1. Introduction

Leaf hoppers (Homoptera: Cicadellidae) are abundant widespread phytophagous insect group. Among the different species under the generic group Cicadella, Cofana spectra (Distant 1908) are known as white leaf hoppers (WLH) (French 2006). They inhabit commonly in paddy plants and grasses (Krishnankutty & Viraktamath 2008). As pest they cause injury to host plants like rice, sugarcane, barley, wheat, and sorghum (Atwal & Dhaliwal 2002; Young 1979; Heinrichs & Barrion 2004). C. spectra are distributed in Oriental, Afrotropical, and Australian regions (Kamitani et al 2004), where rice is one of the staple foods. In India WLHs are prevalent in several regions of West Bengal, North East and Southern states (Young 1979; CAB International 2007). Young (1986) has revised the subfamily of the Old World and included 32 genera and 278 species. Of these, 12 genera and 55 species are recorded from India. Cofana Melichar differs from other Cicadella generic group in lacking basal aedeagal processes and the paraphyses, hind wing without R_{2+3} veins (Young 1979; Krishnankutty & Viraktamath 2008). For identification of species the weakly sclerotized male genitalia is not useful but the external characters especially markings of head and pronotum are more important diagnostic characters (Kamitani et al 2004). Of the 24 worldwide species of Cofana, only 7 are known from Indian subcontinent. They are Cofana spectra (Distant), Cofana bidentata Krishnankutty & Viraktamath 2008, Cofana lineata (Distant), Cofana nigrilinea (Stål), Cofana subvirescens (Stål), Cofana speculata Krishnankutty & Viraktamath 2008, and Cofana unimaculata (Signoret). C. spectra and C. unimaculata are abundant in West Bengal and are considered as minor pest (Reynold et al 1999).

Generally, plant hoppers feed on the basal and the leaf hoppers on the upper part of a paddy plant, but, belong to the same guild, since their mode of feeding is same i.e., both these insect groups are sapsuckers and xylem feeders. During
extensive feeding, and excessive oviposition, the plant systems suffer damage. The fungal and bacterial attacks occur on the oviposition marks and honeydew encourages sooty molds. These insects also act as vector of currently known rice viral diseases (Pathak & Khan 1994; Dahal 1997). Infestations of WLHs cause tillering reduction, moderate infestation leads to loss of ear production and leaves turn brown, and severe infestation result in the death of plants (Sam & Chelliah 1984). *C. spectra* are vectors of pathogenic viruses of rice in South, South-East Asia and Africa (Kathirithamby 1992). In Africa *Cofana* spp. are abundant over *Nephotettix* spp. and some important paddy pests (Heinrich & Barrion 2004). *C. spectra* and *C. unimaculata* are important pests in West Africa (Oyediran 2000, Ignibosa et al 2007). In the warm and humid tropics the species of leaf hoppers and plant hoppers remain active around the year and population fluctuate according to the availability of food plant, presence of natural enemies and environmental conditions (Pathak & Khan 1994). The population of WLH become low during winter as in middle of December, increase with the beginning of the rainy seasons in April but at hot summer they appear in a very few, again increasing in September reaching its peak in November (Oyediran et al 2000).

The endoparasitoid Strepsiptera can be considered as a useful natural enemy of hoppers. The percentage of stylopization of hoppers varies from 1% to 63% according to seasons (Otake et al 1976; Chandra 1978; Miura et al 1978; Barrion & Litsinger 1983; Pena & Shepard 1986). Hirashima and Kifune (1978) first reported parasitization of *Cofana spectra* by *Halictophagus spectrus* Yang in Sarawak Malyasia. Barrion and Litsinger (1983) listed several natural enemies attacking the hopper showing 11-50% variation of stylopization due to Strepsiptera depending on different biological and environmental factors like the host population, weather conditions, rice cultivars, age of the paddy plants and time of occurrence. A
relationship between growth and duration of rice cultivars with population of *Cofana spectra* is known, but no link has been established between the strepsipteran parasitoid and rice cultivars (Oyediran et al 2000). Strepsiptera is the second most frequent form of parasitoid of leaf hoppers after drynidids (Hymenoptera: Drynidae). Stylopization of the leaf hopper genera had also been reported (Baldrige & Blocker 1980; Kathirithamby 1993 b).

