A Review of the Predatory Adaptation and Applications of *Eocanthecona furcellata* (Hemiptera: Pentatomidae) as a Biological Control Agent[1]

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Abstract *Eocanthecona furcellata* (Wolff) (Hemiptera: Pentatomidae: Asopinae) captures and feeds on a wide range of insect pests, making it an important biocontrol agent in agriculture and forestry with significant regional application and promotional potentials. This review summarizes current research information on *E. furcellata* focusing on taxonomy, morphological characteristics involved in predation, its natural prey, mass rearing, regional application and potential, integrated pest management (IPM) usages, ecological safety evaluations, as well as future prospects for its use in IPM programs.

Key Words *Eocanthecona furcellata*, biological control, predatory adaptation, mass rearing

In agroecosystems, predatory bugs of the subfamily Asopinae (Hemiptera: Pentatomidae) play important roles in the management of insect pests (Memmott et al. 2000). All predaceous species in this subfamily possess synapomorphy characterized by a robust and stout rostrum, a combination of genital plates, as well as a thecal shield in the male genitalia (Roca-Cusachs et al. 2020). They prey on various insect pests in agriculture and forestry, occasionally sucking on plants juices in early developmental stages or resorting to cannibalism for survival when their natural insect prey items are unavailable (Gapud 1990, Plata-Rueda et al. 2022). The importance of biological control of insect pests by natural predators has gained the attention of many researchers in recent years with the advancement of technologies for ecologically protecting crops to ensure food safety and security. The investigation and utilization of natural enemies to manage key insect pests have become urgent and necessary especially considering the risks associated with chemical pesticides that kill indiscriminately not only harmful but also beneficial insect species. *Eocanthecona furcellata* (Wolff) is a typical representative predatory stink bug of Asopinae known for its high fecundity and strong predatory skills, enabling it to effectively control a wide range of pests, including Lepidoptera, Coleoptera, Diptera, and some phytophagous Pentatomidae (Hemiptera) (Kaur and Semahagn 2010, Yasuda and Wakamura 1992).

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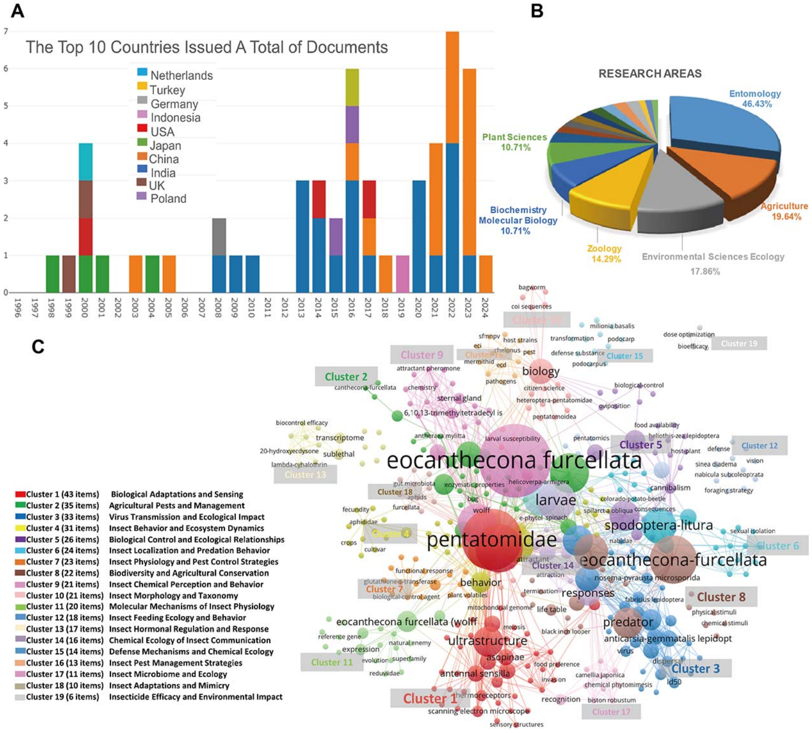

Fig. 1. The bibliometric analysis of published papers related to the *E. furcellata*. (A) Histogram of number of papers published by different countries in different years, (B) Comparison of papers published in different fields, and (C) Clustering diagram of the keywords in published papers on *E. furcellata*, where node size represents frequency and color represents clustering in the research field.

The published papers on *E. furcellata* from the Web of Science Core Collection (WOSCC) were downloaded for bibliometric analyses based on web tools (https://bibliometric.com/). The results revealed that there have been relatively few reports on *E. furcellata* in the past 30 years; however, research has significantly increased in recent years. The publishing fields covered include entomology (46.43%), agronomy (19.64%), environmental science (17.86%), zoology (14.29%), biochemistry and molecular biology (10.71%) as well as plant science (10.71%). The major contributors of the published studies have been primarily from India and China, likely because *E. furcellata* was originally identified and used as a biological control agent in Southeast Asia (Fig. 1A, B). Based on keywords of the downloaded papers, the studies on *E. furcellata* were classified into 19 areas, with biological adaptations and sensing in Cluster 1 (C1, same as below), agricultural pests and managements in C2, virus transmission and ecological impacts in C3, insect behavior and ecosystem dynamics in C4, biological control and ecological relationships in C5 being the top 5 clusters (Fig. 1C). These findings suggest that the current studies on *E. furcellata* focus on predatory habits (Chaudhary et al. 2022, Keerthi et al. 2020), feeding for mass rearing (Gupta et al. 2020, Tuan et al. 2016), and morphology (Shama et al. 2015, Zhao et al. 2021). However, there remains a lack of integration and summary of related studies and applications using *E. furcellata* as a biocontrol agent. This review, therefore, comprehensively elaborates on the current research progress of *E. furcellata* including but not limited to (1) taxonomy and phylogenetic studies, (2) evolution of morphological characteristics involved in predatory habits, (3) potential application and mass rearing, (4) ecological safety evaluation, and (5) the gaps in our knowledge of the development of the predatory bug and future expectations.

