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Genetic diversity of parasitoids and entomopathogenic nematodes of *Spodoptera frugiperda* Smith, 1797 (Lepidoptera: Noctuidae) in Senegal

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ABSTRACT

The pest *Spodoptera frugiperda*, when it invades Africa, is associated with a parasitic fauna, justifying the need to characterize the genetic diversity of its natural enemies in Senegal. Thus the rDNA of the large subunit, 28S was amplified. The study revealed the existence of 12 species of parasitoids obtained and 3 species of entomopathogenic nematodes. Parasitoids are divided into two orders (Hymenoptera and Diptera) and five families (Ichneumonidae, Braconidae, Eulophidae, Encyrtidae and Tachinidae). These parasitoids are *Sinophorus exartemae*, *Chelonus* sp., *Parapanteles* sp., *Dolichogenidea* sp. 1, *Dolichogenidea* sp. 2, *Meteorus* sp., *Meteorus orocrambivorus*, *Euplectrus phthorimaeae*, *Prochiloneurus testaceus*, *Ooencyrtus masii*, *Drino* sp. and *Senometopia cariniforceps*. Nematodes are members of the family Mermithidae and correspond to *Hexamermis* sp., Mermithidae sp. 1 and Mermithidae sp. 2. All these species attack the larval stage except *O. masii* which is oophagous. This study also reports new associations between *S. frugiperda* and the parasitoids *S. exartemae*, *M. orocrambivorus*, *E. phthorimaeae, P. testaceus*, *O. masii* and *S. cariniforceps*. To our knowledge, these six species, in addition to *Drino* sp., have just been known in the entomological fauna of Senegal. Therefore, it is urgent to protect these auxiliaries from the abusive and inappropriate use of chemical insecticides for sustainable management.

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INTRODUCTION

Noctuidae is a family of insects belonging to the order Lepidoptera. The pests of this family are among the most harmful in the world. They can cause economic losses that can be estimated at more than 4500 million US dollars per year (Sisay *et al.,* 2019 ; Riaz *et al.,* 2021 ; Rahmawati and Rahardjo, 2024). Most of the adults in this family have a high migratory capacity, high fertility and a very high reproduction rate (Riaz and Ly., 2021; Altaf *et al.*, 2022; Chen *et al.*, 2022; El-Refaie *et al.*, 2024). In addition, Noctuidae larvae are highly polyphagous and voracious, possessing a wide and diverse host range (Babou *et al.*, 2022; Rahmawati and Rahardjo, 2024). Fall armyworm (FAW), *Spodoptera frugiperda* Smith, 1797 is a perfect illustration of this. It causes economic damage especially to maize, its preferred host plant (Sisay *et al.*, 2019; Zhou *et al.*, 2021). This species has been invasive in Africa since 2016 (Nuambote-Yobila *et al.*, 2022; Nuambote-Yobila, 2023) and Asia from 2018 (Ge *et al.,* 2021). Due to the crop losses caused, especially in sub-Saharan Africa, chemical pesticides have been used (Nuambote-Yobila *et al.,* 2025). However, this method of control is proving to be difficult due to resistance to many classes of insecticides, linked among other things to their overuse but also to the insects' adaptation and detoxification mechanism (Boaventura *et al.,* 2020; Guo *et al.,* 2022; Moustafa *et al.,* 2024; Van den Berg and du Plessis, 2022).

With dificulty of management of the pest, it is essential to develop ecologically respectful and sustainable means of control (Arias *et al.*, 2019; Mansour *et al.*, 2023; Babou *et al.*, 2025). For this reason, beneficial insects are at the forefront, in an invasion context where native natural enemies can be registered as potential pathogens to *S. frugiperda* (Abang *et al.,* 2021; Ganou *et al.,* 2024). Its enemies can be parasitoids or entomopathogenic nematodes (Sun *et al.*, 2020; Kumar *et al.*, 2024). However, identifying these auxiliaries accurately, reliably and quickly can be difficult in some situations (Chen *et al.*, 2021; Ivezić *et al.*, 2021). This is explained on the one hand by the large number of entomophagous present in the agrosystems of the tropical and subtropical zone; on the other hand, it may be linked to a lack of specialists in morphological identification (Delvare, 1991; Chen *et al.*, 2021). This suggests that there could be many more species than are usually recognized. Hence, the use of genetics as an approach to identify the natural enemies of *S. frugiperda* (Sagar *et al.*, 2022). In this respect, this activity aims to genetically characterize the parasitoids and entomopathogenic nematodes of *S. frugiperda* in Senegal.

MATERIALS AND METHODS

Sampling

Spodoptera frugiperda caterpillars found on various plants in the Groundnut Basin ('Bassin arachidier'), Casamance and the Niayes area ('Zone des Niayes') were collected. Egg masses were also collected. The samples were sent to the Entomology and Acarology Laboratory of the Cheikh Anta Diop University in Dakar. They were kept at room temperature. Then the caterpillars were fed with 60g of fresh leaves, replaced every two days. Monitoring was daily and was done until the emergence of adult *S. frugiperda*, parasitoids or entomopathogenic nematodes. The natural enemies emerging from the caterpillar were dipped in 96% alcohol for genetic identification. All individuals are recorded in Table 1 below.

Molecular analysis of entomopathogenic parasitoids and nematodes

Extraction, polymerase chain reaction and DNA sequencing

Total genomic Deoxyribonucleic Acid (DNA) from entomopathogenic nematodes and parasitoids was extracted using the Zymo Research Tissue Kit, according to the manufacturer's instructions, with some modifications. The extraction was carried out on the entire body of the individuals, with the exception of those belonging to the family Tachinidae where the abdomen was removed. A number of 28 samples were extracted for parasitoids and 21 for nematodes. They were chopped into thin pieces or ground according to the stiffness of the specimens' cuticle. The quality of the extracts obtained was approximately assessed by electrophoretic migration using a DNA Ladder size marker, 100 base pairs.

Table 1. Characteristics of the samples to be identified

Orders	Families	Morphotypes	Number of individuals
Hymenoptera	Ichneumonidae	*Charops* sp.	1
	Braconidae	*Chelonus* sp.	2
		Meteorus sp.	4
		Microgastrinae 1	3
		Microgastrinae 2	2
		Undetermined Braconidae	2
	Eulophidae	Eulophidae	2
	Encyrtidae	Encyrtidae 1	1
		Encyrtidae 2	1
	Indeterminate	Hymenoptera Indeterminate	2
Diptera	Tachinidae	Tachinidae 1	6
		Tachinidae 2	2
Mermithida	Mermithidae	Mermithidae	21

The 28S ribosomal DNA (28S rDNA) was then amplified. The 28sF3633 primer pair: 5'-TACCGTGAGGGAAAGTTGAAA-3' and 28sR4076: 5'-AGACTCCTTGGTCCGTGTGTTT-3' were used to amplify this gene, specifically in the D2 domain (28SD2). The study of Schmidt *et al.* (2006) even reveals that at the level of the 28S gene, the D2 region is the most suitable for inferencing relationships, especially for taxonomic purposes. The conditions of the thermal cycler in amplification were as follows: an initial denaturation at 94°C for 3 min; 35 cycles of denaturation at 92°C for 30 s, hybridization at 52°C (45s) characterized by the attachment of the primers and elongation of the complementary strands at 72°C (1 min). Finally, a single period of final elongation at 72°C for 10 min was performed. The sequencing has been outsourced.

Genetic analyses

The resulting sequences were thoroughly checked, corrected and aligned using the Clustal-W algorithm (Thompson *et al.*, 1997) with BioEdit 7.7.1 software (Hall, 1999). The sequences obtained in this study were compared to authenticated sequences available on the GenBank database based on the E-score through the BLAST (Basic Local Alignment Search Tool) program in NCBI (National Center for Biotechnological Information). This made it possible to verify their membership of the different taxonomic groups. The species considered to be identical to the sequences compared were those with the highest percentage of identity and percent coverage and the lowest E value.

