



Review Article

A comprehensive review of *Chelonus* s. str. Panzer (Hymenoptera: Braconidae: Cheloninae) with a special reference to the species associated with fall armyworm, *Spodoptera frugiperda* (J.E. Smith) (Lepidoptera: Noctuidae)

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ABSTRACT: The genus *Chelonus* s. str. (*Chelonus*) Panzer (Hymenoptera: Braconidae: Cheloninae) is reviewed with particular focus on species associated with fall armyworm, *Spodoptera frugiperda* (J.E. Smith) (Lepidoptera: Noctuidae). Additionally, information on the biology and various mass-rearing techniques of the enumerated species are furnished, underlining their significance in biological control and integrated pest management strategies.

KEYWORDS: Fall armyworm, natural enemies, parasitoid, wasp

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INTRODUCTION

The fall armyworm, *Spodoptera frugiperda* (J.E. Smith) (Lepidoptera: Noctuidae), is a highly invasive and polyphagous insect pest capable of infesting over 353 plant species across 76 plant families. This widespread infestation significantly threatens various economically important crops, including essential staple and fibre crops (Early *et al.*, 2018; Montezano *et al.*, 2018; Casmuz *et al.*, 2010; Perier *et al.*, 2022). Since its introduction in continental Africa in early 2016, this pest, known for its migratory nature, has rapidly spread to more than 60 countries across the tropics and sub-tropics (Goergen *et al.*, 2016; Westbrook *et al.*, 2019). The recent incursion of *S. frugiperda* has resulted in profound environmental, economic, and social consequences, particularly affecting the food security and livelihoods of smallholder farmers in developing countries (Durocher-Granger *et al.*, 2021). The larval feeding behaviour of this invasive pest has led to significant crop yield losses and diminished crop quality, with reported losses of up to 20% on various crops in the United States and yield reductions ranging from 17% to 72% on maize in different

global regions (Perier *et al.*, 2022; Mamahit & Kolondam, 2023). Recent occurrences in the Philippines underscore the recurring invasions of fall armyworms in rice nurseries and direct-seeded rice fields, including both previously affected areas and newly designated rice-production regions. This ongoing expansion highlights the persistent challenges posed by the increasing distribution of fall armyworm (Valdez *et al.*, 2023a; Valdez *et al.*, 2023b).

In the Western Hemisphere, the development and wide adoption of genetically modified maize against FAW and other insect pests (Bt maize) has contributed to increased productivity of the crop. However, its potential is continuously challenged by the development of field-evolved resistance, including new pyramided maize varieties that express multiple Bt toxins (Bernardi *et al.*, 2015). While GM maize has been widely adopted in some regions, its use is proscribed in many parts of the world due to a multitude of factors, including regulatory policies, economic pressures, public acceptance, and the ongoing need to address environmental and health concerns.

The extensive global use of synthetic insecticides to tackle *S. frugiperda* has developed resistance across diverse insecticide classes, including pyrethroids, organophosphates, and carbamates. In regions such as India, farmers initially relied on broad-spectrum synthetic insecticides such as lambda-cyhalothrin, emamectin benzoate, and thiamethoxam to address FAW outbreaks. However, the efficacy of chemical control proved to be short-lived and ultimately unsustainable (Prasanna *et al.*, 2018; Sharanabasappa *et al.*, 2019; Sagar *et al.*, 2022; Mamahit & Kolondam, 2023). Recognizing the limitations of synthetic chemical insecticides, Kenis *et al.* (2022) proposed an alternative approach. They identified 24 botanical insecticides sourced from 17 plant families and subjected them to rigorous testing against *S. frugiperda*. This exploration of botanical solutions presents a promising pathway for developing more sustainable and effective pest management strategies.

In economic entomology, employing environment friendly alternative measures, such as augmentative releases or the conservation of Natural Enemies (NE) like insect predators, parasitoids, and entomopathogens, represents a mutually beneficial solution for regulating pest populations at the farmers' field level. Biological pest control plays a crucial role in maintaining the natural balance, or homeostasis, of ecosystems, where certain organisms prey on others as part of their survival strategy (van Lenteren, 2000). Although sudden outbreaks of herbivorous species are common in natural environments, they typically return to their original levels due to the influence of natural regulatory mechanisms (DeBach, 1964). Various approaches have been proposed for conserving NE, including reducing reliance on synthetic pesticides (van Emden, 2002) and manipulating the environment through ecological engineering (Mitsch, 1998; 2012; Fiedler *et al.*, 2008). One widely accepted method involves the mass production and subsequent release of NE, known as "augmentative" or "inundated" biological control (Parrella *et al.*, 1992; Collier & van Steenwyk, 2004). The primary goal is significantly reducing pest populations below the Economic Threshold Level (ETL) (Parrella *et al.*, 1992). However, it is important to note that these NEs often have a broad range of hosts, such as Lepidoptera, in the field, which may distract the parasitoid from targeting the primary insect pest (Carrillo-Sánchez, 1985). Therefore, it is crucial to recognize that many NEs have diverse ranges of hosts and prey, underscoring the importance of conserving alternative hosts to maintain NE populations.

INSECT NATURAL ENEMIES OF *S. frugiperda*

The utilization of parasitoids presents a cost-effective, environment friendly, and comparatively long-term approach with minimal risk of inducing resistance (Molina-

Ochoa *et al.*, 2003). A diverse array of approximately 172 parasitoid and parasite species targeting *S. frugiperda* has been documented in the American continents, including the Caribbean Islands (Molina-Ochoa *et al.*, 2003). Notably, trichogrammatids and braconids are prevalent, with 20 and 12 recorded species, respectively. For the latter, this includes one species of *Campoletis sonorensis* (Cameron) (Campopleginae), three species of *Cotesia* (Microgastrinae), and four species of *Coccygidium* (Agathinidae). Globally, 11 species of *Chelonus* associated with FAW have been recorded (Figure 1 and Table 1). Colmenarez *et al.* (2022) conducted a detailed review of the use of the egg parasitoid *Telenomus remus* Nixon (Hymenoptera: Scelionidae) in four Latin American countries (Venezuela, Honduras, Brazil, Colombia), encompassing the frequency of releases and the percentage of FAW egg parasitism. Recent findings by Kenis *et al.* (2022) extended the global understanding, documenting 37 parasitoid species, including four species of *Chelonus* in various African countries and 41 parasitoid species in Asia. In Ghana, Agboyi *et al.* (2020) reported larval parasitism by other parasitoids ranging from 18% to 42% during the maximum level of the rainy season but significantly lower in the minimum level of the rainy season. Additional insect groups acting as NE of *S. frugiperda* include two species of tachinid flies (Diptera: Tachinidae), *Drino quadrizonula* (Thomson), and an undetermined species, two species of minute pirate bugs *Orius insidiosus* (Say) and *Orius similis* Zheng (Hemiptera: Anthocoridae), and one pentatomid bug *Eocanthecona furcellata* (Wolff) (Hemiptera: Pentatomidae) (Bahena & Cortez 2015; Subramaniam, 2022). Noteworthy recent reports from the Philippines by Valdez *et al.* (2024) highlight two hymenopteran parasitoids, *Brachymeria lasus* Walker (Hymenoptera: Chalcididae), and *Copidosoma floridanum* (Ashmead) (Hymenoptera: Encyrtidae), while Calcetas *et al.* (2023) documented the egg-larval parasitoid *Chelonus formosanus* Sonan.

THE FAMILY BRACONIDAE AND SUBFAMILY CHELONINAE

The Braconidae is the second-most species-rich family of parasitoid wasps in the animal kingdom (Chen & van Achterberg, 2019). They are morphologically more diverse and better studied because a greater proportion of the species are important to agriculture and have been used in biological control (Huber, 2009). The parasitoid wasp family Braconidae is one of the most biodiversity-rich families of Hymenoptera and with more than 1,100 genera, and >21,220 valid described species it is also considered one of the largest families of Metazoan (Yu *et al.*, 2016; Chen & van Achterberg, 2019). It encompasses representatives in more than 40 accepted subfamilies, which are approximately 1–30 mm in length and are currently recognized as monophyletic