Taxonomy and Phylogeny

Eocanthecona furcellata was initially described as *Cimex furcellata* by Wolff in 1801 and re-described as *Canthecona furcellata* by Dallas in 1851 (Mangi et al. 2021). Subsequent taxonomic revisions named it *Cantheconidea furcellata* by Schouteden (1907) who further divided the genus *Cantheconidea* into two categories, with clade A including the model species *Cantheconidea javana*, featuring a modified mesosternum rising to embrace the rostrum, while clade B lacks this feature. Bergroth (1915) established the genus *Eocanthecona* (i.e., Clade B of *Cantheconidea*) which, at that time, only included *E. furcellata* and *Eocanthecona eburnea* (Distant). Currently, more than 20 species have been discovered and identified worldwide, such as *Eocanthecona formosa* (Horváth), *Eocanthecona japanicola* (Esaki & Ishihara), *Eocanthecona thomsoni* (Distant), *Eocanthecona concinna* (Walker), and *Eocanthecona tibialis* (Distant) (Grazia et al. 2015, Thomas 1994).

Most insects of the superfamily Pentatomoidea are herbivorous species, with a small number (Asopinae subfamily) being predatory. Previous studies have shown that specific gene family expansions and contractions due to adaptive evolution likely contributed to the diversification of species within Pentatomidae (Hemiptera) (Wu et al. 2024). Additionally, clades of phytophagous Pentatomidae were found to be sistered with the clade of Asopinae (Lian et al. 2022). Based on the phylogenetic tree constructed with mitogenomic genes, the predatory subfamily of Asopinae likely diverged from the most recent common ancestor (MRAC) of the extant phytophagous subfamilies (Chen et al. 2023).

Circumscribing and classifying the genus *Eocanthecona*, which has highly variable species and complex relationships within Asopinae due to rapid diversifications and radiation, have been challenging due to the limited data of phenotypical observations. The molecular taxonomy of *E. furcellata* was referenced by complete mitochondrial sequence of 13 species of Pentatomoidea by analysis of the 13 protein-coding genes and two rRNA genes (Guo et al. 2021). By utilizing the DNA barcode of cytochrome oxidase subunit I (*coxI*), a total of 65 species (including 5 species of the *Eocanthecona* genus) with 124 *coxIs* accessions of Asopinae were obtained from the National Center for Biotechnology Information (NCBI,

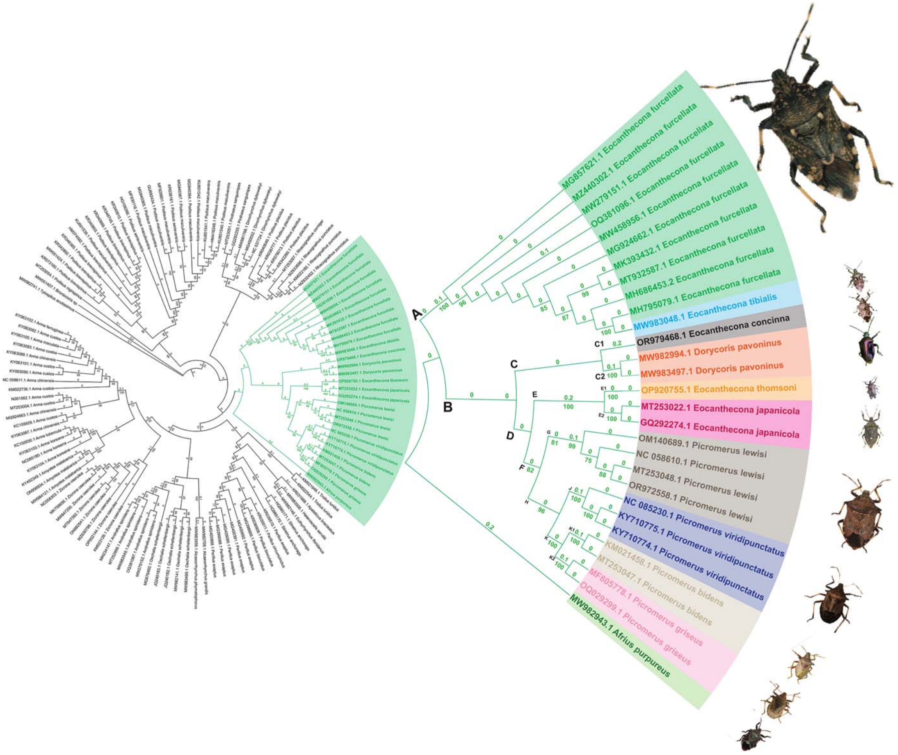

Fig. 2. The phylogenic tree constructed by mitochondrial cytochrome oxidase subunit I (*Mt-CoxI*) sequence download from NCBI (https://www.ncbi.nlm.nih.gov/) for taxonomy referring. Note: The *CoxI* genes were labeled with NCBI access ID followed by species name of Asopinae subfamily.

https://www.ncbi.nlm.nih.gov) for phylogenetic analysis in this review. The resulting phylogenetic tree showed that available species of *Eocanthecona* (i.e., *E. furcellata*, *E. tibialis*, *E. thomsoni*, *E. japanicola* and *E. concinna*) were divided into two clades with *E. furcellata* and *E. tibialis* clustered together in clade A, while *E. thomsoni*, *E. japanicola*, and *E. concinna* were clustered together in clade B, containing species from the genera of both *Dorycoris* and *Picromerus*. Interestingly, clade B can be further divided into subclades: subclade C, where *E. concinna* was clustered together with *Dorycoris pavoninus* (Westwood) and subclade D, in which *E. thomsoni* and *E. japanicola* were grouped as a minor clade sistered with another minor clade F encompassing species of *Picromerus* (Fig. 2, heighted part). Given the limited available data, the results of the phylogenetic tree rejected that the *Eocanthecona* genus has a monophyletic clade remains inconclusive. Further taxonomic research with increasing number of species from Asopinae, based on the their mitogenomes as well as nuclear genomes, is needed for a reasonable tribal classification of the *Eocanthecona* genus.