Phylogenetic reconstructions were performed using the Bayesian inference (with 1,000,000 generations and 4 Markov chains) and the maximum parsimony method (Fitch 1971) using Mr. Bayes version 3.2 and MEGA version 10.2 software (Kumar *et al.,* 2016) and the GTR (General Time Reversible) model with a gamma distribution. Branch robustness was assessed by bootstrapping with 1,000 replications for maximum parsimony. To the sequences obtained from the present study, others have been added from the Genbank database and which are associated with their accession number. The reconstructions were rooted with a sequence of *Helicoverpa armigera* Hübner, 1808 (Lepidoptera: Noctuidae) for parasitoids and *Daubaylia* sp. (Nematoda: Daubayliidae) for nematodes.

RESULTS

Sequences obtained

Of the forty-nine (49) samples sequenced, including twenty-eight (28) parasitoids and twenty-one (21) entomopathogenic nematodes, seven (7) were eliminated with regard to chromatograms, due to poor adhesion of the primers during sequencing. Of the seven, two are nematode samples and five are insect samples, including the 2 undetermined Braconidae, 1 of the two individuals of Eulophidae and two of the 6 Tachinidae 1. The rest of the analyses were carried out on 23 parasitoid sequences and 19 nematode sequences.

Identification and phylogenetic reconstruction of parasitoids

Table 2 shows that twelve (12) insect species parasitized the pest *Spodoptera frugiperda,* based on the Blast performed. The percentages of identities are recorded in the table below. Two orders of insects are confirmed. These are the Hymenoptera with four families (Braconidae, Ichneumonidae, Eulophidae and Encyrthidae) and which make up most of the species (10) which are *Sinophorus exartemae*, *Chelonus* sp., *Parapanteles* sp., *Dolichogenidea* sp. 1, *Dolichogenidea* sp. 2, *Meteorus* sp., *Meteorus orocrambivorus*, *Euplectrus phthorimaeae*, *Prochiloneurus testaceus*, and *Ooencyrtus masii*. The second order concerns the Diptera consisting of a single family (Tachinidae) and two (2) species: *Drino* sp. and *Senometopia cariniforceps*.

Table 2. List of *S. frugiperda* parasitoid species identified from 28S rDNA

Orders/Families	Morphotypes identified	Species identified	Accession No.	Identity (%)	E-value
Hymenoptera: Ichneumonidae	*Charops* sp.	*Sinophorus exartemae*	EF406253.1	94,61	0,0
Braconidae	*Chelonus* sp.	*Chelonus* sp. 2	AF029124.1	96,45-97,09	0,0
	Hymenoptera indeterminate	*Chelonus* sp. 2	AF029124.1	95,32-96,45	0,0
	Microgastrinae 1	*Parapanteles* sp.	MN645200.1	98,71-98,31	0,0
	Microgastrinae 2	*Dolichogenidea* sp. 1	PV468782.1	94,57	0,0
	Microgastrinae 2	*Dolichogenidea* sp. 2	MK568812.1	95,37	2.10^{-160}
	Meteorus sp.	*Meteorus orocrambivorus*	KJ591259.1	98,02-98,23	0,0
	Meteorus sp.	*Meteorus* sp.	LC632021.1	97,67-96,88	0,0
Eulophidae	Eulophidae	*Euplectrus phthorimaeae*	MW586890.1	96,82	0,0
Encyrtidae	Encyrtidae 1	*Prochiloneurus testaceus*	MT783605.1	88,53	5.10^{-151}
	Encyrtidae 2	*Ooencyrtus masii*	PQ790242.1	88,48	3.10^{-148}
Diptera:	Tachinidae 1	*Drino* sp.	OR082818.1	82,47-96,90	2.10^{-86}-0,0
Tachinidae	Tachinidae 2	*Senometopia cariniforceps*	AB466064.1	96,93 -95,55	9.10^{-169}-0,0

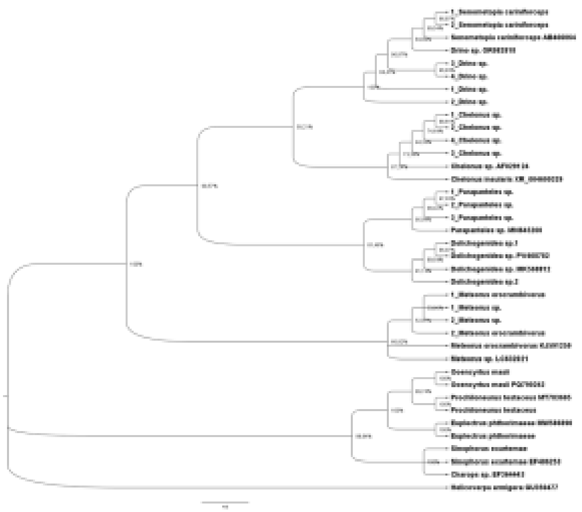

Fig. 1. Phylogenetic tree of parasitoids, inferred using the Bayesian approach

The species names associated with accession numbers are taken from the Genbank database. Bootstrap values are indicated in front of the nodes.

The analysis of the tree obtained by the Bayesian approach (Fig. 1) reveals the existence of 2 clades: The first clade is made up of individuals of the family Braconidae and Tachinidae. Tachinidae individuals have a strong genetic affinity for each other. Specimens of *Senometopia cariniforceps* separated from those of *Drino* sp. with a bootstrap value of 96% and 84% depending on the individual. However, the individuals sampled in Senegal are phylogenetically closer. As for the Braconidae, the sequences of *Chelonus* sp. and that of *Chelonus insularis* are genetically very close and are grouped together in a well-supported cluster (87%). The subclade made up only of Microgastrinae 1 (Parapanteles) and Microgastrinae 2 (Dolichogenidea) individuals reveals that they belong to the same taxonomic group (81%). Individuals of *Dolichogenidea* sp. 1 and those of *Dolichogenidea* sp. 2 share a well-supported subclade (81%). This shows the similarity between these sequences. This same remark is noted for the second subclade formed by *Parapanteles* sp. (95%). The two species *Meteorus orocrambivorus* and *Meteorus* sp.

obtained, have a genetic affinity of 100%. There is also an individual of *M. orocrambivorus* which formed a cluster with the two individuals of *Meteorus* sp. (53%). The second clade groups the individuals of Ichneumonidae, Eulophidae and Encyrtidae in one clade but in different subclades supported by strong bootstrap (99% and 100%). Individuals of the family Ichneumonidae, *Sinophorus exartemae* and *Charops* sp. (EF364443.1) share the same node for a maximum bootstrap of 100%. However, a stronger genetic affinity (100%) is noted between the species of Eulophidae (*Prochiloneurus testaceus* and *Ooencyrtus masii*) and Encyrtidae (*Euplectrus phthorimaeae*).

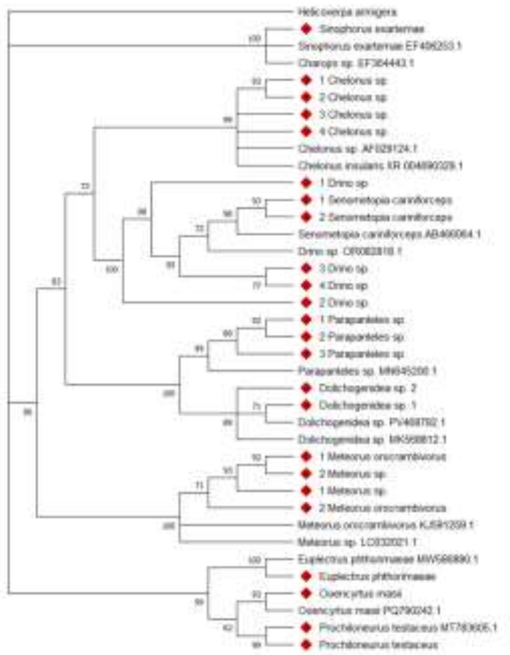

Fig. 2. phylogenetic tree of parasitoids inferred by the maximum parsimony method

The red diamonds indicate the species sampled and the others come from the Genbank database. The bootstrap values are shown below the node.

Unlike the Bayesian method, the maximum of parsimony (Fig. 2) forms 3 clades, one of which includes individuals of Ichneumonidae, the second individuals of the family Braconidae and the third is formed by the species Eulophidae and Encyrtidae but in different subclades. Just like the first method, the branches are well supported with a slight difference in the bootstrap values.