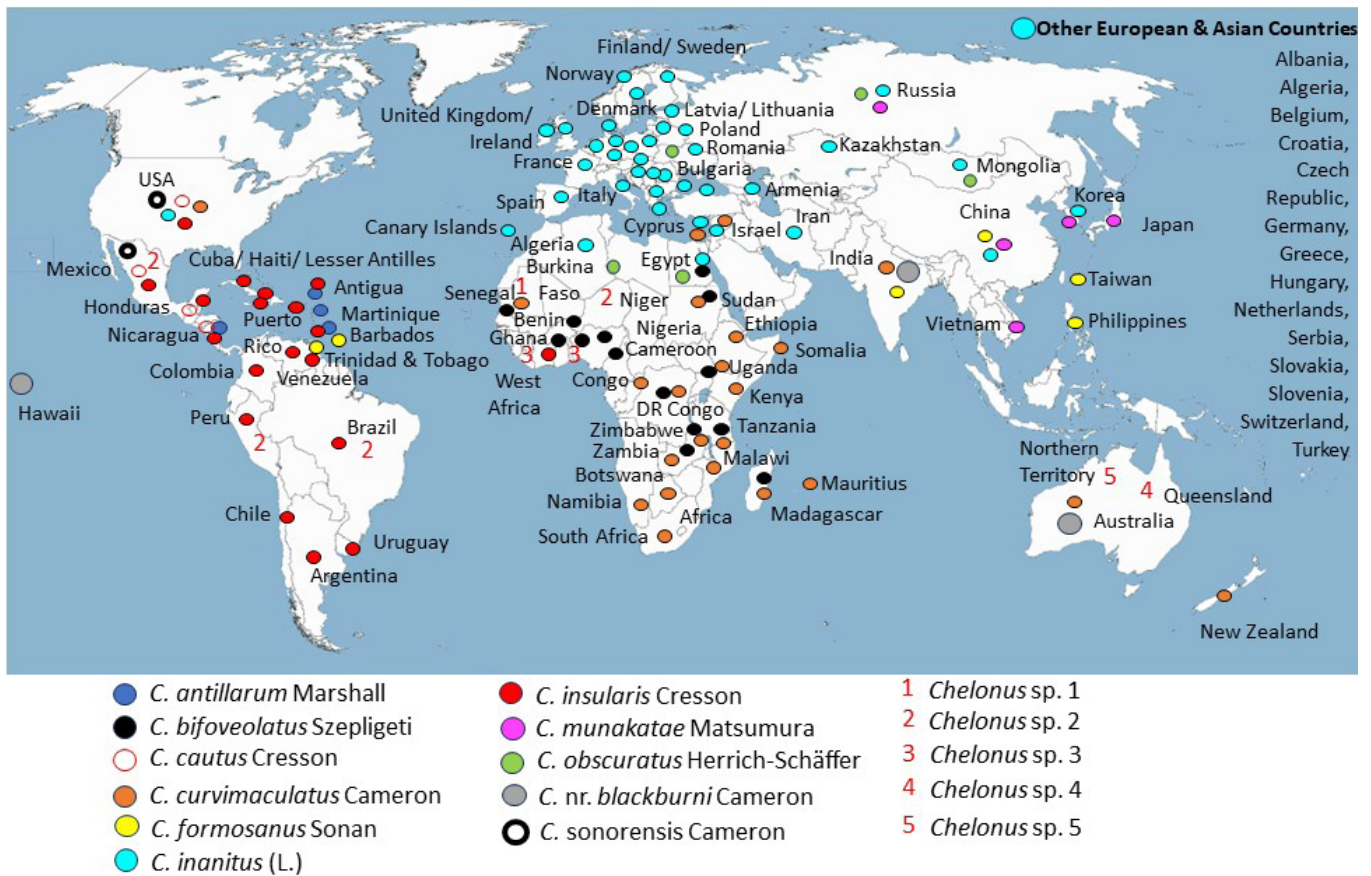


Figure 1. Geographic distribution of *Chelonus* s. str. Panzer associated with fall armyworm, *Spodoptera frugiperda* (JE Smith) (after Li *et al.*, 2023) (Template of the map courtesy of Wikimedia, 2023).

Table 1. Updated geographic distribution of egg-larval parasitoid *Chelonus* s. str. Panzer associated with fall armyworm, *Spodoptera frugiperda* (JE Smith), and references (after Li *et al.*, 2023)

<i>Chelonus</i> Panzer spp.	Distribution	References
<i>C. antillarum</i> Marshall	Antigua, Barbados, Martinique, Nicaragua	Ashley (1986); Molina-Ochoa <i>et al.</i> (2003); Yu <i>et al.</i> (2016); Zenner (2006)
<i>C. bifoveolatus</i> Szepligeti	Benin, Burkina Faso, Cameroon, DR Congo, Ghana, Madagascar, Nigeria, Senegal, Sudan, Tanzania, Uganda, Zambia, Zimbabwe	Madl and van Achterberg (2014); Yu <i>et al.</i> (2016); Tang <i>et al.</i> (2019); Tendeng <i>et al.</i> (2019); Agboyi <i>et al.</i> (2020); Koffi <i>et al.</i> (2020); Ngangambe and Mwatawala (2020); Ahissou <i>et al.</i> (2021); Durocher-Granger <i>et al.</i> (2021); Otim <i>et al.</i> (2021); Zang <i>et al.</i> (2022); Shen <i>et al.</i> (2023); Georgen (2024, personal communication)
<i>C. cautus</i> Cresson	Honduras; Mexico; Nicaragua; USA	Gutierrez-Ramirez <i>et al.</i> (2015); Yu <i>et al.</i> (2016)
<i>C. curvimaaculatus</i> Cameron	Australia, Botswana, Congo, DR Congo, Egypt, Ethiopia, India, Israel, Kenya, Madagascar, Malawi, Mauritius, Namibia, Senegal, Somalia, South Africa, Sudan, Tanzania, Uganda Zambia, Zimbabwe	Legner and Thompson (1977); Kittel (2014); Yu <i>et al.</i> (2016); Sisay <i>et al.</i> (2019); Koffi <i>et al.</i> (2020); Durocher-Granger <i>et al.</i> (2021)
<i>C. formosanus</i> Sonan	Barbados, China, India, Philippines, Trinidad and Tobago	Baringbing (1982); Baringbing and Baringbing (1984); Varshney (1999); Yu <i>et al.</i> (2016); Gupta <i>et al.</i> (2019); Firake and Behere (2020a, b); Gupta <i>et al.</i> (2020a); Tang <i>et al.</i> (2020); Jindal (2022); Liu <i>et al.</i> (2022); Sagar <i>et al.</i> (2022); Keerthi <i>et al.</i> (2023); Calcetas <i>et al.</i> (2023)

Table 1. Continued...

<i>Chelonus</i> Panzer spp.	Distribution	References
<i>C. inanitus</i> (L.)	Albania, Algeria, Armenia, Belgium, Bulgaria, Canary Islands, China, Croatia, Cyprus, Czech Republic, Denmark, Egypt, Finland, France, Germany, Greece, Hungary, Iran, Ireland, Israel, Italy, Kazakhstan, Korea, Latvia, Lithuania, Mongolia, Netherlands, Norway, Poland, Romania, Russia, Serbia, Slovakia, Slovenia, Spain, Sweden, Switzerland, Turkey, USA, United Kingdom	Rechav (1975, 1978); Rechav and Orion (1975); Hafez <i>et al.</i> (1980); Kaeslin <i>et al.</i> (1985)
<i>C. insularis</i> Cresson	Antigua, Argentina, Barbados, Brazil, Chile, Colombia, Cuba, Haiti, Honduras, Lesser Antilles, Mexico, Nicaragua, Peru, Puerto Rico, Trinidad and Tobago, USA, Uruguay, Venezuela	Zenner <i>et al.</i> (2006); Yu <i>et al.</i> (2016); Lopez <i>et al.</i> (2018); Prasanna <i>et al.</i> (2018); Tang <i>et al.</i> (2019); Garcia-Gonzales <i>et al.</i> (2020); Jaraleno-Teniente <i>et al.</i> (2020); Zang <i>et al.</i> (2022)
<i>C. munakatae</i> Matsumura	China, Japan, Korea, Russia, Vietnam	Yu <i>et al.</i> (2016); Li <i>et al.</i> (2019)
<i>C. obscuratus</i> Herrich-Schäffer	Egypt, Europe, Mongolia, North Africa, Russia (Central, East and South)	Goergen 2024, personal communication; Edmardash <i>et al.</i> (2011)
<i>C. nr. blackburni</i> Cameron	India	Nagarkatti and Singh (1989); Varshney (1999); Kittel (2014); Sagar <i>et al.</i> (2022); Keerthi <i>et al.</i> (2023); TNAU (2023)
<i>C. sonorensis</i> Cameron	Mexico, USA	Yu <i>et al.</i> (2016)
<i>Chelonus</i> sp. 1	West Africa (Senegal)	Tendeng <i>et al.</i> (2019)
<i>Chelonus</i> sp. 2	Brazil, Mexico, Peru, Niger	Molina-Ochoa <i>et al.</i> (2003); Amadou <i>et al.</i> (2018)
<i>Chelonus</i> sp. 3	Ghana, Benin	Shen <i>et al.</i> (2023)
<i>Chelonus</i> sp. 4	Queensland, Australia	Subramaniam (2022)
<i>Chelonus</i> sp. 5	Northern Territory, Australia	Subramaniam (2022)

(Huber, 2009; Chen & van Achterberg, 2019). Current records indicate that more than 2,600 species of braconids have been documented for the Afrotropical region, however, this number significantly underestimates the actual diversity of braconids in this region (Yu *et al.*, 2013).

