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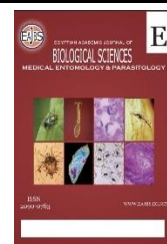
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Entomopathogenic Nematodes and their Symbiotic Bacteria as Bioagents to Combat the Mosquito Vectors of Human Diseases in the World: A Comprehensive Review

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ABSTRACT

Medically, the most dangerous genera are *Anopheles*, *Aedes* and *Culex* due to their ability to transmit mosquito-borne human diseases, such as malaria, yellow fever, chikungunya, lymphatic filariasis, dengue fever, hemorrhagic fever and encephalitis. Mosquito control is a prerequisite work for fighting the increasing mosquito populations and mosquito-borne diseases. Generally, chemical insecticides have been widely used to suppress mosquito populations but these chemicals were evidenced to be less-than-perfect solutions for the long-lasting control of mosquitoes due to the development of insecticide resistance in all mosquito species and different hazards all over the world. Therefore, the search for alternative agents is urgent to avoid or minimize the insecticidal hazards on ecosystem components. One of the potential alternatives is biological control which received great research attention in the world. One of these biocontrol agents is Entomopathogenic Nematodes (EPNs). Therefore, the objective of the present article was primarily to review the current knowledge focusing on the use of EPNs for controlling mosquito vectors. It highlighted the global attention to EPN application as a novel strategy for combating mosquito vectors. Also, this review discussed the pathogenic efficiencies of three EPNs, Mermithidae, Steinernematidae and Heterorhabditidae. Other important issues had been reviewed, such as diverse susceptibility of mosquito larvae and variation of EPN virulence, Key parameters and environmental conditions affecting the virulence of EPNs against mosquito larvae, EPN-symbiotic bacteria and their potential role for the control of mosquito vectors and Suppressive activity of EPN/symbiotic bacteria complex against innate immune defences of mosquito larvae. This review provided, also, some future prospects for the EPN application for controlling mosquito vectors. In conclusion, EPNs can be equal to chemical pesticides against human-disease-transmitting mosquitoes if they are applied in critical concentration under suitable environmental conditions and precautions for application.

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INTRODUCTION

Systematically, mosquitoes belong to the family Culicidae, in the suborder Nematocera: order Diptera: class Insecta: phylum Arthropoda (Gaugler, 2016). This family includes three subfamilies: Toxorhynchitinae, Anophelinae, and Culicinae (Mullen and Durden, 2009) and contains 112 genera comprising over 4500 species of mosquitoes in the world (Chandra *et al.*, 2013; Harbach and Besansky, 2014). The genus *Aedes* only includes over 950 described species (Elbers *et al.*, 2015). Geographically, mosquitoes are found in temperate and tropical regions of the world except the Polar Regions (Lancaster and Briers, 2008). Through trade and travel, key mosquito species are being introduced into new habitats (Kilpatrick, 2011; Vila and Hulme, 2017). From the medical point of view, the serious genera are *Anopheles*, *Aedes*, *Culex*, *Psorophora*, *Mansonia*, *Haemagogus* and *Sabethes* due to their ability to transmit mosquito-borne human diseases (Gubler, 2010; Mullen and Durden, 2019).

In tropical and subtropical countries, mosquito-borne diseases represent one of the main problems (Kalita *et al.*, 2013). Some mosquito species transmit disease-causing pathogens to people causing different human diseases affecting many millions of people annually, such as malaria, yellow fever, chikungunya, lymphatic filariasis, dengue fever, hemorrhagic fever and encephalitis (Ghosh *et al.*, 2005; Onyido *et al.*, 2008; Farajollahi *et al.*, 2011; Mwangangi *et al.*, 2012; WHO, 2014; Sarwar, 2015; Benelli *et al.*, 2016; Afolabi *et al.*, 2019). Moreover, some mosquitoes can transmit animal diseases, such as myxomatosis in rabbits, fowl-pox in poultry, encephalitis in horses and birds, heartworm diseases in dogs and rift-valley fever in sheep (Rabiu and Ahmed, 2019; Dahmana and Mediannikov, 2020). However, three main genera of dangerous

mosquitoes, *Anopheles*, *Aedes* and *Culex*, transmit the causative agents of numerous severe diseases to humans as well as animals (Barretto *et al.*, 2015; Benelli and Beier, 2017; Achee *et al.*, 2019). These mosquito genera transmit various pathogens causing nearly 350 million cases and nearly half a million deaths per year (Moyes *et al.*, 2017). Therefore, accurate action is urgent to get away from the disease as soon as possible (Gaddaguet *et al.*, 2016; Naseem *et al.*, 2016).

For instance, malaria is currently an endemic disease being transmitted by anopheline mosquitoes in more than 80 countries inhabited by about three billion people, especially in sub-Saharan Africa (Dahmana and Mediannikov, 2020) and worrying outbreaks have recently spread through many areas in the world (Rahmah *et al.*, 2015; Amato *et al.*, 2018; Lok and Dijk, 2019). Of the approximately 430 *Anopheles* species, while over 100 are known to be able to transmit malaria to humans, only 30–40 commonly do so in nature (Cox, 2010; Sinka *et al.*, 2010; Harbach, 2013; Elbers *et al.*, 2015; Adugna *et al.*, 2021). Annually 200–450 million infections are caused by the *Anopheles* mosquito leading to 2.7 million deaths in more than 100 developing countries (Koech and Mwangi, 2014).

With regard to dengue fever, the World Health Organization recently reported about 400 million infections annually with about half of the world's population at risk of dengue transmission (Katzelnick *et al.*, 2017). This serious problem can be exacerbated through the adaptation of mosquitoes to the polluted water, which could make control an intractable challenge in the foreseeable future mostly in Central and South America, Africa and Asia (Bhatt *et al.*, 2013; Villamil-Gómez *et al.*, 2016). According to the current knowledge, the yellow fever mosquito *Aedes aegypti* and Asian tiger mosquito *Aedes albopictus* are

the major mosquito vectors of dengue fever worldwide (Silva *et al.*, 2008), in addition to other severe diseases, such as dengue hemorrhagic fever, Zika virus and yellow fever (Rodriguez *et al.*, 2007; WHO, 2009; Simmons *et al.*, 2012; Mahesh Kumar *et al.*, 2013; Ansari and Hussain, 2020) as well as chikungunya fever which has afflicted hundreds or thousands of people annually in more than 100 tropical and subtropical countries (CDC, 2015) and other arboviruses, like dog heartworm and filarial nematodes (Bonizzoni *et al.*, 2013).

In recent years, Zikavirus outbreaks are terrifying human health problems. The mosquito *Ae. aegypti* is considered to be the main vector of this horrifying disease (Diallo *et al.*, 2014), while *Ae. albopictus* is considered a secondary vector (Grard *et al.*, 2014). In addition, several other mosquito species are involved in the existence and transmission of this rapidly spreading virus (Musso *et al.*, 2014; Song *et al.*, 2017; Dahmana and Mediannikov, 2020). Zika virus causes ongoing epidemics in several countries in Latin America and the Pacific (Ledermann *et al.*, 2014; Brady and Hay, 2019; Dahmana and Mediannikov, 2020). The daytime biting mosquito *Ae. albopictus* is known to transmit several arboviruses including West Nile virus, eastern equine encephalitis virus, and Japanese encephalitis virus (Sardelis *et al.*, 2002; Bonizzoni *et al.*, 2013; De Wispelaere *et al.*, 2017). Also, it is an important vector of dog heartworm parasites, *Dirofilaria immitis* and *D. repens* (Morchón *et al.*, 2012).

In this context, other zoophilic mosquito species, especially *Culex* spp., are responsible for the transmission of arboviruses, including Japanese encephalitis virus and West Nile virus (Solomon and Vaughn, 2002). The northern house mosquito, *Culex pipiens*, is a dominant mosquito species worldwide (Elhawary *et al.*, 2020) and the southern house mosquito *Culex quinquefasciatus* is a common nuisance mosquito widely distributed in tropical and subtropical areas.

It is a vector of urban filariasis (Abagli and Alavo, 2019).

It should not be forgotten that the first step in fighting mosquitoes is the avoidance of their bites. There are simple methods to protect from these bites, such as wearing long pants inserted into socks and long-sleeved shirts outdoors (Kamareddine, 2012). Indoor, persons should be present in the areas that are screened, live in air-conditioned and can use bed nets (Mandal, 2011). Mosquito repellents and plant-borne molecules are also required to combat the increasing mosquito populations (Mandal, 2011; Mehlorn, 2016; Naseem *et al.*, 2016).

The most important reasons for the terrible increase in dengue fever, for example, are the increasing oviposition and breeding sites for *Aedes* mosquito, less effective control of mosquitoes, more urbanization and enhanced growth of population (Sritabutra and Soonwera, 2013). Mosquito breeding can be stopped by clearing the standing water from the drains, improving water storage and proper solid waste disposal (Patel *et al.*, 2012). Also, the destruction of the breeding sites is an effective means to decrease the mosquito population (Knio *et al.*, 2008). The sluggish nature and confined population of larvae of different mosquito species make them easy to control at the larval stage (Kishore *et al.*, 2011). However, the removal of habitats in the environment is still an efficient measure for the population reduction of disease vectors.

On the other hand, mosquito control is an urgent demand for fighting the increasing number of mosquito-borne diseases (Xu *et al.*, 2014). In the middle of the 20th century, synthetic pesticides were first used for pestcontrol (Phasomkusolsil and Soonwera, 2011). Generally, chemical insecticides have been widely used to suppress the epidemics of mosquito-transmitted diseases (Neelakanta and Sultana, 2015; Yooyangket *et al.*, 2018; Agumba *et al.*, 2019). At that time, these chemicals were considered the best control agents for mosquitoes, but it was evidenced

to be a less-than-perfect solution for the long-lasting control of mosquitoes (Gaddaguti *et al.*, 2016).

The chemical control targeted both larvae and adults, but larvae and pupae are the important developmental stages that live in water. The insecticides are usually used as larvicides (Reiter and Nathan, 2001; Rodriguez *et al.*, 2007). However, field works have provided controversial reports on the prospect of these approaches to prevent mosquito-borne disease outbreaks (Horstick and Runge-Ranzinger, 2018; Achee *et al.*, 2019). Also, the use of indoor residual spray is more likely to be effective in controlling indoor species, such as *Ae. aegypti*, but has a limited impact on the outdoor populations of various *Culex* species mosquitoes (WHO, 2006).

Moreover, the intractable problem facing insecticide usage for mosquito control is the development of insecticide resistance which was evidently confirmed in all mosquito species all over the world (Hemingway and Ranson, 2000; Chareonviriyaphapet *et al.*, 2013; Naqqash *et al.*, 2016; Moyes *et al.*, 2017). Therefore, the control success is limited by resistance to the majority of widely marketed insecticides (Seccacini *et al.*, 2008; Bisset-Lazcano *et al.*, 2009). For example, resistance to insecticides is emerging in natural *Ae. albopictus* populations and is widespread in *Ae. aegypti*, challenging the sustainability of this control measure (Xu *et al.*, 2016; Moyes *et al.*, 2017; Pichler *et al.*, 2018). It may be important to mention that mosquito insecticide resistance at the larval stage is extremely high compared to the adult stage (Zohdy *et al.*, 2013; Ansari and Hussain, 2020). This problematic insecticide resistance has increased rapidly in recent years (Moyes *et al.*, 2017), and the extremely challenging or downright impossible task of finding and treating all mosquito breeding sites. This has made the fight against mosquitoes increasingly difficult (Balkew *et al.*, 2006; Ranson and Lissenden, 2016).

In addition to the insecticide resistance of mosquitoes, intensive and improper uses of many broad-spectrum currently marketed insecticides usually cause serious toxicological problems to all ecosystems including water, air and soil pollution (Haq *et al.*, 2004; Ibarra *et al.*, 2006; Tiryaki and Temur, 2010; Gunstone *et al.*, 2021). Also, synthetic insecticides drastically affect the natural enemies, allowing an exponential increase in pest population (Calvo-Agudo *et al.*, 2019; Demok *et al.*, 2019) and adversely affecting human health and domestic animals (Vattikonda and Sangam, 2017; Shahzad *et al.*, 2020) beside the accumulation of pesticide residues in food (Moustafa *et al.*, 2021). Additionally, conventional pesticides have negative impacts on both target and non-target organisms including birds, fish, amphibians, and earthworms (Gill and Garg, 2014). The widespread use of chemical pesticides could easily interfere with the normal physiological behavior of butterflies and bees, such as visiting flowers, foraging, pollination and other ecological functions (Williamson *et al.*, 2014; Xue *et al.*, 2014).

Taking these hazards and problems of insecticides into consideration, it is urgent to search for alternative agents to suppress the mosquito populations (Laznik and Trdan, 2012; Benelli *et al.*, 2016; Moyes *et al.*, 2017; Thomas, 2018; Achee *et al.*, 2019) and to avoid or minimize the insecticidal hazards on ecosystem components (Glare *et al.*, 2016; Roiz *et al.*, 2018). These alternatives should be effective, eco-environmentally safe, cheap, and reliable mosquito control strategies (Benelli, 2015; Jeffries and Walker, 2015; Yakob and Walker, 2016; Liao *et al.*, 2017; Kunbhar *et al.*, 2018) and targeting the aquatic immature stages and adults (Wilke and Marrelli, 2012; Dahmana and Mediannikov, 2020). Also, they should be effective at low concentrations (Walkowiak *et al.*, 2015).

One of these effective alternatives to synthetic insecticides is biocontrol

agents. During the last few decades, biological control of mosquitoes received a great research attention in the world (Platzer, 2007; Abagli *et al.*, 2019; Edmunds *et al.*, 2021) as environmentally friendly agents to control mosquito vectors (Liu *et al.*, 2020; Kendie, 2020). Biocontrol agents are highly promising because they are safe for humans and the environment (Amutha *et al.*, 2021), as well as they have little or no effect on other non-targeted organisms (Jagodič *et al.*, 2019). However, there are several different biological control approaches: killing the mosquito vector, changing vector behavior to increase self-fatality, and producing vectors that are either sterile or unable to transmit diseases (Benelli *et al.*, 2016). Moreover, these diverse biocontrol approaches influence different developmental stages of the vector (Benelli *et al.*, 2016; Kendie, 2020). Several pests have been successfully targeted and suppressed by biocontrol agents, such as parasitoids, predators and pathogens (Scholte *et al.*, 2004; Cameron and Lorenz, 2013; Chaudhary *et al.*, 2017).

Microbial control is a type of biological control using entomopathogenic microorganisms. This approach has been applied throughout the world with great advantage and success (Butt *et al.*, 2001). Because microbial biocontrol agents have complex modes of action, it is very difficult for a pest to develop resistance against them (Khan *et al.*, 2012). Various microbial control agents, such as nuclear polyhedrosis viruses, entomopathogenic bacteria, entomopathogenic fungi, entomopathogenic nematodes and protozoa, have been assessed for the control of several pests as an alternative to the synthetic insecticides (Regis *et al.*, 2001; Scholte *et al.*, 2007; Halouane *et al.*, 2013; Cameron and Lorenz, 2013; Cardoso *et al.*, 2015; Alkhaibari *et al.*, 2016). Additional strategies aim at identifying natural symbionts of mosquitoes and either alter them genetically to express anti-pathogen effectors or disrupt their natural symbiosis with the insect host (Coutinho-Abreu *et al.*,

2010; Ramirez *et al.*, 2014; Kean *et al.*, 2015; Saraiva *et al.*, 2018 a, b).

It may be important to shed some light on the entomopathogenic fungi, entomopathogenic bacteria and entomopathogenic viruses in the following few paragraphs. Fungus species that are used for controlling the majority of mosquito vectors belong to the genera *Beauveria*, *Coelomomyces*, *Metarhizium*, *Culicinomyces*, *Entomophthora* and *Lagenidium* for their mosquitocidal activities (Sritabutra and Soonwera, 2013). Fungal preparations can be used for indoor house services and outdoor traps (Tawatsin *et al.*, 2006). Also, entomopathogenic fungi can be used for insecticide-resistant mosquitoes. These fungi produce infective spores (conidia) that attach to and penetrate the cuticle of mosquitoes, releasing toxins that result in mosquito death (Scholte *et al.*, 2004).

Fungal treatments have been reported to adversely affect the fitness conditions, behavior and feeding habits of the mosquito vectors (Chandra *et al.*, 2008). The use of *Metarhizium* against mosquitoes induces the production of anti-malarial peptides, obstructing the communication of the malarial parasite from the vector (Iturbe-Ormaetxe *et al.*, 2011). If the mosquito develops resistance against the fungi, it will be temporary because weak selection for this resistance would occur (Pattanayak and Dhal, 2000). Some authors (Noskov *et al.*, 2019; Lovett *et al.*, 2019) reported that none of these fungi have been specifically adapted as larvicidal agents against important vector species while other authors (Achee *et al.*, 2019; Lee *et al.*, 2019) reported the efficiency of *Beauveria bassiana* and Ascomycete fungi against *Ae. albopictus* and *Cx. pipiens* mosquito adults. Also, many other fungus species infect and kill mosquitoes at the larval stage (Scholte *et al.*, 2004). In addition, *Metarhizium anisopliae* has the potential to be a biological control agent for *Cx. pipiens* and it is an appropriate candidate for further study and development (Benserradj and

Mihoubi, 2014). Some studies documented the pathogenic effect of fungi on malaria mosquito vectors (Blanford *et al.*, 2005; Knols *et al.*, 2010) and on *Ae. aegypti* (Paula *et al.*, 2011a, b; Darbro *et al.*, 2012).