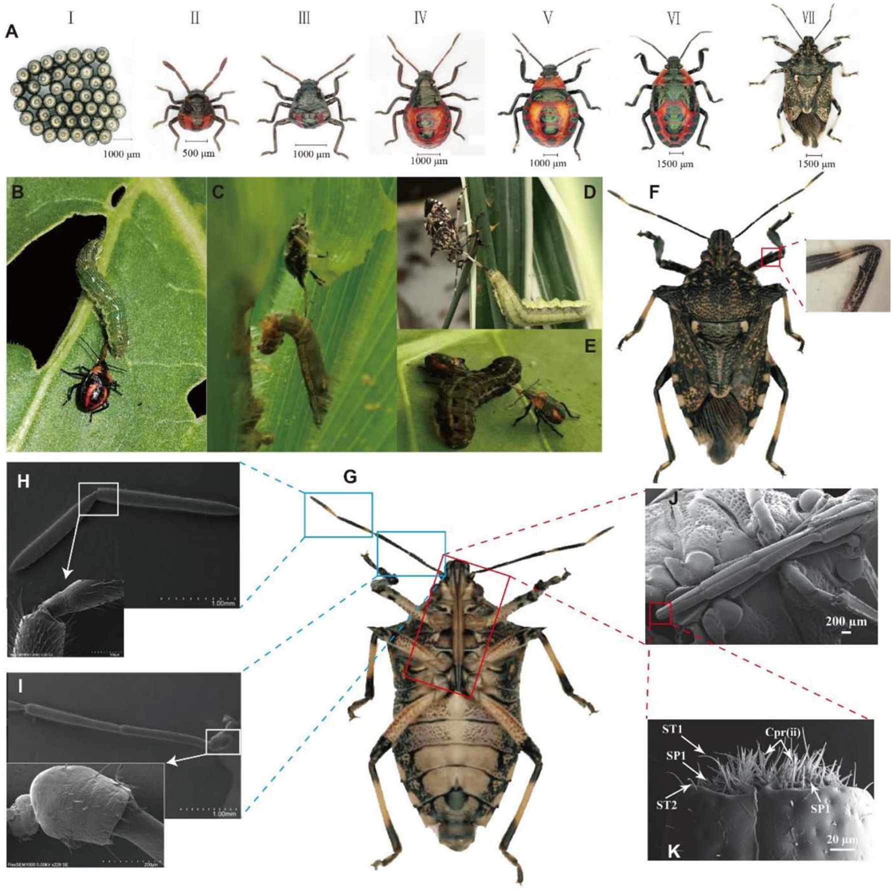

Fig. 3. Developmental characteristics and morphological adaptability to predation. (A) Morphology of *E. furcellata* eggs (I), nymphs (II: 1st instar nymph; III: 2nd instar nymph; IV: 3rd instar nymph; V: 4th instar nymph; VI: 5th instar nymph), and adults (VII, female), (B-D) The predation of different crop pests by *E. furcellata*, (E) joint predation of two *E. furcellata*, (F-G) enlarged images of the back, abdomen, and forefoot of *E. furcellata* adult (male), (H-I) microstructure of *E. furcellata* antennae (Zhao et al. 2021), (J-K) microstructure of *E. furcellata* mouthparts (Shama et al. 2015).

Morphological Characteristics and Development

The life cycle development of *E. furcellata*, a paurometabolous insect, consists of eggs, 1–5 instar nymphs, and adult female as well as male stages, with a total average developmental period of about 1 month (Fig. 3A, G). Eggs and body sizes of each stage are listed in Table 1. The eggs, with an average of 134.88 produced

Table 1. Body size of different insect states of *E. furcellata*.

Stage	Length (mm)	Width (mm)	Weight (mg)	References
eggs	1.1	0.9	NA*	(Lin et al. 1997)
1st instar nymph	0.050 ± 0.001	0.030 ± 0.001	0.00028	(Zhang et al. 2022)
2nd instar nymph	2.070 ± 0.040	1.370 ± 0.020	0.00065	
3rd instar nymph	3.880 ± 0.086	2.140 ± 0.050	5.45 ± 0.42	
4th instar nymph	6.120 ± 0.080	3.570 ± 0.050	18.10 ± 1.18	
5th instar nymph	10.670 ± 0.080	6.509 ± 0.080	111.95 ± 6.62	
adult female	14.480 ± 0.160	8.960 ± 0.100	175.85 ± 4.98	
male adult	12.240 ± 0.170	7.720 ± 0.110	152.75 ± 2.51	

* NA in the table indicates that no relevant data has been found.

per imaginal female, are cylindrical in shape with a metallic luster color. The egg cap is circular, with 10–12 spiny aero-micropylar projections at the edges. The fine structure of *E. furcellata* eggs was first observed and described with electron microscopy by Kumar et al. (2002). Newly oviposited eggs are silver gray or silver white, gradually turning gray-black or brown. Virgin female adults can also lay eggs with light color, but do not hatch with the shrinking of shapes in the later stage (Zhang et al. 2022).

