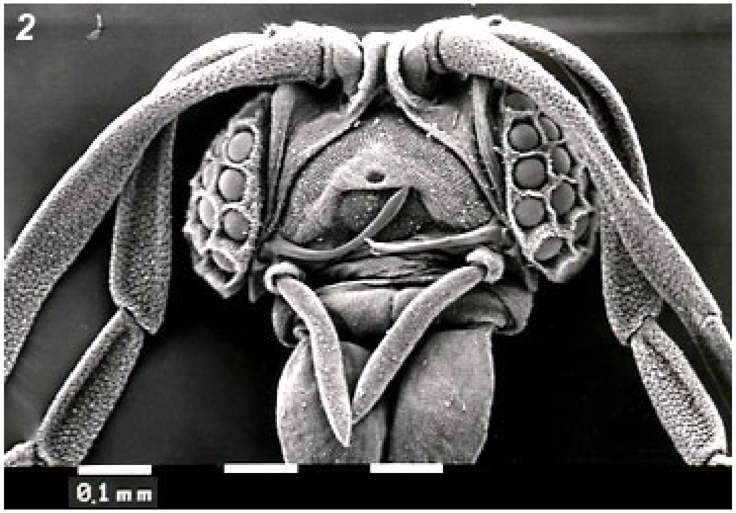
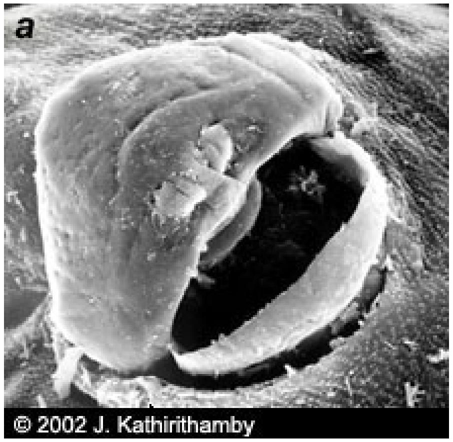
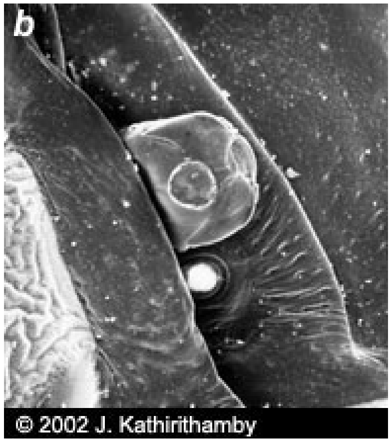


Figure 2. Adult male: *Myrmecolax rossi* Bohart (Myrmecolacidae) (Queensland & Northern Territory, Australia). From Kathirithamby (1993). Copyright © 1993 CSIRO, reproduced by permission.

Strepsiptera exhibit extreme sexual dimorphism, which is most pronounced in the suborder Stylopidia. Strepsipteran males emerge from the host after endoparasitic pupation in the host. Adult males are free-living, and their sole mission is to find and fertilize a female. They have reduced forewings and fan-shaped hind wings, branched antennae, and raspberry-like eyes (title image and fig. 2); the latter are very unusual among living insects and form a modern counterpart to the structural plan proposed for eyes of trilobites (Kinzelbach 1971, 1990, Kathirithamby 1989, Buschbeck et al. 1999).



a. *Elenchus varleyi* Kathirithamby (Elenchidae). (Queensland, Australia).



b. *Coriophagus rieki* Kinzelbach (Halictophagidae). (Canberra, ACT, Australia)

c. *Dipterophagus daci* (Drew & Allwood) (Halictophagidae). (Queensland, Australia)

Figure 3. Cephalothorax of adult females. Micrographs copyright © 2002 Kathirithamby

Females of the family Stylopidae are neotenic (i.e., they retain juvenile features even in adulthood) and totally endoparasitic in their hosts. They are highly modified morphologically, lacking adult external characteristics such as eyes, antennae, legs, wings and external genitalia (fig. 3). Apart from the adult males, the only free-living stages in this suborder are the viviparous 1st instar host-seeking larvae (fig 4). In contrast, males and females in the family Mengenillidae leave the host at the end of the last larval instar to pupate externally (fig. 5, 6). After eclosion, the females are free-living, with the presence of all other adult characteristics such as eyes, mouthparts, antennae, legs and a ventral genital opening, but with the absence of wings (fig. 7).