Mosquitocidal bacteria are reported as environmentally friendly alternatives to synthetic pesticides for controlling mosquito vectors. Therefore, great efforts have been made to identify new mosquitocidal bacteria within the natural ecosystem (Poopathi *et al.*, 2014). For controlling the mosquito vectors, like the malarial vector, *Bacillus sphaericus* (*Bs*) and *Bacillus thuringiensis* (*Bt*) can be used because they are highly effective, exert selective effects and are non-toxic in nature (Kayedi *et al.*, 2014). As compare to the *Aedes*, *Culex quinquesfasciatus* and *An. arabiensis*, the effect of *Bs* and *Bt* is more on *An. gambiae* (Chandra *et al.*, 2008; Singh *et al.*, 2012). *Bs* and *Bt* cause the production of the endotoxin proteins that damage the stomach of larvae leading to death (Ogoma *et al.*, 2012). Currently, *Bacillus thuringiensis* var. *israelensis* (*Bti*) is the most common mosquito larvicide employed in European countries. Application of *Bti* has been used to reduce the number of larvae of *Ae. aegypti* (Armengol *et al.*, 2006; Ritchie *et al.*, 2010) and *Ae. albopictus* (Lam *et al.*, 2010).

Concerning the entomopathogenic viruses, there are many groups capable of causing diseases in mosquitoes but only four major groups may be used, including baculoviruses, cytoplasmic polyhedrosis viruses, densovirus and iridovirus (Becnel and White, 2007; Huang *et al.*, 2017). Although thousands of entomopathogenic viruses that are active against insect pests have been described, only very few are commercially accessible (Pirali-Kheirabadi, 2012). Recently, there has been a great research development in the ability to transmit baculoviruses and cypoviruses to mosquitoes with the finding that transmission is mediated by divalent cations (Becnel, 2006).

Although the available literature contains many reviews for the microbial control of mosquitoes, entomopathogenic nematodes (EPNs) received little attention (Benelli *et al.*, 2016; Huang *et al.*, 2017) although they have broad potential to kill the soil-dwelling insect pests and other above-ground insects which have soil-dwelling stages, in addition to mosquitoes (Laznik and Trdan, 2011; Lacey and Georgis, 2012; James *et al.*, 2018; Du Preez *et al.*, 2021). Therefore, the main objective of the present review was to follow up the available research publications focusing on the EPNs as recent biocontrol agents against different mosquito vectors. This review described also some of the main control strategies for mosquito vectors and highlighted the use of the most efficient EPN families against mosquito vectors. In addition, this review discussed the main immune interactions between the mosquito hosts and the invading EPNs. Finally, it provided some research priorities and future prospects for the control of mosquito vectors by EPNs.

1. Entomopathogenic Nematodes and Their Role in Insect Pest Control: Basic Knowledge:

1.1. General Outline:

Nematodes are colorless non-segmented, elongated roundworms (Sikandar *et al.*, 2019) classified in phylum Nematoda. They have no appendages and are usually microscopic in size (Adams and Nguyen, 2002). They have no circulatory or respiratory systems (Sikandar *et al.*, 2020b). Nematodes can be termed according to the habitat in which they are found, like free-living marine and freshwater, soil, saprophytes, parasitizing plants, microphagous or animals (Gaugler, 2002). In nature, terrestrial nematodes are soil-dwelling attacking insect pests that live in, on, or near the soil surface (Vashisth *et al.*, 2013). In addition, there is an order Mermithida including Mermithidae (aquatic nematoda) (Poinar, 2001; Keiser *et al.*, 2005; Shamseldean *et al.*, 2007).

Geographically, nematodes can inhabit almost all around the world with different climatic conditions and in almost all types of ecosystems and biomes, such as cultivated fields, forests, grasslands, deserts and even on beaches or in the ocean (Hominick, 2002; Devi and Nath, 2017; Aashaq *et al.*, 2020). They may be parasitic, predaceous, or free-living and have an abundance of various associations from useful to harmful (Ferris *et al.*, 2012). The non-beneficial nematodes are also called "plant parasitic nematodes" and cause damage to crops and other plants. Beneficial nematodes attack soil-borne insect pests and other insects (Denno *et al.*, 2008; Abbas, 2020). Depending on their association, they can be divided into four basic groups; facultative parasitism, obligate parasitism, necromenic and phoretic (Askary *et al.*, 2018). Beneficial nematodes are those that cause diseases within an insect or death. They are known as "Entomopathogenic Nematodes" (EPNs) (order: Rhabditida). They have been recorded on all continents except Antarctica (Adams *et al.*, 2006; Abate *et al.*, 2017).

Systematically, phylum Nematoda has five orders including 14 families of obligate parasites. Some of these EPNs are significantly interested because of their potential as biological control agents. The mermithid EPNs (aquatic beneficial nematodes) have been found in natural populations of mosquitoes (Platzer, 1981). In addition to Mermithidae, eight important nematode families, such as Allantonematidae, Diplogasteridae, Heterorhabditidae, Neotylenchidae, Rhabditidae, Sphaerulariidae, Steinernematidae and Tetradonematidae, include species that attack, kill, and sterilize insects, or alter host growth, development and physiology (Petersen, 1985; Piralikheirabadi, 2012b). On the other hand, many authors (Lacey and Georgis, 2012; Vashisth *et al.*, 2013; Sujatha and Jeyasankar, 2018) reported almost 40 nematode families of EPNs in association with insects, but not all cause host mortality

and only 23 of these families include species described as EPNs and widely available in the world for using as biological control agents against many insect pests (Lacey *et al.*, 2001; Stock and Hunt, 2005; Griffin, 2012). However, a total of 86 species of EPN have been identified worldwide: 64 belonging to *Steinernema*, one to *Neosteinernema*, and 21 to *Heterorhabditis* (Kepenekci, 2014). Some authors (Hunt, 2016; Bhat *et al.*, 2020) reported that *Steinernema* (100 species) and *Heterorhabditis* (16 species) are found globally in diverse geographical regions.

Economically, EPNs have a considerable ability to infect and kill soil insects but are not harmful to animals, plants, or earthworms (Shapiro-Ilan *et al.*, 2006) and exhibit negligible effects on non-target insects (Zolfagharian *et al.*, 2016; Sujatha and Jeyasankar, 2018; Kumar *et al.*, 2022; Peçen and Kepenekci, 2022). They are regarded as exceptionally safe for the environment and pollinators (Akhurst and Smith, 2002; Lewis *et al.*, 2006; Sujatha and Jeyasankar, 2018). Unlike chemical insecticides, EPNs are target-specific with a wide range of insect pests (Ehlers, 2003; Odendaal *et al.*, 2015; Devi and Nath, 2017). Despite widespread use in fields, gardens, and pasture lands, no significant acute or chronic toxicity to humans or vertebrates has been reported (Akhurst and Smith, 2002; Jagodič *et al.*, 2019).

Also, EPNs have high reproductive potential, the ability to kill hosts quickly, high virulence and a broad host range (Kaya and Gaugler, 1993). EPNs can be easily mass-produced (Yağci *et al.*, 2021a, b). Importantly, EPNs can be easily applied using common irrigation and pesticide equipment (Grewal *et al.*, 2001; Shapiro-Ilan *et al.*, 2012). EPNs can be used individually or in combination with other biocontrol agents, such as entomopathogenic bacteria and entomopathogenic fungi in order to improve their efficacy in controlling insect pests (Laznik *et al.*, 2012). Therefore, EPNs have been reported since the 1980s to

be effective biocontrol agents for managing many insect pests of crops including those living on foliar, soil surface and cryptic or subterranean habitats (Lacey and Georgis, 2012; Cooper and Eleftherianos, 2016; Abate *et al.*, 2017; Labaude and Griffin, 2018; Abd-Elgawad, 2019; San-Blas *et al.*, 2019) as well as those insect pests spending a part of their life cycle inside the soil or cryptic habitats (Laznik and Trdan, 2011; Shaurub *et al.*, 2016; James *et al.*, 2018; Nouh, 2022). For these reasons, EPNs have attracted much interest globally to study their distribution, virulence, and usage in integrated pest management (IPM) programs (Çağlayan *et al.*, 2021; Ali *et al.*, 2022). For more details, see Vashisth *et al.* (2013), Sujatha and Jeyasankar (2018), Jagodič *et al.* (2019); Askary and Abd-Elgawad (2021); Kumar *et al.* (2022) and Shaurub (2023).

Recently, commercial preparations of EPNs and EPN-based products have already been available in different countries (Gaugler *et al.*, 2000; Shapiro-Ilan and Gaugler, 2002; Ehlers, 2003; Shapiro-Ilan *et al.*, 2012, 2014; Ehlers and Shapiro-Ilan, 2005; Askary *et al.*, 2017; Caoili *et al.*, 2018). In some countries, commercial EPN-based products and EPN-symbiotic bacteria products have already been incorporated into IPM programs for some agricultural insect pests (Dolinski *et al.*, 2012). The EPN products are marketed under various brands, in developing countries of the world (for review, see Sikandar *et al.*, 2021).

1.2. Life Cycle of EPNs:

The life cycle of EPNs can be divided into five distinct phases: (1) penetration into the haemocoel of the potential insect host, (2) recovery into the haemolymph, (3) development to mature stage and reproduction, (4) production of new infective juveniles, and (5) host searching and host acceptance by the infective juveniles (Forst and Clarke, 2002). As reported in the available literature, some families of EPNs, such as Steinernematidae, Heterorhabditidae and Rhabditidae, have a life cycle including the egg stage, four

juvenile stages and the adult stage (Poinar, 1990; Kaya and Gaugler, 1993; Shapiro-Ilan, 2009; Shapiro-Ilan and Gaugler, 2019). The 3rd juvenile stage (J3) is known as the "infective juvenile stage (or infective juveniles, IJs)", or "dauer" stage which is the only free-living stage and can survive a long time without feeding (Koppenhöfer *et al.*, 2000). A common feature of *Heterorhabditis* and *Steinernema* EPNs, IJs harbor the mutualistic *Photorhabdus* and *Xenorhabdus* bacteria, respectively (Ciche, 2007). At this stage, the EPNs do not feed but instead focus on dispersal throughout the soil searching for host species (Poinar, 1990; Shapiro-Ilan *et al.*, 2017).

According to their searching behavior for hosts, EPNs have been divided into two categories including cruisers and ambushers. Cruisers such as *Heterorhabditis bacteriophora* and *Steinernema glaseri* are subterranean, and more active in finding suitable hosts, while ambushers, like *Steinernema carpocapsae*, usually wait to attack suitable hosts in the upper surface of the soil (Mohan, 2015; Lewis *et al.*, 2006; Lortkipanidze *et al.*, 2016; Hussaini, 2017). They can allocate their host in different ways, like vibration, CO₂, or other chemicals (Lortkipanidze *et al.*, 2016; De Brida *et al.*, 2017). They showed significant potential as natural pest control agents in the soil environment (Du Preez *et al.*, 2021, 2022).

It is well known now that IJs invade the host's body cavity through natural openings, such as the mouth, anus, or spiracles; or, in some cases, directly through the intersegmental membranes and other delicate areas of the thin cuticle of certain insects (Griffin *et al.*, 2005; Atwa, 2014; Gozel and Gozel, 2016; Ávila-López *et al.*, 2021). In the case of *Heterorhabditis*, their entry is done with the help of a cuticle projection resembling a tooth since some authors (Peters and Ehlers, 1997; Nguyen *et al.*, 2006) even speak about a dorsal tooth. Also, Dowds and Peters (2002) reported that these IJs may disrupt the cuticle of insect hosts using a dorsal tooth in the

anterior region of their head, or by secreting enzymes that promote tissue breakdown. Then, they penetrate into the haemocoel cavity of the host from its gut (Fetoh *et al.*, 2009; Triggiani and Tarasco, 2011).

In the host haemocoel, IJs release specialized symbiotic bacteria within the haemolymph. These bacteria then convert the internal contents of the insect into a "nutrient soup" for easy feeding and multiplication by the EPNs and produce a range of antibiotics to prevent putrefaction of the host cadaver (Hazir *et al.*, 2003; Chaston *et al.*, 2011). These bacteria grow rapidly and proliferate in the insect haemocoel and produce toxins eventually inducing septicemia for killing the insect host usually within 24-72 hours post-infection (Ehlers, 2001; Griffin *et al.*, 2005). The invading EPNs feed on the digested host tissues and reproduce for two or three generations, depending on the availability of food resources and the size of the host (San-Blas *et al.*, 2008). When the food is depleted or the host resources diminish, higher concentrations of CO₂ and NH₃ signal the EPN to produce IJs which leave the host and disperse back into the soil searching for new hosts, continuing the life cycle (Chaston *et al.*, 2011; Mahmoud, 2016).

Moreover, emergence of IJs from the host cadaver requires about 6–11 days in the case of *Steinernematidae* and 12–14 days in the case of *Heterorhabditidae* (Kaya and Koppenhöfer, 1999; Geisert *et al.*, 2018). The IJs complete their development and reproduce for two or three generations inside their host, depending on their size (Cruz-Martínez *et al.*, 2017). In the case of *Steinernema* spp., the first generation develops into males and females, while in *Heterorhabditis* spp. the first-generation nematodes are hermaphrodites (Griffin *et al.*, 2005). For more details on the biology and ecology of EPNs, see Dembilio *et al.* (2010); Triggiani and Tarasco (2011); Koppenhöfer *et al.* (2020) and Sikandar *et al.* (2021).

1.3. Mechanism of the Insect Death by EPNs:

In general, the virulence of EPNs against the insect host results from their ability to find the host, invade it and, in cooperation with symbiotic bacteria, overcome its immune response and kill it (Grewal and Peters, 2005). When IJs of EPNs become inside the insect haemocoel, they release their symbiotic bacteria. The subsequent death of the insect is mainly due to bacteria-induced septicemia in the late phase of infection (Ffrench-Constant *et al.*, 2007a,b). As for example, the mutualistic bacteria *Xenorhabdus*, symbiotic to *Steinernema*, and *Photorhabdus*, symbiotic to *Heterorhabditis*, are released to kill the host within about two days (Gaugler, 2002; Griffin, *et al.*, 2005; Kaya *et al.*, 2006). Thus, mutualistic association of *Steinernema* and *Heterorhabditis* with their symbiotic bacteria is found to be the primary cause of insect mortality (Leonar *et al.*, 2022).

For some detail, a successful infection of an EPN is subjected to interactions with the host, which can culminate in the unaffected growth and reproduction of the EPN inside the insect body (Castillo *et al.*, 2011; Toubarro *et al.*, 2013). In addition to the action of bacteria, physiological interactions between the EPN and its host must be considered, since the life-cycle of an endoparasite is strongly related to its ability to evade and/or suppress the host immune responses in the early phase of infection. Also, symbiotic bacteria contribute to overcoming the insect immune system resulting in the death of the insect within 24-48 hours post-infection (Adams and Nguyen, 2002). This suppression of the host immune system is a prerequisite process for successful infection of EPNs (Lewis and Clarke, 2012; Shapiro-Ilan and Brown, 2013; Lacey *et al.*, 2015; Kaliaskar *et al.*, 2022).

In this context, it may be important to take a closer look at the immune interaction between EPN and its insect host. Once the IJs have entered the insect

haemocoel cavity, the symbiotic bacteria are released and try to suppress the insect defences (Shi *et al.* 2012) by producing a mixture of molecules responsible for modulation of the host immune system (Bode, 2009; Liao *et al.*, 2017), resulting in the death of the insect host. In addition, these bacteria multiply and produce a diverse group of components, such as bacteriocins, antibiotics, antimicrobials and a scavenger-deterrent compound that suppresses the growth of antagonistic microorganisms to provide a safe niche (Rodou *et al.*, 2010; Chaston *et al.*, 2011), and breaks down the host tissue causing the death of the host (Ffrench-Constant *et al.*, 2007a,b; Devi and Nath, 2017).

On the other side, EPNs are able to secrete insecticidal active substances, including toxins and proteases, contributing to the lethal effect on infected host insects (Gaugler, 2002; Toubarro *et al.*, 2009). Results of numerous studies revealed that IJs of the EPN *Steinernema feltiae* use their cuticle to block the immune defences of the host (Brivio *et al.*, 2004). Furthermore, the delayed activation of phenoloxidase in the insect host is a criterion of humoral immune defense (Song *et al.*, 2011). Another point of interest in this respect is the act of EPNs themselves because they must neutralize a complex series of adverse immune reactions of the host (Brivio *et al.*, 2005, 2010). Some research works confirmed that EPNs can survive and in the case of the steinernematid species, even kill their host, without mutualistic bacteria (Han and Ehlers, 2000; Sicard *et al.*, 2003).

In other words, EPNs suppress the host immune system early in infection causing it to tolerate not only EPNs but also their endosymbiotic bacteria until the host succumbs to infection (Toubarro *et al.*, 2013). Shortly after infection, and before the bacteria is released from the gut of EPN, there is a considerable reduction in total hemocytes in the insect haemocoel, suggesting that EPN itself is capable of suppressing the host immune system, to the benefit of its endosymbiotic bacteria (Abd

El-Aziz and Awad, 2010; Gabarty, 2011; Shaurub *et al.*, 2014; Bobardt *et al.*, 2020). Therefore, the success of EPNs for insect control depends on their stress potential and capability to impair certain physiological processes and biochemical constituents of the insect hosts.