Following embryological development, the first-instar nymphs usually live in groups and are oblate shapes with a red color. At the end of the 2nd-instar nymphal stage, the bugs start to prey with the body color becoming darker, while the 3rd and 4th instar nymphs develop into a pear-like shape; however, they have an oval appearance in the 5th instar. The mouthpart of the 1st-instar nymph is dark-red, but turns black as a 2nd-instar nymph. The length of the mouthpart in the 1st–2nd instar nymphs is close to the body length, while the mouthpart is about one-half the length of the body in the 3rd through 5th nymphal stages and as adults because body size increases rapidly in those stages. The notum is black in the 1st–2nd instar nymphs. It lacks punctations at these stages but appear after molting to the 3rd-instar nymph. The sternum is red with three black horizontal lines of the 1st–2nd instar nymph, the number of black horizontal lines increases from 4–5 at the 3rd–5th instar nymph. The antennae of *E. furcellata* have four segments. The first segment is short, while the 2–4 segments are reddish yellow in the 1st–4th instar nymph, but become gradually darker in the 5th-instar nymph and adults (Fig. 3). The external morphology of the antennae and the ultrastructure of sensilla for semiochemicals or volatile compounds perceptions in both the adult and 5th-instar nymphs were reported by Zhao et al. (2021) (Fig. 3H, I).

Eocanthecona furcellata exhibits a bizarre appearance with a robust mouthpart, presumably as an adaptation to predatory feeding habits. The mouthpart structures of *E. furcellata* have apparently evolved as defensive structures while capturing and feeding upon prey. The pronotum, for example of obvious protective structure, has an angled anterior covered protrusion in a sword-like shape, slightly curved upwards with two branches at the terminal. Another protective appendage structure is scutellum with a large, triangularly shaped and round shield at the end. Rani (2009) conducted ultrastructural observations on the tip of the mouthpart to discover three unique types of sensilla on the terminal mouthpart (Fig. 3J, K) which may play a role in detecting suitable food sources as well as the ability to probe both soft and hard tissues of its prey (Barsagade and Gathalkar 2016).

A black spot occurs on the front wing of adults, with many longitudinal veins on the wing membrane and a gray-black longitudinal band in the center. The forelegs have a slightly enlarged anterior tibia, quite distinct from the middle and hind legs, equipped with spines likely for holding prey. Additionally, the genital structures on the abdomen of males are nearly triangular, while those of females are oval-shaped (Fig. 3). The pigmented coloration of *E. furcellata* typically incorporates red and black, with unknown chemical-emitting structures possibly forming warning patterns to signal unpalatability to its natural enemies and/or to provide camouflage for avoiding detection by its natural prey.

The morphology of *E. furcellata* supports the predatory adaptation in terms of body development and form. However, there remains a lack of relevant studies on the molecular mechanisms underlying the evolution of ultrastructure for predatory adaptation and their impacts on individual development, population differentiation, success, and survival.

During development, the 1st- and early 2nd-instar nymphs do not prey as they only imbibe water or plant juices, while the 2nd- through 5th-instar nymphs and adults require natural prey as food for normal growth and development. This may involve recognizing the food source through visual detection and olfactory perception by antennae sensing of volatile chemicals emitted by the prey itself or from damaged parts of plants upon which the prey is feeding. Upon locating a prey item, the bugs extend their mouthparts and make multiple attempts to pierce into the prey. Once it captures the prey, *E. furcellata* exhibit extraoral digestion, sometimes performing aerial sucking behavior (Fig. 3C) (Barsagade and Gathalkar 2016). The digestion process involves the rostrum, salivary glands, and gut which function together for ingesting and digesting the prey, similar to most species of Asopinae. The rostrum is the piercing or stylet type mouthpart of *E. furcellata*, with the salivary glands producing enzyme-rich (e.g., protease, lipase, nucleases, glycosidases) secretions and various compounds that are injected into the prey body through salivary ducts within the mouthpart, causing prey paralysis, death, and tissue disrupting as an initial (extra-oral) step in digestion. Subsequent intermediary and final digestion, followed by nutrient absorption, occur primarily in the midgut (Yasuda and Wakamura 1992).

The range of prey for *E. furcellata* is extremely wide, including Lepidoptera, Coleoptera, and Hemiptera, with Lepidoptera being the preferred targets. Relevant literature on *E. furcellata* prey is listed in Table 2; however, this list does not represent all the natural prey for *E. furcellata*. As we observed, *E. furcellata* can also prey on *Phthorimaea operculella* (Zeller) as well as measuring worms (e.g., *Buzura thiberaria* [Oberthur]) (unpubl. data).

Pheromones and Pheromone Perception

Stink bugs, in general, emit sex or aggregation pheromones derived from terpene or fatty acid biosynthetic pathways for defense or as intraspecific communications (Rebholz et al. 2023). However, knowledge of the biosynthesis and regulation of these diversified and specialized metabolites remain limited in stink bugs including *E. furcellata*. Some insects do not directly synthesize pheromones. For example, male neotropical orchid bees (Euglossini) collect volatile terpenes and other volatiles from orchid flowers to attract conspecific females (Pokorny et al. 2017), while males of the oriental fruit fly (*Bactrocera dorsalis* [Hendel]) attract females by emitting a pheromone produced by bacteria in the rectal glands (Ren et al. 2021).

