



## DIVERSITY AND BIOLOGY OF THE INDIAN STREPSIPTERA WITH A PICTORIAL KEY

POULAMI HUI<sup>1</sup>, SUKHENDU ROY<sup>2</sup> AND NILADRI HAZRA<sup>1\*</sup>

<sup>1</sup>Entomology Research Unit, Department of Zoology, The University of Burdwan, Burdwan, Purba Bardhaman 713104, West Bengal, India

(moupou1997@gmail.com; ORCID ID: 0000-0003-1455-7427);

<sup>2</sup>Department of Zoology, Gushkara Mahavidyalaya, Guskara, Purba Bardhaman 713128, West Bengal, India

(sukhenduroy2512@gmail.com; ORCID ID: 0009-0008-2584-6762)

\*Email: nhazra@zoo.buruniv.ac.in (corresponding author): ORCID ID 0000-0001-8149-9445

### ABSTRACT

**Strepsiptera is a monophyletic group of entomophagous, obligate endoparasites, styloping a wide range of insect hosts belonging to 34 families of Zygentoma, Polyneoptera, Paraneoptera, and Holometabola. So far 30 species in 14 genera and six families of Strepsiptera are known from India. The zoogeographic distribution of the Indian species of Strepsiptera and their known hosts are presented. The biology of *Halictophagus australensis* Perkins has been explored in detail. Stylopisation of *Cofana spectra* Distant (Hemiptera: Cicadellidae) by *H. australensis* lengthens the life span of *C. spectra*. A pictorial key to the Indian species of Strepsiptera is presented.**

**Key words:** Strepsiptera diversity, biology, endoparasite, key, hypermetamorphosis, primary larva, stylopization, ecology, distribution, India

The Strepsiptera (commonly stylops, twisted-winged parasites) are a highly perplexing group of the Insecta that include entomophagous, obligate endoparasitic taxa (Greek *strepsi* – twisted, *pteron* – wing) (Pierce, 1909; Ulrich, 1943; Kinzelbach, 1971; Kathirithamby, 1989, 2009; Tröger et al., 2023). The Strepsiptera exhibit haemocoelous viviparity and also hypermetamorphosis, where the primary larva is the host-seeking, free-living stage. The Strepsiptera display a wide range of peculiar phenotypic and genetic traits along with conspicuous sexual dimorphism, whereby little external morphological similarities occur between adult males and females. The females are strongly morphologically simplified and their legs, wings, and external genitalia are completely absent. They exhibit a mosaic pattern of paedomorphic characters such as features of the nervous system and the presence of stemmata (the single-lensed eyes positioned bilaterally on the female head) but also non-paedomorphic structures such as the spiracles (Weingardt et al., 2023). Endoparasitic existence of female depends exclusively on the insect hosts throughout the course of their lives (except, the Mengenillidae).

Thus, being devoid of external morphological adult characters, larviform females are difficult to identify using traditional taxonomic methods and tools. On the other hand, although the adult males are short-lived, many of the known species are scientifically described

using only the males, since these are free-living and also display characteristic insect attributes. Approximately 650 species are known today (Cook, 2019; Kogan and Poinar, 2019; Pohl et al., 2021; Benda et al., 2022; Kathirithamby, 2023) including 30 from India (Roy, 2018; Hui et al., 2023). In addition to clarifying taxonomic ambiguity, the biology of Strepsiptera requires to be better explored, partly because of how infrequently encountered this group is, due to its complex life history. Strepsiptera, a monophyletic insect group, parasitises a wide range of insects belonging to 34 families from the Zygentoma, Polyneoptera, Paraneoptera and Holometabola (Kathirithamby, 2009). The Strepsiptera induce striking effects on their hosts. Such effects may lead to parasitic castration and concomitant effects on the organisation of the host insects. The endoparasitic insects exhibit unique genetic characteristics with minute genomic material (Johnston et al., 2004) and unusual insertions in the sequences of 18S rRNA sequences (Gillespie et al., 2005) showing high rates of sequence evolution (McMahon et al., 2011). These insertions and high-substitution rates have resulted in the unique ‘Strepsiptera problem’ in placing them in their phylogenetic position (Kristensen, 1981).

Explaining the phylogenetic position of lineages such as those of the Strepsiptera that display high rates of sequence evolution, extremely derived lifestyles, and morphological characters is often challenging. The

current evidence-based genomics strongly supports the Strepsiptera as the sister clade of the Coleoptera (Coleoptera + Strepsiptera = Coleopterida), rather than an internal clade of the Coleoptera, and Neuropterida as the sister clade of Coleopterida. This presently resolved phylogeny confirms Strepsiptera to be a valid and distinct order of the Insecta (Wiegmann et al., 2009; Beutel et al., 2011, 2019; Niehuis et al., 2012; Misof et al., 2014; Peters et al., 2014; Boussau et al., 2014).

The Strepsiptera usually castrate their hosts and the reproductive death of the host is usually either a direct or indirect consequence of stylopisation (Lefèvre et al., 2009a, b; Beani et al., 2011, 2017). Some of the hosts are economically important, pestiferous species. For example, *Nilaparvata lugens* (Stål) (Hemiptera: Delphacidae) and *Sogatella furcifera* (Horváth) (Hemiptera: Delphacidae), which spread virus-induced hopper-burn disease in *Oryza sativa* (Poaceae) are styloped by *Elenchus japonicus* Esaki and Hashimoto (Strepsiptera: Elenchidae). *Halictophagus bipunctatus* (Strepsiptera: Halictophagidae) styloped both *Nephotettix virescens* (Distant) and *N. nigropictus* (Stål) (Hemiptera: Cicadellidae) in Philippines (Barrion and Litsinger, 1983). *Cofana spectra* Distant (Cicadellidae), the vector of a viral disease of *O. sativa* in South and East-Asia is styloped by both *Halictophagus australensis* Perkins (Chaudhuri and Mazumdar, 2000) and *H. spectrus* Yang (Hirashima and Kifune, 1978). *Halictophagus compactus* Pierce parasitises many taxa of the Fulgoridae (Hemiptera) and Cicadellidae in Bihar and southern India (Pierce, 1911). Barrion and Litsinger (1983) and Reissig et al. (1986) made a list of several natural enemies of *Cofana spectra* in Asia. *Halictophagus palmae* Kathirithamby and Ponnamma styloped *Protutista moesta* (Westwood) (Hemiptera: Derbidae) spreading phytoplasma diseases in *Cocos nucifera*, *Elaeis guineensis*, and *Areca catechu* (Arecaceae) in Kerala (Kathirithamby and Ponnamma, 2000). The life cycle and bionomics of *Halictophagus australensis* Perkins that parasitises *Cofana spectra* Distant (Hemiptera: Cicadellidae) were studied by Chaudhuri and Mazumdar (2000).

### 1. Historical resumé

The earliest scientific record of *Xenos vesparum* (Strepsiptera: Stylopidae: Xenidae) parasitising *Polistes gallicus* (Hymenoptera: Vespidae) was made by Pietro Rossi (1793) in Pisa, Italy. British entomologist William Kirby described *Stylops melittae* (Stylopidae) that parasitises *Andrena nigroaenea* (Hymenoptera:

Andrenidae) in 1802. Swiss entomologist Louis Jurine in 1816 commented that the Strepsiptera are ‘one of the strangest and most interesting groups that nature can offer’. In 1909, Harold Maxwell-Lefroy, in *Indian Insect Life: a manual of the insects of the plains (Tropical India)* mentioned that the endoparasitic female of a species of *Xenos* protruded as a brownish structure (now coined it as cephalothorax) from the abdomen of its host *Polistes hebraeus* (Hymenoptera: Vespidae). Lefroy also quoted Charles Horne, who in his notes on the habits of the Indian aculeate Hymenoptera, stated that species of *Stylops* were harboured by many females of *P. hebraeus* in their second-abdominal segment. William Dwight Pierce, an American entomologist, in 1911, described *Tachytixenos indicus* (Xenidae) (earlier *Paraxenos indicus*) from one male and one female collected in Deesa, Banaskantha District (Gujarat) by Charles George Nurse, a senior British military officer and an amateur naturalist in June 1898. *Tachytixenos indicus* Pierce, 1911 was found to parasitise predatory, solitary wasps of *Tachytes* (Hymenoptera: Crabronidae). Charles Pierce (1914) described both sexes of a new *Pyriloxenos compactus* (presently *Halictophagus compactus*) collected as three females and one male by Chandra Shekar Misra from Pusa, Bihar, between 1907 and 1914. *Halictophagus compactus* (Halictophagidae) parasitises a species of *Pyrilla* (Hemiptera: Lophopidae). A new species *Indoxenos membraciphaga* (presently *Halictophagus membraciphaga*, Halictophagidae), parasitizing *Otinotus pallescens* (Hemiptera: Membracidae), and *Tridactylophagus mysorensis* (Halictophagidae) parasitizing a small, but active species of *Tridactylus* (Orthoptera: Tridactylidae), were described by Taracad Vythianathan Subramanian of Mysore Agricultural Service in 1927 and 1932, respectively (Subramanian 1927, 1932).