Over the past two decades, there has been increasing evidence that some EPNs influenced certain metabolic processes (Shaurub *et al.*, 2020; Ghoneim *et al.*, 2022) and some important enzymatic activities (Abdel-Razek *et al.*, 2004; Shaurub *et al.*, 2015; Ibrahim *et al.*, 2015; Shairra *et al.*, 2016; Vidhya *et al.*, 2016; Ghoneim *et al.*, 2023b). However, the potential role of the EPN-symbiotic bacteria in the biocontrol of insect pests will be discussed in some detail under the subtitle "EPN-symbiotic bacteria and their potential role for the control of mosquito vectors" in the present review. Also, it may be necessary to describe the major components of the immune system in insects and their immune defenses of different types against the invading EPNs under the subtitle "Suppressive activity of EPN/symbiotic bacteria complex against innate immune defences of mosquito larvae" in this review.

2. Increasing Global Attention to the EPN Application as A Novel Strategy for Combating Mosquito Vectors:

Many nematodes belonging to numerous orders and families are known to be parasites of insects (Poinar, 2018). Over the past decades, EPNs have great global attention in the field of biocontrol of serious agricultural insect pests (Trdan *et al.*, 2007; Laznik *et al.*, 2010; Davari and Parker, 2018; Trdan *et al.*, 2020; Sikandar *et al.*, 2020a). For instance, EPNs of the genera *Steinernema* (Steinernematidae) and *Heterorhabditis* (Heterorhabditidae) provide an environmentally safe and economic alternative against a variety of serious insect pests and some of them could be used commercially for biocontrol (Cagnolo *et al.*, 2010; Mbata and Shapiro-Ilan, 2010; Yan *et al.*, 2013; Zadji *et al.*, 2013). However, relatively few studies

were conducted to investigate the effectiveness of EPNs against mosquitoes (Poinar and Kaul, 1982; Molta and Hominick, 1989; Cagnolo and Almirón, 2010). By that time, EPNs have attracted much attention from researchers and research institutions worldwide as effective and safe biocontrol agents for suppressing mosquito populations (Abagli *et al.*, 2012).

Historically, Welch (1961); Welch and Bronskill (1962), Dadd (1971), and Poinar and Kaul (1982) were the pioneers of studying the potential of EPNs and their symbiotic bacteria against mosquitoes. Welch (1961) was the first to test EPNs for controlling populations of *Aedes* spp., including the yellow fever mosquito *Aedes aegypti*, in laboratory and field. According to his results, larval population and adult emergence had been reduced by the application of EPN *S. carpocapsae*. Also, early studies indicated that 3rd and 4th larval instars of mosquitoes readily ingest EPN infective juveniles (IJs). Most IJs are injured by larval mouthparts, but some enter the haemocoel and overcome the insect's defenses, causing mortality (Daad, 1971; Poinar and Kaul, 1982; Molta and Hominick, 1989).

Some years later, the study of Pandii *et al.* (2008) showed that EPN *S. carpocapsae* was effective as bio-control against 3rd and 4th larval instars of the frosty mosquito *Culex gelidus* under laboratory conditions. Also, a laboratory colony of the mosquito *Culex apicinus* was parasitized by the terrestrial EPN *Steinernema rarum* (Cagnolo and Almirón, 2010). Moreover, many studies have demonstrated the efficacy of EPNs *Steinernema* spp. and *Heterorhabditis* spp., isolated from different countries, against larvae of different mosquito species including *Ae. aegypti* and the common house mosquito *Culex pipiens* (Cagnolo and Almirón, 2010; Peschiutta *et al.*, 2014; Chaudhary *et al.*, 2017; Toksoz and Saruhan, 2018; Edmunds *et al.*, 2020). In Egypt, Zohdy *et al.* (2013) recorded that the EPN *Heterorhabditis bacteriophora* killed the southern house

mosquito *Culex quinquefasciatus* faster than *Steinernema* species.

In addition, various authors have reported a dramatic reduction of larval density following the release of the mermithid nematode *Romanomermis iyengari* in countries such as Cuba and Mexico (Pérez-Pacheco *et al.*, 1998; Santamarina *et al.*, 1999; Santamarina and Bellini, 2000; Pérez-Pacheco *et al.*, 2004, 2005). Also, several assays were carried out using different mermithid spp. against larvae of *Ae. aegypti* and other mosquito species (Santamarina *et al.*, 2000; Achinelly *et al.*, 2004, Achinelly and Micieli, 2012; Sanad *et al.*, 2013). In Brazil, the laboratory assays of Cardoso *et al.* (2015) revealed the potential of the EPN *Heterorhabditis indica* LPP35 to be used as an agent for biocontrol of 3rd and 4th instar larvae of *Ae. aegypti*.

Some authors (Abagli and Alavo, 2019; Dahmana and Mediannikov, 2020) reported that EPNs are naturally adapted to their hosts, such nematodes are highly specific to their hosts, which they can kill by producing high levels of parasitism. They are free swimming and disseminate easily in the infective stage and species, such as *R. iyengari*, are widely suggested to be a component of integrated mosquito control programmes in lymphatic filariasis endemic countries. Also, many authors (Paily and Balaraman, 2000; Abagli *et al.*, 2012; Lacey *et al.*, 2015) demonstrated the effectiveness of different EPNs against malaria vectors and several other important mosquito species, such as *Ae. aegypti*, the Asian tiger mosquito *Aedes albopictus*, *Cx. quinquefasciatus*, and the African malaria mosquito *Anopheles gambiae*. Abagli *et al.* (2019) evaluated the effectiveness of *R. iyengari* for the control of *An. gambiae* using the pre-parasitic stage (J2) for laboratory and field experiments. In field experiments, separate natural *Anopheles* breeding sites were sprayed with concentrations of 3500, 4000 and 5000 J2/m². The larval density of mosquitoes was dramatically reduced five days after the first treatment in all treated breeding sites. Also,

larval density was maintained at a very low level during the whole experimental period.

According to Liu *et al.* (2020), larval mortality (about 90%) of *Ae. albopictus* was caused by EPN *Steinernema abbasi* isolate within 72 h which was similar to that exhibited by *S. carpocapsae* in an aquatic environment of mosquitoes. Therefore, the *S. abbasi* isolate when

applied to larvae of *Ae. albopictus* can be a potential biocontrol agent for managing this vector mosquito in water. However, many studies have demonstrated the effectiveness of various EPNs for mosquito control in different countries of the world indicating the increasing attention to these potential biocontrol agents (see Table 1).

Table 1. Some global efforts to use EPNs as biocontrol agents against different mosquito species in the world.

Tested EPN	Targeted mosquito	Country	Reference
<i>Romanomermis culicivorax</i> and <i>R. iyengari</i>	<i>Anopheles</i> spp., <i>Culex</i> spp.	Tajikistan	Vladimirova <i>et al.</i> (1990)
<i>R. iyengari</i>	<i>Anopheles</i> spp.	Uzbekistan	Pridantseva <i>et al.</i> (1990)
<i>R. iyengari</i>	<i>Anopheles sacharovi</i> and <i>Culex theileri</i>	Azerbaijan	Alirzaev <i>et al.</i> (1990)
<i>R. iyengari</i>	Ten species from five genera	India	Paily and Balaraman (2000)
<i>R. yunanensis</i>	<i>Culex</i> spp.	China	Peng <i>et al.</i> (1998)
<i>Steinernema</i> spp. and <i>Heterorhabditis</i> spp.	<i>Ae. aegypti</i> , <i>Ae. albopictus</i> , <i>Cx. quinquefasciatus</i>	Thailand	Ardpairin <i>et al.</i> (2023)
<i>Strelkovimermis spiculatus</i>	<i>Culex pipiens</i>	Iran	Allahverdipour and Talaei-Hassanloui (2017)
<i>R. iyengari</i>	<i>Anopheles</i> spp.	Cuba	Santamarina <i>et al.</i> (1992)
<i>R. iyengari</i>	<i>An. pseudopunctipennis</i>	Mexico	Santamarina <i>et al.</i> (1999)
<i>R. iyengari</i>	<i>An. pseudopunctipennis</i>	Mexico	Mijares <i>et al.</i> (1999)
<i>R. iyengari</i>	<i>An. pseudopunctipennis</i>	Mexico	Pérez-Pacheco <i>et al.</i> (2005)
<i>R. culivorax</i>	<i>Aedes aegypti</i>	Mexico	Santamarina <i>et al.</i> (2000)
<i>R. culicivorax</i>	<i>An. albimanus</i>	Nicaragua	Mendoza <i>et al.</i> (2014)
<i>R. iyengari</i>	<i>An. albitarsis</i> , <i>An. rondoni</i>	Brazil	Santamarina and Bellini (2000)
<i>S. spiculatus</i>	different mosquito species	Argentina	Achinelly and Micieli (2012)
<i>Heterorhabditis bacteriophora</i>	<i>Cx. pipiens</i>	Argentina	Poinar and Kaul (1982)
<i>S. spiculatus</i>	<i>Ae. albifasciatus</i>	Argentina	Poinar and Camino (1986)
<i>Steinernema rarum</i>	<i>Cx. apicinus</i>	Argentina	Cagnolo and Almirón (2010)
<i>R. culicivorax</i>	<i>Anopheles</i> spp.	Colombia	Rojas <i>et al.</i> (1987)
<i>R. culicivorax</i>	<i>Anopheles albimanus</i>	Cuba	Santamarina and Perez Pacheco (1997)
<i>R. iyengari</i> and <i>S. spiculatus</i>	<i>Ae. albopictus</i>	Cuba	Díaz <i>et al.</i> (2018)
<i>R. culicivorax</i>	<i>An. albimanus</i>	El Salvador	Willis <i>et al.</i> (1980)
<i>Steinernema</i> spp. and <i>Heterorhabditis</i> spp.	<i>Ae. aegypti</i> and <i>Ochlerotatus detritus</i>	United Kingdom	Edmunds <i>et al.</i> (2021)
<i>R. iyengari</i>	<i>Cx. pipiens</i>	Egypt	Elbrenseet <i>et al.</i> (2022)
<i>Steinernema scapterisci</i>	<i>Cx. pipiens</i>	Egypt	Sayed <i>et al.</i> (2018)
<i>R. culicivorax</i>	<i>An. quadrimaculatus</i>	Egypt	Shamseldean <i>et al.</i> (2006)
<i>H. bacteriophora</i> and <i>S. carpocapsae</i>	<i>Cx. quinquefasciatus</i>	Egypt	Zohdy <i>et al.</i> (2013)

<i>R. iyengariis</i>	<i>An. gambiae</i>	Benin	Abagli <i>et al.</i> (2012)
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3. Pathogenic Efficiency of Family Mermithidae (Aquatic Epns) Against Various Mosquito Vectors:

Nematodes of the order Mermithida (phylum Nematoda, class Adenophorea) parasitize arthropods and snails and some other invertebrates. This order comprises both terrestrial and aquatic species. Adults are a few-millimeter or at most a few centimeter-long, thread-like in shape (Petersen, 1985; Platzer, 2007). They are obligate parasites of arthropods, mainly insects, but have also been found in spiders, crustaceans, earthworms, leeches, and mollusks (Kendie, 2020). Numerous mermithids have been found in mosquitoes on every continent except Antarctica (Blackmore *et al.*, 1993; Vythilingam *et al.*, 2005). As shown in the available literature, Mermithidae is one of three nematode families that are well-studied in the world for controlling mosquito populations (Poinar, 2001; Keiser *et al.*, 2005; Platzer, 2007; Bisen and Raghuvanshi, 2013).

3.1. Life Cycle of Mermithidae and Their Mechanism of the Host Death:

Eggs of aquatic mermithids are deposited in the external environment and the newly hatched pre-parasites (2nd stage infective juveniles, IJ) search for hosts. They infect their hosts *via* infiltration of the cuticle, invasion through spiracles or anus, or after ingestion by the host insect (Pirali-Kheirabadi, 2012b). For some detail, Shamseldean and Platzer (1989) reported that the mermithid pre-parasites use a needle-like stylet to inject "venom" into the host haemocoel to initiate the infection. This causes an inhibition of the host heart rate and a concurrent temporary paralysis which facilitates nematode entry *via* a cuticular wound. Although the host immune system rapidly recognizes and encapsulates many invading mermithids, these mermithids secrete an extracellular surface coat which aids in immune evasion. This coat serves as a disposable, renewable

barrier between parasite and host that is intermittently shed to cleanse the nematode of adhering host immune products (Shamseldean *et al.*, 2006).

Unlike insect parasitoids of which the ovipositing females take infection decisions, pre-parasitic juveniles of Mermithidae must take the decision whether to penetrate and infect an already parasitized host. A single pre-parasite can inspect a host to identify earlier conspecific parasitism and what is the impact of superparasitism on the parasite and host. These critical questions might be answered by a study by Sanad *et al.* (2017).

Then, the pre-parasites develop in the haemocoel of mosquito larva and escape from it as post-parasitic juveniles through mechanical rupture of the integument, forcing their way out of the larvae and in the process killing them (Platzer, 2007). These post-parasitic juveniles then undergo two additional moults to transform into adults, and burrow into the moist substrate at the bottom of their aquatic habitat (Shamseldean *et al.*, 2007). After copulation, the gravid females lay eggs in the soil. After finishing the embryogenesis in eggs, they hatch when submerged in water (Platzer, 2007). The killing behavior of these mermitid species seems an inevitable part of their life cycle (Platzer, 1981). Mosquito death upon its emergence has sparked interest in using mermithids as biological control agents (Platzer, 2007). In addition, sex determination in mermithids has been done within the host post-infection and it is dependent on the EPN density. Sex ratios are female-biased at low parasite loads and male-biased at high parasite loads. Superparasitism in mermitid EPNs is essential for male production because single infections invariably produce a female (Sanad *et al.*, 2013).

3.2. The Most Important Identified Species of Mermithidae:

Until 2001, seven genera of Mermithidae were detected in the bodies of mosquito larvae all over the world, *viz.*, *Culicimermis*, *Empidomermis*, *Hydromermis*, *Octomyomermis*, *Perutilimermis*, *Romanomermis* and *Strelkovimermis* (Poinar, 2001). There are at least 25 species worldwide that belong to these genera (Blackmore, 1994). According to the available literature, the mermithid species that have gained more attention in research are *Romanomermis culicivorax*, *Romanomermis iyengari*, *Romanomermis yunanensis*, *Romanomermis wuchangensis* and *Strelkovimermis spiculatus*. Based on the available literature, also, the most attracting species to the research attention are *R. culicivorax* and *R. iyengari*. These two species have gained great interest for the control of mosquito breeding in different types of habitats, such as larvae of mosquitoes *Culex* and other genera (Pérez-Pacheco *et al.*, 2004; Keiser *et al.*, 2005).

The mermithid nematode *R. culicivorax* is a temperate-zone species and was found effective in rice fields, lakes and ponds (Santamarina and Perez, 1997). Mosquito-parasitic mermithids, particularly *R. culicivorax*, have been field-tested successfully against different culicidal mosquitoes (Platzer *et al.*, 2005). It can be used by over 90 different mosquito species as a host (Bisen and Raghuvanshi, 2013). It has received intensive study of their pathogenicity, ecology, mass production, specificity and biology (Platzer, 2007).

Another mosquito-parasitic mermithid that was examined for biological control is *R. iyengari*. It is one of several species of EPNs that parasitize and kill mosquito larvae (Platzer, 2007). It is a tropical species originally indigenous to India (Gajanana *et al.*, 1978) and is successful in suppressing mosquito breeding in rice fields, grassland, and other natural habitats (Santamarina *et al.*, 1999; Santamarina and Bellini, 2000; Pérez *et al.*, 2005). Paily and Balaraman (2000) identified 10 species of mosquitoes, belonging to five genera, which were

susceptible to *R. iyengari*. Likewise, Pérez-Pacheco *et al.* (2015) examined the susceptibility of culicine mosquito larvae to *R. iyengari*. In laboratory experiments, Abagli *et al.* (2019) showed that all instar larvae of *Cx. quinquefasciatus* were susceptible to *R. iyengari* infection.

3.3. More Research Efforts to Use Mermithids against Mosquitoes in the World:

Because of a host range that includes mosquitoes of the public health vectors, several studies were carried out using mermithids against larvae of mosquitoes, such as *Culex* sp. and other genera (Santamarina, 2000; Achinelly *et al.*, 2004; Perez-Pacheco *et al.*, 2004; Trujillo-González *et al.*, 2021). Field releases have demonstrated the ability of mermithids to reduce mosquito populations (Perez-Pacheco *et al.*, 2005; Achinelly and Micieli, 2009; Abagli *et al.*, 2012). A comprehensive report or complete list of publications documenting the global efforts for assessing mermithid EPNs against different mosquito species could not be available. Therefore, it may be enough to give an insight into the following few works in different parts of the world.

Some mermithid species have been detected in the mosquito vectors, such as *Culex* spp. larvae in Finland (Levander, 1904), *Ochlerotatus hexodonus* larvae in Norway (Nielsen *et al.*, 1981), *Ochlerotatus communis* adults in Sweden (Blackmore, 1994) and *Ochlerotatus cantans* adults in Denmark (Nielsen, 2001). In Azerbaijan, Alirzaev *et al.* (1990) examined the effect of *R. culicivorax* and *R. iyengari* against the larvae of biting mosquitoes. Gerik *et al.* (1990) examined the effect of *R. culicivorax* on the biting mosquito species in Russia.