Identification and phylogenetic reconstruction of entomopathogenic nematodes

Sequence analysis indicates the existence of 3 species of Mermithidae nematodes: *Hexamermis* sp. (LC844941.1) (4 individuals), Mermithidae sp. (PQ811687.1) (12 individuals) and Mermithidae sp. (LC788416.1) (3 individuals). The latter two are named in the study Mermithidae sp.1 and Mermithidae sp. 2 respectively. The percentages of identity are shown in Table 3.

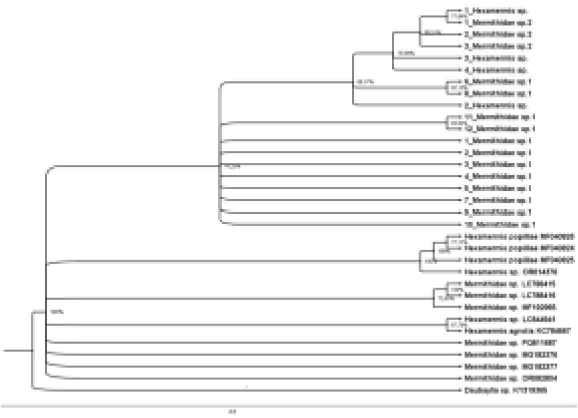

Fig. 3. Phylogenetic tree of entomopathogenic nematodes, inferred using the Bayesian approach

The species names associated with accession numbers are taken from the Genbank database. Bootstrap values are indicated in front of the nodes.

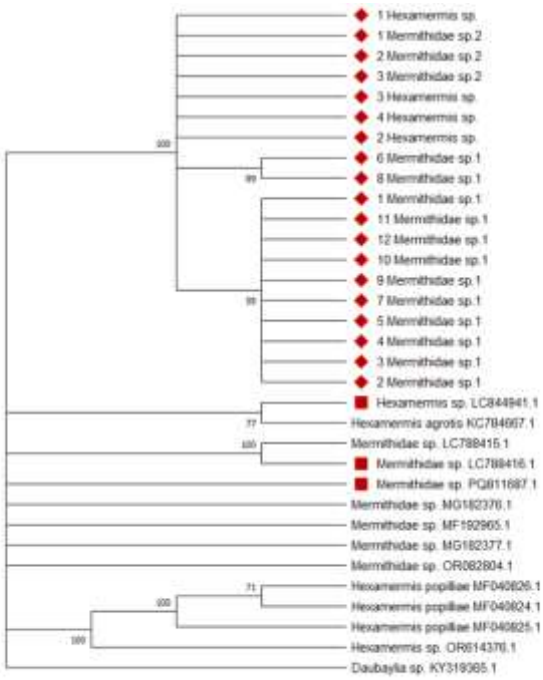

Fig. 4. phylogenetic tree of entomopathogenic

nematodes inferred by the maximum method of parsimony
The red diamonds indicate the species sampled and the others come from the Genbank database. The bootstrap values are shown below the node.

The trees of the individuals of bayesian inference (Fig. 3) and the maximum parsimony (Fig. 4), show the existence of 4 very distinct clades supported by high bootstrap values, between 67 and 100%. The Mermithidae species collected in this study form a single clade with a bootstrap of 76% and 100% depending on the methods (Fig. 3 and Fig. 4). In this clade, individuals of Mermithidae sp. 1 group into two subclades while individuals of Mermithidae sp. 2 and *Hexamermis* sp. are not resolved in this clade, according to maximum parsimony. The Bayesian method shows a grouping of individuals of *Hexamermis* sp. and *Mermithidae* sp. 2, in addition to two *Mermithidae* sp. 1. The species *Hexamermis* sp. (LC844941.1), which has more similarity to some sequences of the study and the species *Hexamermis agrotis* (KC784667.1) shares a clade that seems to have a strong affinity with a bootstrap of 82% and 93%. The species Mermithidae sp. 2 (LC788416.1) identified forms a subclade (Fig. 3) (73%) or a clade (Fig. 4) (100%) with another Mermithidae sp. (LC788415.1). However, Mermithidae sp.1 (PQ811687.1) does not form a clade with individuals of the genus *Hexamermis*, nor with other Mermithidae species, so does not seem to be resolving for both types of reconstructions performed. The species *Hexamermis popilliae* (3 sequences) and *Hexamermis* sp. (OR614376.1) constitute a clade backed by a bootstrap of up to 100%.

Table 3. List of identified Spodoptera frugiperda entomopathogenic nematode species

Morphotypes	Species identified	Accession No.	Identity (%)	E value
	Hexamermis sp.	LC844941.1	89,29-89,32	3.10^{-148}
Mermithidae	Mermithidae sp. 1	PQ811687.1	89,15-89,61	6.10^{-150}-1.10^{-146}
	Mermithidae sp. 2	LC788416.1	88.71-89.17	4.10^{-147}-$8.\ 10^{-144}$

DISCUSSION

The present study, which aimed to genetically characterize the entomopathogenic parasitoids and nematodes of *S. frugiperda* in Senegal, revealed the presence of 12 species of insects and 3 species of entomopathogenic nematodes. This pest first reported in Africa by (Sisay *et al.*, 2018) and in Senegal by Brévault *et al.* (2018) has been described with its community of parasitic species (Ruiz-Nájera *et al.*, 2013; Sisay *et al.*, 2018; Gani *et al.*, 2023). In America, more than 130 species, parasitoids of *S. frugiperda* are listed by (Molina-Ochoa *et al.,* 2003; Murúa *et al.,* 2006) and fewer than five species of entomopathogenic nematodes in the Americas and Asia (Ruiz-Nájera *et al.*, 2013; Sun *et al.*, 2020). The first reports on its natural enemies in Africa reveal a dozen parasitoids (Sisay *et al.*, 2018; Kenis *et al.*, 2019; Chipabika *et al.*, 2023) and Mermithidae nematodes (Gani *et al.* 2023). This is in line with the results of this study where parasitoids and nematodes parasitized the FAW.

Of the 12 parasitoid species revealed by molecular identification, eleven (11) emerged from the larval stage versus one from the embryonic stage of *S. frugiperda*. These species belong to the orders Diptera and Hymenoptera.

Diptera have long parasitized Lepidoptera, a pest of maize in Africa (Chinwada *et al.*, 2014 ; Faithpraise *et al.*, 2015). According to the study conducted by Molina-Ochoa *et al.* (2003) in America, more than fifty species of *Tachinidae* are in association with *S. frugiperda*. Several studies conducted on the African continent show that *Tachinidae* can cause parasitism rates of up to more than 15%. The parasitoid *Tachinidae* of *S. frugiperda* including species of the genus *Drino*, are well distributed across the African continent (Sisay *et al.*, 2018; Durocher-Granger *et al.*, 2021; Chipabika *et al.*, 2023) particularly in West Africa (in Benin and Ghana) (Agboyi *et al.*, 2020; Blakely *et al.*, 2022). This is in line with the results of this study. A species, *Drino* sp. is observed in Burkina

Faso (Ahissou *et al.*, 2021; Gani *et al.*, 2023) and Zambia (Chipabika *et al.*, 2023). Indeed, it predominates among the Tachinidae parasitoids of *S. frugiperda,* and has a wide distribution in these two countries (Chipabika *et al.*, 2023; Gani *et al.*, 2023). This confirms the results of this study, due to its presence in the Groundnut Basin and Casamance. This species is often cited in the literature, which may be the same or different species and may not yet be described. Concerning *Senometopia cariniforceps* Chao and Liang, 2002 (*Carcelia cariniforceps*), she is a solitary parasitoid. According to Pernek *et al.* (2016), the species of *Senometopia* can be generalist parasitoids. *S. cariniforceps* is first encountered in China (O'Hara *et al.*, 2009). It should be noted that it is not yet reported in Africa, except in this study. However, two species of *Senometopia* were collected in Cameroon from *Helicoverpa armigera* by Di Giovanni *et al.* (2019). Also *Senometopia illota* Curran, 1927 is identified as a new association with *S. frugiperda* in Indonesia by Lestari *et al.* (2024). This same observation is noted by Shima and Tachi (2023) Come in *S. cariniforceps* and *Catocala columbina* Leech, 1900 in Japan. In fact, in parasitoids, It is common to meet associations with new guests (Efil and Kara, 2004). This is in line with the results of this research. *S. cariniforceps* has never been registered as a parasitoid of *S. frugiperda* and probably a new association.