Braconids typically parasitize the immature stages of butterflies, moths, beetles, and flies, although they may infest other insect orders as well (Huber, 2009). They exhibit various lifestyles, being either solitary or gregarious, and can live externally on the surface of their host (ectoparasitoid) or internally within the host's body (endoparasitoid). Some species demonstrate polyembryony, a phenomenon where multiple individuals develop from a single egg, while a few are capable of parasitizing already parasitized insects or hyperparasitoids, and a handful are classified as phytophagous (Wharton, 1993). They constitute one of the primary groups

of biological control agents of major plant pests and nearly all are major parasitoids of predominantly larval or adult forms belonging to over 120 insect families (Chen & van Achterberg, 1997). The former subfamily Adeliinae is clustered (in-group) of the Cheloninae (Belshaw *et al.*, 1998; Kittel *et al.*, 2016) and is treated as a tribe. Notably, two genera of Cheloninae are represented in the fossil records (*Eobracon* Cockerell 1921 and *Diodontogaster* Brues 1933), while the remaining 15 extant genera include *Ascogaster* Wesmael 1835, *Austroascogaster* Kittel and Austin 2013, *Chelonus* Panzer 1806, *Dentigaster* Zettel 1990, *Huseyinia* Koçak and Kemal 2008, *Leptochelonus* Zettel 1990, *Megascogaster* Baker 1926, *Odontosphaeropyx* Cameron 1910, *Phanaustrotoma* Kittel and Austin 2013, *Phanerotoma* Wesmael 1838, *Phanerotomella* Szépliget 1900, *Phanerotomoides* Zettel 1990, *Pseudo phanerotoma* Zettel 1990, *Siniphanerotomella* He, Chen and van Achterberg 1994, *Wushenia* Zettel 1990.

The subfamily Cheloninae Foerster, 1863, also known as chelonines, is widely distributed, comprising 23 genera, five tribes, and 1,523 described species worldwide, making it one of the largest lineages within the family Braconidae (Yu *et al.*, 2016; Kittel & Austin, 2014; Chen & van Achterberg, 1997). Divergence dating analyses and the reconstruction of ancestral ranges suggest that the Cheloninae originated in the Neotropics approximately 150 million years ago, indicating an older lineage than previously believed, which was estimated at 65–75 million years ago. The current biogeography of the Cheloninae is thought to be shaped by a dynamic process involving both vicariance and long-distance dispersal (Kittel & Austin, 2014). This subfamily is characterized by a large and homogeneous group of endoparasitoids targeting lepidopteran larvae, occupying a sub-basal position in the microgastroid lineage (Shi *et al.*, 2005; Sharanowski *et al.*, 2011). Chelonine parasitoids are frequently employed in biological control programs targeting lepidopterous insect pests worldwide (Legner & Thompson, 1977). They play a crucial role as biological control agents (BCAs) in regulating the population dynamics of phytophagous insects, particularly economically significant lepidopterous pests belonging to families such as Noctuidae, Geometridae, Tortricidae, Pyralidae, and Gelechiidae (Kaeslin *et al.*, 2005; Shaw & Huddleston, 1991; van Achterberg, 1990).

GENUS *Chelonus* s. str. PANZER, 1806

Distribution: The genus *Chelonus* s. str. Panzer, 1806 has 973 described species worldwide and is one of the diverse genera of the subfamily Cheloninae (Yu *et al.*, 2016). Recently, the list was updated by Sharkey *et al.* (2021) to more than 1,000 species when he described 79 new species, which were mainly from Costa Rica, a global biodiversity hotspot. However, many more undescribed species of *Chelonus* and the hosts include a wide range of lepidopterous families (Sharkey *et al.*, 2021; Yu *et al.*, 2016). The type species of *Chelonus* is *Ichneumon oculator* Fabricius 1775, a species commonly occurring in the Palearctic region. The genus is also the most widespread and broadly distributed parasitoid of FAW in the American continent and Africa (Otim *et al.*, 2021). *Chelonus* species have received much importance globally as contender parasitoids for FAW control (Li *et al.*, 2023). Currently, an updated list of *Chelonus* spp. Li *et al.* (2023) showed that there are 11 species affiliated with FAW; five distributed in Central America, four in Africa, and five in Asia.

Diagnosis of the subfamily Cheloninae: Members of this subfamily are usually black, yellow, or orange, and they vary in size from 1.8 to 11 mm (Ghahari *et al.*, 2022). They can be easily distinguished from other braconid wasps by their wing venation (with three submarginal cells) and the presence of a

complete postictal carina. These wasps are black, compact in appearance, and have a body length of 2–6 mm (Dudarenko, 1974). The carapace is the most prominent character and is formed by the fusion of the first three metasomal tergites covering the rest of the gaster; however, the rest of the parts of the metasoma are usually covered ventrally (Dudarenko, 1974; van Achterberg, 1976; Shaw, 1997). However, a carapace also appears convergently in several other braconid subfamilies (e.g. Brachistinae, Ichneutinae, Microgastrinae, and Sigalphinae), but it generally seldom occurs outside of the subfamily Cheloninae (Dudarenko, 1974). In layman's terms, the subfamily Cheloninae can be readily discerned by the shape of its abdomen or ventral side of the carapace, which looks similar to an inverted bathtub or a turtle shell. However, the last instar larvae have thin and cylindrical mandibles, usually with the presence of indeterminate hypostomal sutures (Kaeslin *et al.*, 2005).

Higher classification of the genus *Chelonus* Panzer:

The higher-level classification of the genus *Chelonus* s. l. is a subject of ongoing debate and lacks clarity. Several authors have questioned *Microchelonus Szépligeti*, 1908 and other experts classified *Microchelonus* as a subgenus of *Chelonus* (Zettel 1990; van Achterberg & Polaszek 1996; Zhang *et al.*, 2008). However, others recognized it as a valid genus (Papp, 1995; Tobias, 2000, 2011; Zhang *et al.*, 2008). Furthermore, the genus was split into six subgenera (*Carinichelonus* Tobias, 2000, *Microchelonus* s. str., *Parachelonus* Tobias, 1995, *Rasnichelonus* Tobias, 2011, *Scabrichelonus* Chen and van Achterberg, 1997 and *Stylochelonus* Hellén, 1958) by Tobias (2000, 2011). However, Kittel *et al.* (2016) reached a different conclusion, suggesting that the subgenus *Microchelonus* should be synonymized with *Chelonus* based on molecular and morphological phylogenetic analyses, which also encompassed three other subgenera (*Baculonus*, *Carinichelonus*, and *Scabrichelonus*). Nonetheless, uncertainties persist regarding the status of other subgenera within *Chelonus* s. l. primarily due to limitations in sample size and the scope of conclusions drawn. Each of the three subgenera synonymized by Kittel *et al.* (2016) exhibits distinct apomorphic characteristics, and *Microchelonus* was recognized as a valid subgenus in the study conducted by Zhou *et al.* (2022).

Chelonus (Chelonus) Panzer, 1806: Currently, there are 12 subgenera under the genus *Chelonus*: *Areselonus* Braet, 1999; *Arichelonus* Viereck, 1913; *Baculonus* Braet and van Achterberg, 2001; *Carinichelonus* Tobias, 2000; *Chelonus* Panzer, 1806 s. str.; *Cubochelonus* Baker, 1926; *Megachelonus* Baker, 1926; *Microchelonus* Szépligeti, 1908 s. str.; *Mirachelonus* subgen. nov.; *Parachelonus* Tobias, 1995; *Scabrichelonus* He, Chen and van Achterberg, 1997; and *Stylochelonus* Hellén, 1958 (Zhou *et al.* 2022).

Furthermore, a revisional work on the Cheloninae of China resulted in the establishment of a new subgenus, *Mirachelonus*, and the description of a new species *C. (M.) miraventris*, underscoring thereby the limitation of the generic concept and specific boundaries of the genus *Chelonus* s. l. (Zhou *et al.* 2022). Recently, Zhou *et al.* (2024) revised the genus *Chelonus* (*Chelonus*) Panzer, 1806 in China, adding 21 new species and bringing the total number of described species to 73.

Diagnosis of the genus *Chelonus*: *Chelonus* species can be easily compared to other genera of Cheloninae by the following distinguishing morphological characteristics: vein 1-SR+M of fore wing absent and vein SR1 nearly always completely sclerotized, metasomal carapace without distinct transverse sutures, eyes distinctly setose and usually vein R of fore wing emitted near middle from the pterostigma (van Achterberg & Polaszek, 1996). The head is transverse in dorsal view, and the temple is narrow. The mesoscutum is short and 0.7–0.8 as long as wide. The fore wing has 3 cubital cells present; cell 2 is small and more or less triangular and distinctly smaller than cell 3. Abscissa 1 of cubitus is absent, and the first cubital and first discoidal cells are confluent. The abdomen length is less than 3X the greatest width. The abdominal sutures are erased, and the tergites 1–3 are forming a solid carapace. Furthermore, at most 2 sutures are visible on the abdomen dorsally. Males can be distinguished from females by their thin and long bodies having somewhat setaceous antennae. Also, the female wasp has a short ovipositor, occasionally concealed inside the carapace (Yousuf & Ray, 2009). Furthermore, it has antennae thickened in the middle with depressions in the apical flagellar segments. In species of the subgenus *Microchelonus*, the apex of the male carapace bears an opening, the foramen. There are numerous keys to species covering specific world regions, among which the most important are Varshney (1999) for the oriental region, Papp (1995) for the western Palearctic, McComb (1968) for the Holarctic region, Tobias (2000) for the Russian far East, Zhang (2008) for S.E. Asia and De Saeger (1948) for the Afrotropical region.