Since then, no significant progress has occurred in the study of the Indian Strepsiptera until 1978, when Prasanta Kumar Chaudhuri and his team at the University of Burdwan described *Parastylops plantipes* (presently *Myrmecolax plantipes*, Myrmecolacidae) obtained from Pasighat, Arunachal Pradesh Union Territory (Chaudhuri et al., 1978). Following that, a number of new species from India have been described by Sujit Kumar Das Gupta, Apurba Kumar Chatterjee, Mayabi Ghosh, Alpana Mazumdar, Abhijit Mazumdar, Niladri Hazra, and Sukhendu Roy. A special mention needs to be made of Jeyarany Kathirithamby, who is currently an emeritus fellow at St. Hugh’s College, University of Oxford, England, who has contributed

to the biology and taxonomy of the Strepsiptera of the world, and also that of India.

## 2. Status of the Strepsiptera

Around 650 species have been described globally belonging to 68 genera under 15 families (five extinct and 10 extant) (Table 1) (Cook, 2019; Kogan and Poinar, 2019; Pohl et al., 2021; Benda et al., 2022; Kathirithamby, 2023), although many more are awaiting descriptions including the cryptic taxa.

Table 1. Global diversity of Strepsiptera

Families	Genera	Species
Bahiaxenidae	01	01
Bohartillidae	01	03
Corioxenidae	15	49
Cretostylopidae <sup>†</sup>	01	01
Elenchidae	05	29
Halictophagidae	07	139
Lychnocolacidae	01	23
Mengeidae <sup>†</sup>	01	02
Mengenillidae	05	17
Myrmecolacidae	03	94
Phthanoxenidae <sup>†</sup>	03	03
Protoelencolacidae <sup>†</sup>	01	01
Protoxenidae <sup>†</sup>	01	01
Stylopidae	10	170
Xenidae	13	119
Total = 15	68	652

<sup>†</sup> = Extinct

Information on the Indian Strepsiptera is meagre. So far only 30 extant species under 14 genera placed in six families are known from the Indian subcontinent (Table 2) (Mazumdar and Chaudhuri, 2004; Cook, 2019; Kathirithamby, 2023). Among these, 29 have been described either as only males or both males and females. Among the 30 known, 21 belonging to eight genera, have been reported only from India, the remainder – nine – are known elsewhere as well (Table 3). Distribution of Indian Strepsiptera and their hosts (Cook, 2019; Benda et al., 2022; Kathirithamby, 2023) reveal that the hosts of Indian Strepsiptera are little studied. However, hosts of nine widely distributed Strepsiptera are known from other countries (Table 3).

## 3. General morphology of adult males (Kinzelbach, 1971; Kathirithamby, 1989; Pohl and Beutel, 2005; Kogan, 2012 and Lu and Liu, 2014)

An adult male (1.5–6 mm long, Fig. 1) displays an

Table 2. Strepsiptera of the Indian subcontinent

Families	Genera	Species
Corioxenidae	04	04
Elenchidae	01	01
Halictophagidae	03	17
Lychnocolacidae	01	01
Myrmecolacidae	02	04
Xenidae	03	03
Total = 06	Total = 14	Total = 30

unusual set of characters. Head is laterally elongate in the frontal area and the posterior end being concave. The head bears conspicuous flabellate antennae and protruded ‘raspberry’ like compound eyes each having 15–150 individual ommatidia. The mouth parts comprise maxillae and mandibles. Mandible is blade-like, conical or acuminate but strongly reduced in the Corioxenidae. The head is connected to a short, inconspicuous pronotum. The mesonotum bears strongly modified forewings (halter), large metathorax bearing the asynchronous-type flight muscles (Smith and Kathirithamby, 1984) and the large fan-shaped hind wings with radially arranged longitudinal veins. For names of veins and the abbreviations used, we have followed Kinzelbach (1971) in the present article. The longitudinal veins are — costa (C), subcosta (Sc), radius ( $R_1$ ,  $R_2$ ,  $R_3$ ,  $R_4$  and  $R_5$ ), anterior cubitus ( $CuA_1$  and  $CuA_2$ ), and posterior cubitus (CuP). Two detached fragmentary veins  $R_2$  and  $R_3$  are present; when present,  $R_5$  is always detached. Cross-veins are absent. A special feature of the Strepsiptera is the absence of a true trochanter in the fore- and midlegs except in the extinct genus *Kinzelbachilla* Pohl and Beutel. The trochanter on the fore- and midlegs appear to be fused with the femur to form a single-leg segment, the trochanterofemur. The fore- and midlegs are long, tarsi often modified differing in the numbers of tarsal segments, endowed with claws (e.g. *Triozocera pugiopennis* Chaudhuri and Das Gupta, 1979 (Corioxenidae)) and occasionally without as in *Viridipromontorius aequus* (Roy and Hazra, 2016a) (Corioxenidae). Adhesive structures consisting of hairy surfaces are common in many male Strepsiptera are presumed to have a role in copulation (Pohl and Beutel, 2004). The first two segments of the abdomen remain concealed beneath post-scutellum, the ninth segment always ventrally produced beyond the 10<sup>th</sup> segment, forming a dorsal cover. The aedeagus articulated at the tip of the ninth segment is a chitinous, unpaired median tube with a subapical pore. Aedeagus is nearly straight to hook- or anchor like in shape (Kathirithamby, 1989).

Table 3. Distribution of Strepsiptera from India and their hosts

Strepsiptera	Distribution	Host species
<b>Elenchidae</b>		
<i>Elenchus japonicus</i> Esaki and Hashimoto, 1931 (Elenchidae).	India (West Bengal), Japan, Philippines, Sri Lanka, Thailand.	<i>Nilaparvata lugens</i> (Stål), <i>Sogatella furcifera</i> (Horváth), <i>S. longifurcifera</i> (Esaki and Ishihara), <i>S. panicicola</i> (Fallén), <i>Laodelphax striatellus</i> (Fallén) (Hemiptera: Delphacidae).
<b>Xenidae</b>		
<i>Tachytixenos indicus</i> Pierce, 1911 (Xenidae).	India (Gujarat), Algeria, Sri Lanka, Thailand, China, Denmark.	<i>Tachytes vicinus</i> Cameron, <i>T. maculicornis</i> Saunders, <i>T. modestus</i> Smith, <i>T. vischnu</i> Cameron, <i>T. xeniferus</i> Rohwer, a species of <i>Tachytes</i> (Hymenoptera: Sphecidae).
<i>Xenos ropalidia</i> (Kinzelbach, 1975) (Xenidae).	India, Indonesia (Java), Malaysia, Nepal, Laos, Papua New Guinea, Pakistan (Karachi), Philippines.	<i>Ropalidia cincta</i> (Lepeletier), <i>R. fulvopruinosa</i> (Cameron), <i>R. marginata</i> (Lepeletier), <i>R. nobilis</i> (Gerstäcker) <i>R. variegata</i> (Smith), <i>R. malayana</i> (Cameron) (Hymenoptera: Vespidae).
<i>Xenos hebraei</i> Kinzelbach, 1978 (Xenidae).	India (Bihar), Iraq, Oman.	<i>Polistes olivaceus</i> (DeGeer), <i>P. wattii</i> Cameron (Hymenoptera: Vespidae).
<b>Corioxenidae</b>		
<i>Corioxenos raii</i> Baliga, 1967 (Corioxenidae).	India (Karnataka).	<i>Antestiopsis cruciate</i> (Fabricius) (Hemiptera: Pentatomidae).
<i>Dundoxenos kinzelbachi</i> Luna de Carvalho, 1985 (Corioxenidae).	India (West Bengal), Republic of Cape Verde, Macronesia.	<i>Aethus lindbergi</i> Wagner (Hemiptera: Cynidae).
<i>Triozocera pugiopennis</i> Chaudhuri and Das Gupta, 1979 (Corioxenidae).	India (West Bengal), Pakistan.	Not presently known.
<i>Iridipromontorius aequus</i> (Roy and Hazra, 2016a) (Corioxenidae).	India (West Bengal).	Not presently known.
<b>Lychnocolacidae</b>		
<i>Lychnocolax similis</i> Chaudhuri, Ghosh and Das Gupta, 1983 (Lychnocolacidae).	India (Arunachal Pradesh).	Not presently known.
<b>Myrmecolacidae</b>		
<i>Myrmecolax comparilis</i> Roy and Hazra, 2017 (Myrmecolacidae).	India (West Bengal).	Not presently known.
<i>Myrmecolax pierci</i> (Chattopadhyay and Chaudhuri, 1980) (Myrmecolacidae).	India (West Bengal).	Not presently known.
<i>Myrmecolax plantipes</i> (Chaudhuri, 1978) (Myrmecolacidae).	India (Arunachal Pradesh, West Bengal).	Not presently known.
<i>Stichotrema sagax</i> Roy and Hazra, 2017 (Myrmecolacidae).	India (West Bengal).	Not presently known.
<b>Halictophagidae</b>		
<i>Coriophagus calcanus</i> Roy and Hazra, 2016b (Halictophagidae).	India (West Bengal).	Not presently known.