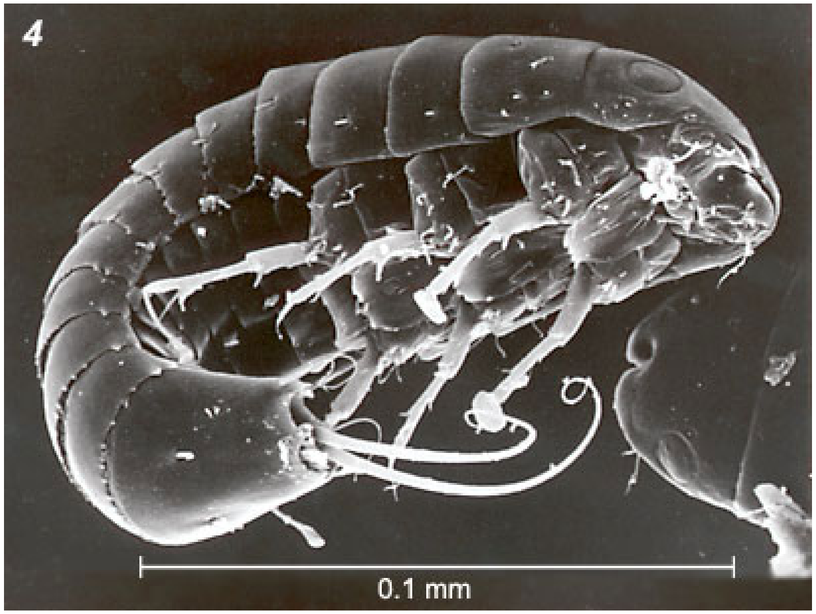


Figure 4. 1st instar free-living larva: *Stichotrema dallatorreanum* Hofeneder (Myrmecolacidae) (Papua New Guinea). From Kathirithamby & al. (1998). Copyright © 1998 [Taylor & Francis](#).

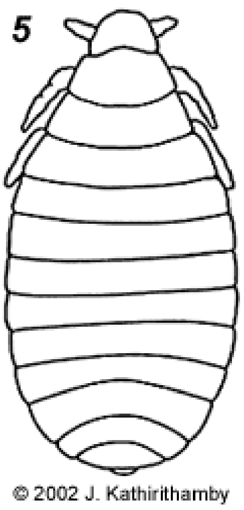


Figure 5. Free-living female pupa: *Mengenilla chobauti* Hofeneder

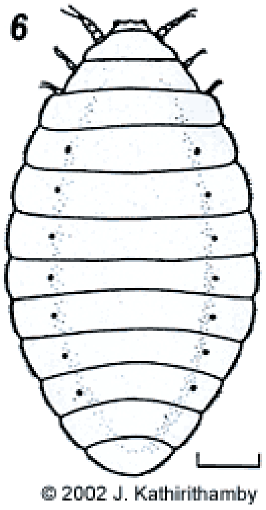


Figure 6. Free-living male pupa: *Eoxenos laboulbenei* De Peyerimhoff

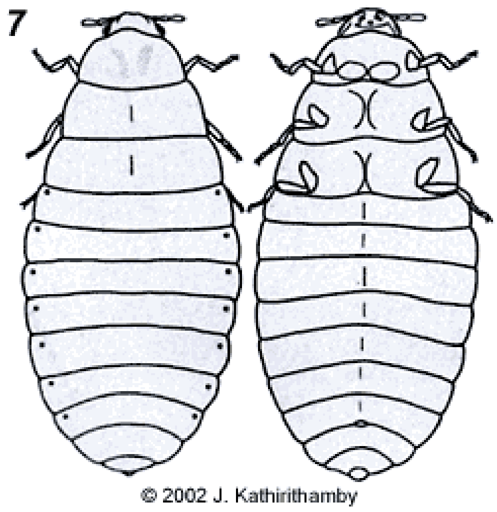


Figure 7. Free-living female of *Eoxenos laboulbenei* De Peyerimhoff (Mengenillidae)

(Mengenillidae) (Mengenillidae)

Drawings after Kinzelbach 1971.