BIOLOGY, ECOLOGY AND PARASITISM

Bio-ecology of Cheloninae: Oviposition in host eggs is a common behaviour among chelonines. Members of the genus *Ascogaster* are typically found in shrubby areas, while *Chelonus* species inhabit steppes, prairies, and grasslands, showing a high tolerance to heat and drought. *Phanerotoma* species are often encountered in arid and seasonally dry habitats (Shaw, 1997; Beyarslan, 2021). Certain species exhibit nocturnal behaviour and are frequently captured in light traps, such as *Phanerotoma* and *Phanerotomella*, while females of various species forage in vegetation during the

daytime and can be collected using sweep nets on foliage (Shaw, 1997).

Bio-ecology of *Chelonus* Panzer: Adults of *Chelonus* are free-living, contrasting with the larvae that parasitize host larvae (Yousuf & Ray, 2009). They are predominantly solitary, and the mode of development is egg-larval concerning the host stage and koinobiont concerning its effect on the host insect. Upon hatching, the larva becomes an internal parasitoid, and the host's development continues even after parasitization (Baltazar, 1962; Khajeh *et al.*, 2020). Members of *Chelonus* spp. display arrhenotoky, a reproductive mode common among aculeate and parasitic Hymenoptera, in which unfertilized eggs produce male offspring and fertilized eggs yield female offspring (Yu *et al.*, 2016). Nearly all koinobionts are endoparasitic, laying their eggs directly inside the host insect. Larval development of the parasitoid typically occurs when the host larva is nearing maturity (Baltazar, 1962). Additionally, eggs are deposited into the host egg, delaying larval development at the first instar until the host larva matures (Tang & Marsh, 1994). FAW larvae parasitized by *Chelonus* experience a gradual reduction in food intake, consuming less than 10% of the biomass ingested by healthy larvae (Prasanna *et al.*, 2018).

Life history and parasitism of *Chelonus formosanus* Sonan

Gupta *et al.* (2020a) investigated the life history and parasitism of *C. formosanus* in Karnataka, India, finding that adult longevity ranged from 2 to 7 days, and the developmental period on *S. frugiperda* was 20 to 25 days in the BOD incubator (KCS/BI-50) set at 27±2°C and 65±2% RH. The per cent parasitism varied from 10.0% to 19.4%, with 45.0% to 57.5% of *C. formosanus* adults successfully emerging from cocoons. In a concurrent study in the same region, Jindal *et al.* (2022) observed a parasitism rate of 6.67% to 32% by *C. formosanus*, with a peak in the second and third week of November 2020 and an overall mean parasitism rate of 16.33%. Firake and Behere (2020b) reported a parasitism rate of 5% by *C. formosanus* on *S. frugiperda* in northern India, while Keerthi *et al.* (2023) identified *C. formosanus* as the most active parasitoid contributing to the highest total parasitism in India. In Hainan, China, Kenis *et al.* (2022) reported parasitism rates of 12%, 7%, and 4% by *C. formosanus*, the larval parasitoid *Microplitis pallidipes*, and the pupal parasitoid *Tetrastichus howardi*, respectively.

In Flores Island, Indonesia, Baringbing and Baringbing (1984) conducted mass rearing of the introduced parasitoid *C. formosanus* in the laboratory conditions, utilizing the potato tuber moth *Phthorimaea operculella* as the host to control the coconut moth *Batrachedra arenosella*. Each female parasitoid in the laboratory produced an average of 14

offspring, with a male-biased sex ratio favouring 2.27. Males exhibited an incubation period of 26 days, while females had a slightly longer incubation period of 27 days within the host body of *P. operculella*. In contrast, the sex ratio of the same parasitoid in the field, parasitizing *B. arenosella*, was 1:1, while the sex ratio of the pest in the field was 1:1.26. A 10% honey solution served as suitable food for both the parasitoid and adult *P. operculella*. Laboratory observations suggested that achieving a sex ratio close to 1:1 for the parasitoid is preferable for effective biological control of *B. arenosella*, indicating that the observed increase in the proportion of males to females in the laboratory may be due to deficient fertilization.

Rao and Patel (1974) investigated the biology of *C. formosanus* using *Spodoptera litura* (F.) and *Spodoptera exigua* (Hübner) in India. Their findings revealed that at a temperature of $26.7 \pm 1.5^\circ\text{C}$, females exhibited an average pre-oviposition period of 3.7 ± 0.77 days and an oviposition period of 6.6 ± 1.06 days. Mated females had an average egg-laying capacity of 299 ± 71 eggs, with a parasitoid egg incubation period of 23.9 hours. The parasitoid larva underwent five instars, and the entire egg-larval duration, including cocoon formation, was 14.16 days. After the 11th day of parasitization, the parasitized host larvae exhibited smaller lengths than larvae that were not parasitized. Male cocoons were smaller than female cocoons in the soil. Pupal duration in cocoons averaged 5.57 ± 0.97 days for males and 6.12 ± 0.79 days for females.

Life history and parasitism of *Chelonus insularis* Cresson

The average incubation period of *Chelonus insularis* is approximately 1.8 days, with no pre-oviposition period for adults. The larval stage typically lasts between 17 and 23 days at a temperature of $25 \pm 2^\circ\text{C}$, with an average duration of 20.4 days. Pupal development averages 6.2 days, resulting in a total cycle duration of 28.6 days. Mated females exhibit an average longevity of 11.6 days, ranging from a maximum of 18 days to a minimum of 5 days. The number of parasitized eggs and the longevity of individual female wasps vary considerably, decreasing notably towards the end of their lifespan. Females of *C. insularis* deposit their eggs within the egg masses of their host, emerging from *S. frugiperda* larvae during the 4th instar, ultimately leading to the host's death (Zenner *et al.*, 2006). The peak parasitism rate occurs in females aged three days, ranging from a maximum of 92.2 to a minimum of 48.1 eggs parasitized during this period. Between the 3rd and 6th days, females maintain a parasitism rate of 72% to 80% (Prasanna *et al.*, 2018). However, under natural conditions, the parasitism of *C. insularis* on *S. frugiperda* ranges from 6.63% to 21.96% (Tang *et al.*, 2019). Notably, *Chelonus* species, including *C. insularis* and *C. bifoveolatus* exhibit larger body sizes and greater egg-

carrying capacity compared to other egg parasitoids such as *Telenomus remus* and *Trichogramma* spp. (Tang *et al.*, 2019; Zang *et al.*, 2022).

Life history and parasitism of *Chelonus bifoveolatus* Szépligeti

The wasp *C. bifoveolatus* parasitized 0-to-2-day-old *S. frugiperda* eggs and it successfully parasitized and developed on eggs in all tested samples (Shen *et al.*, 2023). Notably, 1-day-old eggs of FAW eggs exhibited a higher parasitism rate, pupation rate, and emergence rate compared to 2-day-old FAW eggs, albeit with a shorter development time. The sex ratio of females-to-males sex was nearly 1:1 across all stages examined (Shen *et al.*, 2023). Under laboratory conditions, *C. bifoveolatus* required an average of 40.2 ± 3.88 days at 25°C and 33.3 ± 2.47 days at $30 \pm 1^\circ\text{C}$ ($n=35$) to develop from egg to adult when feeding on *S. frugiperda* (C.E.F. Kassa, unpublished data). Moreover, at these same temperatures and with the same host, female *C. bifoveolatus* produced an average of 117 and 98 offspring, respectively, with a sex ratio ranging from 0.27 to 0.45. The adult lifespan ranged between 10.2 days at 25°C and 6.2 days at 30°C . In a survey conducted across 54 maize fields in central and southern Benin, the average rate of parasitism of *S. frugiperda* by *C. bifoveolatus* ranged from 12.3% to 2.4%, respectively (Personal communication, Goergen, unpublished data), indicating that the parasitoid is better adapted to conditions prevalent in the dry savannas.

Parasitism of *Chelonus blackburni* Cameron

In India, Keerthi *et al.* (2023) conducted a study documenting the overall parasitism rates of *S. frugiperda* by various parasitoids, ranging from 28.37% to 42.44%. Notably, *Chelonus* nr. *blackburni* emerged as the predominant species, contributing significantly with 18.57% parasitism during July 2021.