(contd.)

(contd. Table 1)

<i>Halictophagus acerbus</i> Mazumdar and Chaudhuri, 1997 (Halictophagidae).	India (West Bengal).	Not presently known.
<i>Halictophagus australensis</i> Perkins, 1905 (Halictophagidae).	India (West Bengal), Australia (Queensland), Borneo, Malaysia, China (Szechuan), Japan, Mozambique, Sri Lanka.	<i>Cofana spectra</i> (Distant), <i>C. unimaculata</i> (Signoret), <i>Conognimula coeruleopennis</i> (Fabricius) (Hemiptera: Cicadellidae).
<i>Halictophagus bipunctatus</i> Yang, 1955 (Halictophagidae).	India (West Bengal), China (Kwantung, Fujian, Jiangzi, Guangdong, Kiangsi, Kiangsu, Henan, Honan, Hupeh, Szechuwan, Fukien), Japan (Honshu, Kyushu, Okinawa), Borneo, Malaysia, Luzon, Philippines, Thailand.	<i>Nephotetix nigropictus</i> (Stål), <i>N. virescens</i> (Distant), <i>N. cinciteps</i> (Uhler) (Hemiptera: Cicadellidae).
<i>Halictophagus compactus</i> (Pierce, 1914) (Halictophagidae).	India (Bihar).	<i>Pyrilla abberans</i> (Kirby), <i>P. perpusilla</i> (Walker) (Lophopidae), <i>Idioscopus clypealis</i> (Lethierry), <i>Amritodus atkinsoni</i> (Lethierry) (Hemiptera: Cicadellidae).
<i>Halictophagus indicus</i> Bohart, 1943 (Halictophagidae).	India (Karnataka).	<i>Idiocerus niveosparvus</i> Lethierry, <i>I. atkinsoni</i> Lethierry, <i>I. clypealis</i> Lethierry (Hemiptera: Cicadellidae).
<i>Halictophagus membraciphaga</i> (Subramanian, 1927) (Halictophagidae).	India (Karnataka).	<i>Otinotus pallescens</i> Distant (Hemiptera: Membracidae).
<i>Halictophagus palmae</i> Kathirithamby and Ponnamma, 2000 (Halictophagidae).	India (Kerala).	<i>Protista moesta</i> (Westwood) (Orthoptera: Derbidae).
<i>Halictophagus prominens</i> Roy and Hazra, 2016b (Halictophagidae).	India (West Bengal).	<i>Idioscopus clypealis</i> (Lethierry) (Hemiptera: Cicadellidae).
<i>Halictophagus tenebrosus</i> Chaudhuri Ghosh and Das Gupta, 1983 (Halictophagidae).	India (West Bengal).	Not presently known.
<i>Tridactylophagus aduncus</i> Maxumdar and Chaudhuri, 1999 (Halictophagidae).	India (West Bengal).	Not presently known.
<i>Tridactylophagus carinatus</i> Maxumdar and Chaudhuri, 1999 (Halictophagidae).	India (West Bengal).	Not presently known.
<i>Tridactylophagus confertus</i> (Yang, 1964) (Halictophagidae).	China, India (West Bengal).	<i>Tridactylus japonicus</i> Shiraki (Orthoptera: Tridactylidae).
<i>Tridactylophagus maculatus</i> Chaudhuri, Ghosh and Das Gupta, 1983 (Halictophagidae).	India (West Bengal).	Not presently known.
<i>Tridactylophagus mysorensis</i> Subramanian, 1932 (Halictophagidae).	India (Karnataka).	<i>Tridactylus</i> sp. (Orthoptera: Tridactylidae).
<i>Tridactylophagus orientalis</i> (Chaudhuri and Das Gupta, 1979) (Halictophagidae).	India (West Bengal).	Not presently known.
<i>Tridactylophagus sufflatus</i> Hui, Mukherjee and Hazra, 2023 (Halictophagidae).	India (West Bengal).	Not presently known.

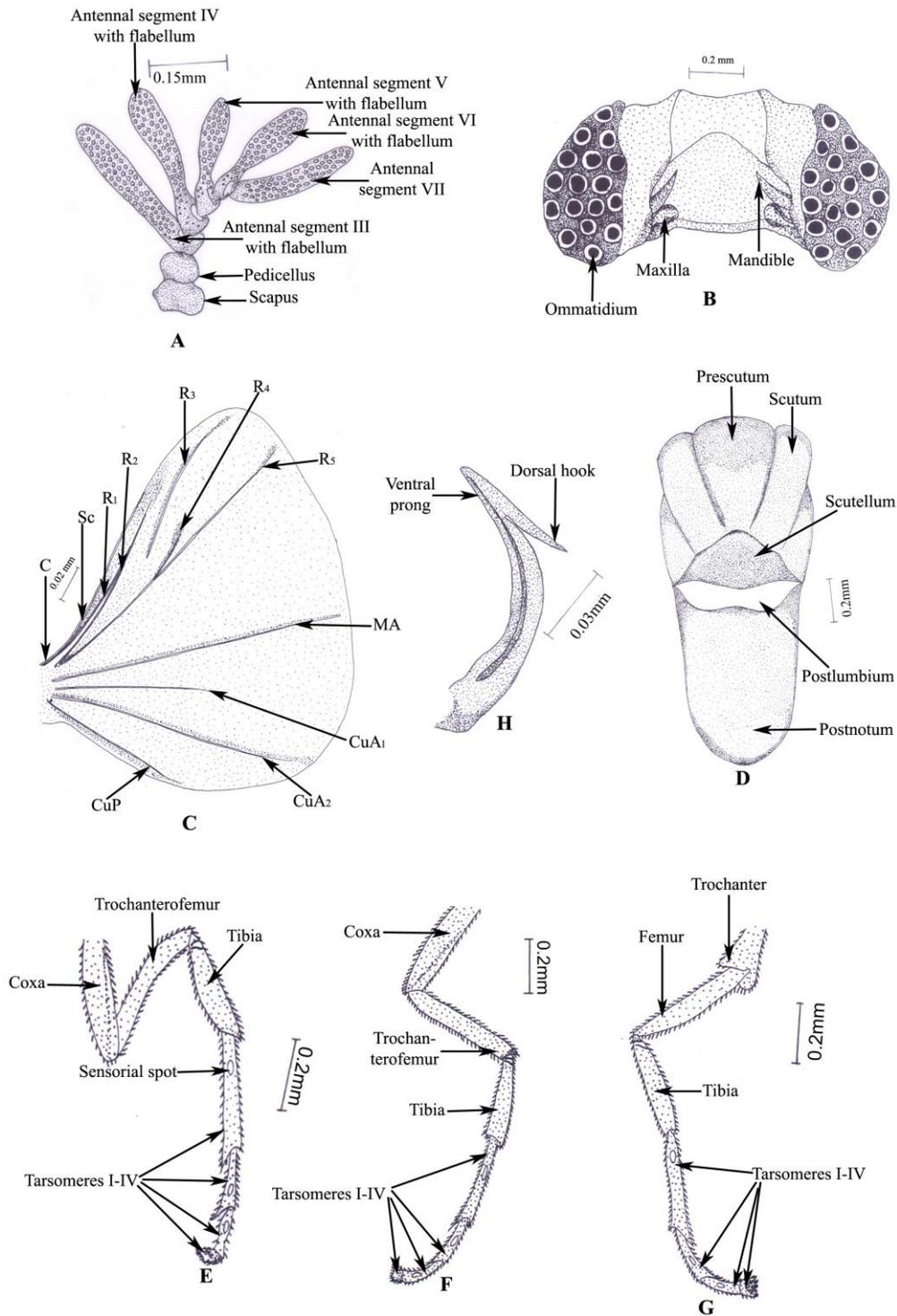


Fig. 1. Morphology-male Strepsiptera. a. antenna (*Coriophagus calcaneus* Roy and Hazra). b. head showing compound eyes, maxillae and mandibles (*Coriophagus calcaneus*) (ventral view). c. hind wing (*Viridipromontorius aequus* (Roy and Hazra)). d. metathorax (*Halictophagus prominens* Roy and Hazra). e. foreleg (*Viridipromontorius aequus* (Roy and Hazra)). f. midleg (*Viridipromontorius aequus* (Roy and Hazra)). g. hindleg (*Viridipromontorius aequus* (Roy and Hazra)). h. aedeagus (*Myrmecolax comparilis* Roy and Hazra) (Roy, 2018).