In Hemiptera, the central terpene backbone metabolism, including isoprenyl diphosphate synthases (IDSs) catalyzing the condensation of the terpene biosynthetic precursors of isopentenyl diphosphate (IPP) and dimethylallyl diphosphate (DMAPP) to form different-sized prenyl diphosphate intermediates (e.g., geranyl diphosphate [GPP], farnesyl diphosphate [FPP], and geranylgeranyl diphosphate [GGPP]) were elucidated by Noriega (2014) and Tholl et al. (2023). Isoprenyl diphosphate synthases (IDS)-type terpene synthase (TPSs) of *Nezara viridula* (L.)

Table 2. Insects that are reported to be prey of *E. furcellata*.

Species Name	Order	References
Antheraea mylitta (Drury)	Lepidoptera	(Barsagade and Gathalkar 2016)
Athalia proxima (Klug)	Hymenoptera	(Mohan et al. 2022)
Bombyx mori (L.)	Lepidoptera	(Gupta et al. 2020)
Calopepla leayana (Latreile)	Coleoptera	(Ahmad et al. 1996, C et al. 2022)
Chilo partellus (Swinhoe)	Lepidoptera	(Bhatnagar et al. 2022)
Clostera cupreata (Butler)	Lepidoptera	(Mohan et al. 2022)
Cnaphalocrocis medinalis (Guenee)	Lepidoptera	(Bhatnagar et al. 2022)
Corcyra cephalonica (Stainton)	Lepidoptera	(Chaudhary et al. 2022, Gupta et al. 2020, Rustam et al. 2019)
Craspedonta leayana (Latreille)	Coleoptera	(Tuan et al. 2016)
Eutectona machaeralis (Walker)	Lepidoptera	(Ahmad et al. 1996, Mohan et al. 2022)
Galleria mellonella (L.)	Lepidoptera	(Gupta et al. 2020)
Helicoverpa armigera (Hübner)	Lepidoptera	(Bhatnagar et al. 2022)
Hyblaea puera (Cramer)	Lepidoptera	(Ahmad et al. 1996, Mohan et al. 2022)
Hyposidra talaca (Walker)	Lepidoptera	(Sarkar et al. 2021)
Latoia lepida (Cramer)/*Parasa lepida* (Cramer)	Lepidoptera	(Senrayan 1988)
Maruca vitrata (F.)	Lepidoptera	(Bhatnagar et al. 2022, Tiwari et al. 2016)
Mythimna separata (Walker)	Lepidoptera	(Bhatnagar et al. 2022)

Table 2. **Continued.**

Species Name	Order	References
Nephopteryx rhodobasalis (Pyralidae)	Lepidoptera	(Ahmad et al. 1996, Mohan et al. 2022)
Oecophylla smaragdina (F.)	Hymenoptera	(Rustam et al. 2019)
Pericallia ricini (F.)/*Olepa ricini* (F.)	Lepidoptera	(Sahayaraj 2014)
Plecoptera reflexa (Guenée)	Lepidoptera	(Ahmad et al. 1996, Mohan et al. 2022)
Plutella xylostella (L.)	Lepidoptera	(Tuan et al. 2016)
Prodenia litura (F.)	Lepidoptera	(Ahmad et al. 1996)
Spilarctia obliqua (Walker)	Lepidoptera	(Chaudhary et al. 2022)
Spodoptera frugiperda (J. E. Smith)	Lepidoptera	(Keerthi et al. 2020)
Spodoptera litura (F.)	Lepidoptera	(Mohan et al. 2022)
Tenebrio molitor (L.)	Coleoptera	(Zhang et al. 2022)

were found to catalyze the conversion of (E, E)-FPP to (+)-(S, Z)-α-bisabolene as the likely common precursor of most pheromones biosynthesis (Lancaster et al. 2019). Additionally, the harlequin bug (*Murgantia histrionica* [Hahn]) also uses IDS-type TPSs to convert (1S,6S,7R)-1,10-bisaboladien-1-ol (sesquipiperitol) to murgantiol as an aggregation pheromone (Khrimian et al. 2014a). *Halyomorpha halys* (Stål) also uses terpene analogs as pheromone or semiochemicals for communication (Khrimian et al. 2014b). These discoveries suggest that the predatory *E. furcellata* may also use terpenes as major components in the blending of semiochemicals for communications. Ho et al. (2005) reported that the male specific compound, 6,10,13-trimethyltetradecyl isovalerate secreted by the sternal gland (SG) of *E. furcellata*, was dramatically changed by isolated rearing, with higher levels averaging 1,948 ng per male bug compared to group rearing of approximately 5–8 bugs with only 4 ng per male bug (Fig. 4A). This compound may play a role as an aggregation or sex pheromone for attracting females (Ho et al. 2005). Ho et al. (2003) reported that the metathoracic gland (MTG) secreted volatiles with higher levels of (E)-2,9-decadienal in females than in males, with converse patterns of (E, Z)-2,4-decadienal (Fig. 4A). The volatiles from the dorsal abdominal gland (DAGs) contained geraniol, which was specific in males, while both limonene and α-terpineol were detected only in females (Fig. 4A), indicating their potential involvement in sexual behavior of *E. furcellata* adults.

Insects detect volatile odorants/pheromone molecules using olfactory receptors (ORs) or pheromone receptors (PRs), typically located on cell membrane of sensilla located on their antennae and/or maxillary palps (Hansson and Stensmyr 2011). The sensillum lymph contains soluble pheromone binding proteins (PBPs) that bind with pheromones/odorants, passing through the pores on the cuticular surface of the olfactory sensillum to activate PRs or ORs (Leal 2012) (Fig. 4B). The peripheral olfactory sensilla house olfactory sensory neurons that play a role in odorant perception and signal transduction to the central nervous system. Many studies in model insects have revealed the odorant-binding proteins (OBPs)/PBPs, sensory neuron membrane proteins (SNMPs), PRs or ORs, as well as their co-receptors (Orcos) are involved in the chemoreception and signaling of pheromone molecules (Fig. 4B). This process also involves ion transportation mediated by ion receptors (IRs) either directly or indirectly through G protein-coupled signaling pathway, including phospholipid degradation and secondary calcium signaling mediated by both diacylglycerol (DAG) and inositol-3-phosphate (IP3) (Brito et al. 2016, Sakurai et al. 2014).