Parasitism of *Chelonus oculator* Panzer

Özmen (2004) investigated the biological interactions between the egg-larval parasitoid *C. oculator* and two different hosts under laboratory conditions. The study also assessed the impact of Aldicarb on the parasitoid using radioisotope tracer techniques. The optimal host age for successful parasitization was determined to be eggs older than 24 hours of the Mediterranean flour moth *Ephestia kuehniella* Zeller. Female *C. oculator* exhibited a maximum longevity of 16.3 ± 2.3 days, with a mean development time of 58.6 ± 0.09 days, while males had a longevity of 14.1 ± 2.3 days and a mean development time of 55.9 ± 0.09 days both at optimum temperature. The parasitoid demonstrated high fecundity, with a mean of $2,344 \pm 222.5$ parasitoids, a sex ratio of 2.5:1 (male: female), and a net reproduction rate of 668.8 female/female. The presence of a mating partner more

than doubled the number of produced females. Additionally, the development time of *C. oculator* on its natural host, the Egyptian cotton leafworm *Spodoptera littoralis*, was 18.4 ± 0.3 days. Parasitization significantly reduced the food consumption of *S. littoralis*, with parasitized larvae consuming 32.9 ± 0.6 sq. cm leaf area compared to 143.3 ± 6.5 sq. cm in unparasitized larvae. The study also revealed that C^{14} Aldicarb residues applied to parasitized *S. littoralis* larvae were retained at $75.4 \pm 3.2\%$ sq. cm of the initially applied radioactivity, indicating that the parasitoid was not adversely affected by Aldicarb residues. Overall, the research highlighted the high fecundity of the parasitoid when reared on *E. kuehniella*, its ability to reduce the food consumption of harmful hosts like *S. littoralis*, and its resilience to Aldicarb residues in the context of cotton field protection.

Biology and parasitism of *Chelonus* sp. 1 in West Africa

Tendeng *et al.* (2019) provided a concise account of the biology and parasitism of an unidentified *Chelonus* species. Parasitized *S. frugiperda* larvae completed their development until the parasitoid's emergence. Upon emergence, the host larvae became moribund, losing mobility and feeding capability. Although positioned externally, the parasitoid remained attached to the larval track, continuously extracting hemolymph. After the larval contents were emptied, the parasitoid larvae detached and proceeded with pupal development, secreting a silk cocoon for protection until adulthood. The resulting larvae were pearly white, ranging in size from 8 to 10 mm, with emergence occurring 8 to 9 days later. There were 28 individuals of *Chelonus* sp. 1 emerged from FAW larvae, resulting in a calculated parasitism rate of 10.9% (n=255). The adult parasitoids' size ranged from 8 to 9 mm. The undetermined species has two white spots in the anterior part of the abdomen. The relationship between antenna length and the body length and that of the wing and body were 0.8 mm and 0.75 mm, respectively.

Parasitism of *Chelonus* spp. on other *Spodoptera* spp.

In Africa and Asian continents, various *Chelonus* species, originally parasitoids of local *Spodoptera* spp. (Lepidoptera: Noctuidae) have been observed and reported as significant parasitoids that have adapted to *S. frugiperda* (Agboyi *et al.*, 2020; Durocher-Granger *et al.*, 2021; Firake & Behere, 2020a, 2020b; Gupta *et al.*, 2020a).

ALTERNATE HOSTS

Chelonus has numerous associations with various lepidopterous species, including some significant agricultural pests worldwide (Baltazar, 1962; Jones, 1985). Notably, it can target insect pests from the superfamily Tortricoidea and Pyraloidea (Yousuf & Ray, 2009). This genus of wasps has been successful in controlling economically important agricultural

pests such as the common cutworm *S. litura* Fabricius, beet armyworm *S. exigua* (Hübner), and corn earworm or cotton bollworm *Helicoverpa armigera* (Hübner). *Chelonus* spp., reared in laboratories using factitious hosts, have effectively contributed to the control of various lepidopterous pests, including *Batrachedra arenosella* (Walker) (Lepidoptera: Batrachedridae), *Earias villa* (F.) (Lepidoptera: Noctuidae), *H. armigera* (Hübner) (Lepidoptera: Noctuidae), *Pectinophora gossypiella* (Saunders) (Lepidoptera: Gelechiidae), *Prays oleae* Bernard (Lepidoptera: Praydidae), and *S. littoralis* (Boisduval) (Lepidoptera: Noctuidae) (Pawar *et al.*, 1983; Baringbing & Baringbing, 1984; Hafez *et al.*, 1980; Legner & Thomson, 1977; Arambourg *et al.*, 1970).

The wasp *C. formosanus* has demonstrated effective control of various noctuid pests, including *H. armigera* (Hübner) (Yadav, 1980; Liu, 2022), *Leucania (Mythimna) loreyi* (Duponchel) (Sonan, 1932; Chou, 1981), *S. exigua* (Chou, 1981; Liu, 2022), *S. frugiperda* (Molina-Ochoa *et al.*, 2003; Liu, 2022), and *S. litura* (Sonan, 1932; Sonan, 1937; Rao & Patel, 1974; Chou, 1981; Liu, 2022). In addition to *S. frugiperda*, a comprehensive list of other lepidopterous insect pests, along with moths utilized in the rearing of *Chelonus* spp., is provided and summarized in Table 2. The utilization of alternative hosts by all currently recorded *Chelonus* species plays a pivotal role in sustaining populations of these parasitoids during periods when FAW availability is reduced, such as the maize off-season. This ecological strategy and adaptability are paramount for Integrated Pest Management (IPM) systems, ensuring the resilience of *Chelonus* spp. populations, which are crucial for regulating FAW populations upon the resumption of the maize growing season.

GEOGRAPHIC DISTRIBUTION OF *CHELONUS* SPP. PANZER

North and South America

The presence and impact of Fall armyworm, *S. frugiperda* have been documented since its initial observation on grains and grasses in Georgia, USA, dating back to 1797 (Westbrook *et al.*, 2019). In the Caribbean Islands, *Chelonus* spp., particularly *Chelonus antillarum* Marshall, is among the earliest recorded parasitoids of *S. frugiperda*, targeting its eggs (Ashley, 1986; Zenner *et al.*, 2006). Notably, *S. frugiperda* larvae exhibit increased susceptibility to chlorpyrifos, methomyl, and cypermethrin upon infestation by the egg-larval parasitoid of *S. frugiperda*.

In Nicaragua, key parasitoids of *S. frugiperda* in maize include braconids, with up to 30% parasitism of collected larvae, predominantly *Aleiodes* (= *Rogas*) *laphygmae* (Viereck) and *C. insularis* (van Huis, 1981). Another ectoparasitoid of *S. frugiperda*, *Diapetimorpha introita*

Table 2. Lepidopterous insect hosts and rearing hosts of egg-larval parasitoid *Chelonus* s. str. Panzer