The combination of morphological reduction and modification, and the bizarre and unusual life history of Strepsiptera, have puzzled biologists for over two centuries (Rossi 1793; Latreille 1809; Kirby 1802, 1813. 1815; Lamark 1816 Pierce 1909; Crowson 1960, 1981; Arnett 1963; Kinzelbach 1971, 1990; Kathirithamby 1989), and the Strepsiptera's phylogenetic position has been the most enigmatic question in ordinal level insect systematics (the "Strepsiptera problem", Kristensen 1981, see below).

Strepsiptera are cosmopolitan in distribution (Table 1), but are extremely difficult to locate, and one often has to find the host in order to find the female. To date, 596 species of Strepsiptera have been described and many more await description. Many of the described species are of free-living males that have come into traps. At present, since sites have been located where Strepsiptera can be collected, some of the species are being reared in the laboratory. Work on the extraordinary reproductive and developmental biology and behavioural ecology of this group is under way.

Table 1: Geographical distribution of the extant families of Strepsiptera.

Family	**Geographical Range**					
	Palaearctic	Afrotropical	Australian	Oriental	Neotropical	Nearctic
Mengenillidae	+	+	+	+	-	-
Corioxenidae	+	+	+	+	+	+
Halictophagidae	+	+	+	+	+	+
Elenchidae	+	+	+	+	+	+
Myrmecolacidae	+	+	+	+	+	+
Stylopidae	+	+	+	+	+	+
Bohartillidae	-	-	-	-	+	-
Callipharixenidae	-	-	-	+	-	-

Characteristics

Strepsiptera are characterized by the following synapomorphies:

1. Free-living host-seeking 1st instar larvae, which are produced viviparously by the neotenic female. Several hundred are produced which emerge from the female and seek new hosts. Sexual dimorphism does not exist in the 1st instars. These 1st instars are often known as "triungulin" larvae. This term was initially applied to the Meloidae, because of the presence of three claws on the legs. The term was later extended to the Rhipiphoridae and Strepsiptera, and refers to the active host-seeking larvae. However, morphologically, the 1st instar larvae of Strepsiptera do not resemble the Meloidae. The pulvillus of the 1st pair of legs is disk-like, and slender; single, spine-like tarsi are present on the 2nd and 3rd pair of legs, while there is absence of claws. In addition, the 1st instars have highly serrated tergites and sternites, presumably to enable them to cling to the hosts and/or vegetation while awaiting entry. The head bears antennae, mandibles, and labrium, and the abdominal setae are long, and are about a third or half the body length.
2. The 1st instar larvae moult, on entry into the host, to an apodous 2nd instar. Therefore, all Strepsiptera exhibit hypermetamorphosis (two morphologically distinct larval instars—the 1st larva and subsequent endoparasitic stages).
3. The endoparasitic larvae undergo apolysis without ecdysis (Kathirithamby et al. 1984) whereby the larvae moult but do not shed the old cuticle. It was found that *Elenchus tenuicornis* (Kirby) and *Stichotrema dallatorreanum* Hofeneder have four larval instars (Kathirithamby 1998).
4. In the male, at the last larval instar, the cuticle is sclerotized to form the puparium (fig. 8) (Kathirithamby 1983).

Figure 8. Male pupa of *Pseudoxenos* sp. (Stylopidae) between sternites of *Odynerus bicolour* Saussure (Hymenoptera).

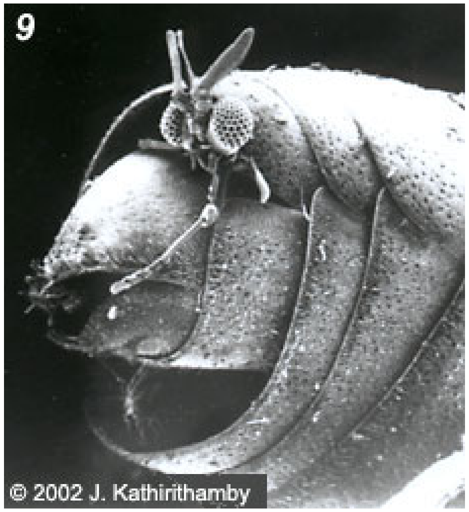


Figure 9. Adult male *Pseudoxenos* sp. (Stylopidae) emerging from puparium in *Odynerus bicolour* Saussure (Hymenoptera).