Strepsiptera (*Strepsi-*“twisted”; *pteron-*“wing”) are one of the most complex groups of unusual obligate endoparasitoid. On account of its sparseness, the study of this insect group had not been made much in comparison to other insects. They are unusual in their morphology, life history, genetics and host-parasitoid relationship, and exhibit extreme sexual dimorphism (Kathirithamby 2009). Free living males possess flabellate antennae, large, unique, raspberry-like eyes, reduced club shaped forewings (pseudohalteres), large fan shaped hind wings with reduced radial venation, absence of trochanter in the fore- and mid legs and usually hook-like aedeagus but the females are neotenic and permanently endoparasitic in the host abdomen, except the family Mengenillidae in which the late larva of both male and female emerge to pupate externally, the cephalothorax of the female extrudes outside from the host where a brood canal opening remains by which the female is inseminated by the male (Pierce 1909; Kathirithamby 1987, 1989, 1991, 1992; Mazzini et al 1991; Chaudhuri & Mazumdar 2000). Both male and female infect same host except in Myrmecolacidae where the male and female parasitize the host of different species even of different orders of the insects. The male parasitizes (Hymenoptera: Formicidae) the female of the members of Tettigonidae, Gryllidae, Gryllotalpidae (Orthoptera) and Mantidae (Dictyoptera). This phenomenon is called ‘heterotrophic heteronomy’ which makes impossible to distinguish the sexes
due to extreme sexual dimorphism and only molecular tools can prove their
conspecificity (Kathirithamby 2009).

Strepsiptera has been recorded from all the major zoogeographical regions.
Among the families, Corioxenidae, Halictophagidae, Elenchidae, Stylopidae,
Myrmecolacidae are cosmopolitan while Mengenillidae being unrepresented from
Nearctic and Neotropical and Bohartillidae were only found in Neotropical and
Callipharixenidae from Oriental region (Kathirithamby 1989, 1992). So far 596
species of Strepsiptera have been described in the world (Kathirithamby 2007) and
112 species were recorded from the Oriental region (Kathirithamby 1993; Pohl &
Melber 1996; Mazumdar & Chaudhuri 2004). Till date only 21 species belonging to
the 8 genera have been reported from this subcontinent (Mazumdar & Chaudhuri
2004).

The phylogenetic position of Strepsiptera is controversial and yet to be
resolved (Kathirithamby 2009). Strepsiptera are considered as a separate line in
insect evolution in respect to spermatology, animal taxonomy and phylogeny
(Mazzini et al, 1991; Kathirithamby et al 1992) while Whiting (1998) have taken
Strepsiptera as the sister group of true flies (Diptera) on the basis of morphological
and molecular evidence. Recently, a fossil of Protoxenos janzeni was discovered
which may be considered as the most archaic strepsipteran reducing the
"morphological gap" between Strepsiptera and other insects. It weakens current
hypotheses advocating the following clusters Coleoptera+Strepsiptera and
Diptera+Strepsiptera (= Halteria) (Pohl & Beutel 2008).

Major part of the lifecycle of both the sexes of Strepsiptera is spent in the
host haemolymph. Only the gut is present in the larval stages, which is redundant
in adult female and a modified structure "apron" is developed for absorption of
nutrients (Kathirithamby 2000, Johnston 2004). Strepsiptera exhibit haemocoelic fertilization
and haemocoelous viviparity. The first instar larva is a freeliving host seeking stage called triungulins. Ovaries develop in the earlier instar and break up in the third instar stage. These are present freely in the fat body of hosts in the absence of oviducts (Kathirithamby 1989). Adult male also possesses an unusual type of eye, a combination of a single and compound lens, and each unit functions as independent image forming unit and contributes a partial image of the visual field (Buschbeck 2005). Strepsiptera possess one of the smallest insect genome as revealed through study of flow cytometry. It is observed that higher level of endoreduplication occurs in strepsipteran thorax, which is not found in other insects possessing small genome. They also demonstrate unique mechanisms of immune avoidance after getting entrance in the host body and the triungulin wraps itself with epidermal tissue derived from the host and moult therein (Kathirithamby 2003).