#### 4. Biology

Strepsiptera have a complex life cycle that includes an obligate endoparasitic phase. Only members of the Stylopida include obligate endoparasitic females. Because of the peculiar characteristics in their life cycles, their biology is known only in a handful of species. Life cycle of *Halictophagus australensis* parasitizing *Cofana spectra* was first studied by Chaudhuri and Mazumdar (2000) and subsequently in detail by Hazra et al. (unpublished data). *Halictophagus australensis* will be used here as an example.

##### a. *Halictophagus australensis* (Figs. 2-4)

Experimental set up was made by transplanting germinated seedlings of *O. sativa* in earthen pots in a net house. A few adult males and females of *C. spectra* (both normal and parasitised) as well as their nymphs captured from the experimental rice farm in the Crop Research and Seed Multiplication Centre of the University of Burdwan using sweep nets were released in the net house. Adults were allowed to mate. Eggs were laid by *C. spectra* within the paddy plant leaves. The leaves of *O. sativa* bearing the egg masses of *C. spectra* were transferred onto a Petri plate to observe egg hatching in

unparasitised and parasitised *C. spectra*. For studying the fecundity of both unparasitised and parasitised (stylopised) *C. spectra* lactophenol-acid-fuchsin stain (Backus et al., 1988) was used. Host seeking free living primary larvae were allowed to discharge through birth opening located in the cephalothorax of viviparous female *H. australensis* residing in the stylopised *C. spectra*. Entry of the primary larvae within *C. spectra* nymphs occurred for 3–4 consecutive days to obtain a large number of parasitised hosts. Life cycle of the endoparasite *H. australensis* within *C. spectra* was allowed to complete. Adult females are described as ‘larviform’ that resemble other insect larvae measuring 2–6 mm in overall length. The cephalothorax usually extrudes through the intersegmental region of the integument of the *C. spectra* retaining the abdomen within the host. The neotenic female produces a potent sex pheromone from the Nasonow’s gland (‘stylopsal’ *sensu* Cvačka et al., 2012) that attracts the male (Cvačka et al., 2012; Tolasch et al., 2012; Hrabar et al., 2015). The male *H. australensis* locates the receptive female with the chemoreceptor Hofender’s organ on the antenna, inseminates her through the birth opening (Hrabar et al., 2014). In the ‘haemocelous viviparity’ process, the



Fig. 2. Adult male Strepsiptera, unstylopised and stylopised *Cofana spectra* from an *Oryza sativa* rice agroecosystem. a. Application of sweep net. b. Battery operated CDC-type fabricated light trap which will trap both *C. spectra* and *H. australensis*. c. Open light trap. d. Malaise trap for trapping *H. australensis*.



Fig. 3. a. *Oryza sativa* seedlings maintained in net house. b–c. Rearing and maintenance of *Cofana spectra* for completion of lifecycle of *Halictophagus australensis*

embryo develops in the female's haemocoel obtaining nutrients from the mother and the primary larvae hatch within the haemocoel of mother. Thus one female produces several 1000s of free-living primary larvae that escape through the birth opening. The primary larvae are smallest known metazoan with an average size of 230  $\mu\text{m}$  (smallest species: 70  $\mu\text{m}$ , largest species: 850  $\mu\text{m}$ ) (Pohl, 2002; Fischer et al., 2021) and highly mobile, as they only have a limited time to locate a new host — *C. spectra* — before exhausting food reserves. These primary larvae have stemmata and once they latch onto *C. spectra*, head of them continuously punches the cuticle of the *C. spectra* with the help of mandibles mostly in the abdominal region of nymphal stage of *C. spectra* for penetration. The larval entry into the exocuticle and endocuticle might occur by piercing. The primary larvae moult within the haemocoel of the host into an apodous, trophic and endoparasitic secondary larval stage belonging to the oversimplified larvae of the Holometabola (Tröger et al., 2020; Beutel et al., 2022) and feed within the host's haemocoel. From there the larvae of *H. australensis* undergo holometabolous development. The life cycle of these insects is described as hypermetamorphosis, a term used to describe wherein the primary larva is strikingly morphologically different from the secondary larva. The male secondary larva undergoes metamorphosis through pupation, and then, it extrudes through the abdomen of the host cuticle. The apolysed cuticle of the larva forms the puparium. The free-living male ecloses from the puparium. In contrast, the female

secondary larva does not metamorphose into pupa but develops a cephalothorax extruding through the mobile host (Roy and Hazra, 2016b).

#### b. Primary larva

The primary larvae (Fig. 4) are free-living, highly mobile host-seeking stages of the Strepsiptera, which emerge from the endoparasitic viviparous females. These larvae vary in length from 0.18 to 0.21 mm ( $n = 10$ ) and the caudal bristles are 0.06–0.09 mm long ( $n = 10$ ). They are pale brown, fusiform and sclerotised. The head is triangular, anterior margin slightly bowed, and narrowly fixed to prothorax. Stemmata are large and antennae are absent. Thorax is  $2.5 \times$  wider than the head. Legs are slender; coxae are large and globular; trochanterofemur and tibia are slender; tarsi filiform with no claws. Abdomen is 11-segmented, posterior edge of the sternites fringed with minute microtrichia, posterior margin of the 9<sup>th</sup> segment bearing two setae while the 11<sup>th</sup> bearing a pair of long strongly developed caudal bristles placed close to midline.

#### c. Endoparasitic secondary-larval stage

On entering the host the free-living primary larvae molt into apodous second-instar larvae. A mouth and a gut are evident in the endoparasitic larval stages (Kathirithamby, 2009). Larvae are creamy white with faint segmentation. Length varies between 0.3 and 0.35 mm ( $n = 5$ ). Head is differentiated with small black eye patches. Sexes are indistinguishable at this stage. Males are elongate, smooth, white with distinct segmentations

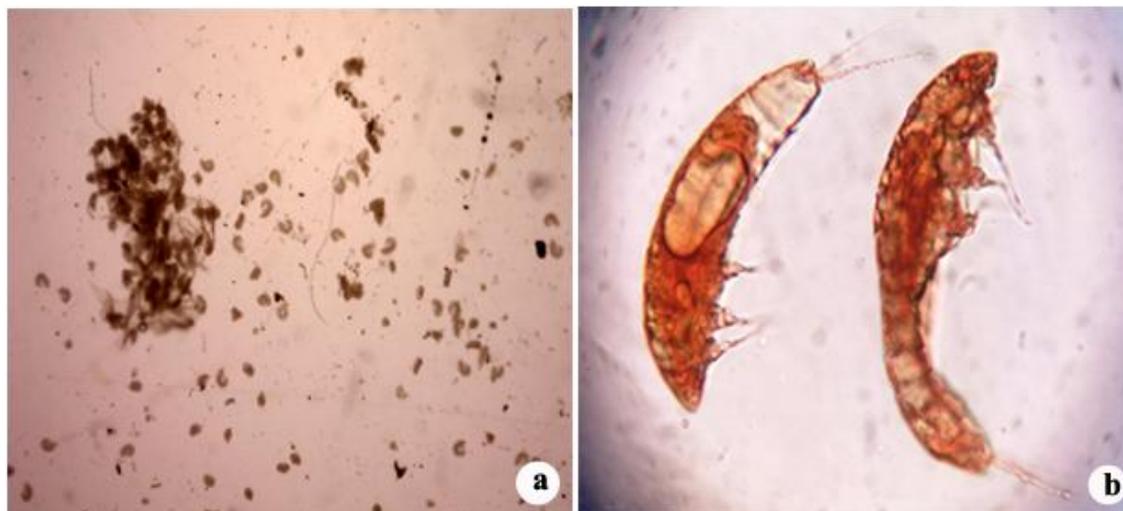


Fig. 4. a. Numerous primary larvae dissected out from the styloipised *Cofana spectra*. b. Primary larvae (enlarged).

and a bulbous hemispherical head, broader at its posterior margin, and as wide as thoracic segments. Eye spots are discrete.

#### d. Pupal stage

The male secondary larvae extrude through the host abdomen and undergo pupation, while the neotenic females without any pupal stage become mature in adult *C. spectra*. The head of the male thereafter is sclerotised to form the cap of the puparium — the cephalotheca. The metamorphosis of the male occurs in two stages within the puparium: the pupal and pre-adult stages. During pre-adult stage (the cuticle of the pupa is shed and therefore is not a pharate adult), cuticle hardened and darkened, sperm mature, wings expand and flight muscles develop (Kathirithamby, 2009). Free-living adult males emerge by breaking open the cephalotheca (Kathirithamby et al., 1989).

#### e. Endoparasitic adult female

The female extrudes the cephalothorax through the abdomen of the *C. spectra* and becomes a neotenic one without undergoing a pupal instar and the abdomen remained within the host. Cephalothorax has a birth opening containing varying numbers of birth organs leading to the haemocoel.