The parasitoids of *S. frugiperda* are mainly Hymenoptera with the family Braconidae dominating (Molina-Ochoa *et al.*, 2003). This is in line with the results of this study where six species of Braconidae are recorded against two species of Encyrtidae, one species of Ichneumonidae and one species of Eulophidae.

Species of the genus *Chelonus* are often reported as parasitoids of *S. frugiperda* in the world (Gupta *et al.*, 2020; Sagar *et al.*, 2022). They are reported in parasitic East and West Africa *S. frugiperda* or species of the same genus (Agboyi *et al.*, 2020; Ahissou *et al.*, 2021; Durocher-Granger *et al.*, 2021; Koffi *et al.*, 2022; Shen *et al.*, 2023; Ganou *et al.*, 2024). The results of the study are in line with those of Tendeng *et al.* (2019) in Senegal and those of Chipabika *et al.* (2023) in Zambia, which recorded the presence of a species of *Chelonus* not identified morphologically and genetically respectively. Our study indicated, based on the phylogenetic tree, that *Chelonus* sp. is 87% or 99% related to *Chelonus insularis* Cress, 1865, a promising biological control agent against *S. frugiperda* (Rezende *et al.*, 1994). The results obtained indicate three species of the subfamily Microgastrinae: *Parapantels* sp. *Dolichogenidea* sp. 1 and *Dolichogenidea* sp. 2. Species of the genus *Parapantels* have a wide host range and are distributed in many countries. Some of its species have been recorded on *Spodoptera cosmioides* Walk, 1858 and *Spodoptera eridania* Stoll, 1782 (Whitfield *et al.*, 2018; Freitas *et al.*, 2019). A species named *Parapantels* sp. was newly associated with *S. frugiperda* Zambia (Durocher-Granger *et al.*, 2021). This is in line with the results of the study. A strong affinity was observed between the genus *Parapanteles* and *Dolichogenidea*, either 81% or 100% depending on the approach. In Senegal, three species of *Dolichogenidea* are listed by Crash *et al.* (2021). However, molecular identification does not show resemblance to these three species. The study of Crash *et al.* (2021) confirms that there are no keys to distinguish African species from *Dolichogenidea*, which can justify the existence of both *Dolichogenidea* sp. Indeterminate. Species in this genus have a very restricted host range and often attack *Tuta absoluta* Meyrick, 1917 (tomato pest) (Agboka *et al.*, 2022; Aigbedion-Atalor *et al.*, 2022) explaining his first report on *S. frugiperda* in a context where market gardening crops that shelter their main hosts are not very present in an area such as the groundnut Basin, especially during rainy periods when field crops are promoted.

Concerning *Meteorus orocrambivorus* and *Meteorus* sp. species of the same genus are known as parasitoids of *Spodoptera* and among which *S. frugiperda* (Molina-Ochoa *et al.*, 2001; Freitas *et al.*, 2019). Species of the genus *Meteorus* have increased the list of native parasitoids of the pest in the invaded areas. Mano *et al.* (2023) and Dickson *et al.* (2022) were able to show in Burkina Faso and Senegal respectively, the presence of the parasitoid *Meteorus laphygmarum* Brues, 1926 on moths. It is also a potential regulator of *S. frugiperda* in America, highlighting the ability to *Meteorus* to parasitize the FAW. This corroborates the results of this study. *M. Orocrambivorus* is not yet reported on *S. frugiperda* and in Senegal as well, according to the research carried out. This confirms the continuous adaptation of *Meteorus* to the FAW.

The species *Sinophorus exartemae* Uchida, 1928 (*Limnerium exartemae*) is a family of Ichneumonidae. Studies have shown that species of this genus are distributed in central and northern America, where they are endemic, and in part of Asia and Europe (Sanborne, 1983; Sheng and Sun, 2014). In the Afrotropical zone, 3 species of *Sinophorus* are known among the 114 (Sheng and Sun, 2014). Studies have shown that this genus often parasitizes the larvae of Noctuidae, a pest of maize in the same way as *S. frugiperda* (Sertkaya and Bayram, 2005; Fortuna *et al.*, 2023). *S. exartemae* is an endoparasitoid, solitary. However, it is can be documented and never seems to be reported in Senegal and even less as a parasitoid of *S. frugiperda*. Even if *Charops* sp., a species with which it is phylogenetically closely related (100%), is recorded on the FAW in Zambia (Durocher-Granger *et al.*, 2021), in Mozambique (Caniço *et al.*, 2020) and *Charops ater* Tanzania, Kenya (Sisay *et al.*, 2018) and Niger (Moussa *et al.*, 2023).

The results of the genetic analysis were able to reveal the presence of *Euplectrus phthorimaeae* Ferrière, 1941. Studies show that wasps *Euplectrus* are parasitoids of Lepidoptera including Noctuidae, distributed in Africa (Burkina Faso) (Mano *et al.*, 2023) (*Euplectrus* sp.) and in other continents (Hansson *et al.*, 2015; Žikić *et al.*, 2017). The species *Euplectrus laphygmae* Ferrière, 1941 is listed in Zambia as a new association with *S. frugiperda* (Durocher-Granger *et al.,* 2021; Lestari *et al.* 2024). This is in line with the results of this study because indeed, *Euplectrus phthorimaeae* also is not yet registered on *S. frugiperda*. Referring to the study of Nagoshi and Meagher (2008), the females of *Euplectrus* prefer to lay their eggs on the corn strain of *S. frugiperda*. While individuals from *Euplectrus phthorimaeae* collected are sampled from maize and sorghum. Two preferred host plants of the maize strain according to Pashley (1986). This proves the possibility of new associations between *Euplectrus* at *S. frugiperda*. Moreover, a species *Euplectrus frugiperda* was recently discovered in Australia on *S. frugiperda* for the first time by Fagan-Jeffries *et al.* (2024), hence its name.

The sample of Encyrtidae 1 analyzed, corresponds to at *Prochiloneurus testaceus* Agarwal, 1965 (*Achrysopophagus testaceus*). Gender *Prochiloneurus* Silvestri, 1915 is cosmopolitan (Hayat *et al.*, 2008). These species are known to be hyperparasitoids of species of the same family as it (Encyrtidae), Pteromalidae, Coccinellidae, among others (Noyes and Hayat, 1984; Pillai *et al.*, 2009). In West Africa *Prochiloneurus insolitus* Alam, 1961 is recognized as the most abundant native hyperparasitoid on Pseudococcidae (Goergen and Neuenschwander, 1992). The author Godfray (1994) In his book, he points out that if the primary host is not parasitized, the hyperparasitoid can lay eggs in it and the larvae will develop as primary parasitoids. The authors Shivakumara *et al.* (2022) also claim to have found six species of hyperparasitoids *Prochiloneurus* sp. as primary parasitoids of two species of mealybugs. In the case of *P. testaceus*, it is difficult to say whether the parasitoid directly attacked the non-parasitized FAW or not, since it has never been recorded on the latter. In this study of Encyrtidae species in the same way as *P. testaceus* are sampled in the Groundnut Basin, in maize cultivation and at the same time. So the presence of these species could attract *P. testaceus* on *S. frugiperda*. Also, since the caterpillar has infested maize more than other pests since its invasion in Africa, its abundance could attract the native primary and secondary parasitoids that were once dependent on other

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pests. However, its status as a hyperparasitoid or primary parasitoid of *S. frugiperda*, remains undetermined.

Molecular analysis reveals that individuals of morphotype 2 of Encyrtidae are found to be *Ooencyrtus masii* Mercet, 1921. Species in this genus are parasitoids of a wide host range (Laraichi *et al.*, 1979). The parasitized species can be of different orders, including the Lepidoptera (Laraichi *et al.*, 1979; Žikić *et al.*, 2017; Polaszek *et al.*, 2023; Acheampong *et al.*, 2024). This is consistent with the results of this study, where the species *O. masii* is found among the parasitoids of *S. frugiperda*. However, according to the research results obtained, this oophagous parasitoid has never been recorded on *S. frugiperda*. But insects, in certain conditions, can adapt according to the availability of the hosts in the wild (Abrams and Kawecki, 1999). This species was already considered to be solely dependent on the eggs of *Malacosoma neustria* Linnaeus, 1758 (Laraichi *et al.*, 1979). The authors Fusu and Andreadis (2023) emphasize that*Ooencyrtus* seems to be able to adapt very quickly to invasive pests. This is in line with our results. To our knowledge, this study is the first recording of*O masii* in Senegal. Proving Laraichi's words *et al.* (1979) on the restricted or wide distribution of*Ooencyrtus*.