Mass Rearing Considerations

Expanding the global range of *E. furcellata* to control of harmful phytophagous insect pests in agricultural crops and forests has led to a gradual increase in market demand for the predatory insect. However, in the face of competition from other predatory insects in China (e.g., *Arma custos* [F.]), the development of mass rearing of *E. furcellata* will inevitably require the prerequisite of low costs and high yields, necessitating a breakthrough in less expensive artificial foods for the rearing process as well as automatic rearing lines for reducing labor fees.

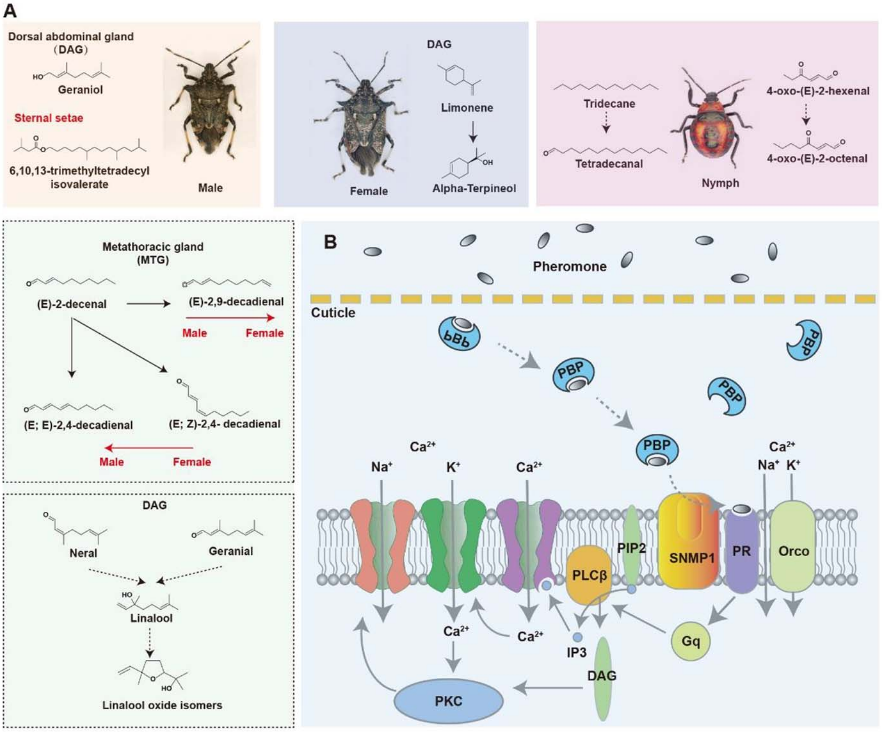

Fig. 4. The semiochemicals and perception of the *E. furcellata*, (A) the reported semiochemicals, (B) possible diagram of volatile pheromone perception and signaling (Fleischer and Krieger 2018). Note: Compounds in the orange, purple and pink backgrounds are specific to males, females and nymph respectively, and green background is compounds common to both males and females. PBP: pheromone-binding protein, PR: pheromone receptor, SNMP1: sensory neuron membrane protein 1, Orco: OR co-receptor, Gq: G protein, PLCβ: phospholipase C type β, PIP2: phosphatidylinositol 4,5-bisphosphate, IP3: inositol 1,4,5-trisphosphate, DAG: diacylglycerol, PKC: protein kinase C.

Many studies, plus our current rearing practices, have established an optimal mass rearing environmental control for *E. furcellata* by maintaining a temperature of 28–30°C, with a photoperiod of 16L/8D, a relative humidity of 70%, a male to female ratio of 1:1–2, and a rearing density of 7,307–10,961 per m^3. Our rearing practices showed that overly high rearing densities of the bugs can lead to self-destruction or cannibalism. Mass rearing of *E. furcellata* in China uses primarily natural or semi-natural prey insects, such as *Spodoptera frugiperda* (J.E. Smith), *S. litura* (F.), *Bombyx mori* L., and *Tenebrio molitor* L., as food which, in turn, requires a significant amount of manpower and plant resources, resulting in higher rearing costs. Successful propagation of *E. furcellata* using frozen *B. mori* pupae effectively reduces rearing costs and promotes off-season reproduction (Gupta et al. 2020), as *B. mori* have been efficiently and cheaply mass reared on mulberry (*Morus alba* L.) leaves for thousands of years in China.

In Hemiptera, many endosymbionts in guts have nutritional roles by synthesizing essential amino acids, vitamins, carotenoids, or purines that cannot be made by their insect hosts and are lacking in their diets (Hansen and Moran 2014). Therefore, saps from certain host plant with beneficial microorganisms are required in culturing *E. furcellata*, especially in the 1st- and 2nd-instar nymphal stages. During the mass rearing of *E. furcellata*, population degradation (reduced viability, poorer disease resistance, slower growth, smaller individuals, and low fecundity) was often observed, which were associated with inbreeding within the rearing populations. Therefore, attention should be placed on the collection of wild *E. furcellata* or *ex situ* introductions of gene sources by crossing in the process of large-scale rearing of the stink bugs to retain their genetic diversities.