#### f. Free-living adult male

Total length is *c.* 1.75 mm; length of the metathorax is *c.* 0.85 mm; width of the metathorax is *c.* 0.40 mm; length of the antenna is *c.* 0.40 mm. Males of the *H. australensis* have seven segmented antennae with segments III–VI bearing flabella (therefore, flabellate); segment III is the longest and broadest,

while segment V is the shortest. Hind wings have five primary and two detached veins. Thorax is dark brown with prescutum 0.15 mm long and 0.08 mm in width, roughly curved anteriorly, fairly obscured from the scutum. Mesothoracic wing is 0.16 mm in length with globular apical end and slender basal end. Legs have no claws. Abdomen is light brown and sclerotised. Aedeagus is 0.033 mm long with terminal hook 0.009 mm long, at *ca.* 106° angle bearing a plump shaft, 0.018 mm long, bent with an extension of 0.012 mm.

The male puparia (cephalotheca) protruded through the integument of *C. spectra*, while the female cephalothorax projected between the reflexed lateral margins of the tergites of *C. spectra*. In general, the protrusion took place on both sides of the abdominal tergites. Emergence of primary larvae took place by jumping with the aid of caudal bristles through the birth opening of female cephalothorax. The majority of *C. spectra* died in the day of emergence of primary larvae, but few remained alive for 3–4 days. The period of emergence of the primary larvae varied from 46–72 hrs. The life-span of primary larvae appeared to be 1–2 hrs, but they were found to survive a little longer of 4–5 hrs in humid condition.

In the laboratory, free living males of *H. australensis* required 12–14 days to emerge from the puparia during summer. Generally, the emergence occurred in the morning and afternoon. The eclosion of the imago happened by breaking the cephalotheca. The antennae and fore legs made exit first from the puparium eventually dragging the remaining part out of the puparium. Immediately after emergence, the males reposed for a while before performing flight (Fig. 5).

A comparison of oviposition scar made by the unparasitised gravid and stylopised gravid females *C. spectra* was studied from February 2015 to January 2016. A cluster of eggs laid by unparasitised *Cofana spectra* in a leaf of *Oryza sativa* is shown after staining with lactophenol-acid-fuchsin (Fig. 6). It revealed that number of scars in *O. sativa* made by unparasitised gravid females of *C. spectra* (Fig. 7) was much greater (mean = 59) in number than the parasitised ones (mean = 20). Each oviposition scar made by unparasitised *C.*

*spectra* included 18–20 eggs, whereas the stylopised *C. spectra* laid 9–11 eggs under each scar. Eggs laid by stylopised *C. spectra* did not hatch, when the experiment was conducted in the net house and it appears that the reproductive fitness of the stylopised *C. spectra* was reduced owing to parasitisation. However, more experiments are necessary before a firm conclusion can be drawn.

Strepsiptera can extend the life span of their hosts

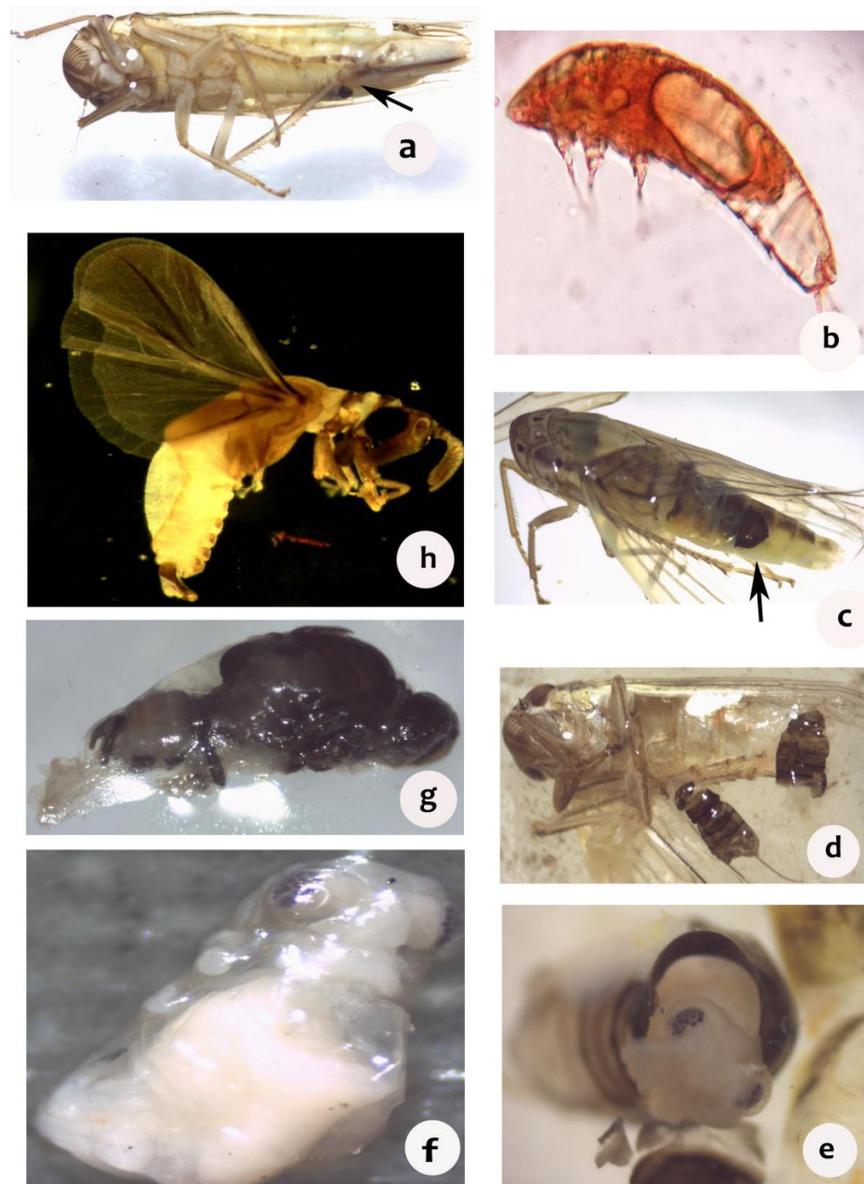


Fig. 5. Life cycle of *Halictophagus australensis* Perkins. a. Stylopised female *Cofana spectra* indicated by arrow. b. Primary larva of *H. australensis*. c. Stylopised male *C. spectra* indicated by arrow. d. Dissected *C. spectra* with male cephalotheca of parasite. e. Removal of the pupal cap showing the head of the pharate adult male of *H. australensis* with remains of *C. spectra* abdomen. f. Early pharate adult male of *H. australensis* dissected out from puparium. g. Late pharate adult male of *H. australensis* dissected out from puparium. h. Free living adult male *H. australensis*.

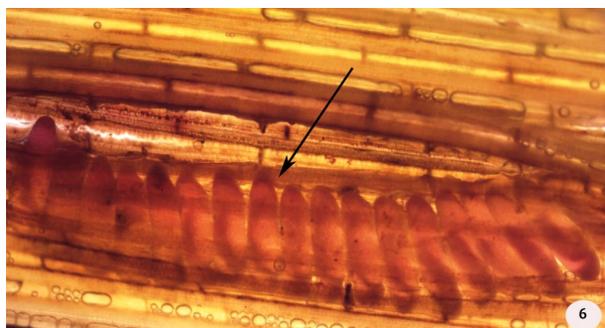


Fig. 6. Egg cluster of unstyloised *Cofana spectra* in a paddy leaf

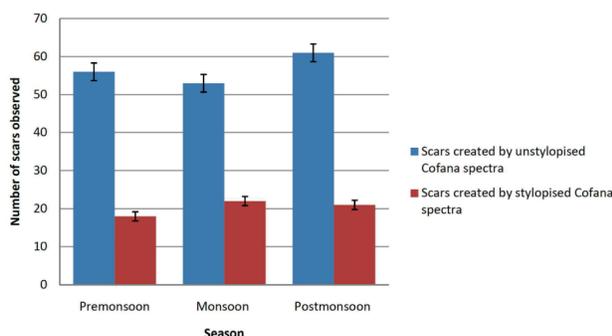


Fig. 7. Comparison of oviposition scar between the unstyloised gravid and the styloised gravid female of *Cofana spectra*. (Premonsoon: February–May; Monsoon: June–September; Postmonsoon: October–January)

until their own life cycle is completed. The term macrynobionts (macryno — lengthen; bionts — organisms) was proposed by Kathirithamby (2009). Styloisation of *C. spectra* by *H. australensis* lengthens the life span of *C. spectra*. Normal life span of unstyloised *C. spectra* was 28–32 days whereas in the styloised *C. spectra* it was 38–40 days (Hazra et al. unpublished observations), which corroborates with the findings of Kathirithamby (2009) and Beani et al. (2021). A single *C. spectra* may be styloised by a primary larva (Fig. 8) or by more than one (superparasitism) (Fig. 9) (Roy and Hazra, 2016b). This superparasitism phenomenon has also been observed in two host species of the Strepsiptera in India: *Cofana spectra* parasitised by two females of *H. australensis*, and *Idioscopus clypealis* (Hemiptera, Cicadellidae) parasitised by two males of *Halictophagus prominens* (Figs. 10–11). If there are two males or a male and a female Strepsiptera within one individual of *C. spectra*, the male emerges first leaving an empty puparium that provides a large opening to the haemocoel through which dehydration of the visceral organs ensues and also acquires an infection by a fungus (Perkins, 1918a, b; Misra, 1917). This results in killing of the most hosts along with the remaining parasites

within it (Kathirithamby, 2009).