5. The free-living males have prominent branched antennae and raspberry-like eyes, reduced forewings and large hindwings (title image and fig. 2). They are short-lived, and their sole mission on emergence from the host (fig. 9) is to find and fertilize a female. There is no trochanter on the fore and middle legs, and the metacoxae are fused to the pleurosternum. The male has an aedeagus but no copulatory apparatus, such as parameres.
6. The females are neotenic (fig. 3) and totally endoparasitic in their hosts (except in the family Mengenillidae). The external cuticle on the ventral surface is analogous to the peritrophic membrane (found in the midgut of other insects) in adult females (Kathirithamby 2000). The whole abdominal cavity of the adult female is filled with developing embryos. Fertilization is by haemocoelic insemination, and reproduction is by haemocoelous vivipary.

Discussion of Phylogenetic Relationships

Kinzelbach (1971) divided the Strepsiptera into two suborders (Mengeillidia and Stylopidia) and nine families. Seven of these families are here united in the suborder Stylopidia, which is defined by many shared derived characteristics. The monophyly of this group has recently also been confirmed by Pohl's (2002) analysis of the 1st instar larvae of nearly all extant strepsipteran families.

The family Mengeidae is known only from a few fossil males from Baltic amber, all representing a single species, *Mengea tertiaria* (Menge). *Mengea* shares many plesiomorphic characters with the Mengenillidae, such as:

a. Similar round head capsule
b. Inwardly directed mandibles
c. Presence of abdominal stigmata
d. 5-jointed tarsi
e. Straight aedeagus.

Therefore, the two groups have often been associated with one another (Pierce 1908, 1909, 1918; Ulrich 1927, 1956; Bohart 1941, Luna de Carvalho 1956, 1959 1961, 1967; Kinzelbach 1969a; Riek 1970). Since all of the traits shared by *Mengea* and the Mengenillidae may be plesiomorphic, and there are a few tentative morphological similarities between *Mengea* and the stylopidian family Corioxenidae, Kinzelbach (1971)included the Mengeidae in the Stylopidia. However, in

1978 Kinzelbach placed the Mengeidae in the Mengenillidia. He says the formation of the labrium, free metacoxa, number of antennal joints, wing vein CuP are more plesiomorphic than the Mengenillidae, and the recent Mengenillidae may be thought to be derived from Mengeidae. Since females are unknown it will be regarded as a sister group of the Mengenillidae. Hence the phylogenetic position of the Mengeidae will remain uncertain until additional specimens are found which allow a more detailed analysis of the morphology and life history of this fossil group.

Relationship of Strepsipterans to Other Insects

Strepsiptera are a monophyletic group (Henning 1981). In recent years, four phylogenetic placements of these insects have been proposed:

1. Sister group to the Endopterygota. Kristensen (1991, 1995) noted that the position of Strepsiptera may not be within Endopterygota since:
   - the pupal stage is preceded by a couple of pharate instars (Whiting et al. 1997 interpreted this as the 2nd instar) with external wing buds
   - larval eyes are carried over to the adult stage

   These two characters are plesiomorphic within Endopterygota. However, neither the 2nd instar nor any of the other endoparasitic larval stages in the male have external wing buds (Kathirithamby et al. 1984). The pupal stage in the male begins when the 4th instar larval cuticle is sclerotized to form the puparium (Kathirithamby et al. 1984). Within this puparium there are three pupal instars which have external wing buds. The endoparasitic development in the male is therefore holometabolous. In the neotenic female (except in the Mengenillidae), the pupal stage is lost secondarily (Kathirithamby 2000). The structure of the larval eyes is being investigated (Kathirithamby unpublished).
2. Crowson (1960, 1981) placed Strepsiptera within the coleopteran suborder Polyphaga, as sister to Rhipiphoridae. This theory was based on derived features in rhipiphorids which he said were similar to Strepsiptera:
   - active host-seeking 1st instar larva
   - hypermetamorphosis from a 1st instar larva to apodous endoparasitic larvae
   - flabellate antennae
   - reduced forewings (in some genera)