Molecular identification of Mermithidae nematodes indicated the existence of 3 species. These are *Hexamermis* sp., of Mermithidae sp.1 and Mermithidae sp. 2. This family of nematodes often attacks species of Lepidoptera that may belong to the family Noctuidae and specifically to the genus *Spodoptera* (Villemant *et al.*, 2015; Babu *et al.*, 2019). The species *S. frugiperda* since its invasion of Asia and Africa, Mermithidae have been associated with it.

Species *Ovomermis sinensis* and *Hexamermis* cf. *albicans* are reported in China and India respectively between 2019 and 2020 (Firake and Behere, 2020; Sun *et al.*, 2020). In two studies carried out in Burkina Faso, species or a species of Mermithidae, because it is undetermined, parasitized the caterpillar with very high rates (Ahissou *et al.*, 2021; Gani *et al.*, 2023). In Senegal, an undetermined species of the genus *Hexamermis* was collected from larvae of *S. frugiperda* by Tendeng *et al.* (2019). This is related to the results of this study, even if in the previous one only a morphological identification was applied. In addition Babu *et al.* (2019) have also found a species *Hexamermis* sp., parasitizing *Spodoptera litura* Fabricius, 1775 et *S. exigua*. This reinforces the idea that, *Hexamermis* can parasitize *S. frugiperda*. For the other two species whose molecular identification was limited to the family, one is similar to a species from Japan (Mermithidae sp. 2) and the other from Italy. The study of Kakui and Shimada (2022), carried out two years earlier in Japan and on the same host species (*S. calcitrans*), assigns nematodes to the genus *Ovomermis*, *Hexamermis* and *Amphimermis* thanks to the associated molecular data, the analysis of phylogenetic trees. This would also mean that Mermithidae sp. 2 would certainly not come out of these three genres. Since for the amplified region, there are already sequences of *Hexamermis* in the database while there is no one for the genera *Ovomermis* and *Amphimermis*. It can then be assumed that Mermithidae sp. 2 can correspond to *Ovomermis* or *Amphimermis*. It should be noted that individuals from Mermithidae sp. 2, due to the presence of a caudal appendage in post-parasitic juveniles and the presence of the stylet, it may be suspected that it is the genus *Ovomermis* although it has not yet been reported in Senegal. Moreover, in Senegal, apart from the morphological study of Tendeng *et al.* (2019) and that of Faye *et al.* (2024) that identified the family, only the genetic study of Kobylinski *et al.* (2012) was carried out on mosquito parasites and where an indeterminate Mermithidae was identified. The authors Kakui and Shimada (2022) confirm by adding that this is certainly linked to the unavailability of data in the databases. This can therefore minimize the number of sequences with which the sequences of a study could be compared. It may also be explained by the fact that the species is a new to the genus *Hexamermis*. The species *Hexamermis* sp. similar to the sequences of *Hexamermis* of this study, seems to be very similar to *Hexamermis agrotis* with which it forms a well-supported clade (67% ou 77%).

CONCLUSION

The present study on the genetic diversity of *Spodoptera frugiperda* auxiliaries in Senegal shows the existence of various species of entomopathogenic parasitoids and nematodes. The results confirm new associations between FAW and the parasitoids *Sinophorus exartemae, Meteorus orocrambivorus, Euplectrus phthorimaeae, Prochiloneurus testaceus, Ooencyrtus masii* and *Senometopia cariniforceps*. To our knowledge, these species, in addition to *Drino* sp., have just been known in the entomological fauna of Senegal. Hence, the need to protect these auxiliaries.

REFERENCES

Abang AF, Nanga SN, Fotso Kuate A, Kouebou C, Suh C, Masso C, Saethre MG, Fiaboe KKM. 2021. Natural Enemies of Fall Armyworm *Spodoptera frugiperda* (Lepidoptera: Noctuidae) in Different Agro-Ecologies. Insects. **12**(509), 1-23.

Abrams PA, Kawecki TJ. 1999. Adaptive host preference and the dynamics of host-parasitoid interactions. Theoretical Population Biology. **56**(3), 307–324.

Acheampong A, Bempah O, Osei-Owusu J, Osafo-Acquaah S. 2024. Composition chimique des composés volatils de l'espace de tête des gousses de niébé intactes et des gousses de niébé infestées par les ravageurs *Riptortus dentipes* et *Nezara viridula*. Scientific African. **23**, 1-10.

Agboka KM, Tonnang HEZ, Abdel-Rahman EM, Odindi J, Mutanga O, Mohamed SA. 2022. A Fuzzy-Based Model to Predict the Spatio-Temporal Performance of the *Dolichogenidea gelechiidivoris* Natural Enemy against *Tuta absoluta* under Climate Change. Biology (Basel) **11**(1280), 1-13.

Agboyi LK, Goergen G, Beseh P, Mensah SA, Clottey VA, Glikpo R, Buddie A, Cafà G, Offord L, Day R, Rwomushana I, Kenis M. 2020. Parasitoid Complex of Fall Armyworm, *Spodoptera frugiperda*, in Ghana and Benin. Insects **11**(68), 1-15.

Ahissou BR, Sawadogo WM, Dabiré GT, Kambiré FC, Bokonon-Ganta AH, Somda I, Verheggen F. 2022. Susceptibility of fall armyworm *Spodoptera frugiperda* (JE Smith) to microbial and botanical bioinsecticides and control failure likelihood estimation. Biotechnologie, Agronomie, Société et Environnement **26**(3), 136-143.

Ahissou RB, Sawadogo WM, Bonzi S, Baimey H, Somda I, Bokonon-Ganta AH, Verheggen FJ. 2021. Natural enemies of the fall armyworm *Spodoptera frugiperda* (Smith) (Lepidoptera: Noctuidae) in Burkina Faso. Tropicultura **39**(3), 1-21.

Aigbedion-Atalor PO, Hill MP, Azrag AGA, Zalucki MP, Mohamed SA. 2022. Disentangling thermal effects using life cycle simulation modelling on the biology and demographic parameters of *Dolichogenidea gelechiidivoris*, a parasitoid of *Tuta absoluta*. Journal of Thermal Biology **107**, 103260.

Altaf N, Idrees A, Ullah MI, Arshad M, Afzal A, Afzal M, Rizwan M, Li J. 2022. Biotic Potential Induced by Different Host Plants in the Fall Armyworm, *Spodoptera frugiperda* (Lepidoptera: Noctuidae). Insects **13**(10), 921.

Arias O, Cordeiro E, Corrêa AS, Domingues FA, Guidolin AS, Omoto C. 2019. Population genetic structure and demographic history of *Spodoptera frugiperda* (Lepidoptera: Noctuidae): implications for insect resistance management programs. Pest Management Science **75**(11), 2948–2957.

Babou FF, Badiane D, Diome T, Sembène M. 2025. Evaluation of three biopesticides on the invasive pest *Spodoptera frugiperda* Smith, 1797 (Lepidoptera : Noctuidae), infesting maize crops (*Zea mays* L., 1753) in upper Casamance. International Journal of Biosciences **27**(1), 375–385.

Babou FF, Diome T, Sembène M. 2022. *Spodoptera frugiperda* (Smith, 1797) (Lepidoptera: Noctuidae) expands its food spectrum in Senegal. International Journal of Entomology Research **7**(3), 107–114.

Babu S, Phani V, Meena P, Chauhan K, Khan M, Somvanshi V. 2019. Report of a mermithid nematode infecting *Amyna axis*, *Chrysodeixis* spp. and *Spodoptera* spp. from India. Journal of Biological Control **33**(3), 217–221.