Many workers studied on mating through use of tactile, visual, auditory and chemical senses in recognition of sexes. Copulation occurs immediately after the insects have paired or need an interval before resuming next copulation (Chapman 1998). General account on mating and oviposition behaviour on the leaf and planthoppers owes to Raatikainen (1967), Oh (1979), Viraktamath and Viraktamath (1981, 1982), Bhandari (1982), Duan and Messing (2000), Atwal and Dhaiwal (2002), Bailey and Nuhardiyati (2005), Hummel et al (2006), Hattori and Sogawa (2002) monitored the oviposition behaviour and oviposition capacity, which determined the population level of insect, hatching, development survival and egg production in Nilaparvata lugens (Stål) (Hattori & Sogawa 2002). The behaviour depends on the host availability, quality and environment (Papaj 2000). The eggs are cylindrical in shape and their micropyle protruding from leave sheath. Some aspects on ovipositing behaviour and biology of Cofana spp. are on record (Sam & Chelliah 1984; Atwal & Dhaliwal 2002; Heinrichs & Barrion 2004). Insects reared at higher temperature do survive but they are less fertile and often many eggs do not hatch (Pathak & Khan 1994).

Contrast to these, information on the reproductive biology of female Cicadellidae is scanty (Hummel et al 2006). The structure and development of the reproductive system is known from the works of Singh Purthi (1924), George (1928) and Kathirimuthy (1974). Structure of ovary and process of oogenesis were extensively studied in Heteroptera (Bonhag 1958; Telfer 1975; Bunning 1994; Santos et al 2002; Lemos et al 2005) and in Homoptera (Auchenorrhyncha and Stenorrhyncha) (Bonhag 1958; Szklarzewicz 1997, 1998a, 1998b; Szklarzewicz et al 2000, 2005; Tsai & Perrier 1996; Ksiazkiewicz 1980; Buning 1994). The basic structure of ovary is same in all hemipterans, characterized by the occurrence of telotrophic meroistic ovarioles. The number of ovarioles is species specific and
some times family specific; it usually varies from 4-7 in numbers (Buning 1994). The organization of trophic chamber and number of germ cell cluster varies species wise. The number of germ cells in the tropharium per ovarioles bears significance in the evolution of ovary (Buning 1994) and external genitalia of homopteran male.

The studies on the host-parasitoid relationship and its impact on the host are well documented (Jervis et al 2008). It is known that most species of Strepsiptera are host specific, barring few, like Deinelenchus australensis Perkins (Elenchidae), which parasitize 8 species of three different homopteran families (Kathirithamby 1989). Strepsipteran species, which maintain a large host range, are closely related with a similar life cycle (Maeta & Kifune 1990). Stylopization is known to cause many noticeable changes of their orthopteran, hymenopteran and hemipteran host group. Most of the information concerns qualitative alteration in host character as on morphology, colour and behaviour but work on physiology is largely lacking (Solulu et al 1998).