Temperature Adaptations

Exposure of *E. furcellata* 4th–5th nymphs and adults to high temperatures induced diapause in oviposited eggs (Wen et al. 2017). The diapausing eggs tolerated high temperatures at a cost of low viability. The trade-off between survivability and viability is probably a strategy to adapt to unpredictability in seasonally hot temperatures for survival (Wen et al. 2017). Future research will focus on the characterization of physiological and metabolic changes in egg development in response to high temperatures.

In addition, endosymbionts impact insect fitness, influencing insect host fecundity, viability, tolerance of extreme temperatures, and resistance to both pathogens and parasitoids should be considered (Fellous et al. 2011, Ghanim and Kontsedalov 2009, Himler et al. 2011, Montllor et al. 2002).

Due to its occurrence in tropical and subtropical regions, *E. furcellata* is more sensitive to lower temperatures. The two distinct peaks in the population distribution of the stink bug throughout the year, due to temperature changes, were discovered. Extremely high temperature induced diapause with the highest proportion of egg diapause occurring at a treatment of 35 and 33°C in light and dark periods, respectively, was reported by Wen et al. (2017). The adult bugs overwinter on fallen leaves, but no nymphs were found overwintering (Lin et al. 1997) indicating that adults are the major overwintering form of the bugs and were more tolerant to lower temperatures than nymphs. Additionally, recent research shows that, when the bugs were reared at lower temperatures (16–20°C), the adult's ovarian development slows or halts, leading to dormancy (Zhu et al. 2023). This suggests that *E. furcellata* likely undergoes the “bet hedging” strategy in which both diapausing and non-diapausing dormancy of individuals coexist to protect the species from extinction due to unpredictable environmental fluctuations of extreme temperatures due to seasonal changes (Waldbauer 1978, Wen et al. 2017).

Distribution and Potential Usage as Predators of Crop Pests

Eocanthecona furcellata is mainly distributed in Southeast Asia (e.g., southern parts of China, India, Malaysia, Philippines, Myanmar, Indonesia, Thailand, and

Sri Lanka) (Shylesha and Sravika 2018, Yao et al. 2023). The Maximum Entropy (MaxEnt) model was used to predict the potential geographical distribution of *E. furcellata* globally (Zhao et al. 2022) with the results revealing that precipitation of the warmest season and the average temperature of the coldest season are the main environmental factors influencing the distribution and population size of *E. furcellata*. Based on the overlap of geographic areas in which *E. furcellata* will succeed in the areas of agricultural production areas, we postulate that *E. furcellata* has significant potential for use in managing economically-important crop pests, such as *Galleria mellonella* (L.) (Hosni et al. 2022), *Cydia pomonella* (L.) (Kumar et al. 2015), and *S. frugiperda* (Ramasamy et al. 2022) on a variety of crops.

Ecological Safety Assessments for Introductions

Assessment of the ecological safety of introducing *E. furcellata* into geographic areas where the predator is not indigenous is an important consideration in expanding the range of these biological control agents. In the food chain, *E. furcellata* mainly functions as a secondary consumer and sometimes as a primary consumer by imbibing on plant sap. Therefore, establishing an effective and efficient method for evaluating ecological safety is essential for ensuring the success of the predator and its large-scale release, while not causing ecological disruption or negatively impacting existing agricultural production. Unfortunately, there are currently no reports of such an assessment for *E. furcellata*. Hence, following the requirements of the ecological security policy and obtaining permissions from both the central and local government agencies, we propose (1) to establish ecological safety evaluation bases in forests, meadows, farmlands, etc. in accordance within the *E. furcellata* high suitability area; (2) to preliminarily evaluate its ability to control the pests and its possible destructiveness to the ecological environment in both laboratory as well as field testing with methods of cage catching (Fox et al. 2004, Gardiner et al. 2009), stable isotope assessment (Baker and Tann 2013, Gould et al. 2002) as well as molecular labelling (Wolf et al. 2009); (3) to collect data on the number, density, incidence rate, disease index, and populations of various pests as well as beneficial insects to establish a scientific and efficient ecological security evaluation protocol based on the Internet of Things by designating at least 2 or more ecological trial zones with at least an area of 2–10 ha^2 and sampling of 30–50 experimental sites for each trial zone. Such an assessment will require interdisciplinary collaboration.

Integration with Pest Management Tactics

When *E. furcellata* predators were fed *S. litura* larvae infected with a nucleopolyhedrovirus (NPV), the NPV did not infect *E. furcellata* and had no negative effects on the insect's normal growth and development. Thus, using a combination of NPV $+$ *E. furcellata* may have potential in controlling NPV $-$ sensitive lepidopteran pests (Gani et al. 2013; Gupta et al. 2013, 2014). *Bacillus thuringiensis* (Bt) as well as its Bt toxins are widely used for controlling lepidopteran, coleopteran, hymenopteran, dipteran pests, as well as pathogenic nematodes (Bravo et al. 2007, Soberón et al. 2007). Porcar et al. (2009) further showed that Bt Cry has weak-to-moderate activity against hemipteran species, especially aphids. Meanwhile, many reports suggest that Bt Cry can effectively exert insecticidal activity in an alkaline midgut environment (Berenbaum 1980, Rajan 2023). Based on our research, the pH of the *E. furcellata* intestinal tract is 5.5–6.0, suggesting that *E. furcellata* may tolerate the Bt toxins and, thus, the combination of Bt/Bt Cry with *E. furcellata* has potential against pest species susceptible to Bt/Bt Cry. Additionally, biological control of pests with egg parasitoids (e.g., *Trichogramma* spp. and *Telenomus remus* Nixon) has attracted extensive attention (Fortes et al. 2023, Garcia et al. 2024). Our trials on preventing damage from lepidopteran pests (e.g., *S. litura*, *S. frugiperda*, and *Heliothis assulta* [Guenée]) to major crops (e.g., corn, tobacco) in Yunnan, China, using both *E. furcellata* and *T. remus*, showed that the use of both agents had significant synergistic effects (unpubl. data), thus, suggesting that combined use of *E. furcellata* and egg parasitoids is also a promising management tactic.