### 5. Key to the Indian Strepsiptera (males)

1. Antennae four segmented with flabellum only on antennomere III ..... 2
  - Antennae five to seven segmented with flabellum either on antennomere III only, or antennomeres III–IV or antennomeres III–VI ..... 4
- 2(1). Flabellum of antenna rounded (Fig. 12); tarsi two segmented (Fig. 13)..... Elenchidae ..... *Elenchus japonicus* Esaki and Hashimoto, 1931
  - Flabellum of the antenna flattened; tarsi four segmented ..... Xenidae ..... 3
- 3(2). Palpi of maxilla tapering but not acute at apex; posterior margin of postlumbium sinuate ..... *Tachytixenos indicus* Pierce, 1911
  - Palpi of maxilla tapering and acute at apex (Fig. 14); posterior margin of postlumbium straight (Fig. 15) ..... *Xenos ropalidiae* (Kinzelbach, 1975)
- 4(1). Mandibles strongly reduced ..... Corioxenidae ..... 5
  - Mandibles well developed ..... 8
- 5(4). Antenna seven segmented, flabella present on antennomeres III and IV (Fig. 16) ..... *Triozocera pugiopennis* Chaudhuri and Das Gupta, 1979
  - Antenna five segmented, flabella present either on antennomeres III and IV or III–V ..... 6
- 6(5). Antenna five segmented, flabella present on antennomeres III–V; tarsi three segmented, without any claw (Fig. 17) ..... *Corioxenos raoi* Baliga, 1967
  - Antenna five segmented, flabella present on antennomeres III and IV; tarsi more than three segmented, with or without claws ..... 7
- 7(6). Tarsi five segmented with claws (Fig. 18);



Fig. 8. *Cofana spectra* styloped by one endoparasite, *Halictophagus australensis*



Fig. 9. *Cofana spectra* styloped by four endoparasites, *Halictophagus australensis* (superparasitism)

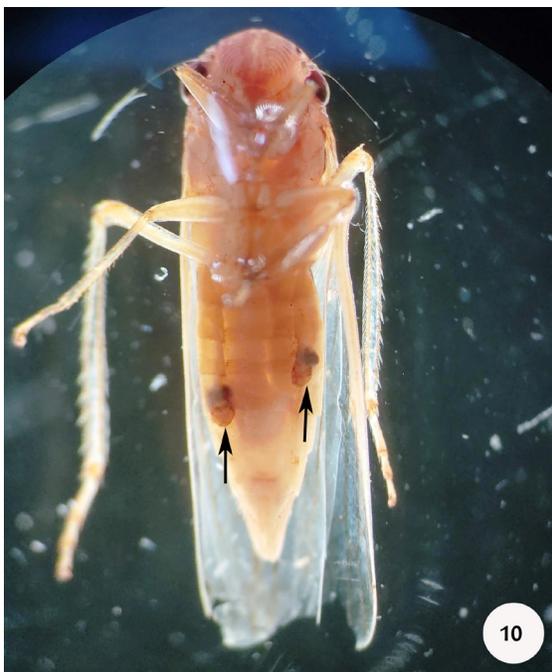


Fig. 10. *Cofana spectra* styloped by two females *Halictophagus australensis* (arrows)



Fig. 11. *Idioscopus clypealis* styloped by two males *Halictophagus prominens* (arrows)



Fig. 12. Antennae of *Elenchus japonicus*.

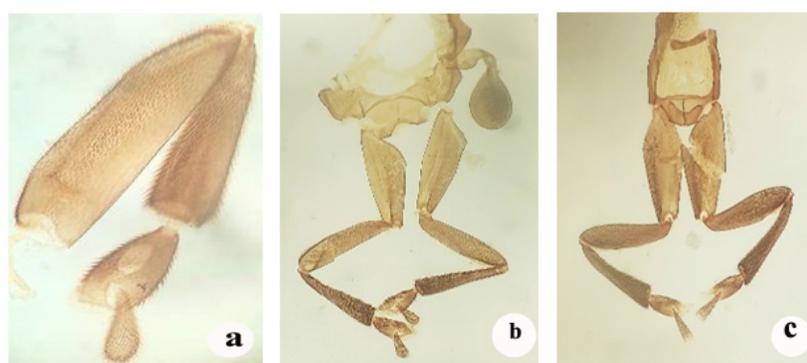


Fig. 13. Legs with two segmented tarsi of *Elenchus japonicus*. a. fore leg. b. Mid legs. c. Hind legs.



Fig. 14. Maxilla of *Xenos ropalidiae*.  
 Source: Kinzelbach R K. 1975.

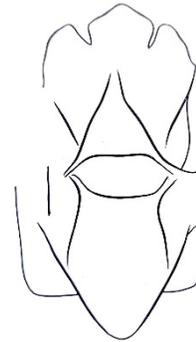


Fig. 15. Metathorax of *Xenos ropalidiae*.



Fig. 16. Antenna of *Triozocera pugiopennis*.  
 Source: Baliga H. 1967.

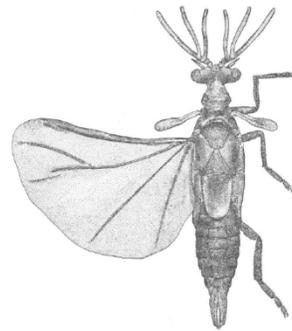


Fig. 17. *Corioxenos raoi*

two detached veins present between radius (R) and media (M) (Fig. 19) .....  
*Dundoxenos kinzelbachi* Luna de Carvalho, 1985

– Tarsi four segmented without any claws (Fig. 20); one detached vein present between radius (R) and media (M) (Fig. 21) .....  
 ... *Viridipromontorius aequus* (Roy and Hazra, 2016a)

8(4). Tarsi four segmented ..... 9

– Tarsi three segmented .....  
 Halictophagidae ..... 13

9(8). Wing venation with  $CuA_1$  and  $CuA_2$  (Fig. 22) .....  
 Lychnocolacidae .....  
*Lychnocolax similis*  
 Chaudhuri, Ghosh and Das Gupta, 1983

– Wing venation with only  $CuA_1$  .....  
 Myrmecolacidae ..... 10

10(9). One detached vein ( $R_5$ ) present on hind wing, veins  $R_2$  and  $R_3$  absent (Fig. 23); aedeagus

more or less straight with unequal prongs (Fig. 24) .....  
*Stichotrema sagax*  
 Roy and Hazra, 2017

– Hind wings with two detached veins between  $R_1$  and  $R_4$ ; aedeagus not straight .....  
 11

11(10). Flabellum of antennomere III reaching tip of antennomere VII (Fig. 25); maxillary palp knife shaped (Fig. 26); aedeagus axe shaped (Fig. 27) .....  
*Myrmecolax plantipes*  
 (Chaudhuri, 1978)

– Flabellum of antennomere III not reaching tip of antennomere VII; maxillary palp long, slender; aedeagus not like above .....  
 12

12(11). Flabellum of antennomere III reaching about 1/3<sup>rd</sup> of antennomere VII (Fig. 28); aedeagus plough shaped, dorsal hook and ventral prong unequal in length (Fig. 29); postnotum broadly triangular in shape (Fig. 30) .....  
*Myrmecolax pierci* (Chattopadhyay and Chaudhuri, 1980)

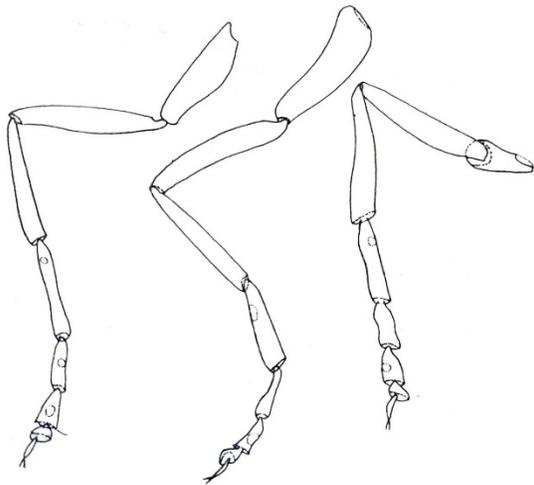


Fig. 18. Legs of *Dundoxenos kinzelbachi*.