The impacts of strepsipteran parasitism on the hymenopteran families like Formicidae, Andrenidae, Vespidae, Sphecidae and Eumenidae have been evaluated (Pierce 1918; Bohart & Irwin 1978; Kifune & Maeta 1978; Jones & Jones 1981; Kathirithamby 1989; Maeta, & Kifune 1990; Cook 2000; Kitamura et al 2002; Kathirithamby 2009). For instance, changes were observed in the number of antennal segment due to strepsipteran infection that may not differ otherwise. Stylopization affects the instinctive behaviour and changes of pollen collection apparatus and the mechanisms of collection of some hymenopteran families (Pierce 1918). Among other effects, ovary is reduced (Pierce 1918) and anal fimbria become reduced or lost (Kathirithamby 1989). Kathirithamby (1989, 2009) made significant observations of the effect of stylopization and behaviour of the stylopized ants in the nest, which were opposite to stylopized wasps.
The effects of the strepsipteran parasitoid on orthopteran host are well recognized (Kathirithamby et al 1998; Solulu et al 1998; Kathirithamby et al 2001; Douropit et al 2001). It was observed that the Strepsiptera *Stichotrema dallatorreanum* Hofeneder reduced the fitness, feeding and reproductive capacity with its number of the host insects (Kathirithamby 1998). The morphological characters, gut content, body composition and reproductive variables are analysed and compared with normal all are more or less affected. Reproductive features were most affected, with impaired ovarian development, reduced egg number, and gonadal weight of both sexes (Sollulu et al 1998).

Several morphological and reproductive features are viewed as life history traits and are useful parameters to gauge the fitness of the individual insect (Agnew et al 2000, 2002; Via et al 1995). Life history traits are those that are associated with the survival and reproduction (Stearns 1989a, b; Stearns & Hoekstra 2005), which include growth rate, size at birth, age and size at maturity, fecundity, longevity and frequency of reproduction. Variations in life history traits may be due to genotypes and its interactions with the environmental factors (Nylin & Gothard 1998; Gotthard & Nylin 1995). Even if the genotypic variations are absent or minimal, the life history traits may be different quantitatively due to environmental impacts, which are substantiated through observations in the insects of the orders Lepidoptera (Nylin & Gothard 1998), Hemiptera (Heteroptera) (Pfenning & Poethke 2006) and Diptera (Agnew et al 2000, 2002; Sharmila Bharati et al 2003, 2004). Thus life history traits can differ quantitatively in a population bearing similar genotype but under different environmental regulations. Adjustment in the life history traits of an individual insect is obvious in response to varied abiotic conditions for its survival. For a pest species, this can be verified by alteration of abiotic environmental factors like food and temperature alone or in
combination with the biotic factors like crowding, predators and parasitoids. As evident, in many of the host-parasitoid systems, parasitoid induces change in the life history traits of hosts. For instance, the parasitoid *Elenchus tenuicornis* Kirby bears an effect on the morphology, anatomy, ethology and mortality of its host *Javesella pellucida* (Fabricius) (Raatikainen 1967). External genitalia are lost in delphacid host, *Sogatella furcifera* and *Nilaparvata lugens* due to parasitization by Elenchids and Drynids (Otake 1976).