<i>Chelonus</i> spp.	Insect Hosts / Factitious Hosts	References
<i>C. antillarum</i> Marshall	<i>Spodoptera frugiperda</i> (JE Smith)	Ashley (1986); Molina-Ochoa <i>et al.</i> (2003); Zenner <i>et al.</i> (2006)
<i>C. bifoveolatus</i> Szepligeti	<i>Spodoptera frugiperda</i> (JE Smith); <i>S. exigua</i> (Hübner), <i>S. littoralis</i> (Boisduval), <i>S. litura</i> (Fab.), <i>Helicoverpa armigera</i> Hübner (Noctuidae); <i>Haritalodes derogata</i> (Fab.) (Crambidae)	Van den Berg (1988); Madl and van Achterberg (2014); Tang <i>et al.</i> (2019); Ngangambe and Mwatawala (2020); Yu <i>et al.</i> (2016); Zang <i>et al.</i> (2022)
<i>C. cautus</i> Cresson	<i>Spodoptera frugiperda</i> (JE Smith); <i>Herpetogramma phaeopteralis</i> (Guenée) (Crambidae); <i>Pectinophora gossypiella</i> (Saunders) (Gelechiidae)	Shenefelt (1973); Gutierrez-Ramirez <i>et al.</i> (2015)
<i>C. curvimaculatus</i> Cameron	<i>Spodoptera frugiperda</i> (JE Smith); <i>S. exigua</i> (Hübner), <i>Busseola fusca</i> (Fuller), <i>Helicoverpa armigera</i> (Hübner), <i>Helicoverpa assulta</i> (Guenée), <i>Heliothis peltigera</i> Denis and Schiffermüller, <i>Sesamia calamistis</i> Hampson, <i>Trichoplusia ni</i> (Hübner), <i>Thysanoplusia oricalcea</i> (Fab.) (Noctuidae); <i>Piezotrachelus varium</i> (Wagner) (Apionidae); <i>Chilo orichalcociliellus</i> Pinhey, <i>Chilo partellus</i> (Swinhoe), <i>Chilo zacconius</i> Błeszyński (Crambidae), <i>Loxostege frustalis</i> (Zeller) (Crambidae); <i>Pectinophora gossypiella</i> (Saunders), <i>Phthorimaea operculella</i> (Zeller), <i>Platyedra cunctatrix</i> Meyrick, <i>Scrobipalpa aptatella</i> (Walker), <i>Scrobipalpa ergasima</i> (Meyrick) (Gelechiidae); <i>Earias insulana</i> (Boisduval), <i>Nola pumila</i> Snellen (Nolidae); <i>Plutella xylostella</i> (L.) (Plutellidae); <i>Phycita diaphana</i> (Staudinger) (Pyralidae)	Legner and Thompson (1977); Kittel (2014); Yu <i>et al.</i> (2016); Sisay <i>et al.</i> (2019)
<i>C. formosanus</i> Sonan	<i>Spodoptera frugiperda</i> (JE Smith); <i>S. exigua</i> (Hübner) and <i>S. litura</i> (Fab.) (Noctuidae); <i>Helicoverpa armigera</i> (Hübner) (Noctuidae); <i>Leucania (Mythimna) loreyi</i> Duponchel (Noctuidae); <i>Batrachedra arenosella</i> Walker (Batrachedridae); <i>Phthorimaea operculella</i> (Zeller) (Gelechiidae)	Sonan (1932); Sonan (1937); Morghan and Crumb, 1941; Rao and Patel (1974); Yadav (1980); Chou (1981); Baringbing (1982); Baringbing and Baringbing (1984); Molina-Ochoa <i>et al.</i> (2003); Wang and Chen (2009); Yousuf and Ray, 2009; Ramani and Ballal, 1994; Varshney (1999); Liu (2022)
<i>C. inanitus</i> (L.)	<i>Spodoptera frugiperda</i> (JE Smith), <i>S. exigua</i> (Hübner), <i>S. littoralis</i> (Boisduval), <i>Agrotis segetum</i> (Denis and Schiffermüller), <i>Longalatedes elymi</i> (Treitschke), <i>Leucania (Mythimna) loreyi</i> Duponchel, <i>Mesoligia literosa</i> (Haworth), <i>Mythimna unipuncta</i> (Haworth), <i>Oligia strigilis</i> (L.), <i>Peridroma saucia</i> (Hübner) (Noctuidae); <i>Haritalodes derogata</i> (Fab.), <i>Ostrinia nubilalis</i> (Hübner) (Crambidae); <i>Phthorimaea operculella</i> (Zeller) (Gelechiidae); <i>Etiella zinckenella</i> (Treitschke) (Pyralidae); <i>Aethes francillana</i> (Fab.), <i>Eucosma aemulana</i> (Schläger) (Tortricidae)	Hafez <i>et al.</i> (1980); Khanjani, 2006; Yu <i>et al.</i> (2016)
<i>C. insularis</i> Cresson	<i>Spodoptera frugiperda</i> (JE Smith); <i>S. eridania</i> (Cramer), <i>S. exempta</i> (Walker), <i>S. exigua</i> (Hübner), <i>S. mauritia</i> (Boisduval), <i>S. ornithogalli</i> (Guenée), <i>S. praefica</i> (Grote), <i>Agrotis ipsilon</i> (Hufnagel), <i>Anomis flava</i> Fab., <i>Autographa californica</i> (Speyer), <i>Feltia subterranean</i> (Fab.), <i>Helicoverpa zea</i> (Boddie), <i>Chloridea virescens</i> (Fab.), <i>Lycophotia porphyria</i> (Denis and Schiffermüller), <i>Peridroma saucia</i> (Hübner), <i>Mythimna unipuncta</i> (Haworth), <i>Trichoplusia ni</i> (Hübner) (Noctuidae); <i>Achyra rantalis</i> (Guenée), <i>Loxostege sticticalis</i> (L.) (Crambidae); <i>Elasmopalpus lignosellus</i> (Zeller), <i>Ephestia elutella</i> (Hübner) (Pyralidae)	van Huis (1981); Wheeler <i>et al.</i> (1989); Molina-Ochoa <i>et al.</i> (2003); Zenner (2006); Yu <i>et al.</i> (2016); Tang <i>et al.</i> (2019); Jaraleno-Teniente <i>et al.</i> , 2020; Zang <i>et al.</i> (2022)

Table 2. Continued...

<i>Chelonus</i> spp.	Insect Hosts / Factitious Hosts	References
<i>C. munakatae</i> Matsumura	<i>Spodoptera frugiperda</i> (JE Smith); <i>Chilo suppressalis</i> (Walker), <i>Cnaphalocrocis medinalis</i> (Guenée), <i>Diatraea</i> sp., <i>Omiodes indicata</i> (Fab.) (Crambidae)	Yu <i>et al.</i> (2016); Li <i>et al.</i> (2019)
<i>C. obscuratus</i> Herrich-Schäffer	<i>Spodoptera frugiperda</i> (JE Smith)	Goergen 2024, personal communication; Edmardash <i>et al.</i> (2011)
<i>C. nr. blackburni</i> Cameron	<i>Spodoptera frugiperda</i> (JE Smith); <i>Helicoverpa armigera</i> (Hübner) (Noctuidae); <i>Pectinophora gossypiella</i> (Saunders), <i>Phthorimaea operculella</i> (Zeller) (Gelechiidae); <i>Earias</i> spp. (Nolidae); <i>Corcyra cephalonica</i> (Stainton) (Pyralidae)	Pawar <i>et al.</i> (1983); Nagarkatti and Singh (1989); Varshney (1999); Kittel (2014); Keerthi <i>et al.</i> (2023); TNAU (2023)
<i>C. sonorensis</i> Cameron	<i>Spodoptera frugiperda</i> (JE Smith) (Noctuidae); <i>Eoreuma loftini</i> (Dyar) (Crambidae)	Yu <i>et al.</i> (2016)
<i>Chelonus</i> sp. 1	<i>Spodoptera frugiperda</i> (JE Smith)	Tendeng <i>et al.</i> (2019)
<i>Chelonus</i> sp. 2	<i>Spodoptera frugiperda</i> (JE Smith)	Molina-Ochoa <i>et al.</i> (2003); Amadou <i>et al.</i> (2018)
<i>Chelonus</i> sp. 3	<i>Spodoptera frugiperda</i> (JE Smith)	Shen <i>et al.</i> (2023)
<i>Chelonus</i> sp. 4	<i>Spodoptera frugiperda</i> (JE Smith)	Subramaniam (2022)
<i>Chelonus</i> sp. 5	<i>Spodoptera frugiperda</i> (JE Smith)	Subramaniam (2022)

(Cresson) (Hymenoptera: Ichneumonidae), has been reported in Georgia, USA (Pair & Gross, 1984). *Chelonus insularis* emerges as the predominant parasitoid of *S. frugiperda* in Central America, while *C. antillarum* is also documented in Barbados (Molina-Ochoa *et al.*, 2003). Together with *Chelonus* sp. 2 from Brazil, Mexico, Peru, and Niger, they represent some of the earliest *Chelonus* spp. parasitoids reported on *S. frugiperda* (Molina-Ochoa *et al.*, 2003; Amadou *et al.*, 2018).

In Colombia, *C. insularis* has been observed parasitizing *S. frugiperda*, though it exhibits high susceptibility to insecticides like chlorpyrifos, methomyl, and cypermethrin, except for *Bacillus thuringiensis* Berliner (Bt) toxin (Zenner, 2006). Wheeler *et al.* (1989) reported in Honduras that the parasitoid complex accounted for 42% of mortality in *S. frugiperda*, with *C. insularis* being the most common, contributing to 15.5% mortality. This suggests insecticide exposure through *S. frugiperda* larvae may diminish the likelihood of successful parasitoid survival.

Research on the non-target effects of spinosad, including its impact on FAW parasitoids, revealed multiple side effects for most tested parasitoids (Biondi *et al.*, 2012). In Mexico, Gutierrez-Ramirez *et al.* (2015) documented the parasitism of *Chelonus cautus* Cresson on *S. frugiperda*, marking it as the fourth *Chelonus* species identified for this invasive pest. Additionally, from May to October of 2017 and 2018 in Guanajuato, Mexico, a survey involving 4,323 sentinel egg masses of *S. frugiperda* exposed at 12 field sites revealed the recovery of *Trichogramma atopovirilia* Oatman and Platner (Hymenoptera: Trichogrammatidae) from three locations and *C. insularis* from two sites (Jaraleno-Teniente *et al.*, 2020).