The indiscriminate use and abuse of conventional chemical insecticides have resulted in significant harm to the environment and pose a threat to biological control agents (Kanga et al. 2016). However, insecticides are indispensable to IPM in agricultural production for rapidly lowering pest populations below economic thresholds and stabilizing agricultural product quality and yield (Tudi et al. 2021).

Whether and how insecticide exposure might affect the predatory efficacy of *E. furcellata* remains largely unexplored. Xu et al. (2024) showed that the exposure of *E. furcellata* to a sub-lethal concentration (LC_{30}) of chlorpyrifos, a broad-spectrum organophosphate, unexpectedly increased predation capacity and the maximum predatory number of *E. furcellata,* while reducing the prey handling time. They also observed a higher expression of detoxification related genes in the exposed vs. control group (Xu et al. 2024). A similar study with λ-cyhalothrin showed that λ-cyhalothrin had no effect on the mortality, body weight, and protein content in the stratum corneum of *E. furcellata*, and there were no observed changes in the activity of major detoxification enzymes (Pang et al. 2023). λ-cyhalothrin, however, significantly reduced the predatory ability and reproductive potential of *E. furcellata* (Yao et al. 2022, 2023).

Additional research is required to elucidate any additive or synergistic activity in combining *E. furcellata* with other biological control agents or insecticidal chemicals. Furthermore, tolerance of *E. furcellata* to commonly used conventional chemical insecticides must be defined.

Future Considerations

Eocanthecona furcellata has great potential for development and use as a biological control agent for pest management in agriculture and forest production with its wide feeding range (Table 2). To date, research on *E. furcellata* has mainly focused on predatory habits (Chaudhary et al. 2022, Keerthi et al. 2020), feeding protocols and methods for artificial rearing (Gupta et al. 2020, Tuan et al. 2016), and morphological studies (Shama et al. 2015, Zhao et al. 2021) (Fig. 1). However additional studies are required to effectively use the predator in IPM programs.

Taxonomic analysis of the genus *Eocanthecona* has proven challenging due to the limited availability of phenotypical data. Using DNA barcoding marker data (*coxI*) of Asopinae, the constructed phylogenetic tree suggests that the postulation that the *Eocanthecona* genus is of non-monophyletic origin is inconclusive (Fig. 2) (Wu et al. 2024). Further taxonomic studies based on mitochondrial genomes and nuclear genomes with additional Asopinae species, as well as detailed descriptions of their morphology, are needed to determine the correct tribal classification of the genus *Eocanthecona*. This knowledge would improve our understanding of the evolutionary history of *E. furcellata* as well as unifying our knowledge of key genes/QTL as possible sources of predatory adaption.

The native range of *E. furcellata* is predominantly in Southeast Asia, with an exceptionally broad habitat. Introduction of the insect to other areas and regions that are characterized by abiotic and biotic conditions that support the insect must, however, be carefully considered and evaluated to avoid potential adverse effects and to ensure that crops and forests in the expanded range remain safe from those adverse effects. For example, *E. furcellata* preys upon a variety of herbivorous insects which are also food sources for other invertebrate and vertebrate predators. In addition, *E. furcellata* can consume plant sap and, thus, could potentially become vectors of plant pathogens in the expanded range.

Development of an active release program for *E. furcellata* will require establishing an automated production process suitable for large-scale production with reduced costs. Production should encompass essential components or modules, such as egg collection, automated sorting of insects in different developmental stages and gender, as well as packaging of insects at the appropriate developmental stages for transport or shipping. Successful implementation of these processes, however, necessitates comprehensive support from various technical aspects and studies including, but not limited to, the following: (1) The *E. furcellata* behavior of randomly ovipositing eggs creates a situation of increased costs for egg collection; therefore, the discovery and effective use of suitable pheromones or attractants that will attract imaginal female adults to a specified location after completing courtship and mating should be explored. (2) Although existing literature reports the occurrence of diapause and dormancy of *E. furcellata* eggs and adults in response to extremely high temperature, challenges persist regarding the survival and hatching rates of diapause eggs of *E. furcellata* (Wen et al. 2017, Zhu et al. 2023). Development of techniques to address diapause/dormancy occurrence may facilitate seasonal regulation of production and storage. (3) The facilities in which *E. furcellata* are reared are plagued with malodorous gases resulting from the decomposition of feces, residual foods, carcasses of dead prey, and *E. furcellata* themselves. Developing deodorization techniques using activated carbon adsorption, biological deodorization, or UV photolysis deodorization, as well developing symbiotic microorganisms for the gut could be an avenue of research. (4) The male-to-female ratio significantly affects the numbers and quality of fertile eggs produced by *E. furcellata*; therefore, developing methods for inexpensive and rapid gender detection, female transformation by genetic modification, as well as easily sorting of male from female adults based on morphological or genomic marker(s) may be possible ways to detect and facilitate separating sexes.

Modern multiomics is providing new insights and opportunities to understand the evolution and dynamics of plant-pest interactions and predatory insects. The application of high-throughput methods for examining variations at the genomic, transcriptomic, proteomic, and metabolomic levels has facilitated thorough investigation of the relationship and interaction among protected crops, pests, and *E. furcellata* and will likely become a major focus for basic and applied studies of *E. furcellata*.

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