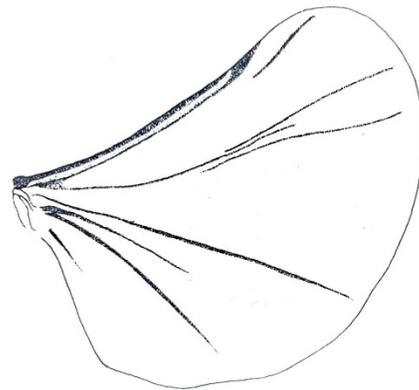


Fig. 19. Wing of *Dundoxenos kinzelbachi*.

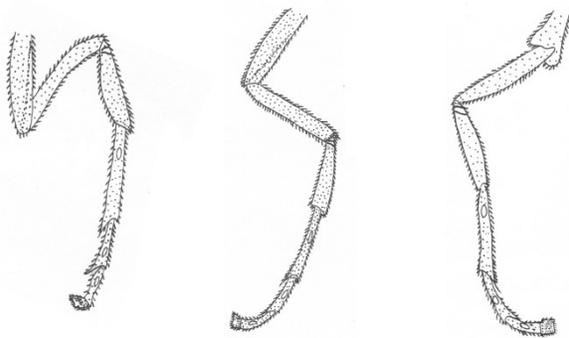


Fig. 20. Legs of *Viridipromontorius aequus*

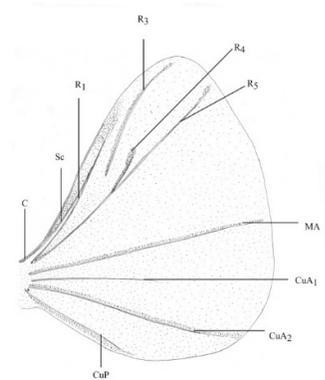


Fig. 21. Wing of *Viridipromontorius aequus*



Fig. 22. Wing of *Lychnocolax similis*  
Source: Chaudhuri P K, Ghosh M, Das Gupta S K. 1983.

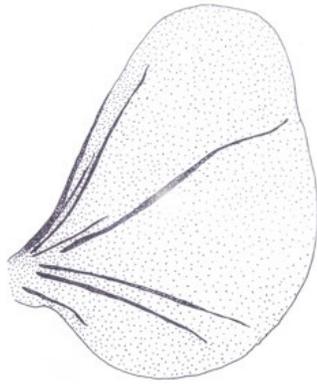


Fig. 23. Wing of *Stichotrema sagax*

Source: Roy S, Hazra N. 2017.

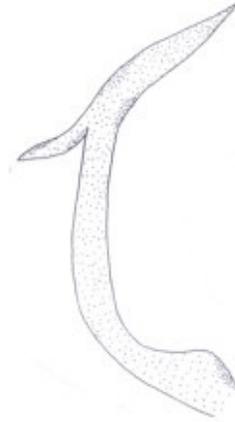


Fig. 24. Aedeagus of *Stichotrema sagax*

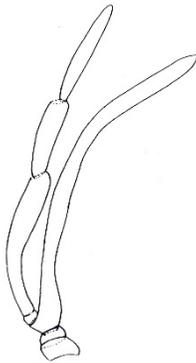


Fig. 25. Antenna of *Myrmecolax plantipes*

Source: Chaudhuri P K, Das Gupta S K, Chatterjee A K. 1978.

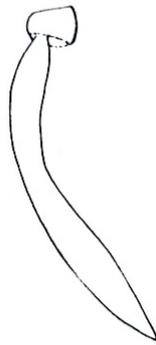


Fig. 26. Maxilla of *Myrmecolax plantipes*

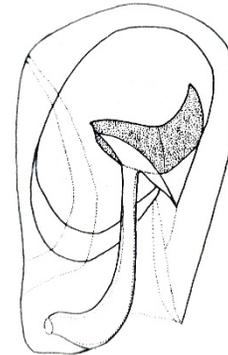


Fig. 27. Aedeagus of *Myrmecolax plantipes*

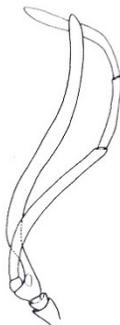


Fig. 28. Antenna of *Myrmecolax pierci*

Source: Chattopadhyay A K, Chaudhuri P K. 1980.



Fig. 29. Aedeagus of *Myrmecolax pierci*

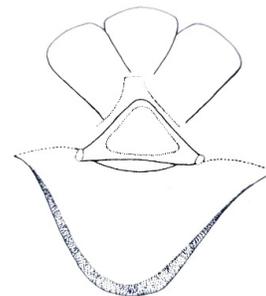


Fig. 30. Metathorax of *Myrmecolax pierci*

– Flabellum of antennomere III reaching base of antennomere VII (Fig. 31); aedeagus arcuately curved, dorsal hook and ventral prong are equal in length (Fig. 32); postnotum narrowly triangular in shape (Fig. 33)  
 ..... *Myrmecolax comparilis* Roy and Hazra, 2017

13(8). Only antennomere III with rounded flabellum; mandibles not sclerotised..... (*Tridactylophagus* spp.)  
 ..... 14

– Antennomeres III–VI with flattened flabella; mandibles sclerotised ..... 20

14(13). Hindwings with one detached vein between radius (R) and media (M)..... 15

– Hindwings with two detached veins between radius (R) and media (M) ..... 16

15(14). Tips of mandibles cross each other (Fig. 34)  
 .....  
 ..... *Tridactylophagus carinatus* Maxumdar and Chaudhuri, 1999

– Tips of the mandibles not cross each other (Fig. 35) ..... 35)

..... *Tridactylophagus mysorensis* Subramaniam, 1932

16(14). Detached vein  $R_3$  shorter than  $R_2$  (Fig. 36)  
 .....

*Tridactylophagus maculatus* Chaudhuri, Ghosh and Das Gupta, 1983

– Detached vein  $R_3$  longer than  $R_2$  ..... 17

17(16). Antennomere IV half length of antennomere V (Fig. 37) .....  
 .....

..... *Tridactylophagus coniferus* (Yang, 1964)

– Antennomere IV longer than half length of antennomere V ..... 18

18(17). Antennomere IV swollen on one side (Fig. 38) .....  
 ..... *Tridactylophagus sufflatus* Hui, Mukherjee and Hazra, 2023

– Antennomere IV not swollen on one side ..... 19



Fig. 31. Antenna of *Myrmecolax comparilis*  
 Source: Roy S, Hazra N. 2017.



Fig. 32. Aedeagus of *Myrmecolax comparilis*

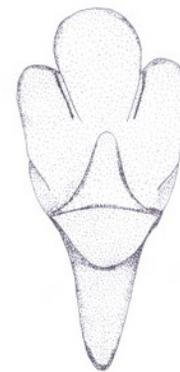


Fig. 33. Metathorax of *Myrmecolax comparilis*

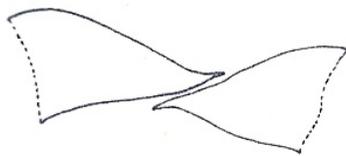


Fig. 34. Mandibles of *Tridactylophagus carinatus*  
 Source: Maxumdar A, Chaudhuri P K. 1999.

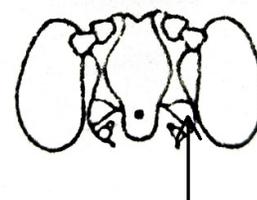


Fig. 35. Mandibles of *Tridactylophagus mysorensis*  
 Source: Subramaniam T V. 1932.

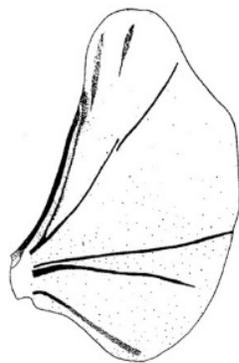


Fig. 36. Wing of *Tridactylophagus maculatus*  
 Source: Chaudhuri P K, Ghosh M, Das Gupta S K. 1983.



Fig. 37. Antenna of *Tridactylophagus coniferus*.  
 Source: Yang C K. 1964.



Fig. 38. Antenna of *Tridactylophagus sufflatus*

19(18).  $R_3$  vein small, narrow, faint and situated close to  $R_2$  (Fig. 39) .....

..... *Tridactylophagus orientalis* (Chaudhuri and Das Gupta, 1979)

–  $R_3$  vein long, prominent, situated near tip of  $R_4$  (Fig. 40) .....

..... *Tridactylophagus aduncus* Maxumdar and Chaudhuri, 1999

20(13). Head Distal end of fore tibia spatulate; fore tarsomere I enlarged (Fig. 41) .....

..... *Coriophagus calcaneus* Roy and Hazra, 2016c

– Smaller body size (<2.5 mm); distal end of fore tibia not spatulate; fore tarsomere I not enlarged .....

..... (*Halictophagus* spp.) .....

21(20). Maxillary palp equal to or shorter than mandible .....