The mermithid *O. muspratti* was isolated from various *Aedes* and *Culex* spp. larvae from Zambia (Muspratt, 1945). Also, mermithids *Empidomermis cozii* and *Reesimermis (Octomyomermis) muspratti* have been discovered in different mosquito species in Africa (Coz, 1966). Subsequent mermithid colonies were established and *O.*

muspratti was found to be capable of parasitizing *Ae. aegypti*, *Anopheles polynesiensis*, *Cx. pipiens*, *An. stephensi*, and *An. albimanus* (Obiamiwe and MacDonald, 1973). Also, the mermithid *E. cozii* was found in *An. funestus* adults from Burkina Faso (Poinar, 1977).

Some years later, mass production of *R. iyengari* could be available. It was used as a cost-effective biocontrol agent against mosquitoes in sub-Saharan Africa (Kerry and Hominick, 2002; Platzer *et al.*, 2005). Sylla *et al.* (2010) and Kobylinski *et al.* (2012) documented the occurrence of numerous mermithids in the adult females of *Anopheles* spp. collected in southeastern Senegal. Abagli and Alavo (2019) evaluated the effectiveness of *R. iyengari* for control of *Cx. quinquefasciatus* in laboratory experiments and field experiments. All tested larval instars were susceptible to nematode infection. They concluded that *R. iyengari* could be easily used as a component of an integrated mosquito control program in lymphatic filariasis endemic countries. In the same year, Abagli *et al.* (2019) found the malaria mosquito larvae, *An. gambiae*, susceptible to *R. iyengari* infection in West Africa. Therefore, *R. iyengari* could be easily used as a component of integrated mosquito control programs in malaria-endemic countries (Alavo *et al.*, 2015).

The mermithid EPN *R. culicivorax* has been used to suppress malaria vector populations of *Anopheles freeborni* in California, USA (Brown-Westerdahl *et al.*, 1982). Also, *R. culicivorax* has been used to suppress malaria vector populations of *An. albimanus* and *An. pseudopunctipennis* in El-Salvador (Willis *et al.*, 1980), *An. albimanus* in Cuba (Santamarina and Perez, 1997), and *An. albimanus* in Colombia (Rojas *et al.*, 1987). The mermithid *R. iyengari* has been used to suppress malaria vector populations of *An. albimanus* in Cuba (Santamarina, 1994), *An. pseudopunctipennis* in Mexico (Santamarina *et al.*, 1999), and *An. salbitarsis* and *An. rondoni* in Brazil

(Santamarina and Bellini, 2000). Some years later, Díaz *et al.* (2018) carried out a study in Cuba to determine the sensitivity of three larval instars of *Ae. albopictus* to the infection of *R. iyengari* and *S. spiculatus*. Depending on their results, both EPN species proved to be good candidates as biocontrol agents of *Ae. albopictus*.

In Argentina, the mermithid *S. spiculatus* was found for the first-time infecting larvae of *Aedes (Ochlerotatus) albifasciatus* (Poinar and Camino, 1986). Later, this mermithid was isolated in natural habitats from the immature stages of five species of *Culex* and a few *Aedes (Ochlerotatus)* sp. and *Psorophora* sp. (Campos and Sy, 2003; Achinelly and Micieli, 2012; Di Battista *et al.*, 2015). Its pathogenic effect was assessed against larvae of *Cx. apicinus*, causing a 100% mortality of larvae (Achinelly *et al.*, 2004). Achinelly and Micieli (2012) demonstrated that this nematode infected some *Anopheles* spp., *Aedes* spp. and *Culex* spp. in laboratory bioassays. In a report by Lopez *et al.* (2016), the mosquito larvae of *Cx. eduardoi* was found as a new host of *S. spiculatus*.

3.4. Some Advantages and Disadvantages of Mermithidae as Biocontrol Agents For Mosquitoes:

As previously reviewed, the family Mermithidae contains species developing in insect pests ending in the host's death. Subsequently, these EPNs had several advantages making them promising biological alternatives to chemical insecticides in the fight against public health insect vectors, including biting mosquitoes (Platzer, 2007; Juliano, 2007; Stock and Goodrich-Blair, 2012; Paily *et al.*, 2013; Di Battista *et al.*, 2020).

Some of their advantages are: (1) they are obligate endoparasites of larvae belonging to at least 100 species of mosquitoes (Platzer, 2007). (2) they adversely affect particular growth stages of the host. (3) they are specialists and are usually specific to a single species or one or two families of insects (Abagli *et al.*, 2019; Kendie, 2020). (4) they produce high levels

of parasitism and they require only one victim/host to complete their life cycle. (5) they are capable of killing all infected hosts after suppressing their immune defenses before their transformation into adults. (6) They are easily handled (Petersen, 1973; Platzer, 2007). (7) they have a high reproductive potential. (8) they are aquatic and free swimming. (9) they can be distributed easily in the infective stage to control mosquitoes (Sáringar-Kenyeres *et al.*, 2017). (10) they have a considerable potential for practical methods of *in vivo* mass rearing and are able to laboratory manipulation of life history (Petersen *et al.*, 1978; Grewal *et al.*, 2001; Alavo *et al.*, 2015). (11) as previously mentioned, mosquito larvae are killed through mechanical rupture of their integument by the emerging parasitic life completed and hence, there is no chance of resistance development by the host (Paily *et al.*, 2013). (12) they pose little or no environmental risk. Because of their lifespan, they pose little threat of competitive displacement of other beneficial creatures (Petersen, 1985). (13) they are safe for non-target organisms including humans (Gajanana *et al.*, 1978). (14) they have characteristics of environmental friendliness and long-term sustainability, suggesting they may be widely used for the biological control of mosquito pests (Xiong *et al.*, 2021). (15) Mermithids have been applied to aquatic habitats as either pre-parasitic forms with a hand-operated spray pump (Petersen and Willis, 1972) or aerial spray pump (Levy *et al.*, 1979) and post-parasitic stages can be applied to moist soil prior to flooding (Brown-Westerdahl *et al.*, 1982; Kerwin and Washino, 1985). (16) The mermithid EPNs are also compatible with the use of chemical insecticides (Grewal *et al.*, 2001).

Although mermithids, such as *R. culicivorax* and *R. iyengari*, are natural parasites of mosquitoes and successfully infect and kill them, the use of EPNs warrants further investigation and precautions for application (Koylinski *et al.*, 2012). For example, the penetration of

mermithids, especially *Romanomermis* spp., into the body cavity of mosquito larvae should be taken into consideration for the development of biological control strategies (Sanad *et al.*, 2013).

In contrast to several advantages of mermithid EPNs, as biocontrol agents of mosquito vectors, their major disadvantages should be known before application. It has proven difficult to commercialize these nematodes because their viability is difficult to maintain in storage and transportation (Huang *et al.*, 2017). Also, mermithids have high specificity towards their hosts and are difficult to mass produce, subsequently, their potential for commercial use has been limited (Walgate, 1994; Campos-Herrera, 2015). They must be grown *in vivo* within mosquitoes, which limits their practicable use (Campos-Herrera, 2015).

An alternative to the mermithid EPNs is the use of EPNs from the families Steinernematidae and Heterorhabditidae, which are natural parasites of many insects and have been developed as biological control agents used widely in agriculture (Campos-Herrera, 2015). Steinernematidae, for instance, would have better characteristics than Mermithidaesince at the end of the mosquito parasitizing cycle they produce a great number of new IJs originating in the first as well as in the second adult generations (Cagnolo *et al.*, 2004) so that mass production would be easier and at a lower cost (Cagnolo and Almiron, 2010). Therefore, it was important to shed some light on these two ENP families in the following paragraphs.

4. Pathogenic Efficiency of Steinernematidae and Heterorhabditidae (terrestrial-living EPNs) Against Various Mosquito Vectors:

4.1. Important Status of Steinernematidae and Heterorhabditidae in the World of Beneficial Nematoda:

Steinernematidae and Heterorhabditidae (order Rhabditida:

phylum Nematoda) are naturally terrestrial-living EPNs. They are the most economically important families among the 23 families of Nematoda (Kumar *et al.*, 2015; Shapiro-Ilan *et al.*, 2017). These two families are established worldwide in diverse ecological habitats (Lacey *et al.*, 2015; Abd-Elgawad, 2020). In Steinernematidae, *Steinernema* is the most interesting genus for researchers worldwide. It includes more than 100 described species until now (Shapiro-Ilan *et al.*, 2017; Koppenhöfer *et al.*, 2020). In Heterorhabditidae, *Heterorhabditis* is the most interesting genus and contains more than 19 species (Abate *et al.*, 2017; Bhat *et al.*, 2020; Machado *et al.*, 2021). In addition, species of genus *Oscheius* are EPNs because they are parasitic to insect pests (Dillman *et al.*, 2012b).

Steinernematidae and Heterorhabditidae have attracted much research interest around the world to study their distribution, virulence, and usage in integrated pest management programs (Koppenhöfer *et al.*, 2020; Yüksel *et al.*, 2022). Different species of these two families have received more attention in the world as effective biocontrol agents against some economically important insect pests belonging to different orders (Burnell and Stock, 2000; Dillman *et al.*, 2012b; Cranshaw and Zimmerman, 2013). In particular, genera *Steinernema* and *Heterorhabditis* have been considered effective biological control agents against diverse agricultural insect pests (Shapiro-Ilan *et al.*, 2012; Lacey and Georgis, 2012; Chitra *et al.*, 2017; Ali *et al.*, 2022; Ardpairin *et al.*, 2023).

EPNs of Steinernematidae and Heterorhabditidae are characterized by mutualistic association with symbiotic bacteria of the genera *Xenorhabdus* and *Photorhabdus*, respectively, in their intestines (Boemare, 2002; Labaude and Griffin, 2018). These symbiotic bacteria are essential agents for the death of insect hosts (Poinar and Grewal, 2012; Ferreria and Malan, 2014; Vicente-Díez *et al.*, 2021).

For more detail, see Lewis and Clarke, 2012; Shapiro-Ilan and Brown, 2013; Lacey *et al.*, 2015; Koppenhöfer *et al.*, 2020; Bhat *et al.*, 2020; Kaliaskar *et al.*, 2022). However, the EPN-symbiotic bacteria have been reviewed in detail under the following subtitle "EPN-symbiotic bacteria and their potential role for the control of mosquito vectors" in this review. These EPNs, with their symbiotic bacteria, kill the targeted insect pests by the suppression of immune defences of the insect host within approximately 48 h (Dillman *et al.*, 2012a; Shapiro-Ilan and Brown, 2013; Lacey *et al.*, 2015; Labaude and Griffin, 2018; Kaliaskar *et al.*, 2022). These immune interactions were reviewed under the following subtitle "Suppressive activity of EPN/symbiotic bacteria complex against innate immune defences of mosquito larvae" in this review.

4.2. Potentiality of Steinernematidae and Heterorhabditidae for Controlling Mosquito Vectors:

Over the last few decades, EPNs of Steinernematidae and Heterorhabditidae have been used to control important agricultural insect pests. Also, different EPN species have been used against insects and arthropods of medical and veterinary significance, including Cat flea (Silverman *et al.*, 1982), spiders (Poinar, 1989), flies, mosquito larvae and black flies (Begley, 1990), body louse (Weiss *et al.*, 1993), ticks (Zhioua *et al.*, 1995) and head louse (De Doucet *et al.*, 1998). In addition, Edmunds *et al.* (2017) reported that the aquatic stages of non-biting midge *Chironomus plumosus* were rapidly killed by invading *Steinernema feltiae*, *S. carpocapsae*, *S. krausseii* and *H. bacteriophora*. However, relatively few studies focused on the potential of these two EPN families for the control of aquatic larvae of mosquito vectors (Cagnolo and Almirón, 2010; Peschiutta *et al.*, 2014; Cardoso *et al.*, 2015; Edmunds *et al.*, 2017, 2021).

Almost like the EPN entry into the haemocoel of an insect host, as previously described under the subtitle "Entomopathogenic nematodes and their

role for the insect pest control: basic knowledge", steinernematid EPNs invade through natural openings and then puncture the gut wall to enter the haemocoel of mosquito larvae (Walsh, and Webster, 2003; Poinar and Grewal, 2012; Ulvedal *et al.*, 2017). Liu *et al.* (2020) found similar results in *Ae. albopictus* after inoculation with the EPN *S. abbasi*. It is interesting to know that the EPN *S. glaseri* is able to release proteolytic enzymes to assist its penetration through the cuticle (Abu Hatab *et al.*, 1995). In addition to entry through natural body openings, *S. abbasi* could insert directly into the larval trumpet, the intersegmental membrane of the cuticle, and the basement of the paddle of *Ae. albopictus* pupae (Liu *et al.*, 2020).

As clearly shown in the current literature, Welch and Bronskill (1962), Dadd (1971) and Poinar and Kaul (1982) were pioneers in investigating the potentiality of heterorhabditid and steinernematid EPNs and their symbiotic bacteria against mosquito larvae. As recorded by some authors (Bronskill, 1962; Welch and Bronskill, 1962), *S. carpocapsae* is able to penetrate through the gut wall of *Ae. aegypti*, *Ae. stimulans* and *Ae. trichurus* resulting in host death (in spite of encapsulation of many nematode individuals). According to Poinar and Kaul (1982), *Cx. pipiens* larvae would ingest *H. bacteriophora*, but at high concentrations, they would escape melanization in the host and cause the death of the mosquito larvae.

Later on, Narksuwan *et al.* (2004) assessed the pathogenicity of EPNs *S. carpocapsae*, *S. siamkayai*, *S. feltiae*, *H. indica*, and *H. bacteriophora* against some mosquito species of different genera. Their results revealed successful suppressing action of all EPNs on *Ae. aegypti*, *Cx. quinquefasciatus* and *Cx. gelidus* populations. Pandii *et al.* (2008) tested *S. carpocapsae* and *H. indica* (local Thai strain) against *Cx. gelidus*. Depending on their results, *S. carpocapsae* exhibited more effectiveness than *H. indica*. In another study, Cagnolo and Almirón (2010)

evaluated the larvicidal effect of *S. rarum* using six different concentrations (OLI strain) against larvae of *Cx. apicinus*. They recorded an increasing larval mortality rate in a dose-dependent course.

In the last decade, *Heterorhabditis bacteriophora* caused 84% mortality in *A. aegypti* larvae (Peschiutta *et al.*, 2014). Peschiutta *et al.* (2014) recorded a mortality rate of *Ae. aegypti* larvae up to 84% after treatment with *H. bacteriophora*. EPN *Steinernema rarum* caused 75% larval mortality in the mosquito *Culex apicinus* at a concentration of 400 IJs/larvae (Cagnolo and Almiron, 2017). In Kyrgyzstan and Turkey, Toksoz and Saruhan (2018) studied the pathogenic efficacy of five EPNs on *Cx. pipiens* larvae under laboratory conditions. Larval mortality was observed after treatment with all EPN species. In addition, *H. bacteriophora* (KG81) and *S. carpocapsae* isolates were found to be the most effective isolates causing 100% larval mortality. Dilipkumar *et al.* (2019) isolated four different EPN species and evaluated their bio-larvicidal potential against mosquitoes *Ae. aegypti*, *An. stephensi* and *Cx. quinquefasciatus*. Among the tested four different EPN species, *S. abbasi* caused the highest mortality against *Ae. aegypti* (97.33%), *H. indica* against *An. stephensi* (97.33%) and *S. siamkayai* against *Cx. quinquefasciatus* (98.67%).

In the current decade, Liu *et al.* (2020) investigated the mosquitocidal effects of *S. abbasi* against *Ae. albopictus* in aquatic habitats. This EPN entered the haemocoel of the 3rd and 4th instar larvae mainly through the mouth and gastric caecum or by penetrating pupae through the intersegmental membrane or trumpet. The mosquito larvae infected with a single EPN demonstrated a high mortality. In México, Ávila-López *et al.* (2021) investigated the effectiveness of different isolates of *Heterorhabditis* on the *Ae. aegypti* larvae. The concentration of 2,520 IJs:1 caused 80% mortality of mosquito larvae during 48 h. In Mexico, also, Treviño-Cueto *et al.* (2021) isolated five strains of local EPNs

(*H. bacteriophora* and *S. carpocapsae*) and assessed their pathogenicity against *Ae. aegypti*. Depending on their results, all EPN strains caused lethal infections in larvae (mortality 3–100%).

Recently, Ardpairin *et al.* (2023) isolated and identified EPNs from soil samples in Thailand and evaluated their efficacy for controlling larvae of three mosquito vector species, *Ae. aegypti*, *Ae. albopictus* and *Cx. quinquefasciatus*. The EPN *H. bacteriophora* showed the highest efficacy against both *Ae. aegypti* and *Cx. quinquefasciatus* because mortality rates were 60.0 and 91.7%, respectively, at 96 h after exposure. In another recent study, Lalitha *et al.* (2023) recorded the highest larval mortality (80–90%) of *Cx. quinquefasciatus* at a concentration of 1000 IJs of EPNs *S. carpocapsae* and *Rhabditis blumi*. In comparison, 70% of mortality was observed in mosquito larvae after infection with *Steinernema monticolum* IJs and *S. carpocapsae*. EPN *R. blumi* exhibited the lowest larval mortality on the first instar larval instar. This may be due to the smaller size of the host larvae. IJs were recognized in the larval guts as early as within minutes after their contact with the host. Following IJ entry into mosquito larval midgut, a change in color from light brown to dark black is observed.