Africa

Four species of *Chelonus* have been documented in Africa following their introduction to the continent. The first is *Chelonus bifoveolatus* Szépligeti, with a parasitism rate ranging between 1.04 and 12.3%, has been identified in Benin, Burkina Faso, Cameroon, DR Congo, Ghana, Kenya, Madagascar, Nigeria, Tanzania, Senegal, Uganda, and Zambia, covering sub-Saharan Africa (Nonveiller, 1984; van den Berg (1988); Madl & van Achterberg, 2014; Tendeng *et al.*, 2019; Agboyi *et al.*, 2020; Koffi *et al.*, 2020; Ahissou *et al.*, 2021; Durocher-Granger *et al.*, 2021; Otim *et al.*, 2021; Shen *et al.*, 2023). Notably, *C. bifoveolatus* is recognized as one of the predominant *S. frugiperda* parasitoids throughout tropical Africa (Agboyi *et al.*, 2020; Ahissou *et al.*, 2021). However, a molecular study by Shen *et al.* (2023) revealed that, although *Chelonus* sp. 3 shares >99% similarity with specimens from Ghana and Benin, it also exhibits >99% similarity to *C. formosanus* found in Guangdong, Taiwan, Hainan, Zhejiang (China), and certain regions of India (Gupta, 2020a). Furthermore, the blast results indicated that *Chelonus* sp. 3 and *C. bifoveolatus* in Benin, Burkina Faso, Ghana, Senegal, Uganda, and Zambia are situated in the same branch, with a 99.99% similarity between them. Additionally, they display >99.69% similarity to *C. formosanus* (Shen *et al.*, 2023).

Chelonus bifoveolatus Szépligeti (sic) was observed in Kenya and Zambia, demonstrating a parasitism rate of 4.8% (Sisay *et al.*, 2019). Unfortunately, in Tanzania, the use of Flubendiamide, an anthranilic diamide insecticide, led to a reduction in *S. frugiperda* parasitism by *C. bifoveolatus* and *Coccygidium luteum* (Brulle) (Ngangambe & Mwatawala, 2020). Recently, *C. bifoveolatus* was identified in Zimbabwe

from a specimen submitted for identification (Georgen 2024, unpublished report). Furthermore, according to Goergen (2024, personal communication), the species *Chelonus intermedius* in Egypt is a synonym of *Chelonus obscuratus* Herrich-Schäffer. *Chelonus obscuratus* is also recorded in Mongolia, Russia (Central, East, and South), Northern Africa, and Europe (Ermardash *et al.* 2011).

Asia and Oceania

In Israel, *Chelonus inanitus* (L.) is recognized as a parasitoid of *S. littoralis*, *S. exigua*, and *S. frugiperda* (Rechav, 1975; Rechav & Orion, 1975; Rechav, 1978). The parasitoid *C. formosanus* was initially identified from a survey conducted in corn areas infested with FAW, cotton, and other host plants in Karnataka in 2018 and in Uttar Pradesh in 2019, India (Gupta *et al.*, 2019; Jindal *et al.*, 2022). *Chelonus* spp. and *Coccygidium* spp. (Gupta *et al.*, 2020b) were identified as more abundant and widely distributed parasitoids in India. Collectively, these parasitoids provided an average of 9.2% *S. frugiperda* larval mortality in various locations. Furthermore, two braconid parasitoids of *S. frugiperda* were documented on corn in India, *Coccygidium transcasicum* (Kokujev) (Gupta *et al.*, 2020b), and *Cotesia ruficrus* (Haliday) (Gupta *et al.*, 2019). The latter parasitoid was also reported in Trinidad and Tobago, with Gupta *et al.* (2019) providing detailed morphological and molecular identification, along with host data, cocoon characters, and geographical distribution. These promising species can potentially be harnessed for the biological control of key forest insect pests, contributing to the effective balance of ecosystems (Yousuf & Ray, 2009).

In ginger (*Zingiber officinale* Roscoe) fields in Meghalaya State of India, Firake and Behere (2020b) documented a 74% larval mortality, primarily attributed to the egg-larval parasitoid *C. formosanus* (5%), mermithid nematodes (10%), *Metarhizium rileyi* (Farl.) Kepler, Rehner, and Humber (38.01%), and SfMNPV (21%). A recent survey of *S. frugiperda* parasitoids in India by Sagar *et al.* (2022) revealed an 80.46% larval mortality due to the natural enemy complex.

Eight species of *Chelonus* have been documented in India, with Varshney (1999) providing a taxonomic key for these chelonine species. The most prevalent parasitoid attacking *S. frugiperda* in India is *C. nr. blackburni* Cameron, causing a larval mortality rate of 49.24%, followed by *C. formosanus*. *Chelonus blackburni* is a notable example of an introduced parasitoid in India, imported from Hawaii, USA, in 1976 by the Indian Station of the Commonwealth Institute of Biological Control, Bangalore, and subsequently released near Bangalore against *H. armigera* Hübner (Nagarkatti & Singh, 1989). Subsequent records indicate its efficacy against *Earias* spp. (Lepidoptera: Nolidae), *Pectinophora gossypiella*

(Saunders) (Lepidoptera: Gelechiidae), and *Phthorimaea operculella* (Zeller) (Lepidoptera: Gelechiidae), providing significant management to these pests (Morgan & Crumb, 1914; Yousuf & Ray, 2009). *Mythimna (Cirphis) loreyi* (Duponchel) (Lepidoptera: Noctuidae) and *S. (Prodenia) litura* (Fabricius) (Lepidoptera: Noctuidae) have also been identified as hosts for *C. formosanus* (Varshney, 1999).

In organic corn areas in New Delhi, India, *C. formosanus* emerged as the dominant parasitoid at 12.55%, followed by *C. nr. blackburni* at 10.98%, and *Coccygidium* sp. (Hymenoptera: Braconidae) at 4.85% (Keerthi *et al.*, 2023). Additionally, *C. formosanus* was recorded as the most abundant egg-larval parasitoid of *S. frugiperda* in the northern part of India (Sagar *et al.*, 2022) and India as a whole (Firake & Behere 2020a; Gupta *et al.*, 2020a).

In Middle Eastern countries, Ghahari *et al.* (2022) reported a total of 219 species within the subfamily Cheloninae, constituting 14.3% of the world species, distributed across five genera and three tribes (Adeliini, Cheloninae, Phanerotomini). The genus *Chelonus* stands out as the most abundant, with 137 recorded species.

In China, a survey conducted in corn plantations infested with *S. frugiperda* in the Hainan Province identified the presence of *Chelonus munakatae* Matsumura. Following its discovery, artificial propagation and field application were initiated (Li *et al.*, 2019). *Spodoptera frugiperda* infestations have also been observed in ginger plants in China (Shankar & Adachi, 2019). The distribution of the parasitoid *C. formosanus* spans Taiwan, Guangdong, Zhejiang, and Hainan provinces (Liu *et al.*, 2022). Notably, a study presenting the chromosome-level genome assembly of *C. formosanus*, sequenced using PacBio®, Illumina®, and Hi-C technologies® by Liu *et al.* (2022), could prove to be a valuable resource for the biological control of lepidopterous pests.

In Southeast Asia, throughout 2019, *S. frugiperda* occurrences were reported in Indonesia (Trisyono *et al.*, 2019), Laos, Malaysia, Vietnam, the Philippines, Cambodia (personal observation by Khay), and in Eastern Asia from the Republic of Korea and Japan in July 2019 (Australian Aid, 2020). The moth's high potential for contaminating specific agricultural trade products (Early *et al.*, 2018) contributed to its success as a pest and facilitated its spread to different countries. The larvae and pupae of *S. frugiperda* can unintentionally contaminate traded commodities, especially plant parts. They have been frequently intercepted on vegetables in Europe, fruits from the Americas, and occasionally on herbaceous ornamentals (Seymour *et al.*, 1985; Cock *et al.*, 2017). Similarly, Taiwan, located just

1,205 km from the northern tip of Luzon, Philippines, as per Watanabe (1937), boasts ten species of *Chelonus*, including *C. formosanus*. However, it is worth noting that *C. formosanus* exhibits a Neotropical and Oriental distribution (Yu *et al.*, 2016).

In the Philippines, the endemic species *Chelonus semihyalinus* Ashmead has yet no recorded host information (Ashmead, 1904; Baltazar, 1962). Recently, Calcetas *et al.* (2023) reported the presence of *C. formosanus*, a well-known parasitoid of FAW in the Philippines, and its association with FAW has been an important aspect of the enhancement of the biological control program in the country. This marks it as the second species of *Chelonus* Panzer, following *C. semihyalinus* Ashmead, in 1904, to be recorded in the country. The global geographic distribution of the *Chelonus* species, including the new record from the Philippines, is presented in Figure 1. Another chelonine species, *Megachelonus* Baker, was recorded in the Philippines.