Boaventura D, Martin M, Pozzebon A, Mota-Sanchez D, Nauen R. 2020. Monitoring of Target-Site Mutations Conferring Insecticide Resistance in *Spodoptera frugiperda*. Insects **11**(8), 545.

Boukari SA, Sinzogan CAC, Sikirou R, Deguenon JM, Amagnidé GAY, Zossou N, Vodounon HST, Adomou AC, Ahanchédé A. 2022. Influence of agricultural practices on *Spodoptera frugiperda* (JE Smith) infestation, natural enemies and biocontrol in maize. Journal of Agricultural and Crop Research **10**(7), 113–130.

Brévault T, Ndiaye A, Badiane D, Bal AB, Sembène M, Silvie P, Haran J. 2018. First records of the fall armyworm, *Spodoptera frugiperda* (Lepidoptera: Noctuidae), in Senegal. Entomologia Generalis **37**(2), 129–142.

Caniço A, Mexia A, Santos L. 2020. First Report of Native Parasitoids of Fall Armyworm *Spodoptera frugiperda* Smith (Lepidoptera: Noctuidae) in Mozambique. Insects **11**(9), 615.

Chen H, Wang Y, Huang L, Xu CF, Li JH, Wang FY, Cheng W, Gao BY, Chapman JW, Hu G. 2022. Flight Capability and the Low Temperature Threshold of a Chinese Field Population of the Fall Armyworm *Spodoptera frugiperda*. Insects **13**(5), 422.

Chen MN, Santander RD, Talamas EJ, Jentsch PJ, Bon MC, Aćimović SG. 2021. Molecular Identification of *Trissolcus japonicus*, Parasitoid of the Brown Marmorated Stink Bug, by Species-Specific PCR. Insects **12**(5), 467.

Chinwada P, Nyamutukwa S, Marandure A, Zitsanza ES. 2014. Biology and Development of *Sturmiopsis parasitica* (Diptera: Tachinidae) on Different Species and Populations of Maize Stemborers in Zimbabwe and an Assessment of Its Suitability for Redistribution in Africa. African Entomology. **22**(4), 828-837.

Chipabika G, Sohati PH, Khamis FM, Chikoti PC, Copeland R, Ombura L, Kachapulula PW, Tonga TK, Niassy S, Sevgan S. 2023. Abundance, diversity and richness of natural enemies of the fall armyworm, *Spodoptera frugiperda* (J.E. Smith) (Lepidoptera: Noctuidae), in Zambia. Front. Insect Sci. **3**, 1-14.

Delvare G. 1991. L'identification et l'étude systématique des insectes sont-elles toujours d'actualité? 13.

Di Giovanni F, Prudent P, Gisondi S, Badano D, Lo Giudice G, Lawe Djague T, Doke NS, Cerretti P. 2019. Tachinid flies (Diptera: Tachinidae) associated with crop pests in northern Cameroon, with the description of a new species of *Carcelia* Robineau-Desvoidy. Annales de la Société entomologique de France (N.S.) **55**(6), 489–496.

Diop P, Labou B, Sylla ES, Tending E, Diatte M, Balde A, Seydi O, Sene SO, Ndiaye IA, Diarra K. 2022. Actualisation de l'entomofaune associée à la culture de pomme de terre dans les Niayes, Sénégal: Update on the entomofauna associated with potato cultivation in the Niayes, Senegal. International Journal of Biological and Chemical Sciences **16**(3), 1314–1319.

Durocher-Granger L, Mfune T, Musesha M, Lowry A, Reynolds K, Buddie A, Cafà G, Offord L, Chipabika G, Dicke M, Kenis M. 2021. Factors influencing the occurrence of fall armyworm parasitoids in Zambia. Journal of Pest Science **94**(4), 1133–1146.

Efil L, Kara K. 2004. Tachinid parasitoids (Diptera: Tachinidae) of *Spodoptera exigua* in cotton fields in Diyarbakır, Turkey. Phytoparasitica **32**(4), 363–366.

El-Refaie RM, Shaurub ESH, Abd-Allah GE, Ebeid AA, Abouelnaga ZS. 2024. Effect of four host plants on the life history and nutritional indices of *Spodoptera littoralis*. International Journal of Tropical Insect Science **44**(3), 1091–1101.

Fagan-Jeffries EP, Miles MM, Atkin-Zaldivar TC, Howe AG, Subramaniam S, Chambers DM, Tadle FPJ, Adnan SM, Sivasubramaniam V, Woodward A, Spafford H, Thistleton B. 2024. Hymenopteran parasitoids of fall armyworm (*Spodoptera frugiperda*) (J.E. Smith) (Lepidoptera: Noctuidae) in Australia, with the description of five new species in the families Braconidae and Eulophidae. Austral Entomology **63**(2), 136–174.

Faithpraise F, Idung J, Chatwin C, Young R, Birch P. 2015. Modélisation du contrôle des infestations de chenilles légionnaires africaines (*Spodoptera exempta*) dans les cultures céréalières en déployant des insectes naturellement bénéfiques. Biosystems Engineering **129**, 268–276.

Faye M, Ndiaye A, Diallo I, Thiaw C. 2024. Natural regulation and bioecology of *S. frugiperda* (J.E. Smith, Lepidoptera Noctuidae) in maize crops in Senegal. International Journal of Entomology Research **9**(8), 254–263.

Firake DM, Behere GT. 2020. Mortalité naturelle de la chenille légionnaire d'automne invasive, *Spodoptera frugiperda* (JE Smith) (Lepidoptera: Noctuidae) dans les agroécosystèmes de maïs du nord-est de l'Inde. Biological Control **148**, 104303.

Fitch WM. 1971. Toward Defining the Course of Evolution: Minimum Change for a Specific Tree Topology. Systems Biology **20**(4), 406–416.

Fortuna TM, Anne M, Gonnidec ML, Capdevielle-Dulac C, Jeannette R, Mougel F, Kaiser L. 2023. Demandes d'autorisation d'entrée sur le territoire et d'introduction dans l'environnement de *Cotesia typhae* (Hymenoptera, Braconidae) non indigènes utiles aux végétaux, notamment dans le cadre de la lutte biologique. Centre National de la Recherche Scientifique. 31pp.

Freitas JG de, Takahashi TA, Figueiredo LL, Fernandes PM, Camargo LF, Watanabe IM, Foerster LA, Fernandez-Triana J, Shimbori EM. 2019. Premier signalement de *Cotesia scotti* (Valerio et Whitfield, 2009) (Hymenoptera: Braconidae: Microgastrinae) comb. nov. parasitant *Spodoptera cosmioides* (Walk, 1858) et *Spodoptera eridania* (Stoll, 1782) (Lepidoptera: Noctuidae) au Brésil. Revista Brasileira de Entomologia **63**(3), 238–244.

Fusu L, Andreadis SS. 2023. *Ooencyrtus mirus* (Hymenoptera, Encyrtidae), discovered in Europe parasitizing eggs of *Halyomorpha halys* (Hemiptera, Pentatomidae). Journal of Hymenoptera Research **96**, 1045–1060.

Gani DA, Issoufou O, Antoine S. 2023. Distribution naturelle des principaux parasitoïdes larvaires inféodés à la chenille légionnaire d'automne (*Spodoptera frugiperda* J.E Smith) au Burkina Faso. Journal of Applied Biosciences **190**, 20037- 20049.

Ganou SF, Sankara F, Agboyi LK, Dao ANC, Dabire R, Nebie K, Zida I, Wangrawa D, Somda I. 2024. Contribution des parasitoïdes dans la lutte contre *Spodoptera frugiperda* (J. E. Smith) (Lepidoptera: Noctuidae) en Afrique de l'Ouest: cas de *Chelonus bifoveolatus* et *Coccygidium luteum* (synthèse bibliographique). International Journal of Biological and Chemical Sciences **18**(1), 279–288.

Ge S, He L, He W, Yan R, Wyckhuys KAG, Wu K. 2021. Laboratory-based flight performance of the fall armyworm, *Spodoptera frugiperda*. Journal of Integrative Agriculture **20**(3), 707–714.

Godfray HCJ. 1994. Parasitoids : Behavioral and Evolutionary Ecology. Princeton University Press, 488 pp.