On the contrary, the available literature contains few contradictory results, *i.e.*, failure of some heterorhabditid and steinernematid EPNs to successfully infect or kill the mosquito larvae. Early, Dadd (1971) recorded *Cx. pipiens* larvae ingesting *S. carpocapsae*, often hundreds at a time, EPN failed to enter into the haemocoel and subsequently could not cause larval mortality. Cardoso *et al.* (2015) found that two strains of *H. indica* and *H. baujardi* could kill *A. aegypti* but *S. carpocapsae* could not kill. Zohdy *et al.* (2013) exposed larvae of *Cx. quinquefasciatus* to IJs of four EPNs under laboratory conditions. Depending on their results, *H. bacteriophora* and *H. indica* successfully established themselves in the

host cadaver and produced IJs, while *S. carpocapsae* and *S. feltiae* failed to establish themselves in the host larvae or cause significant host mortality because they were melanized. The higher virulence of heterorhabditids could be attributed to IJs of these EPNs which develop into hermaphrodites, a single invader can potentially reproduce. Thus, a low number of EPNs entering their mosquito hosts will be capable of establishing the next generation. On the other hand, steinernematids are amphimictic and mating is necessary to reproduce, thus an invasion of high numbers of individuals increases the probability of mating and further reproduction (Koltai *et al.*, 1995).

4.3. Some Advantages of the Families Steinernematidae and Heterorhabditidae as Biocontrol Agents Against Mosquito Vectors:

Some advantages of these two families, as biocontrol agents against insect pests, had been previously reviewed in the first paragraphs. However, other advantages should be highlighted herein. The steinernematid and heterorhabditid EPNs are more advantageous than mermithid nematodes because the former families can be developed *in vivo* in alternate hosts or *in vitro* on artificial media (Friedman, 1990). A second advantage is the longevity of IJs (3~6 months in water at room temperature), and it is also characterized by a short life cycle (Grewal *et al.*, 2005; Peschiutta *et al.*, 2014). As reported by many authors (Molta and Hominick, 1989; Cagnolo and Almirón, 2010; Lacey and Georgis, 2012; Ulvedal *et al.*, 2017; Silva *et al.*, 2019), steinernematids and heterorhabditids can infect a wide range of susceptible mosquito species. Non-toxicity of *Steinernema* spp. and *Heterorhabditis* spp. to humans, target specificity and compatibility with some insecticides enabled these EPNs to accurately in the spectrum of integrated pest management (Grewal *et al.*, 2001; Shapiro-Ilan *et al.*, 2012). EPNs of these two families have high virulence, less killing time, host-finding ability, and fast-acting

generations (Lacey and Georgis, 2012; Bal and Grewal, 2017; Toksoz and Saruhan, 2018; Yüksel *et al.*, 2022).

Although steinernematids and heterorhabditids are naturally terrestrial EPNs, the aquatic habitat offers a suitable environment for their survival (Pandii *et al.*, 2010; Peschiutta *et al.*, 2014; Silva *et al.*, 2019). In aquatic habitat, IJs sink to the aquatic substratum where mosquito larvae frequently feed on the organic detritus and may swim actively looking for hosts resulting in successful infection of mosquitoes (Pandii *et al.*, 2010; Zohdyet *et al.*, 2013; Edmunds *et al.*, 2017). In spite of being *S. raruma* terrestrial EPN, it moves in the interstitial water between the soil particles. According to Cagnolo and Almirón (2010), IJs of this EPN were observed swimming actively searching for the mosquito larvae.

It was reported that *S. abbasi* is able to kill and produce more IJs in host insects under a temperature ranging from 20 to 30°C (Yoshida, 2007; Sunanda, 2009; Aasha *et al.*, 2019; Nagesh *et al.*, 2019). The survival rate of *S. abbasi* was not affected when stored in distilled water for up to 6 weeks at 8 °C (Hussaini *et al.*, 2000), and even up to 90 days at 30°C resulting in 70.22% survival (Sunanda *et al.*, 2012). Temperature ranging from 25 to 32°C was favourable for the pathogenicity of *S. abbasi* (Sunanda, 2009).

The infectivity, reproduction, and size of the progeny of EPNs may be related to the EPN behavior, adaptation to a given host (ability to overcome the defense mechanism of the host) (Kaya, 1990) and different developmental stages and size of the host (Murdoch *et al.*, 1997; Boff *et al.*, 2000). These EPNs have a wide host range, making them a viable option for the biocontrol of insect pests (Arthurs *et al.*, 2004). Also, EPNs can be applied alone, as a biocontrol agent, or combined with other biocontrol agents, such as entomopathogenic bacteria and fungi in order to improve their efficacy in

controlling insect pests (Laznik *et al.*, 2012).

5. Diverse Susceptibility of Mosquito Larvae and Variation of EPN Virulence:

5.1. Dose-dependent Mortality of Mosquito Larvae:

A great body of evidence has been accumulated in the available literature about the positive correlation of the larval mortality of mosquitoes with the EPN concentration. It may suffice to review the following studies. Early, Poinar and Kaul (1982) assessed the parasitism of different larval instars of *Cx. pipiens* by EPN *H. bacteriophora*. They recorded a dose-dependent course of larval mortality. In agreement with these results, Molta and Hominick (1989) observed a positive correlation of 3rd larval instar of *Cx. pipiens* with the applied dose of *H. heliothidis* and *S. feltie*. To a great extent, these results were consistent with many results reporting dose-dependent mortality of mosquito larvae by various EPNs (Cagnolo and Almirón, 2010; Chaudhary *et al.*, 2017).

For some detail, the pathogenic effect of three mermithid nematodes, *R. culicivora*, *R. iyengari* and *S. spiculatus*, was evaluated at different doses in larvae of *Ae. aegypti*. Both the infestation mean and parasitism rate increased as the dose increased (Rodríguez *et al.*, 2005). In Argentina, Cagnolo and Almirón (2010) evaluated the larvicidal effect of *S. rarumon* *Cx. apicinus* and recorded an increasing larval mortality rate in a dose-dependent course. Also, similar results were found in *S. carpocapsae* parasitizing *Cx. gelidus* (Pandii *et al.*, 2010). In addition, Peschiutta *et al.* (2014) studied the infectivity and life cycle of *H. bacteriophora* (Argentinean isolate) on the *Ae. aegypti* larvae. Larval mortality rates of 3rd and 4th larval instars ranged from 0% to 84%. The larval mortality increased with the increase of the EPN dose. Also, a dose-dependent mortality of 3rd and 4th larval instars of *Ae. aegypti* was recorded for *H. indica* LPP35 (Cardoso *et al.*, 2015). In this area of research, Abagli *et al.* (2019) reported

concentration-dependent mortality of *An. gambiae* larvae with the *R. iyengari* infection.

Recently, Shah *et al.* (2021) found a dose-dependent mortality of *Ae. aegypti* 3rd and 4th instar larvae after treatment with different concentrations of some EPN species in Turkey. Also, they recorded a variation in the EPN virulence, since a dose of 100 IJs per larva of *H. bacteriophora* and *S. carpocapsae* caused 90%–100% mortality, whereas *H. downesi* and *S. feltiae* caused only 40%–60% mortality. Even when using 200 IJs/larva, *H. megidis* and *S. krausseii* caused a maximum of 30%–40% mortality. In Egypt, Elbrense *et al.* (2022) recorded a concentration-dependent mortality of mosquito *Cx. pipiens* after infection with *R. iyengari* under laboratory conditions.

5.2. Diverse Susceptibility of Mosquito Larval Instars to the EPN Infection:

With respect to the susceptibility of mosquito larval instars to the EPN infection, the available literature contains contradictory results, since some studies revealed higher susceptibility of the later instars (3rd and 4th instars) while other studies documented the earlier instars (1st and 2nd instars) as more susceptible. Early, Poinar and Kaul (1982) reported that *H. bacteriophora* preferentially infected the later instar of *Culex* species, *i.e.*, the older instars are more susceptible than the early instars to EPN infection. In Brazil, de Oliveira Cardoso *et al.* (2015) demonstrated that *H. baujardi* and two strains of *H. indica* LPP35 were not virulent against 1st and 2nd larval instars of *Ae. aegypti* and only 3rd and 4th instars were affected by these EPNs since no mortality of 1st and 2nd instars (early instars) were recorded. In Egypt, Sayed *et al.* (2018) found that the infection of 3rd and 4th larval instars of *Cx. pipiens* with EPN *S. scapterisci* resulted in more mortality of 4th instar larvae than mortality of 3rd instar larvae. In other words, the 4th instar larvae were more susceptible to nematode infection than the 3rd instar larvae. In

Taiwan, Liu *et al.* (2020) found that the treatment of *Ae. albopictus* larvae with 1000 IJs/mL of *S. abbasi* or *S. carpocapsae* resulted in a high mortality of 3rd and 4th instar larvae, but not the 1st and 2nd instar larvae or pupae, *i.e.*, 3rd and 4th instar larvae were more susceptible to *Steinernema* nematodes. Also, Shah *et al.* (2021) assessed the pathogenicity of some EPN species against the *Ae. aegypti* larvae and found the later larval instars (3rd and 4th) readily ingested EPNs, which ultimately led to their death. The early larval instars (1st and 2nd) did not ingest any EPN and, thus, escaped infection.

Why the Later Instar Larvae Are More Susceptible Than Larvae Of The Earlier Instars To Invading EPN?

Some scenarios can be provided to explain this widespread observation. The lower susceptibility of earlier instar larvae may be due to their small mouthparts or feeding behavior that excludes large particles (Bedding *et al.*, 1983). The nematode IJs are difficult to penetrate directly through the cuticle or pores in the 1st and 2nd instar larvae with very small body sizes (Molta and Hominick, 1989; Ulvedal *et al.*, 2017). For some detail, larger hosts could more readily ingest IJs without damaging them, while small-sized early instar larvae rarely ingest whole EPNs, more often crushing them with their mandibular teeth because of their smaller oral aperture. Once the cuticle was broken, the nematode perished (Zohdy *et al.*, 2013). Also, the haemocoel invasion of 3rd and 4th instar larvae *Cx. pipiens* by IJs of *H. bacteriophora* causes septicemia by the EPN-symbiotic bacteria which normally colonizes the larval gut but only enters the haemocoel after the peritrophic membrane has been perforated by the IJs (Cardoso *et al.*, 2015). However, the fact that EPNs may only infect older instars of mosquitoes does not prohibit their use in the biocontrol programs of mosquito vectors as they are preventing adult emergence, and subsequently, this will lead to a suppression

of the mosquito populations (Poinar and Kaul, 1982).

In contrast, only a few studies found the early larval instars of some mosquito species as more susceptible than the later ones to EPN infection. For example, Santamarina *et al.* (1999) found the later instar larvae of *An. pseudopunctipennis* less susceptible to *R. iyengari* infection than earlier instar larvae in 16 sites of Mexico. Pérez-Pacheco *et al.* (2004) showed that the 3rd instar larvae of *A. pseudopunctipennis* and *Cx. quinquefasciatus* were more susceptible than 4th instar larvae to *R. iyengari* infection. Results of Díaz *et al.* (2018) demonstrated that the 1st and 2nd instar larvae of *Ae. albopictus* were more susceptible to *R. iyengari* infection than 3rd instar larvae. In Benin (Africa), Abagli and Alavo (2019) reported that 1st and 2nd instar larvae of *Cx. quinquefasciatus* were more susceptible to infection with *R. iyengari*, compared to the older larvae. In sub-Saharan Africa, Abagli *et al.* (2019) carried out some laboratory and field experiments to evaluate the effectiveness of *R. iyengari* for the control of *An. gambiae*. In laboratory experiments, the mortality rates of larvae indicated that 1st and 2nd larval instars were more susceptible to EPN infection, compared to later larval instars. In Egypt, Elbrense *et al.* (2022) evaluated the comparative susceptibility of different larval instars of *Cx. pipiens* to *R. iyengari* infection in the laboratory. Based on their results, LC₅₀ values for 1st - 4th larval instars were 3.18, 2.73, 3.79 and 4.00 pre-parasites / larva, respectively. In other words, the earlier larval instars were more susceptible to *R. iyengari* than the later instars.

Why the Earlier Instar Larvae of Mosquitoes Are More Susceptible Than the Later Instars to Invading EPN?

Authors who obtained such results have attributed this higher susceptibility to the fact that the thin cuticle of earlier larvae facilitates the invasion of pre-parasitic IJs, which have more difficulty penetrating the thicker cuticle of later instar larvae. In other

words, the thicker cuticle of later larval instars has assisted them in preventing the pre-parasitic IJs to insert their stylets and penetrate the host body (Achinelly *et al.*, 2004; Pérez-Pacheco *et al.*, 2004). Also, the lower susceptibility of later instar larvae may be interpreted by the violent wriggling behavioural defence by these larvae against EPN attack, making it difficult for the pre-parasitic IJs to search and insert their stylets into the body cuticle and enter the host (Santamarina, 1994). In addition, the mosquito larvae exhibit a special physiological action to combat EPNs that try to invade their haemocoel (Hillyer, 2010). After the invasion of their haemocoel, mosquito larvae have a diverse array of cellular and humoral immune defences. It is reasonable to suggest that the later larval instars have exerted a stronger immune defence than the early instars to combat EPN invasion (Shamseldean *et al.*, 2006; Liu *et al.*, 2020).

5.3. Stronger Virulence of Certain EPNs than other EPNs Against the Same Mosquito Species:

As shown in the current literature, there are many reports about the superior virulence of certain EPN species over other EPN species against the same mosquito species. This is an interesting point and should be highlighted by the following examples. The pathogenic effects of three mermithid nematodes, *R. culicivorax*, *R. iyengari* and *S. spiculatus*, were assessed on larvae of *Ae. aegypti*. Although all tested nematodes caused 100% larval mortality at higher doses, *R. culicivorax* proved to be more virulent at low doses (Rodríguez *et al.*, 2005). According to the results obtained by Cardoso *et al.* (2015) in Brazil, *H. indica* LPP35 was more virulent than *Steinernema* spp. against the 3rd and 4th larval instars of *Ae. aegypti*. In Thailand, Pandiet *et al.* (2008) found mortality rates of 3rd and 4th larval instars of *Cx. gelidus*, caused by *S. carpocapsae*, were higher than mortality caused by *H. indica* (Loyal Thai strain), *i.e.*, *S. carpocapsae* was more virulent than *H. indica* against *Cx. gelidus* larvae. Some

years later, Ansari and Hussain (2020) studied the potential biocontrol of *Ae. aegypti* by commercial EPNs. All EPNs were pathogenic to *Ae. aegypti*, however, their virulence varied significantly because *H. bacteriophora* and *S. carpocapsae* were the most virulent (causing 90-100% mortality at 100 IJs per larva), whereas *H. megidis* and *S. kraussei* showed the least virulence (causing 40-60% mortality).

Recently, Edmunds *et al.* (2021) exposed larvae of two mosquitoes *Ae. aegypti* and *Ochlerotatus detritus* to commercially available EPNs and field-collected EPNs from the UK. The commercially available EPNs were more virulent against *Ae. aegypti* and *O. detritus* but the field-collected EPN species have less virulence to these larvae. According to Shah *et al.* (2021), all tested EPN species against *Ae. aegypti* larvae were pathogenic but differed significantly in their virulence, since *H. bacteriophora* and *S. carpocapsae* were more virulent (causing 90-100% mortality at 100 IJs per larva), whereas *H. downesi* and *S. feltiae* exhibited less virulence and *H. megidis* and *S. kraussei* were found the least virulent EPNs (causing 40-60% larval mortality).

Shortly, some of the previously mentioned authors explained their results as follows. The less virulent EPNs may have been less effective at penetrating the gut and accessing the nutrient-rich haemolymph. Since host suitability is dependent on the ability of the EPN to evade or suppress the insect immune responses (Wang *et al.*, 1995; Peters and Ehlers, 1997), it is possible that the more virulent species were able to suppress host immune defenses more quickly than other species.

5.4. Comparative Susceptibility of Different Mosquito Species to The Same EPN Species:

It is important to shed some light on the variable susceptibility of different mosquito species to the EPN. In a study, Paily and Balaraman (2000) exposed ten species of mosquitoes, from five genera, to *R. iyengari*. When 2nd instar larvae were

exposed, the highest mortality was found in *Cx. sitiens* (95%) followed by *Cx. quinquefasciatus* (90%), *Ae. aegypti* (79%), and other mosquito species. When 4th instar larvae were exposed, the infection was highest in *Ar. subalbatus* (66% mortality), followed by *An. stephensi* (52% mortality), *Cx. quinquefasciatus* (47% mortality), and other mosquito species. In another study, Rojas-Urdaneta *et al.* (2002) assessed the infestation capacity of *R. iyengari* on *Anopheles nuneztovari* and *Ae. aegypti*. Mortality ranked between 95 and 100% for both mosquito species. Thus, *Annuneztovari* showed the highest susceptibility to the nematode infection. However, the variable susceptibility of different mosquito species to the same EPN species can be due to their variation of specific physiological, physical and/or behavioural characteristics of the host larvae (Petersen, 1975; Petersen and Chapman, 1979).