   The above morphological characters shared by Strepsiptera and Rhipiphoridae have been erroneously interpreted:
   - active host-seeking stage and hypermetamorphosis have arisen once in the Exopterygota and five times in the endopterygota;
   - flabellate antennae are found in many insects;
   - as pointed out by Kathirithamby (1989) and Pix et al. (1993), the reduced forewings in Strepsiptera are neither morphologically nor functionally similar to the elytron in Coleoptera.
3. Handlirsch (1903), Boerner (1904) and Shipley (1904) placed Strepsiptera as a sister group to Coleoptera, and Kinzelbach (1971, 1990) and Kathirithamby (1989, 1991) argued that this placement was based on only one character: posteromotorism (use of the hind wings for flight). The venational characters supporting the sister group relationship between the Coleoptera and Strepsiptera (Kukalova-Peck and Lawrence 1993) were disputed by Whiting and Kathirithamby (1995).
4. The hypothesis that the Strepsiptera are a sister group to true flies (Diptera) is based on both morphological and molecular evidence, and has been championed by Whiting and Wheeler (1994) and Whiting et al. (1997), but remains controversial.
   - Whiting and Wheeler (1994) published a short note indicating that a phylogenetic analysis of 18S ribosomal DNA suggested that Strepsiptera were related to Diptera. No data or details of the analysis were included in the note, but this information eventually appeared in Whiting et al. 1997. The authors further suggested that the reduced, mesothoracic wings of strepsipteran males may be homologous to the halteres (on the metathorax) of dipterans, and that their presence on different thoracic segments is due to homeotic mutation.
   - Carmean and Crespi (1995), in response, provided an analysis of 13 18S ribosomal DNA sequences, and showed that the branches leading to Diptera and Strepsiptera were both very long. They suggested that the grouping of these taxa in a parsimony analysis of the data might be artifactual, caused by long-branch attraction (Felsenstein 1978).
   - Chalwatzis et al. (1996) analysed 18S rDNA of 19 insect species, and similarly found a grouping of Strepsiptera plus Diptera, even though they used distance methods (with several distance measures) that would be affected by long-branch attraction under different conditions than parsimony methods.
   - Whiting et al. (1997) presented their complete analysis, using parsimony methods, of 85 18S rDNA sequences and 52 28S rDNA sequences, as well as morphological data. This analysis also supported a grouping of Strepsiptera plus Diptera.
   - Huelsenbeck (1997) showed that the data set of 13 18S ribosomal DNA sequences used by Carmean and Crespi (1995), when analysed with maximum likelihood methods, yielded a tree with Strepsiptera as sister to Coleoptera. He suggested that long branch attraction is the cause of the placement of Strepsiptera with Diptera when parsimony methods are used.
   - Rokas et al. (1999) investigated the potential of an intron insertion site as a phylogenetic character. They found that the en homeobox gene of *Stichotrema dallatorreanum* lacks the derived intron insertion shared by representatives of Diptera and Lepidoptera. They thus argued against a close affiliation

between Strepsiptera and Diptera.
- Huelsenbeck (2001) observed that quality and quantity of morphological data available are limited, and that it is molecular data which hold the promise to solving the problem. The two ribosomal genes available, 18S and 28S, produced different placements of Strepsiptera. He states that more molecular data are needed to solve the phylogenetic placement of Strepsiptera.

Therefore the position of Strepsiptera among Insecta is still not solved, but work is being carried out on molecular and morphological data to try and resolve the question of the placement of Strepsiptera. Collaborating laboratories are: Jeyaraney Kathirithamby and Peter Holland (Oxford), John Huelsenbeck (San Diego) and Spencer Johnston (Texas A&M).

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Information on the Internet

- Strepsiptera. Hans Pohl's Strepsiptera page with many great images.
- Systematics, Developmental Biology and Biodiversity of Strepsiptera (Insecta). Jeyaraney Kathirithamby, Oxford University.
- Checklist for Strepsiptera. Australian Faunal Directory.
- An insect with 100 eyes has left scientists, well, surprised. 1999 Scientific American exhibit about Buschbeck et al.'s research on the eyes of strepsipteran males.

Title Illustrations

Scientific Name	Elenchus tenuicornis
Location	Oxford, UK
Comments	x270
Reference	Kathirithamby, J. 1989. Review of the order Strepsiptera. Systematic Entomology 14:41-92.
Specimen Condition	Dead Specimen
Sex	Male
Life Cycle Stage	adult
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