Goergen G, Neuenschwander P. 1992. A cage experiment with four trophic levels: cassava plant growth as influenced by cassava mealybug, *Phenacoccus manihoti*, its parasitoid *Epidinocarsis lopezi*, and the hyperparasitoids *Prochiloneurus insolitus* and *Chartocerus hyalipennis*. Journal of Plant Diseases and Protection **99**(2), 182–190.

Guo Z, Jin R, Guo Z, Cai T, Zhang Y, Gao J, Huang G, Wan H, He S, Xie Y, Li J, Ma K. 2022. Insecticide Susceptibility and Mechanism of *Spodoptera frugiperda* on Different Host Plants. Journal of Agricultural and Food Chemistry **70**(36), 11367–11376.

Gupta A, Lalitha Y, Varshney R, Shylesha AN, van Achterberg C. 2020. *Chelonus formosanus* Sonan (Hymenoptera: Braconidae) an egg-larval parasitoid of the invasive pest *Spodoptera frugiperda* (J. E. Smith) (Lepidoptera : Noctuidae) amenable to laboratory mass production in India **8**(1), 1521–1524.

Hall TA. 1999. Bioedit : a user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. Nucleic Acids Symposium, 95–98.

Hansson C, Smith MA, Janzen D, Hallwachs W. 2015. Integrative taxonomy of New World *Euplectrus* Westwood (Hymenoptera, Eulophidae), with focus on 55 new species from Area de Conservación Guanacaste, northwestern Costa Rica. ZooKeys **485**, 1–236.

Hayat M, Badruddin S, Khan F.R. 2008. Descriptions of six new and records of eight known species of Encyrtidae from India (Hymenoptera : Chalcidoidea). Oriental Insects- Orient Insect **42**, 103–115.

Ivezić A, Rugman-Jones PF, Trudić B. 2021. Rapid molecular identification of *Trichogramma* (Hymenoptera: Trichogrammatidae) parasitizing the eggs of the European corn borer, *Ostrinia nubilalis* (Lepidoptera: Crambidae) in Serbia. Egypt Journal Biology Pest Control **31**(1), 74.

Kakui K, Shimada D. 2022. Dive into the sea : first molecular phylogenetic evidence of host expansion from terrestrial/freshwater to marine organisms in Mermithidae (Nematoda : Mermithida). Journal of Helminthology **96**, e33.

Kenis M, du Plessis H, Van den Berg J, Ba M.N, Goergen G, Kwadjo KE, Baoua I, Tefera T, Buddie A, Cafà G, Offord L, Rwomushana I, Polaszek A. 2019. *Telenomus remus*, a Candidate Parasitoid for the Biological Control of *Spodoptera frugiperda* in Africa, is already Present on the Continent. Insects **10**(4), 92.

Kobylinski KC, Sylla M, Black W, Foy BD. 2012. Mermithid nematodes found in adult Anopheles from southeastern Senegal. Parasites & Vectors **5**(1), 131.

Koffi D, Kyerematen R, Osae M, Amouzou K, Eziah VY. 2022. Assessment of *Bacillus thuringiensis* and emamectin benzoate on the fall armyworm *Spodoptera frugiperda* (J. E. Smith) (Lepidoptera : Noctuidae) severity on maize under farmers' fields in Ghana. International Journal of Tropical Insect Science **42**(2), 1619–1626.

Krache F, Boualem M, Fernandez-Triana JL, Bass A, Arnó J, Benourad F. 2021. First record in Africa of the parasitoid *Dolichogenidea gelechiidivoris* (Hymenoptera: Braconidae) on tomato leafminer *Tuta absoluta* (Lepidoptera: Gelechiidae) from tomato fields in Algeria. Journal of Hymenoptera Research. **88**, 115–131.

Kumar D, Nagal P, Sidhu H, Ranga P, Mehra P, Sidhu S. 2024. Role of Mermithid Nematodes in the Management of Agricultural and Household Insect Pests: A review. Environment and Ecology **41**(4), 2890–2899.

Kumar S, Stecher G, Li M, Knyaz C, Tamura K. 2018. MEGA X: Molecular Evolutionary Genetics Analysis across Computing Platforms. Molecular Biology and Evolution **35**(6), 1547–1549.

Laraichi M, Remaudiere G, Zomorodi A, Djavameri M, Gallego G, Sanchez-Boccherini J, Stavraki HG, Mineo G, Attiah H, Isa A. 1979. Groupe de travail lutte intégrée en céréaliculture dans le Bassin méditerranéen et en Iran. 102.

Lestari P, Fitriana Y, Suharjo R, Swibawa IG, Utomo SD, Andrianto E. 2024. Nouveaux parasitoïdes de *Spodoptera frugiperda* dans la province de Lampung, Indonésie. Journal of Asia-Pacific Biodiversity **17**(4), 631–643.

Mano E, Ouedraogo B, Kambou G, Somda I. 2023. Diversité, abondance et comportement trophique des parasitoïdes contre le ravageur *Helicoverpa armigera* (Hübner 1808) en culture de tomates biologiques au Burkina Faso. International Journal of Biological and Chemical Sciences **17**(1), 1–12.

Mansour R, Bauer AL, Goodarzi M, Hoffmann C. 2023. Toxicity of Pesticides Applied in European Vineyards on *Anagyrus vladimiri* and *Trichogramma evanescens*, Parasitoids of *Planococcus ficus* and *Lobesia botrana*. Insects **14**(12), 907.

Molina-Ochoa J, Carpenter JE, Heinrichs EA, Foster JE. 2003. Parasitoids and parasites of *Spodoptera frugiperda* (Lepidoptera : Noctuidae) in the Americas and Caribbean Basin : an inventory. Florida Entomologist **86**(3), 254–289.

Molina-Ochoa J, Hamm JJ, Lezama-Gutiérrez R, López-Edwards M, González-Ramírez M, Pescador-Rubio A. 2001. A Survey of Fall Armyworm (Lepidoptera: Noctuidae) Parasitoids in the Mexican States of Michoacán, Colima, Jalisco, and Tamaulipas. The Florida Entomologist **84**(1), 31–36.

Moussa OZ, Laminou S, Zangui H, Amadou L, Boukari IB. 2023. Inventory of Host Plants and Parasitoids of the Fall Armyworm (FAW), *Spodoptera frugiperda* (JE Smith), in the Southern Agricultural Zone of Niger. Journal of Agricultural Chemistry and Environment **12**(1), 16–27.

Moustafa MAM, Osman EA, Mokbel ESMS, Fouad EA. 2024. Caractérisation biochimique et moléculaire de la résistance au chlorantraniliprole chez *Spodoptera littoralis* (Lepidoptera : Noctuidae). Crop Protection **177**, 106533.

Murúa G, Molina-Ochoa J, Coviella C. 2006. Population dynamics of the fall armyworm, *Spodoptera frugiperda* (Lepidoptera: Noctuidae) and its parasitoids in northwestern Argentina. Flen. **89**(2), 175–182.

Nagoshi RN, Meagher RL. 2008. Review of Fall Armyworm (Lepidoptera: Noctuidae) Genetic Complexity and Migration. Flen. **91**(4), 546–554.

Ndiaye A, Faye M, Ba I, Diallo I, Sembene PM. 2021. The fall armyworm *Spodoptera frugiperda* (J.E. Smith), a new pest of maize in Africa: monitoring, damage evaluation and identification of natural enemies on production areas of Senegal. International Journal of Biological and Chemical Sciences **15**(6), 2247–2260.

Noyes JS, Hayat M. 1984. A review of the genera of Indo-Pacific Encyrtidae (Hymenoptera: Chalcidoidea). Bulletin of the British Museum (Natural History) Entomology **48**(3), 131–395.

Nuambote-Yobila O, Bruce A, Makumbi D, Ogola G, Marangu C, Beyene Y, Mahungu NM, Prasanna B, Marion-Poll F, Calatayud PA. 2025. Combining ability for resistance to fall armyworm, *Spodoptera frugiperda* in tropical maize inbred lines. Phytoparasitica **53**(43).

Nuambote-Yobila O, Musyoka B, Njuguna E, Bruce AY, Khamis F, Subramanian S, Marion-Poll F, Calatayud PA. 2022. Influence of Si in maize plants in Kenyan populations of *Spodoptera frugiperda* (Lepidoptera: Noctuidae). Phytoparasitica **50**(5), 1025–1032.