6. Key factors and Environmental Conditions Affecting the Virulence of EPNs against Mosquito Larvae:

6.1. Basic Information:

The virulence of EPNs, as biological control agents of insects, varies greatly depending on their characteristics, such as reproductive capacity, host-seeking behaviors, host specificity and adaptation capabilities (Yan *et al.*, 2020; Acharya *et al.*, 2020). It is well known that EPNs with higher levels of infectivity and reproduction inside a targeted insect may be more effective for controlling this insect under field conditions (Rahoo *et al.*, 2018; Kapranas *et al.*, 2020). Several researchers have mainly focused on the potential of EPNs as inductively applied augmentative biocontrol agents (Grewal *et al.*, 2005; Laznik *et al.*, 2010; Laznik *et al.*, 2011).

As reported in the current literature, the environmental parameters (biotic and abiotic factors), application technique, and others have influenced EPN virulence against insect pests (Lacey and Georgis, 2012). In other words, the effectiveness of EPNs for controlling insects depends on

biotic factors, such as natural enemies, species of EPNs, age of targeted insects, and competition for resources (Shapiro-Ilan *et al.*, 2012; Hazir *et al.*, 2003) and abiotic factors, such as extreme temperatures, pH, UV radiation and aeration (Kaya and Gaugler, 1993). For these reasons, EPNs are less efficient against insect pests outdoors, although the previous laboratory assays showed a much higher efficiency (Laznik and Trdan, 2011; Majić *et al.*, 2019). Another point of interest is the accordance of EPN virulence to the insect species (Ehlers *et al.*, 2003; Ramos-Rodríguez *et al.*, 2006) and the developmental stage of the insect host (Acharya *et al.*, 2019; Yan *et al.*, 2020; Acharya *et al.*, 2020). In other words, the IJs of EPNs rely on their host behaviors, body size of different host developmental stages, and host immunity to maximize their chances of a successful infection (Peschiutta *et al.*, 2014). Also, IJ concentration is an important factor in producing increased larval mortality (Peschiutta *et al.*, 2014).

With regard to mosquitoes, the current literature documented many nematode bioassays that did not examine the key factors determining the virulence of EPNs as biocontrol agents (Chaudhary *et al.*, 2017; Dilipkumar *et al.*, 2019). Also, many studies on the efficacy of EPNs against mosquito larvae have been conducted only in the laboratory (indoor), with a variety of methodological procedures that limit generalizations (for a review see Cardoso *et al.*, 2015). Various environmental factors including temperature, pH, nutrient content, presence of organic matter, UV radiation and others can significantly impact the prevalence and persistence of EPNs in different habitats (Lacey and Georgis, 2012). During a survey on EPNs in North China, the environmental conditions imposing adverse effects on the virulence, survival, and reproduction of *Heterorhabditis* and *Steinernema* spp. were investigated (Ma *et al.*, 2010). Therefore, it is important to understand the environmental factors present in areas

where EPN exists to ensure its success as a biological control agent (Ulvedal *et al.*, 2017; Toksoz and Saruhan, 2018). In other words, for an EPN to become a more effective biocontrol agent, it needs to adapt to the environmental conditions on the application sites (Del Pino *et al.*, 2018).

6.2. Physicochemical Characteristics of the Mosquito Oviposition and Breeding Sites:

In respect of the dependence of EPN efficiency on characteristics of the oviposition and breeding sites of mosquitoes, this important issue has rarely been examined (Powell and Tabachnick, 2013). The physicochemical parameters of water in the oviposition sites should be taken into consideration to be optimal for allowing the EPN to reproduce and to continue parasitizing larval mosquitoes over a long period (Santamarina *et al.*, 1996). Perez-Pacheco *et al.* (2005) indicated that a number of topographical and hydrological factors can play a role in the effectiveness of the nematode *R. iyengari* against malaria vectors.

For instance, Cardoso *et al.* (2016) assessed the efficacy of *H. indica* LPP35 outdoors, in plastic cups, bottles, and buckets, which mimicked typical oviposition sites. Depending on their study, the EPN efficacy was above 75% in cups and bottles but decreased to 40% in buckets. These authors concluded that the key parameters for *H. indica* LPP35 efficacy against larval instars of *A. aegypti* are: (i) the dose of IJs/larva, which should be at least 80 to 100; and (ii) the concentration of IJs/cm² of the bottom internal surface of the oviposition site. To a great extent, similar results have been reported by Silva *et al.* (2019), since adult females of *Ae. albopictus* usually prefer to lay their eggs either in areas of relatively clean water or small containers placed in home yards, such as uncovered barrels, plastic buckets, water storage drums, jars, discarded tires, flower vases, and trash cans (Wong *et al.*, 2011; Kampen and Werner, 2014; Getachew *et al.*, 2015; Dom *et al.*, 2016). Also, high

salinity can affect the EPN activity (Kergunteuil *et al.*, 2016). As an exceptional case, Mijares and Pacheco (1998) reported that the values of the physical and chemical parameters, such as pH, conductivity, oxygen, and chlorides determined in these waters apparently did not affect the infective capacity of the pre-parasitics of the mermithid nematode *R. iyengari* against all larval instars of *Ae. aegypti* in breeding places.

6.3. Effect of the Population Density of EPN within the Mosquito Larva:

Based on the current literature, the fitness of an EPN can be adversely affected by increasing its population density within the host body. This parameter has been reported in mermithid nematodes in mosquito larvae. Density-dependent effects on an EPN include reduced fecundity, increased mortality, change in sex ratio, reduction in adult size, increased generation time and reduced oviposition (Selvan and Muthukrishnan, 1988). Although all EPNs have the same general life history, species differences in the host utilization (Selvan and Blackshaw, 1990) and reproductive strategies (Poinar, 1990) may affect the EPN response to increasing density. In addition, Reyad (2005) reported that the nutritional requirements of *H. bacteriophora* are larger than those required for *S. riobrave*; thus, the principal nutrients of larvae infected with *H. bacteriophora* are lower than in those infected with *S. riobrave*. This finding might explain the superiority of the reproductive potential of *H. bacteriophora* over that of *S. riobrave*.

6.4. Temperature as an Affecting Parameter of EPN Virulence:

The ambient temperature is one of the limiting factors of the EPN virulence. Some research works investigated the effect of the ambient temperature on EPN virulence against insect pests. In general, the optimum range for *H. bacteriophora* is 22 - 26°C (Doucet *et al.*, 1996) and 25°C for *S. feltiae* (Belair *et al.*, 2003). Chaudhary *et al.* (2017) investigated the virulence of *S. kraussei* and *H. bacteriophora* against *Ae.*

aegypti at different temperatures in canal, sewage and tap water. These authors reported that both EPN species were highly effective against the mosquito larvae, causing 100% larval mortality optimally at 20°C and 30 °C. In water, the EPN IJs can survive over 6 months even at temperatures of 20–25 °C (Poinar and Kaul, 1982); therefore, EPNs could provide a sustained control of *Ae. aegypti* over a long period of time. The virulent EPN species, identified in the study of Shah *et al.* (2021), were known to work better at higher temperatures, i.e. 20–30 °C (Kim and Alston, 2008; Power *et al.*, 2009) makes their application in *Ae. aegypti* hot spots are even more practicable and promising.

6.5. Nematode Concentration as an Affecting Factor of Virulence:

For successful mosquito control by EPNs, the nematode effective concentration should be accurately determined. In a study by Abagli *et al.* (2019) to control *An. gambiae* larvae by *R. iyengari* in West Africa, the parasitism intensity depends on the nematode concentration. Monthly application of the concentration 3500 J2/m² was enough to effectively control the mosquito larvae. Trujillo-González *et al.* (2021) determined lethal doses of *R. iyengari* on *Cx. quinquefasciatus*. Habitat complexity had no effect on the pathogenic efficiency of *R. iyengari* at high concentrations (100 parasites per larva) but significantly decreased at low concentrations (10 parasites per larva).

6.6. The EPN IJs Production Determinants:

Concerning the IJs production, differences in the reproduction potential of EPNs may related to the EPN species, isolates, host susceptibility, number of bacteria per infective stage, invasion rate, temperature and other factors (Rahoo *et al.*, 2016, 2017; Nabeel *et al.*, 2018). Apart from mosquitoes, many studies reported the capacity of *Heterorhabditis* species to produce more IJs, hence they can be used for insect pest control (Khan *et al.*, 2017; Kassi *et al.*, 2018). For example, the

production of nematode IJs in *G. mellonella* larvae was significantly affected by the species itself. Significantly higher numbers of IJs were produced by Heterorhabditid species than Steinernematid species in the larval cadaver of the greater wax moth *Galleria mellonella* (Lepidoptera: Pyralidae) (Fateh *et al.*, 2017; Kayani *et al.*, 2017). The production of IJ was the maximum in the case of *H. bacteriophora* while minimum IJs were produced by *S. feltiae* (Rahoo *et al.*, 2018).

6.7. Symbiotic Bacteria as a Prerequisite Contributor to the EPN Virulence:

Among factors influencing the EPN virulence is the symbiotic bacteria in the nematode IJs (Mráček and Běčvář, 2000; Campbell and Lewis, 2002; Stock and Blair, 2008), i.e., symbiotic bacteria of EPNs play a crucial role in the EPN virulence by releasing a wide range of secondary metabolites into host haemolymph (Bode, 2009), i.e., an array of the bioactive larvicidal compounds produced by these symbiotic bacteria are supporting for the EPN activity (Shah *et al.*, 2021). However, this subject will be reviewed in detail under the following subtitle "EPN-symbiotic bacteria and their potential role for the control of mosquito vectors".

7. Deleterious Effects of EPNs on Some Biological and Physiological Parameters of Mosquitoes:

As previously reviewed, death of the insect host is reported within 24-72 h post-infection with EPNs, regardless of the insect species and the EPN species (Gaugler, 2002; Griffin, *et al.*, 2005; Kaya *et al.*, 2006; Shapiro-Ilan and Brown, 2013; Shaurub *et al.*, 2014; Lacey *et al.*, 2015; Leonar *et al.*, 2022; Kaliaskar *et al.*, 2022). On the other hand, many authors (Nappi and Vass, 2001; Peschiutta *et al.*, 2014; Cardoso *et al.*, 2015; Liu *et al.*, 2020; Ansari and Hussain, 2020; Shah *et al.*, 2021) reported the success of some infected individuals to avoid the lethal effects of both EPN and its symbiotic bacteria using some immune defences. These host individuals developmentally transform into the next

stage but are usually unhealthy because certain biological and physiological processes have been adversely affected. In this context, there has been increasing evidence that some EPNs influenced certain metabolic processes in the insect host (Shaurub *et al.*, 2020; Ghoneim *et al.*, 2022) and some important enzymatic activities (Shaurub *et al.*, 2015; Ibrahim *et al.*, 2015; Shairra *et al.*, 2016; Vidhya *et al.*, 2016; Ghoneim *et al.*, 2023a).

Apart from mosquitoes, Ghoneim *et al.* (2023a) observed a few EPN-infected 4th instar larvae of the black cutworm *Agrotis ipsilon* (Lepidoptera: Noctuidae) could pupate at the lower two concentrations of *S. carpocapsae* and *H. bacteriophora*. In their study, also, a similar result was recorded after infection of 5th instar larvae with *S. carpocapsae*. Also, some studies, on various agricultural insect pests, recorded the capability of some EPN-infected pupae to metamorphose into adults indicating some resistance of the pupal stage to EPNs (Malan *et al.*, 2011; Odendaal *et al.*, 2016; du Preez *et al.*, 2021; Steyn *et al.*, 2021). In a study of Filgueiras and Willett (2021), EPNs can alter the developmental durations and changes in the risk of death of the non-susceptible pupal stage of the onion fly *Delia antique* (Diptera: Anthomyiidae), indicating an insect resistance to infection during the pupal stage. The inactivation of EPN during the pupal stage of an insect and the reestablishment of its activity during the adult stage indicate the ability of this EPN to overcome the insect's immune system (Vallet-Geley *et al.*, 2008).

With regard to mosquitoes, the available literature contains scarce information concerning the effects of EPNs on the biological and physiological and adult performance parameters of mosquitoes until 2022. Early, Welch and Bronskill (1962) found the pupation of some EPNs-infected larvae of *Ae. aegypti* with *S. carpocapsae* 1 or 2 weeks longer than the normal congeners (i.e., prolongation of the larval period), while others failed to pupate and then died after 3

or 4 weeks. Also, (Obiamiwe and Mac Donald (1973) recorded a delay in the development of the *Anopheles* larvae after infection with the nematode *Octomyomermis muspratti*. According to Liu *et al.* (2020), *S. abbasi* isolate could cause a delay in the next molt and pupation of *Ae. albopictus*. Recently, Elbrense *et al.* (2022) recorded a significantly prolonged pupal duration of *Cx. pipiens* as an effect of infection with LC₅₀ of *R. iyengari* pre-parasites.

Prolongation of the pupal duration, or delay of the pupal ecdysis, of mosquito larvae after infection with mermithids may be due to a disturbance in their endocrine regulation or due to the insertion of some *R. iyengari* neurosecretory compounds (Petersen and Willis, 1970). Also, this result may be related to the insufficient nutritional reserves, which are essential for building the adult structures during the pupal stage, because EPNs absorb nutrients from the host's body through their body surface (Schmidt and Platzer, 1980; Gordon, 1981). In this regard, the haemolymph protein content of *Cx. pipiens* larvae were depleted to one-sixth of the level in normal larvae after infection with *R. culicivora* (Schmidt and Platzer, 1978). Also, the scarcity of nutritional reserves in mosquitoes may be due to the degeneration of the mid-gut epithelium leading to starvation, as recorded for *Ae. aegypti* larvae after infection with *R. culicivora* (Bailey and Gordon, 1973).

Considering the adult performance of EPN-infected insects, infection of Tobacco thrips *Frankliniella fusca* pupae (the soil-dwelling stage) with *H. bacteriophora* (F11-1), *S. feltiae*, *S. riobrave* or *S. rarum* resulted in reduction of the adult emergence (Gulzar *et al.*, 2021). After treatment of the European grapevine moth *Lobesia botrana* (Lepidoptera: Tortricidae) pupae with high IJ concentrations of four EPN species (*S. feltiae*, *S. carpocapsae*, *S. riojaense* and *H. bacteriophora*), adult emergence of the

insect was significantly blocked (Vicente-Díez *et al.*, 2021). On the other hand, the adult performance of mosquitoes could not be affected by EPNs, since Di Battista *et al.* (2015) reported no influenced survival rate of *Ae. albifasciatus* adult females infected with *S. spiculatus*. Elbrense *et al.* (2022) treated *Cx. pipiens* 4th instar larvae with LC₅₀ of *R. iyengari* pre-parasites and observed partial blockage of adult emergence but recorded no effect on the adult longevity.

Concerning the affected insect reproductivity of mosquitoes by EPN infection, EPNs can induce physiological changes in their insect hosts, leading to a reduction of their reproductive capacity. However, factors affecting the female mosquito fecundity had been summarized by Gordon (1981) who suggested that the EPN-infected adults suffer from being sterilized or biologically castrated. Several decades later, Elbrense *et al.* (2022) reported that the treatment of *Cx. pipiens* 4th larval instar with LC₅₀ of *R. iyengari* pre-parasites resulted in a considerable reduction of the female fecundity. This reduction of fecundity may result from the non-selective use of mosquito energy reserves under the stress of EPN infection (Baudoin, 1975). On the contrary, no effect was recorded on the egg-hatching rate of *Cx. pipiens* after infection of 4th instar larvae with LC₅₀ of *R. iyengari* pre-parasites (Elbrense *et al.*, 2022).

8. EPN-symbiotic Bacteria and Their Potential Role in the Control of Mosquito Vectors:

The role of symbiotic bacteria associating with EPNs for suppressing the host immune defenses resulting in death has been briefly mentioned in some parts of the present review. These mutualistic entomopathogens have received great attention from pest control researchers in some parts of the world, whether included in a mutual association with EPNs or separately isolated from them. Therefore, it is very interesting to review the current knowledge on these bacterial symbionts and

provide new insights into their role in the biocontrol of mosquito vectors.

8.1. The Dual Action of EPN-Symbiotic Bacteria for Killing Insect Pests:

It is important to highlight the mutualistic association between EPN and bacteria because the nematode/bacterium complex usually works together and has high virulence as a biological control unit to kill an insect pest (Lacey *et al.*, 2001). As previously mentioned in the section "Entomopathogenic nematodes and their role for the insect pest control: basic knowledge", IJs of an EPN search for a suitable insect host and enter its body through natural openings. After entering the body, the IJs penetrate through the gut wall, and regurgitate their symbiotic bacteria into the insect haemocoel (Dowds and Peters, 2002; Mastore *et al.*, 2015), at which point the bacteria multiply and produce several toxins and degradative enzymes thereby killing the insect rapidly. The EPNs themselves, also, contribute to this process, and the insect host is killed within 24-72 h (Ffrench-Constant *et al.*, 2007a, b; Simon *et al.*, 2014; Leonar *et al.*, 2022).