– Maxillary palp longer than mandible .....

22(21). Detached vein  $R_2$  shorter than  $R_3$  (Fig. 42)

..... *Halictophagus membraciphaga* (Subramaniam, 1927) – Detached vein  $R_2$  almost equal in length of  $R_3$  (Fig. 43).....

..... *Halictophagus palmae* Kathirithamby and Ponnamma, 2000

23(21). Apices of all antennal flabella almost even with each other .....

– Apices of all antennal flabella not even with each other .....

24(23). Aedeagus with broad base, not bent near apex, rather extended straight like a foot, apical process having sharp point (Fig. 44) .....

..... *Halictophagus tenebrosus* Chaudhuri, Ghosh and Das Gupta, 1983

– Aedeagus broad near base, strongly bent rectangularly near apex, apical process slender, very acute .....

..... *Halictophagus compactus* (Pierce, 1914)

25(23). Posterior margin of postlumbium straight .....

– Posterior margin of postlumbium curved .....

26(25).  $R_2$  vein narrow, thickened same as  $R_3$  (Fig. 45) .....

..... *Halictophagus australensis* Perkins, 1905

–  $R_2$  vein broad, more thickened than  $R_3$  .....

27(26). Presence of a small spot extending from the tip of the  $R_4$  to proximal of  $R_5$  (Fig. 46) .....

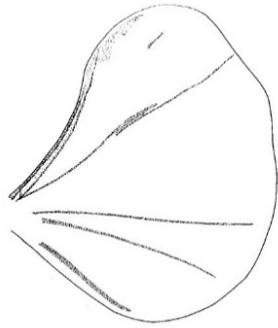


Fig. 39. Wing of *Tridactylophagus orientalis*  
Source: Chaudhuri P K, Das Gupta S K 1979.



Fig. 40. Wing of *Tridactylophagus aduncus*  
Source: Roy S, Hazra N. 2016b.

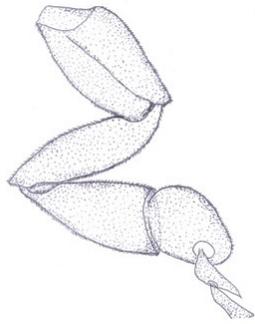


Fig. 41. Foreleg of *Coriophagus calcaneus*  
Source: Roy S, Hazra N. 2016b.

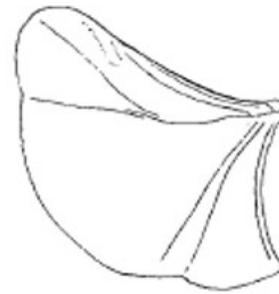


Fig. 42. Wing of *Halictophagus membraciphaga*  
Source: Subramaniam T V. 1927.

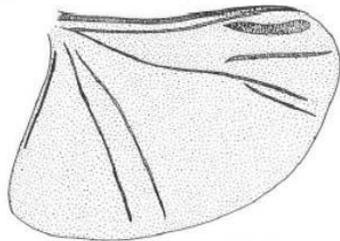


Fig. 43. Wing of *Halictophagus palmae*  
Source: Kathirithamby J, Ponnamma V K. 2000.



Fig. 44. Aedeagus-*Halictophagus tenebrosus*  
(Chaudhuri P K, Ghosh M, Das Gupta S K. 1983)

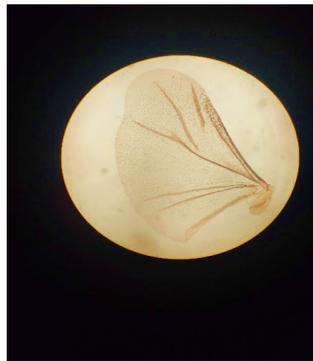


Fig. 45. Wing-*Halictophagus australensis*

..... *Halictophagus acerbus* Mazumdar and Chaudhuri, 1997

– No such spot present in wing (Fig. 47)

..... *Halictophagus indicus* Bohart, 1943

28(25). Hook of aedeagus forming an acute angle with shaft (Fig. 48) .....

.... *Halictophagus prominens* Roy and Hazra, 2016c

– Hook of aedeagus forming almost right angle with shaft (Fig. 49) .....

.... *Halictophagus bipunctatus* Yang, 1955

### 6. Future studies

The Strepsiptera have developed distinct adaptations in response to their long and varied evolution with their hosts (Kathirithamby et al., 2003; Pohl and Beutel, 2008; McMohan et al., 2011). Presently these unusual endoparasites are being explored as model systems in interpreting the evolutionary relationships between parasitic insects and their hosts (Kathirithamby, 2009; Kathirithamby et al., 2015). As the Strepsiptera are found all over the world, cryptic species could be common in this group (Hayward et al., 2011). Several families of the Strepsiptera are currently being studied to clarify cryptic species, host associations, and sexual selection. Stylopisation by the Strepsiptera induces

changes in the host organism's morphology and physiology, mostly rendering the host arthropod sterile. Kathirithamby (1989) reported that stylopised Hemiptera particularly members of the Delphacidae showed the following dramatic changes such as the primary sexual organs are either reduced or lost, the secondary sexual organs such as ovipositor, parameres, aedeagus, and the genital rudiments are also reduced to a greater extent in imagos than in the nymphs and further it is more prominent in males than females irrespective sex of the parasite, and tertiary sexual characters such as colouration, tymbal apparatus and the shape of the pygophore are completely missing in stylopised males.

Because some of their hosts are pestiferous damaging crop plants such as *Oryza sativa* (Poaceae), *Zea mays* (Poaceae), *Elaeis guineensis* (Arecaceae), *Areca catechu* (Arecaceae), *Cocos nucifera* (Arecaceae), *Mangifera indica* (Anacardiaceae), the Strepsiptera may be effective for use in the biological management of diverse pestiferous arthropods. *Stichotrema dallatorreanum* Hofeneder (Myrmecolacidae) stylopises nymphs of *Sexava nubila* Stål, *Segestes decoratus* Redtenbacher, and *Segestidea novaeguineae* (Brancsik) (Orthoptera: Tettigoniidae) in Papua New Guinea and their sterility is seen due to parasitic castration (Solulu et al., 1998). Among them *S. decoratus* and *S. novaeguineae* cause severe defoliation of *Elaeis guineensis* (Arecaceae), and *S. dallatorreanum* keeps them below the economic injury level (EIL) on the main island of Papua New

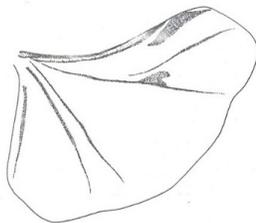


Fig. 46. Wing-*Halictophagus acerbus*

(Mazumdar A, Chaudhuri P K. 1997)

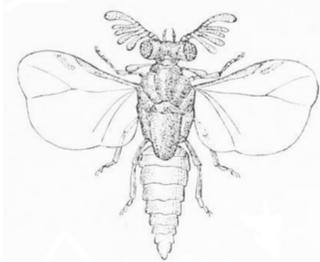


Fig. 47. *Halictophagus indicus*



Fig. 48. Aedeagus *Halictophagus prominens*

(Roy S, Hazra N. 2016b)



Fig. 49. Aedeagus of *Halictophagus bipunctatus*

(Hirashima Y, Kifune T. 1978)

Guinea (Kathirithamby et al., 1998). Due to the difficulty in detecting the females of the Strepsiptera in the field and small sized males with their varied morphology, the Strepsiptera in India has received little attention. Molecular systematics, evolution, sex determination, immunogenetics, and coevolution of these unique parasites require immediate attention.

### CONCLUSIONS

A complete picture of this bizarre group of insects will be of great help to systematists, applied entomologists, reproductive physiologists, agricultural scientists, parasitologists, etc. Discovery of new species will enrich the inventory of the world catalogue of the Strepsiptera, and their distribution should help in establishing their host relations and dispersal patterns. Habitat loss due to expanding agricultural activities, land fragmentation, deforestation, overgrazing and urbanisation is the principal human activity threatening the Strepsiptera. Nevertheless, conservation of these parasitic species should be taken seriously (Dougherty et al., 2016). Yet our inability to quantify economic costs associated with the permanent loss of these natural parasites remains. A more comprehensive understanding of unusual organisms such as the Strepsiptera and their biodiversity indicates that the ecological relationships between host arthropods and their parasites can be critical. The endoparasite, *Stichotrema dallatorreanum* Hofeneder is a good biological-control agent to *Segestidea novaeguineae* (Orthoptera: Tettigoniidae), a pestiferous arthropod of *Elaeis guineensis* in Papua New Guinea (Kathirithamby et al., 1998). The Strepsiptera generally do not show a high percentage of stylopisation due to their low-searching capability and short life span of the primary larvae. However, they have overcome these constraints by producing hundreds to seven hundred thousand first instar larvae (higher fecundity) depending on the species and host size.

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### CONFLICT OF INTEREST

No potential conflict of interest.

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