Nuambote-Yobila O. 2023. Résistance du maïs à la chenille légionnaire d'automne (*Spodoptera frugiperda*) en Afrique. Université Paris-Saclay, 107p.

O'Hara JE, Shima H, Zhang C. 2009. Annotated catalogue of the Tachinidae (Insecta: Diptera) of China. Zootaxa, 1-236.

Pashley DP. 1986. Host-associated Genetic Differentiation in Fall Armyworm (Lepidoptera : Noctuidae): a Sibling Species Complex?. Annals of the Entomological Society of America **79**(6), 898–904.

Pernek M, Lukić I, Lackovic N, Çota E, Tschorsnig HP. 2016. Tachinid (Diptera: Tachinidae) parasitoids of spotted ash looper (*Abraxas pantaria*) in Krka National Park in Croatia. Periodicum Biologorum **117**(4), 532–535.

Pillai KG, Krishnamoorthy A, Gangavisalakshy PN. 2009. First Report of Hyperparasitoids of *Anagyrus dactylopii* (Howard) from India. Journal of Biological Control **23**(2), 193–194.

Polaszek A, Noyes JS, Lugli EB, Schmaedick MA, Peck RW, Banko PC, Fusu L. 2023. *Ooencyrtus pitosina* (Hymenoptera : Encyrtidae)- A natural enemy of Samoan swallowtail butterfly *Papilio godeffroyi* (Lepidoptera : Papilionidae). PLOS ONE **18**(8), 1-15.

Rahmawati AE, Rahardjo BT. 2024. Biology and Demographic Statistics of *Spodoptera frugiperda* on Corn (*Zea mays* L.) and Spinach (*Amaranthus hybridus* L.). Journal of Tropical Plant Protection **5**(2), 79–88.

Rezende M, Cruz I, Della Lucia T. 1994. Biological aspects of the parasitoid *Chelonus insularis* (Cresson) (Hymenoptera, Braconidae) reared on eggs of *Spodoptera frugiperda* (Smith) (Lepidoptera, Noctuidae). Revista Brasileira de Zoologia **12**, 779–784.

Riaz S, Johnson JB, Ahmad M, Fitt GP, Naiker M. 2021. A review on biological interactions and management of the cotton bollworm, *Helicoverpa armigera* (Lepidoptera : Noctuidae). Journal of Applied Entomology **145**(6), 467–498.

Ruiz-Nájera RE, Ruiz-Estudillo RA, Sánchez-Yáñez JM, Molina-Ochoa J, Skoda SR, Coutiño-Ruiz R, Pinto-Ruiz R, Guevara-Hernández F, Foster JE. 2013. Occurrence of Entomopathogenic Fungi and Parasitic Nematodes on *Spodoptera frugiperda* (Lepidoptera: Noctuidae) Larvae Collected in Central Chiapas, México. Flen. **96**(2), 498–503.

Sagar D, Suroshe SS, Keerthi MC, Poorani J, Gupta A, Chandel RK. 2022. Native parasitoid complex of the invasive fall armyworm, *Spodoptera frugiperda* (J. E. Smith) from Northern India. International Journal of Tropical Insect Science **42**(3), 2773–2778.

Sanborne PM. 1983. Classification, zoogeography, and phylogeny of the genus *Sinophorus*' Foerster (Hymenoptera: Ichneumonidae). McMaster University, Hanllton, Ontario, Canada, 633p.

Schmidt S, Driver F, Debarro P. 2006. The phylogenetic characteristics of three different 28S rRNA gene regions in Encarsia (Insecta, Hymenoptera, Aphelinidae). Organisms Diversity & Evolution **6**, 127–139.

Sertkaya E, Bayram A. 2005. Parasitoid community of the loreyi leaf worm *Mythimna* (*Acantholeucania*) *loreyi*: Novel host-parasitoid associations and their efficiency in the eastern mediterranean region of Turkey. Phytoparasitica **33**(5), 441–449.

Shen Z, Zang ZY, Dai P, Xu W, Nkunika POY, Zang LS. 2023. Identification of *Chelonus* sp. from Zambia and Its Performance on Different Aged Eggs of *Spodoptera frugiperda*. Insects **14**(1), 61.

Sheng ML, Sun SP. 2014. A new species of the genus *Sinophorus* Förster (Hymenoptera: Ichneumonidae: Campopleginae) from China, 133–137.

Shima H, Tachi T. 2023. Systematic study of the genus *Senometopia* Macquart (Diptera : Tachinidae) from the eastern Palaearctic and Oriental regions. Oriental Insects **57**(1), 139–420.

Shivakumara KT, Keerthi MC, Polaiah AC, Ankita G, Sunil J. 2022. Incidence of invasive mealybugs, *Phenacoccus solenopsis* Tinsley and *Paracoccus marginatus* Williams & Granara de Willink (Hemiptera: Pseudococcidae) on *Gymnema sylvestre* (R. Br) and its natural enemies in the semi-arid region of India. International Journal of Pest Management **70**(4), 1126–1140.

Sisay B, Simiyu J, Malusi P, Likhayo P, Mendesil E, Elibariki N, Wakgari M, Ayalew G, Tefera T. 2018. First report of the fall armyworm, *Spodoptera frugiperda* (Lepidoptera: Noctuidae), natural enemies from Africa. Journal of Applied Entomology **142**(8), 800–804.

Sisay B, Simiyu J, Mendesil E, Likhayo P, Ayalew G, Mohamed S, Subramanian S, Tefera T. 2019. Fall Armyworm, *Spodoptera frugiperda* Infestations in East Africa: Assessment of Damage and Parasitism. Insects **10**(7), 195.

Sun B, Li F, He X, Cao F, Bandason E, Shapiro-Ilan D, Ruan W, Wu S. 2020. First report of *Ovomermis sinensis* (Nematoda: Mermithidae) parasitizing fall armyworm *Spodoptera frugiperda* (Lepidoptera: Noctuidae) in China. J Nematol. **52**, 1–7.

Tendeng E, Labou B, Diatte M, Djiba S, Diarra K. 2019. The fall armyworm *Spodoptera frugiperda* (J.E. Smith), a new pest of maize in Africa: biology and first native natural enemies detected. International Journal of Biological and Chemical Sciences **13**(2), 1011–1026.

Thompson JD, Gibson TJ, Plewniak F, Jeanmougin F, Higgins DG. 1997. The CLUSTAL_X windows interface: flexible strategies for multiple sequence alignment aided by quality analysis tools. Nucleic Acids Res. **25**(24), 4876–4882.

Van den Berg J, du Plessis H. 2022. Chemical Control and Insecticide Resistance in *Spodoptera frugiperda* (Lepidoptera: Noctuidae). Journal of Economic Entomology **115**, 1761–1771.

van Lenteren JC, Bolckmans K, Köhl J, Ravensberg WJ, Urbaneja A. 2018. Biological control using invertebrates and microorganisms : plenty of new opportunities. BioControl. **63**(1), 39–59.

Villemant C, Zuccon D, Rome Q, Muller F, Poinar GO, Justine JL. 2015. Can parasites halt the invader. Mermithid nematodes parasitizing the yellow-legged Asian hornet in France. PeerJ. **3**, e947.

Whitfield J.B., Austin AD. & Fernandez-Triana J.L. 2018. Systematics, Biology, and Evolution of Microgastrine Parasitoid Wasps. Annual Review of Entomology **63**, 389–406.

Zhou Y, Wu Q, Zhang H, Wu K. 2021. Spread of invasive migratory pest *Spodoptera frugiperda* and management practices throughout China. Journal of Integrative Agriculture **20**(3), 637–645.

Žikić V, Stanković SS, Kavallieratos NG, Athanassiou C, Georgiou P, Tschorsnig HP, van Achterberg C. 2017. Parasitoïdes associés à *Lymantria dispar* (Lepidoptera: Erebidae) et *Malacosoma neustria* (Lepidoptera: Lasiocampidae) en Grèce et analyse comparative de leurs spectres parasitoïdes en Europe. Zoologischer Anzeiger **270**, 166–175.