Upon death of the insect host, the bacteria digest its tissues, providing nourishment needed for the associated EPN to successfully reproduce (Burnell and Stock, 2000; Park *et al.*, 2003). In addition, these symbiotic bacteria produce antibiotics that protect the host cadaver from saprophytes and scavengers (Boemare, 2002; Hazir *et al.*, 2003). In other words, bacteria provide the EPN and themselves a protected niche by producing antibiotics that suppress the competition from other microorganisms as well as protection against various biotic and abiotic factors (Sicard *et al.*, 2004, 2006; Flores-Lara *et al.*, 2007; Snyder *et al.*, 2007; Mahmoud, 2016). The IJs of the next generation leave the host cadaver to the natural environment seeking to infect a new host (Griffin *et al.*, 2005). In the field of pest control, this nematodes/bacteria association is crucial, since Steinernematids are less pathogenic without their symbiotic bacteria and

Heterorhabditids cannot kill an insect without their symbiotic bacteria (Adams and Nguyen, 2002).

8.2. The Most Effective Species of EPN-Symbiotic Bacteria from the Pest Control Point of View:

Steinernematids have been reported to be highly virulent to larvae of mosquitoes *Aedes* spp. (Chaudhary *et al.*, 2017; Dilipkumar *et al.*, 2019). They are symbiotically associated with the Gram-negative bacteria from the genus *Xenorhabdus*, which produce a combination of enzymes and toxins to overcome the host immune system and cause insect death (Shapiro-Ilan *et al.*, 2017, 2020). On the other side, EPNs of Heterorhabditidae are mutualistically associated with bacteria from the genus *Photorhabdus* (Family: Morganellaceae), which are carried within the guts of IJs (Boemare, 2002; Poinar and Grewal, 2012; Ferreria and Malan, 2014; Labaude and Griffin, 2018). These beneficial symbiotic bacteria, with EPNs, are able to kill and reproduce in many insect species (Mahar *et al.*, 2005).

In México, Ávila-López *et al.* (2021) investigated the effectiveness of different isolates of *Heterorhabditis* on larvae of *Ae. aegypti*. Depending on their results, the high mortality of larvae apparently was related to bacteria of the genus *Photorhabdus*, since this genus was numerically dominant compared to other non-symbiotic bacteria reported in this work. The EPN *Steinernema litorale* was first isolated from soil samples in Japan (Yoshida, 2004). Then, it has also been reported in soil samples from China and Pakistan (Shahina *et al.*, 2012; Wang *et al.*, 2014). Recently, *S. litorale* was isolated from Ankara, Turkey (Özdemir *et al.*, 2020). The symbiotic bacteria associated with *S. litorale* had been identified as *Xenorhabdus bovienii* (Kuwata *et al.*, 2006). Until now, some authors (Akhurst *et al.*, 2004; An and Grewal, 2011) have documented 24 species of symbiotic bacteria *Xenorhabdus* and five species of

Photorhabdus worldwide. The symbiotic bacterial species associated with *Neosteinerinema*, in the family Steinernematidae, is still unclear (Thanwisai *et al.*, 2022).

Some symbiotic bacteria, such as *Photorhabdus luminescens* and *Xenorhabdus nematophila* strains, have been shown to present oral toxicity to larvae of *Ae. aegypti* on their own (Ahn *et al.*, 2013; da Silva *et al.*, 2013). Some authors (Waterfield *et al.*, 2001; French-Constant *et al.*, 2007a) reported that *Ph. luminescens* and *X. nematophilus* produce a variety of protein toxins, some forming very large oligomeric tripartite toxin complexes that have high levels of toxicity toward the insect pests. According to other authors (Hurst *et al.*, 2000; Wilkinson *et al.*, 2009), other symbiotic bacteria, including *Photorhabdus asymbiotica*, *Xenorhabdus bovienii*, *Serratia entomophila*, *Yersinia entomophaga* and *Pseudomonas syringae*pv., also, produce similar toxin complexes.

8.3. The Potential Role of Isolated Symbiotic Bacteria from EPNs for Controlling Mosquito Vectors:

The symbiotic bacteria, like *Photorhabdus* and *Xenorhabdus*, with their bioactive compounds including antimicrobial, antiparasitic, insecticidal and other cytotoxic compounds, can effectively control many insect pests, including coleopteran, dipteran and lepidopteran pests (Manachini *et al.*, 2013; Kalia *et al.*, 2014; Mohan, 2015), as well as mosquito larvae (Da Silva *et al.*, 2013; Vitta *et al.*, 2018; Suwannaroj *et al.*, 2020; Thanwisai *et al.*, 2021).

For some detail, some reports have shown that the EPN-symbiotic bacteria *Xenorhabdus ehlersii* and *X. griffinae* serve as effective larvicide agents due to the high mortality against *Ae. aegypti* larvae (Fukruksa *et al.*, 2017; Thanwisai *et al.*, 2021). Tsai *et al.* (2008) isolated and identified the symbiotic bacterium of EPN *S. abbasi* to be *Xenorhabdus indica*. When exposed to *Ae. albopictus* larvae to this

isolated bacterium for 96 h, mortality rate of larvae was recorded between 82% and 96%. Da Silva *et al.* (2013) demonstrated that 73%–83% mortality of *Ae. aegypti* larvae treated with *Ph. luminescens* suspension, whereas *X. nematophila* killed 52% of fed larvae and 42% of unfed larvae in their fed-unfed treatments. Orally ingested cell suspensions of the symbiotic bacteria *Ph. luminescens* and *X. nematophila* exhibited high toxicity against culicine mosquitoes (Shrestha *et al.*, 2011; Da Silva *et al.*, 2020).

In Turkey, Shah *et al.* (2021) conducted a study to investigate the toxic effects of some isolated EPN-symbiotic bacteria on *Ae. aegypti*. Depending on their results, both bacterial supernatant and bacterial cell suspension of *X. nematophila* caused >91% larval mortality after 48 h, whereas only the bacterial cell suspension of *Ph. laumondii* was effective against the mosquito larvae. In Thailand, Vitta *et al.* (2018) assessed the effects of bacterial cell suspensions of *X. stockiae*, *X. indica*, *P. luminescens* subsp. *akhurstii* and *P. luminescens* subsp. *hainanensis* on both *Ae. aegypti* and *Ae. albopictus*. They recorded larval mortality between 66 and 73% for *Ae. aegypti* and 36 and 77% for *Ae. albopictus*, 48 h after treatment. In Thailand, also, Thanwisai *et al.* (2022) isolated some EPNs and their bacterial flora from soil samples and evaluated their efficacies for controlling mosquito larvae. Their bioassays demonstrated that isolates of *Photorhabdus* caused high larval mortality of both *Ae. aegypti* and *Cx. quinquefasciatus*. Also, *Photorhabdus* isolates were more toxic to larvae of these mosquitoes than *Xenorhabdus* isolates. In addition, Yooyangket *et al.* (2018) showed that the symbiotic bacteria *Xenorhabdus stockiae* and *Ph. luminescens* subsp. *akhurstii*, isolated from native EPNs, were highly toxic to larvae of *Ae. aegypti* and *Ae. albopictus*. Three years later, Thanwisai *et al.* (2021) isolated and identified some EPNs and their symbiotic bacteria, and assessed the bacterial toxic effects on *Ae. aegypti* larvae. They identified symbiotic

bacteria *Xenorhabdus stockiae*, *X. griffinae*, *X. indica*, *X. vietnamensis*, *Ph. luminescens* subsp. *akhurstii*, *P. temperata* subsp. *temperata* and *X. griffinae*. These isolated bacteria exhibited effective larvicidal activity against *Ae. aegypti* (91% mortality at 72 and 96 h after exposure). Moreover, some bioactive compounds had been isolated and identified from certain EPN-symbiotic bacteria, and then assessed against mosquitoes, as can be reviewed here. For example, several bioactive compounds/proteins from *Photorhabdus*, such as anthraquinones and PirAB protein, were found to be toxic to mosquitoes (Ahantarig *et al.*, 2009; Ahn *et al.*, 2013). Also, several secreted proteins and secondary metabolites from *Xenorhabdus* spp., including phenethylamides and indol derivatives (McInerney *et al.*, 1991a; Li *et al.*, 1998), xenorhabdins and xenooxides (Li *et al.*, 1998), xenocoumacins (McInerney *et al.*, 1991b), benzylideneacetone (Ji *et al.*, 2004) and iodine (Furgani *et al.*, 2009) were effective in controlling culicine mosquitoes (Bode, 2009; Chaston *et al.*, 2011).

In this context, also, novel formulations of symbiotic bacterial toxins have also been studied (Thanwisai *et al.*, 2022). For example, synthesized gold and silver nanoparticles coated with a supernatant of *Ph. luminescens* strain KPR-8B caused high mortality of *Ae. aegypti*, *An. stephensi*, and *Cx. quinquefasciatus* (Aiswarya *et al.*, 2019), while combining *Xenorhabdus* or *Photorhabdus* with Cry4Ba toxin from *Bacillus thuringiensis* exhibited larvicidal activity against *Ae. aegypti* (Park, 2015). Therefore, it is very important, in the future, to identify and test more strains of symbiotic bacteria in order to develop new potential strategies to control mosquito vectors.

9. Suppressive Activity of EPN/Symbiotic Bacteria Complex against Innate Immune Defences of Mosquito Larvae:

9.1. Major Defences of Insect Larvae against EPNs - A Synopsis:

Although it has been previously pointed out, the major defence reactions of insects against invading pathogens need some detail. The first line of defense against pathogens involves physical barriers, such as the adult exoskeleton, the larval cuticle, the chitinous lining of the tracheae and the peritrophic membrane of the midgut (Ganesan *et al.* 2011; Davis and Engström, 2012; Parsons and Foley, 2016). These primary defences include, also, behavioural avoidance and physicochemical mechanisms (Schmid-Hempel and Ebert, 2003; Kunc *et al.*, 2017). For successful infection, the pathogen, like EPNs, must overcome the external and primary defenses and gain access to the insect haemocoel. It can be recognized as a foreign body by the insect host (Stokes *et al.*, 2015). In the insect, immune recognition leads to the induction of downstream signaling pathways resulting in the production of effector molecules and the activation of immune responses against this invading EPN (Buchon *et al.*, 2014).

To get a deeper understanding of the interaction between insect and invading EPNs, it should not be forgotten that insects have no acquired immune defences like vertebrates, but only innate immunity comprising humoral and cellular defences (Janeway and Medzhitov, 2002; Hoffmann, 2003; Strand, 2008; Berger and Jurcova, 2012). These innate immune defences should be activated to defend against the invading pathogen which succeeded in passing the external defences (Hoffmann, 2003; Irving *et al.*, 2005; Jing *et al.*, 2010; Tsakas and Marmaras, 2010). As reported by some authors (Schmidt *et al.* 2001; Hultmark, 2003; Grewal *et al.*, 2005), any immune reaction of the insect host is preceded by the interaction of characterized pattern-recognition receptors (PRRs) that are used to interact specifically with a broad range of foreign antigenic compounds, commonly known as pathogen-associated molecular patterns (PAMPs) lead to defensive reactions. The PAMPs from invaders are recognized by free or cell-

associated host receptors (PRRs). Following this interaction, insect hemocytes become stimulated and initiate defense mechanisms, such as encapsulation, nodulation, phagocytosis and prophenoloxidase release (Das *et al.*, 2009; Hillyer, 2010; Rosales, 2011; Dubovskiy *et al.*, 2016).

In connection with mosquitoes, when entomopathogens try to enter the adult body, due to an accidental break or lesion in the outer cuticle, several events are activated to prevent pathogen entry, such as coagulation, melanization, hemocyte degranulation, and scar formation (Lai *et al.*, 2001, 2002). Once the pathogen enters the mosquito body, the mosquito uses its innate immune system, comprising of cellular and humoral components, to fight pathogens (Strand, 2008). The immune system of adult mosquitoes has received great attention from researchers because of the ability of females to vector disease-causing pathogens while ingesting blood meals. On the contrary, few research works have focused on the immune system of larvae, although some authors (League and Hillyer, 2016; League *et al.*, 2017) reported its stronger immune defences than that of adults. Therefore, this section in the present review deals with the immune reactions between mosquito larvae and invading EPNs, not between mosquito adults and EPNs.

9.2. Cellular Immune Defences of Mosquito Larvae against EPN/symbiotic Bacteria Complex:

As reviewed by several authors (Ribeiro and Brehelin, 2006; Manachini *et al.*, 2011; Siddiqui and Al-Khalifa, 2014; Ghoneim *et al.*, 2021), there are several types of hemocytes in insects. The most common types are prohaemocytes (PRs), plasmatocytes (PLs), granulocytes (GRs), spherulocytes (SPs), adipohaemocytes (ADs), coagulocytes (CGs) and oenocytoids (OEs). Not all of these hemocyte types exist in all insect species. The immunocyte-mediated responses in insects, like phagocytosis, nodulation,

encapsulation and clotting, are principally achieved by the hemocyte types, like PLs and GRs in the lepidopterous insects (Lavine and Strand, 2002; Ribeiro and Brehelin, 2006; Strand, 2008; Browne *et al.*, 2013). It is important to shed some light on the major mechanisms of the insect cellular immune defenses against EPNs in the following few paragraphs.

Encapsulation of EPNs by the insect larvae: The cellular encapsulation results in a multilayer cellular capsule (overlapping layers of cells) and/or a melanin coat that encloses and kills the intruder (Ling *et al.*, 2005). Also, encapsulation is known to begin within the first minutes after haemolymph penetration by a larger foreign body, where hemocytes attach to it forming a surrounding capsule (Marmaras and Lampropoulou, 2009; Dubovskiy *et al.*, 2016). In respect of the contribution of certain hemocyte types in the encapsulation process, GRs were reported to contact a foreign targeted body, disintegrate or degranulate liberating material that endorses attachment of PLs and subsequently multiple layers of PLs form the capsule. Depending on several reported results, it is well-known that the encapsulation responses of the insects varied according to the insect species and EPN species (Ebrahimi *et al.*, 2011; Rahatkhah *et al.*, 2015; Istkhar and Chaubey, 2019; Ghoneim *et al.*, 2023c).

Nodulation (Nodule formation) of EPNs by the insect larvae: Nodulation in insects is a cellular immune process whereby hemocytes recognize a foreign body, like EPN, and insulate it within the haemocoel as well as aggregate large numbers of invading symbiotic bacteria (Lavine and Strand, 2002; Marmaras and Lampropoulou, 2009). The enzyme phenoloxidase in haemolymph can hydroxylate tyrosine and oxidize *o*-diphenols to quinones (Gorman *et al.*, 2007). These quinones undergo a series of additional enzymatic and non-enzymatic reactions leading to melanin synthesis in the final stages of nodulation against the

invading body (Zibae *et al.*, 2011). In other words, the host hemocytes release humoral factors that form multicellular hemocyte aggregates, called "nodules" against many symbiotic bacterial cells. These nodular aggregates may adhere to host tissues and larger nodules may eventually be encapsulated by the hemocytes (Mullen and Goldsworthy, 2006; Dubovskiy *et al.*, 2016).

Phagocytic activity of the larval hemocytes against EPNs: Specific insect hemocytes migrate towards and engulf several targets, in a process called 'phagocytosis' (Wood and Jacinto, 2007; Marmaras and Lampropoulou, 2009). Some authors (Tojo *et al.*, 2000; Kwon *et al.*, 2014; Melcarne *et al.*, 2019) reported that both GRs and PLs have been shown to be capable of phagocytosis. These two hemocyte types are recognized as the immunocompetent cells in most lepidopterous insects (Brillard *et al.*, 2001). As shown in the available literature, the following release of the symbiotic bacteria *Photorhabdus* from the IJs into the insect haemolymph, the first response of the host immune system is to phagocytose or encapsulate the invading bacteria (Eleftherianos *et al.*, 2010 a, b).

Limited knowledge exists in the available literature on the cellular immune interactions between larvae of mosquitoes and ENPs. Early, Welch and Bronskill (1962) reported that *S. carpocapsae* could kill more than 82% of *Ae. aegypti* larvae before pupating although a great number of EPN individuals were encapsulated shortly after penetrating through the gut wall into the haemocoel. Also, Molta and Hominick (1989) reported that larvae of *A. aegypti* and other *Aedes* spp. could encapsulate a number of the IJs of *S. carpocapsae*, *S. feltiae* and *H. heliothidis*, while the remainder of the EPN/symbiotic bacteria complex caused their death. In a study conducted by Shamseldean *et al.* (2006) on *An. quadrimaculatus* larvae against the invasion of nematode *R. culicivora*, the mosquito hemocyte recognition of *R. culicivora* began immediately after

infection. Cellular encapsulation was detected. The populations of PLs and GRs increased or their products adhered to invading nematodes within minutes of infection. In another study, Shamseldean *et al.* (2007) examined the interactions between mosquitoes, *An. quadrimaculatus* and *Cx. pipiens*, and *R. culicivora* using the scanning electron microscopy. According to their observations, the mosquito immune system rapidly recognized the invading nematodes, as GRs and discharged granules were observed attached to *R. culicivora* within 5 min. On the other hand, *R. culicivora* secreted and shed an extracellular surface coat which aided immune evasion.

More than a decade later, Liu *et al.* (2020) demonstrated that the basement membrane-like structures formed an outer surface of the capsule enclosing the EPN *S. abbasi* in haemocoel of larvae of mosquito *Ae. albopictus* at 48 h after inoculation. These encapsulation structures seem effective in suppressing the development of *S. abbasi*. The death of some EPN was also observed by Poinar and Kaul (1982) with *H. bacteriophora* in *Cx. pipiens* larvae. To a great extent, these results were in agreement with the reported results of Liu *et al.* (1998) for the mosquito *An. quadrimaculatus* after infection with a nematode, *Brugia malayi*. Eventually, the mosquito larvae failed to recover and died a few days after infection but only a few larvae were able to survive to adult emergence.