The first report of *S. frugiperda* in Australia emerged in February 2020, and the moth pest swiftly established itself across various regions in Northern Australia, including northern Queensland, the Northern Territory, and northern parts of Western Australia (Sisay *et al.*, 2019; Plant Health Australia, 2020). In Australia, the pest was also identified in sorghum, chickpea, melons, green beans, and pasture seed crops, with some instances of larvae reported on Rhodes grass in Western Australia. More recently, *S. frugiperda* was detected in Papua New Guinea (Australian Aid, 2020), the Solomon Islands in 2021, and New Zealand in March 2022. Australia records 45 species of Cheloniinae, along with several introduced for biocontrol: *Ascogaster quadridentata* Wesmael, *C. blackburni* Cameron, *Chelonus phthorimaeae* Gahan, *Chelonus curvimaculatus* Cameron, and *Phanerotoma hendecasisella* Cameron (Kittel & Austin, 2014). Comprehensive field surveys carried out between 2021 and 2022, aimed at investigating *S. frugiperda* across two Australian states and two territories spanning 65 locations, resulted in the collection of two *Chelonus* species yet identified at a generic level only (Subramaniam, 2022). Also, a field survey in Queensland, particularly in Bowen and Burdekin locations, *Chelonus* sp. 4 along with *C. ruficrus* strain B and *Coccygidium* spp. as the commonly recorded larval parasitoids (Subramaniam, 2022). However, a survey in the Northern Territory, Australia, showed that the most plentiful larval parasitoids found in the majority of sampling sites were the Tachinid fly *Exorista xanthaspis* and the *Chelonus* sp. 5, exhibiting an average parasitism rate ranging between 12.38% and 25% (Subramaniam, 2022).

The global geographic distribution map of the sixteen (16) different species of *Chelonus* spp. associated with

S. frugiperda and corresponding references are presented in Figure 1 and Table 1. Currently, there are eight (8) species of *Chelonus* associated with *S. frugiperda* in the North and South American continents, where the invasive pest originates (*C. insularis*, *C. antillarum*, *C. cautus*, *C. formosanus*, *C. sonorensis*, *C. nr. blackburni* (Hawaii), *C. inanitus*, *Chelonus* sp. 2), eight (8) species in Africa (*C. curvimaculatus*, *C. bifoveolatus*, *C. inanitus*, *C. insularis*, *C. obscuratus*, *Chelonus* sp. 1, *Chelonus* sp. 2, *Chelonus* sp. 3), and six (6) in Asia (*C. inanitus*, *C. formosanus*, *C. munakatae*, *C. nr. blackburni*, *C. obscuratus*, *C. curvimaculatus*), with two (2) in Europe (*C. inanitus*, *C. obscuratus*) and four (4) in Oceania (*C. curvimaculatus*, *C. nr. blackburni*, *Chelonus* sp. 4, *Chelonus* sp. 5). However, the report of *C. intermedius* in Egypt is excluded, as it is no longer considered a valid taxon, being a synonym of *C. obscuratus* Herrich-Schäffer, and its identity is questionable (Goergen 2024, personal communication).

Mass rearing of *Chelonus* spp.

The mass rearing, quality management, and release methods of parasitoids play pivotal roles in augmentative biocontrol strategies (Agboyi *et al.*, 2020). This approach stands out as the most sustainable pest management strategy, leveraging over a century of global agricultural research and application (Heimpel & Mills, 2017). However, the success of an augmentative biological control program hinges significantly on the quality of natural enemies' production (van Lenteren *et al.*, 2003).

The initiation of the biological control campaign in West Africa involving the importation of the parasitoid *C. insularis* originated from the Americas. Due to the cannibalistic habit of the caterpillars, the mass rearing of *C. marginiventris* utilizing *S. frugiperda* as a host presents significant challenges. Successful reproduction is only achievable within compartmentalized rearing units that maintain relatively low larval densities. Presently, production rates have reached approximately 5 to 6 thousand individuals per week, with its introduction primarily conducted through inoculative field releases, exemplifying classical biological control methods (Goergen 2024, personal communication).

In Karnataka, India, the parasitoid *C. formosanus* is produced on a large scale using the rearing methods outlined by Gupta *et al.* (2020a). Field-collected eggs and larvae infested by the parasitoid are reared to obtain adult parasitoids. They undergo growth in the laboratory through a combination of fresh corn leaves and an artificial diet. Parasitized *S. frugiperda* larvae are collected and allowed to pupate, and the cocoons are subsequently harvested. To achieve mass production, emerging adult parasitoids are encouraged to parasitize *S. frugiperda* eggs and larvae that

are reared in the laboratory. The parasitized *S. frugiperda* eggs and newly emerged adult parasitoids are released into the field while maintaining a cohort of parasitoid individuals that are continuously mass reared in the laboratory. This process ensures a sustainable and scalable production of *C. formosanus* in the laboratory.

On Flores Island, Indonesia, Baringbing and Baringbing (1984) outlined three crucial steps for laboratory production of *C. formosanus* to control the coconut moth *B. arenosella*. The first step involves collecting *B. arenosella* moths. Coconut palm spathes from infested areas are carefully cut and opened in the laboratory. *B. arenosella*, in the pupal stage, are placed in 1 L plastic containers, where adult parasitoids emerge from the parasitized pupae. The second step is the rearing of the host, *B. arenosella*. Adults of *P. operculella* (Zeller) (Lepidoptera: Gelechiidae) are collected from potato plantations and housed in plastic containers with cotton wool soaked in 10% honey as a food source. Eggs are deposited on the undersurface of the cotton fabric used to cover the container. The third step involves the rearing of the parasitoid, *C. formosanus*. Adults of *C. formosanus* emerging from host pupae in the first step are paired in test tubes to facilitate mating. Gravid females are then transferred to new plastic containers, accommodating up to 21 individuals, and provided with cotton wool soaked in 10% honey as food. Container lids from the second step (containing *P. operculella* eggs) are transferred to the container with *C. formosanus* females for parasitization. After two days, the cotton fabric containing parasitized eggs is removed, and the potato (*Solanum tuberosum*) tubers are wrapped around and placed in an empty container. The tuber serves as food for developing parasitized and non-parasitized *P. operculella* larvae. After approximately six days, the cotton fabric is opened, and adults of both *P. operculella* (from non-parasitized eggs) and *C. formosanus* emerge from the pupae, typically around four weeks later.

The parasitoid *C. blackburni*, introduced from Hawaii, is reared on the common rice meal moth *Corcyra cephalonica* (Stainton) (Lepidoptera: Pyralidae) and potato tuber moth *Phthorimaea operculella* (Zeller) in Tamil Nadu Agricultural University (TNAU, 2023). The production procedures for both hosts are outlined below:

Rearing procedure of *Corcyra cephalonica* (Rice Meal Moth)

Start by affixing 24-hour-old *Corcyra* eggs (a set of 100, not exposed to UV) onto a 5 x 5 cm card. Place this card, containing the host eggs, into a 1.5-liter plastic container with 30 *C. blackburni* adults. Inside the container, insert two cotton swabs: one soaked in a 10% honey solution and the other for drinking water. Seal the side opening tightly with

a cotton plug covered with cloth. Expose the card to the *C. blackburni* adults for 24 hours, then remove it and transfer it onto 500 g of sterilized stubble medium. After 30 days, adult parasitoids begin emerging from cocoons, indicating the completion of development on *Corcyra* larvae. These adult parasitoids have a lifespan of 25 days, during which they can produce approximately 400 eggs.

Mass production procedure using *Phthorimaea operculella* (Potato Tuber Moth) (PTM)

The mass production of the parasitoid on the Potato Tuber Moth (PTM) involves utilizing a set of 1,500 PTM eggs laid on a cloth and stapled to a card, which is then exposed to 30 adult parasitoids of *C. blackburni* for 24 hours in a plastic rearing container with windows and plastic mesh for aeration. Inside the container, a 50% honey solution and drinking water are provided, covered with a cotton plug wrapped in cloth. After this exposure, the PTM eggs are transferred onto punctured potatoes in a similar plastic container lined with sterilized sand at the bottom. Following a period of 25–27 days, adult parasitoids start emerging from the cocoons. They are formed either in the sand at the cage bottom or occasionally inside the punctured potatoes. These adult parasitoids have a lifespan of 23–31 days, during which their fecundity ranges from 288 to 390 eggs. It is essential to maintain a parasitoid-host ratio of 1:50, and fresh eggs are provided daily to ensure successful rearing.

In France, Arambourg *et al.* (1970) conducted large-scale breeding of *Chelonus elaeaphilus* (Silvestri) in a laboratory environment. They utilized the Mediterranean flour moth, *Ephestia (Anagasta) kuehniella* (Zeller) (Lepidoptera: Pyralidae), as the host with the aim of controlling the olive moth, *Prays oleae* Bernard (Lepidoptera: Praydidae).

In conclusion, the mass rearing of *Chelonus* spp. stands out as a pivotal component of augmentative biocontrol strategies, offering a sustainable and effective approach to *S. frugiperda* management. The success hinges on precise quality management and release methods for parasitoids. Historical instances, like the importation of *C. insularis* and the mass production of *C. formosanus*, underscore the method's adaptability and significance globally. The versatility of mass rearing, demonstrated with *C. blackburni* on different hosts, highlights its practical application across diverse agricultural landscapes. Overall, mass rearing of *Chelonus* spp. proves to be an essential tool for ecologically friendly and economically viable pest control against *S. frugiperda*.

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