In insects, fecundity is a positive function of the body size and longevity (Ambruster & Hutchinson 2002; Via et al 1995; DeWitt et al 1998). Longevity, on the other hand, depends on the feeding pattern and calorie content in the food (Agnew et al 2000, 2002). Thus variations in these life history traits are adaptive providing maximal fitness return to the species that can be explained in terms of the trade-offs in the life history traits (Stearns 1989a). The trade-offs are significant determinants for individual survival and maintenance of the population. Pest and vector insects face a continuous threat from environmental stochastic factors and the synthetic chemicals. Similarly a parasitoid may induce a significant variation in these important life history traits in the host species (Kathirithamby 1982; Jervis et al 2008). This is evident from the effects of parasitoid on the internal and external reproductive structures, as a manifestation of parasitoid infection in *Javesella pelucida* (Raatikainen 1967), *Ulopa reticulata* (Fabricius) (Waloff 1981a, b) and various hoppers (Kathirithamby 1974, 1975, 1977a, b, c, 1979, 1998). According to Kathirithamby (1977b, 1979, 1989), stylopization lengthens the life of the host, sex characters of stylopized male Delphacidae lost and the male resembles superficially a normal /unstylopized female but all other homopteran families appear normal from outside but internal genitalia may be affected (Kathirithamby 1998).
The interactions between host and strepsipteran parasitoid affects primary, secondary and tertiary sexual characters, owing to the physical presence of the parasitoid in the host body (Kathirithamby 1974, 1975, 1977a, b, c, 1998). The internal reproductive structure reduces or totally lost due to the presence of parasitoid. The external reproductive structure as ovipositors, parameres, aedeagus and genital rudiments suffer reduction to lesser degree in nymphs and to a greater degree in the adult, which are more pronounced in male than female. Tertiary or body characters are also changed. The rate of parasitism is related to the volume and biomass of the host. Parasitism by the strepsipteran species \textit{Halictophagus pontifex} Fox arrests development of the ovaries of female cercopid host. Ovaries may be reduced following emergence of male parasite but not after extrusion of the female, due to reinfection by triungulins (Greathead 1970). Otake (1976) found loss of external genitalia as the symptom of parasitization by Elenchids and Drynids in delphacid host, \textit{Sogatella furcifera} and \textit{Nilaparvata lugens}. According to Kathirithamby (1977a) and Waloff (1981a), parasitic castration occurred in \textit{Ulopa} sp. when parasitized by \textit{Halictophagus silwoodensis} Waloff. External genitalia were found modified but sex reversion was not there. Pena and Shepard (1986) showed highest stylopization in \textit{Sogatella furcifera} than other enemies in the summer season of the Philippines. The population growth of plant hopper may normally be in check due to natural enemies (Chandra 1980). The hosts die after emergence of male or triungulins. All these facts provide evidence that the life history of hosts is detrimentally influenced by the parasitoids. These changes in the life history features due to parasitoids may be used as indicators to deduce the potential population size and thus framing effective control strategies for host pests (Nylin 2001). Presence of Strepsiptera damages the sex organs of the host resulting lower population due to strepsipteran parasitism (Oyediran et al 2000) but the host may
remain alive in the sterilized condition. From these observations, it is apparent that the strepsipteran parasitism can be an important component in the suppression of Cofana spp. population in the rice fields. Therefore, studies involving the biology of C. spectra and its regulation through the strepsipteran endoparasitoid Halictophagus australensis are justified.

1.1 Aims and Objectives of the study

Keeping in view the paddy pest status of leaf hoppers, and following the findings of Chaudhuri and Dasgupta (1979), Chaudhuri and Mazumdar (2000) and Mazumdar and Chaudhuri (2004), it appears that the Strepsiptera as parasitoids bears high potential as biocontrol agent. The aim of the present study was to assess the effects of strepsipteran parasitoid on the paddy pests using C. spectra as a model hopper species. The objectives were -

1. Description of the morphological details including the reproductive structures of C. spectra and its strepsipteran parasitoid H. australensis.

2. To assess the seasonal variation of the white leaf hopper C. spectra and its parasitoid H. australensis in their common habitat – ricefields.

3. To make an estimate of the life history stages of normal and parasitized C. spectra.

4. To study the morphometric details and correlates of different life history traits of normal and infected C. spectra.

5. To assess the effect of H. australensis on the reproductive structure of C. spectra.

Apart from the life history traits, the survival and perpetuation of a pest species in nature depends on mating success (Nylin 2001). Successful mating assures the reproductive success and thus fitness at the individual and population
level. Mating behaviour of several pest species has revealed useful information that has been used to formulate strategies to avert the loss due to pest infestation (Carey 2001). In view of this, the mating and oviposition behaviour of C. spectra have been carried out under semi field and laboratory conditions.

In the present study an attempt has been made to quantify the life history traits such as longevity, body size and fecundity of the host, Cofana spectra. The effects of the strepsipteran parasitoid, H. australensis, on these life history traits have been compared. Such variations may predict the effect of the parasitoid on the host C. spectra parasitized by Strepsiptera and may be used to determine the potentiality for regulation of population of C. spectra (Oyediran 2000). Besides providing an illustration on the morphology and general biology of the minor paddy pest C. spectra, the results are expected to highlight the effect of the specific strepsipteran parasitoid on its life history and biology. The usefulness morphometric studies of pest can be justified. Further the data on the effects of parasitization may be useful to predict the usefulness of H. australensis as biological control agent.