9.3. Humoral Immune Defences of Mosquito Larvae against EPN/Symbiotic Bacteria Complex:

Humoral immune responses in insects include some processes, such as the production of antimicrobial peptides (Schmid-Hempel, 2005; Wang and Zhang, 2008), reactive intermediates of oxygen or nitrogen (Vass and Nappi, 2001), and the complex enzymatic cascades that regulate coagulation or melanization of haemolymph (also called 'humoral encapsulation') (Gillespie *et al.*, 1997;

Cerenius *et al.*, 2008). The melanization is achieved as a consequence of the activation of the inactive prophenoloxidase (proPO) to phenoloxidase (PO) (Cerenius and Soderhall, 2004; Shelby and Popham, 2006; Cytrynska *et al.*, 2007). This enzymatic activation requires protease cascades triggered by the detection of specific microbial patterns (Cerenius *et al.*, 2008; Eliáš *et al.*, 2020). Shortly, the melanization response in insects, as a humoral immune defence, involves the deposition of melanin to invading pathogens. The melanization reaction needs PO which catalyzes the oxidation of mono- and diphenols to orthoquinones (Eleftherianos and Revenis, 2011; Lu *et al.*, 2014).

According to the current literature, scarce studies investigated the humoral immune interactions between larvae of mosquitoes and ENPs. Molta and Hominick (1989) detected a decreasing melanization of EPNs *H. heliothidis* and *S. feltie* with the increasing number of IJs entering *A. aegypti* larvae. Such a result disagreed with the result of Peschiutta *et al.* (2014) who found that the number of melanized *H. bacteriophora* was higher when the number of IJs inside the *Ae. aegypti* larvae increased. However, IJs can release their symbiotic bacteria into haemocoel of the host although a certain number of IJs were melanized (Poinar and Kaul, 1982). Back date, Petersen and Willis (1974) suggested that the largest number of melanized IJs can be found in the abdomen and thorax of mosquito larvae, although Pandii *et al.* (2010) found that the nematode infestation was greatest in the thorax and the head of the host and the non-melanized IJs continued their development within the host.

A decade later, Ansari and Hussain (2020) assessed the pathogenic effects of the EPNs *H. bacteriophora*, *H. downesi*, *H. megidis*, *S. carpocapsae*, *S. feltiae* and *S. krausseii* against the 3rd instar larvae of *Ae. aegypti*. Based on their results, larvae indiscriminately overfed EPNs triggering melanization but the ingested

EPNs succeeded in suppressing the defence system resulting in the death of larvae and reproduced within their cadavers. However, some EPN individuals were melanised, suggesting a strong humoral defence response by *Ae. aegypti* larvae. A year later, Shah *et al.* (2021) observed a melanization of some *Heterorhabditis* and *Steinernema* EPNs in the 3rd and 4th instar larvae of *Ae. aegypti*, suggesting a strong humoral immune defense of these larvae. However, the degree of melanization was quite variable since some EPNs were completely enveloped in a melanin sheath while others were partially coated with melanin. Moreover, melanization did not prevent the EPN from multiplying and killing the *Aedes* larvae, since IJs released from infected larvae would have the potential to infect healthy larvae of *Ae. aegypti*.

Another point of interest in this context is the production of some secondary toxic metabolites against insects by the EPN-symbiotic bacteria. The pathogenicity of these toxins to insects occurs *via* the suppression of insect immune responses (Ullah *et al.*, 2014). These toxic metabolites result in the generation of reactive oxygen species (ROS). The high levels of these free radicals usually result in detrimental effects on cells and tissues in the host (Wang *et al.*, 2001; Wu and Liu, 2012). Therefore, insects must remove or scavenge ROS before cell damage occurs (Feig *et al.*, 1994). On the other hand, certain components of the insect immune system produce ROS as a tool to limit microbial growth (Lalitha *et al.*, 2018). In addition, insects mainly protected themselves with antioxidant enzymes, such as Superoxide dismutase (SOD) could effectively remove O²⁻ and convert it into H₂O₂, Catalase (CAT) and Peroxidase (POD) work together to remove H₂O₂, which these antioxidant enzymes coordinated to regulate ROS in insects to keep them in dynamic balance (Felton and Summers, 1995; Federico *et al.*, 2012).

In recent years, Xiong *et al.* (2021) infected the *Ae. aegypti* larvae with the EPN

R. wuchangensis, and investigated the activities of SOD, POD and CAT during the lethal period of the host. Compared to control group, the quantitative real-time PCR analysis results demonstrated that SOD, POD and CAT genes had obvious high expression levels in the nematodes parasitic groups. The antioxidant enzyme test results also exhibited obvious differences in SOD, CAT and POD during the nematode parasitic period.

It is important to point out that not only the EPNs but also their symbiotic bacteria collaborate to suppress the immune response of the insect (Dowds and Peters, 2002). For instance, the EPN *S. carpocapsae* and its symbiotic bacterium *X. nematophila* can inhibit the antibacterial peptide immune reaction of insects (Binda-Rossetti *et al.*, 2016). In a study, Toubarro *et al.* (2013) found *S. carpocapsae* displaying destructive approaches for host immunity through proteolytic secretion which inhibits host immunological defenses. Both EPN-symbiotic bacteria, *Photorhabdus* and *Xenorhabdus* have displayed similar lifestyles but have different molecular defensive mechanisms (Goodrich-Blair and Clarke, 2007). The symbiotic bacteria *Xenorhabdus* spp. inhibits the host's immune system by producing a variety of toxins and carrying type III effector molecules that may interfere with the actin cytoskeleton and prevent phagocytosis (Dillman *et al.*, 2012a). *Photorhabdus* used lipopolysaccharide (LPS) modification to resist the action of the host-derived antimicrobial peptide (AMPs) (Eleftherianos *et al.*, 2006), while *Xenorhabdus* prevents induction of insect AMP expression altogether (Istkhari *et al.*, 2019). In insects, the pathogenic impacts of symbiotic bacteria and the anti-bacterial resistance mechanisms have been well described, however, nematode-associated defenses are nowadays primarily the focus of research (Sikandar *et al.*, 2021). To the best of our knowledge, no information exists in the available literature concerning

the mechanism of immune suppression in mosquito larvae by EPN-symbiotic bacteria.

10. Important Research Priorities and Future Prospects:

When the EPNs were applied against mosquito larvae in critical concentration under suitable environmental conditions, they will be highly potential biocontrol agents fighting the mosquito vectors and they are considered to be equal to chemical pesticides against these human-disease transmitters. It is important to take into consideration that the environmental parameters (biotic and abiotic factors), application technique, and other factors influencing the EPN virulence against insect pests. An EPN to become more effective biocontrol agent, it is needed to adapt to the environmental conditions on the application sites. Also, the physicochemical parameters of water in the oviposition and breeding sites should be taken into consideration to be optimal for allowing the EPN to reproduce and to continue parasitizing larval mosquitoes over a long period.

However, the majority of EPNs bioassays had been conducted in the laboratory. This does not provide an assurance of field efficacy of EPNs. Therefore, field application studies at greater scales represent a fundamental task for the future. Nevertheless, they guaranteed the promising value of using EPNs for controlling the aquatic mosquito larvae. In addition, it is very important, in the future, to identify and test more strains of EPN-symbiotic bacteria in order to develop new potential strategies to control mosquito vectors, especially some isolated bioactive compounds of these bacteria.

11. Summary Points:

* The mosquito family Culicidae contains 112 genera comprising over 4500 species of mosquitoes in the world. The genus *Aedes* only includes over 950 described species. Medically, the most dangerous genera are *Anopheles*, *Aedes* and *Culex* due to their ability to transmit mosquito-borne human

diseases. These mosquito genera transmit various pathogens causing nearly 350 million cases and nearly half a million deaths per year worldwide.

* The mosquito control is urgent for fighting with the increasing number of mosquito-borne diseases. Generally, chemical insecticides have been widely used to suppress the epidemics of mosquito-transmitted diseases. These chemicals were evidenced to be less-than-perfect solutions for the long-lasting control of mosquitoes. The serious problem facing insecticide usage for mosquito control is the development of insecticide resistance which was evidently confirmed in all mosquito species all over the world.

* It is urgent to search for alternative agents to suppress the mosquito populations and to avoid or minimize the insecticidal hazards on ecosystem components. During the last few decades, biological control of mosquitoes received a great research attention in the world, as environmentally friendly agents to control mosquito vectors. Various microbial control agents, such as nuclear polyhedrosis viruses, entomopathogenic bacteria, entomopathogenic fungi, entomopathogenic nematodes and protozoa, have been assessed for the control of several pests as an alternative to synthetic insecticides.

* Terrestrial nematodes are soil-dwelling attacking insect pests that live in, on, or near the soil surface. Also, they can inhabit almost all around the world with different geographical and climatic conditions. "Entomopathogenic Nematodes" (EPNs) have been recorded on all continents except Antarctica.

* Unlike chemical insecticides, EPNs are target-specific with a wide range of insect pests. Despite widespread use in fields, gardens, and pasture lands, no significant acute or chronic toxicity to humans or vertebrates has been reported. EPNs, which infect and kill their insect hosts within a few days, are currently used for controlling

agricultural pests, as well as mosquito vectors.

*The EPN families Steinernematidae, Heterorhabditidae and Rhabditidae have a life cycle including the egg stage, four juvenile stages and adult stage. The 3rd juvenile stage is known as the "infective juvenile stage (IJs)", or "dauer" stage which is the only free-living stage and can survive a long time without feeding. A common feature of *Heterorhabditis* and *Steinernema* EPNs is IJs harbor the mutualistic *Photorhabdus* and *Xenorhabdus* bacteria, respectively.

* The IJs invade the host's body cavity through natural openings, such as the mouth, anus, or spiracles; or, in some cases, directly through the intersegmental membranes and other delicate areas of the thin cuticle of certain insects. In the insect haemocoel, the IJs release specialized symbiotic bacteria which grow rapidly and proliferate in the insect haemocoel and produce toxins eventually inducing septicemia for killing the insect host usually within 24-72 hours post-infection.

* Over the past decades, EPNs have been a great global consideration in the field of biocontrol of serious agricultural insect pests. However, relatively few studies were conducted to investigate the effectiveness of EPNs against mosquitoes. By that time, EPNs have attracted much attention from researchers and research institutions worldwide as effective and safe biocontrol agents for suppressing mosquito populations.

* Nematodes of the order Mermithida parasitize arthropods and snails and some other invertebrates. This order comprises both terrestrial and aquatic species. Numerous mermithids have been found in mosquitoes on every continent except Antarctica. Until 2001, seven genera of the Mermithidae were found in the larval bodies of mosquitoes all over the world.

* The most attracting species of Mermithidae to the research attention are *Romanomermis culicivorax* and *R. iyengari*. These two species have gained a great

interest in the control of mosquito breeding in different types of habitats. Because of a host range that includes mosquitoes of the public health vectors, several studies were carried out using mermithids against larvae of mosquitoes, such as *Culex* sp. and other genera.

* In contrast to the several advantages of mermithid EPNs, as biocontrol agents of mosquito vectors, their major disadvantages should be known before application. It has proven difficult to commercialize these nematodes because their viability is difficult to maintain in storage and transportation. Also, mermithid EPNs have high specificity towards their hosts and are difficult in mass production, subsequently, their potential for commercial use has been limited.

* An alternative to the mermithid EPNs is the use of EPNs from families Steinernematidae and Heterorhabditidae, which are natural parasites of many insects and have been developed as biological control agents used widely in the agricultural field.

* Steinernematidae and Heterorhabditidae are naturally terrestrial-living EPNs. They are the most economically important families among the 23 families of Nematoda. These two families are established worldwide in diverse ecological habitats.

* Steinernematid and Heterorhabditid EPNs are characterized by mutualistic association with specialized symbiotic bacteria of the genera *Xenorhabdus* and *Photorhabdus*, respectively, in their intestines. These symbiotic bacteria are essential agents for the death of insect hosts by the suppression of mosquito immune defences within approximately 48 h.

* Steinernematid and heterorhabditid EPNs are more advantageous than mermithid nematodes because the former families can be developed *in vivo* in alternate hosts or *in vitro* on artificial media. A second advantage is the longevity of IJs (3~6 months in water at room temperature), and it is also characterized by a short life

cycle. Non-toxicity of *Steinernema* spp. and *Heterorhabditis* spp. to humans, target specificity and compatibility with some insecticides enabled these EPNs are accurately in the spectrum of integrated pest management.

*Although steinernematids and heterorhabditids are naturally terrestrial EPNs, the aquatic habitat offers a suitable environment for their survival. Also, EPNs can be applied alone, as a biocontrol agent, or combined with other biocontrol agents, such as entomopathogenic bacteria and fungi in order to improve their efficacy in controlling insect pests.

*Many results report dose-dependent mortality of mosquito larvae by various EPNs. Some studies revealed higher susceptibility of later instars (3rd and 4th instars) while other studies documented the earlier instars (1st and 2nd instars) as more susceptible. Many studies reported superior virulence of certain EPN species over other EPN species against the same mosquito species. The variable susceptibility of different mosquito species to the same EPN species can be due to their variation of specific physiological, physical and/or behavioural characteristics of the host larvae.

* The virulence of EPNs against insect pests varies greatly depending on their characteristics, such as reproductive capacity, host-seeking behaviors, host specificity and adaptation capabilities. Also, the environmental parameters (biotic and abiotic factors), application technique, and others have influenced the EPN virulence against insect pests. In addition, the physicochemical parameters of water in the oviposition sites should be taken into consideration to be optimal for allowing the EPN to reproduce and to continue parasitizing larval mosquitoes over a long period.

* The fitness of an EPN can be adversely affected by increasing its population density within the host body. This has been reported in mermithid nematodes in mosquito larvae. Density-dependent effects on an EPN

include reduced fecundity, increased mortality, change in sex ratio, reduction in adult size, increased generation time and reduced oviposition.

* The ambient temperature is one of the limiting factors of EPN virulence. Some research works investigated the effect of the ambient temperature on EPN virulence against insect pests. Also, for successful mosquito control by EPNs, the nematode effective concentration should be determined.

* Concerning the IJs production, differences among the reproduction potential of EPNs may related to the EPN species, isolates, host susceptibility, number of bacteria per infective stage, invasion rate, temperature and other factors. Among factors influencing the EPN virulence, also, is the symbiotic bacteria in the nematode IJs.

* Many authors reported the death of insect hosts within 24-72 hrs post-infection with EPNs, regardless of the insect species and the EPN species. On the other hand, other authors reported that some infected individuals of the insect can avoid the lethal effects of EPN and its symbiotic bacteria by some immune defences and developmentally transform into the next stage. However, these insects seem to be unhealthy because certain biological and physiological processes have been adversely affected.

*Until now, some authors have documented 24 species of symbiotic bacteria *Xenorhabdus* associating steinernematid EPNs and five species of *Photorhabdus* associating heterorhabditid EPNs worldwide. Some *Photorhabdus* and *Xenorhabdus* strains have been shown to present oral toxicity to larvae of *A. aegypti* on their own. Moreover, some bioactive compounds had been isolated and identified from certain EPN-symbiotic bacteria and then assessed against mosquitoes.

* With regard to the immune interactions between mosquito larvae and invading EPN, once EPN overcomes the external defenses and gains access to the insect

haemocoel, they are recognized as foreign bodies by the insect. Immune recognition leads to the induction of downstream signaling pathways resulting in the production of effector molecules and the activation of immune responses against the invading EPN. Insects, in general, have innate immunity comprising humoral (melanization of the intruder using phenoloxidase and some secondary toxic metabolites) and cellular (encapsulation, nodulation, phagocytosis) defences. These innate immune defences should be activated to defend against the invading EPN which succeeded in passing the external defences. On the other hand, EPN and its symbiotic bacteria produce several active and toxic products to suppress and overcome the insect immune defences to gain successful infection.

12. Conclusions:

It is urgent to search for alternative agents to suppress the mosquito populations and to avoid or minimize the insecticidal hazards on ecosystem components. Entomopathogenic nematodes (EPNs) have been reported as good alternatives to synthetic insecticides because EPNs are target-specific with a wide range of mosquito species with no significant acute or chronic toxicity to non-target organisms, humans and the environment. Some advantages of EPNs, also, are their high reproductive potential, the ability to kill hosts quickly, high virulence, and easy mass rearing.

Although EPNs have been reported as very effective biocontrol agents against many agricultural insect pests, they, also, have attracted much attention from research institutions worldwide as effective and safe biocontrol agents for suppressing mosquito populations. Some identified species of families of Mermithidae (aquatic nematodes), Steinernematidae and Heterorhabditidae (terrestrial nematodes) had gained intensive research for control of mosquito vectors with promising results. Moreover, their mutualistic bacteria are

widely used in biological control programs, as an alternative to chemical insecticides.

Also, the application of EPNs in an integrated approach in combination with certain insecticides or transgenic mosquitoes expressing insecticidal proteins can function in synergy to substantially increase their efficacy in controlling insect pests in the field. In addition to pest control, EPNs form excellent models for dissecting the molecular and mechanistic basis of nematode parasitism, bacterial virulence, microbial mutualism and elucidating the interaction among these important biological functions. In addition, these EPNs and their symbiotic bacteria are outstanding pathogenic organisms for probing the insect host anti-nematode and antibacterial immune response.

Declarations:

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