Entomopathogenic Nematodes for Control of Insect Pests Above and Below Ground with Comments on Commercial Production

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Abstract: Entomopathogenic nematodes (EPNs) have been utilized in classical, conservation, and augmentative biological control programs. The vast majority of applied research has focused on their potential as inundatively applied augmentative biological control agents. Extensive research over the past three decades has demonstrated both their successes and failures for control of insect pests of crops, ornamental plants, trees and lawn and turf. In this paper we present highlights of their development for control of insect pests above and below ground. The target insects include those from foliar, soil surface, cryptic and subterranean habitats. Advances in mass-production and formulation technology of EPNs, the discovery of numerous efficacious isolates/strains, and the desirability of reducing pesticide usage have resulted in a surge of commercial use and development of EPNs. Commercially produced EPNs are currently in use for control of scarab larvae in lawns and turf, fungus gnats in mushroom production, invasive mole crickets in lawn and turf, black vine weevil in nursery plants, and Diaprepes root weevil in citrus in addition to other pest insects. However, demonstrated successful control of several other insects, often has not lead to capture of a significant share of the pesticide market for these pests.

Key words: biological control, commercialization, cryptic habitats, Epigeal habitats, entomopathogenic nematode, Heterorhabditis bacteriophora, Heterorhabditis megidis, Heterorhabditis zealandica, Steinernema carpocapsae, Steinernema feltiae, Steinernema glaseri, Steinernema riobrave, Steinernema scapterisci, Steinernema scarabaei, subterranean habitats.

Nematodes that parasitize insects, known as entomopathogenic nematodes (EPNs), have been described from 23 nematode families (Koppenhöfer, 2007). Of all of the nematodes studied for biological control of insects, the Steinernematidae and Heterorhabditidae have received the most attention because they possess many of the attributes of effective biological control agents (Kaya and Gaugler, 1993; Grewal et al., 2005a; Koppenhöfer, 2007) and have been utilized as classical, conservational, and augmentative biological control agents. The vast majority of applied research has focused on their potential as inundatively applied augmentative biological control agents (Grewal et al., 2005a). Extensive research over the past three decades has demonstrated both their successes and failures for control of insect pests of crops, ornamental, and lawn and turf (Shapiro-Ilan et al., 2002; Georgis et al., 2006). The main advantages and disadvantages of EPNs are presented in Table 1. They can be considered good candidates for integrated pest management and sustainable agriculture due to a variety of attributes in addition to those presented in Table 1: some species can recycle and persist in the environment; they may have direct and/or indirect effects on populations of plant parasitic nematodes and plant pathogens; can play an indirect role in improving soil quality; and are compatible with a wide range of chemical and biological pesticides used in IPM programs. This paper will review selected literature on the successful use of EPNs for control of insect pests above and below ground and discuss aspects of their commercialization.

Entomorathogenic Nematodes for Control OF INSECT PESTS

Selection of an EPN for control of a particular pest insect is based on several factors that include the nematode's host range, host finding or foraging strategy, tolerance of environmental factors and their effects on survival and efficacy (temperature, moisture, soil type, exposure to ultraviolet light, salinity and organic content of soil, means of application, agrochemicals, and others). The 4 most critical factors are moisture, temperature, pathogenicity for the targeted insect, and foraging strategy (Kung et al., 1991; Kaya and Gaugler, 1993; Campbell et al., 2003; Grewal et al., 2005a). Within a favorable range of temperatures, adequate moisture and a susceptible host, those EPNs with a mobile foraging strategy (cruisers and intermediate foraging strategies) could be considered for use in subterranean and certain above-ground habitats (foliar, epigeal and cryptic habitats). Those with a sit and wait foraging strategy (ambushers) will be most effective in cryptic and soil surface habitats.

The effects of environmental factors (such as temperature, moisture, aeration, and soil type [esp. texture and chemistry]) and biotic factors (species of EPN, targeted insect, age of insect, soil fauna) have been documented by numerous researchers (Gaugler and Kaya, 1990; Kaya and Gaugler, 1993; Shapiro-Ilan et al., 2012; Grewal et al., 2005a; Georgis et al., 2006). Temperature range for survival and infectivity will depend on the species of EPN and its native habitat and center of origin (Kaya, 1990). For example, Steinernema feltiae can be infective from 2-30°C, whereas some heterorhabditids can infect host insects from 7 to 35°C and Steinernema carpocapsae is nearly inactive at 10°C (Kaya, 1990; Georgis et al., 2006; Lacey et al., 2006a).

Subterranean habitats. EPNs are predominantly isolated from soil habitats and not surprisingly, many

Received for publication March 6, 2012.

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This paper was edited by Nancy Kokalis-Burelle.

Advantages and disadvantages of entomopathogenic nematodes (modified from Shapiro-Ilan et al., 2012). Table 1.

Disadvantages Broad pest insect host range Cost of production Rapid speed of kill Limited shelf-life and refrigerated storage required Environmental limitations: requirements for adequate moisture (to enable Can actively seek or ambush host survival and infectivity) and temperatures (above or below that required for optimal infectivity), sensitivity to UV radiation, lethal effect of several pesticides (nematicides, fumigants and others), lethal or restrictive soil chemistries (high salinity, high or low pH, etc.). Mass in vivo and in vitro production capability Possible to use conventional application equipment Safety: for all vertebrates, most non-target invertebrates, and the food supply Little or no registration required

subterranean insects have received attention for control efforts with EPNs, notably white grubs of the family Scarabaeidae and weevils (Coleoptera:Curculionidae). Scarab larvae are the principle insect pests of lawn and turf while many of the adults are polyphagous pests of flowers and foliage. Damage caused by larvae (grubs) in golf courses has resulted in implementation of control using chemical pesticides and increasingly, EPNs.

White grubs are among the more difficult insects to control with EPNs because they have developed various morphological and behavioral barriers to infection (Klein et al. 2007). Among white grub species that are important pests of turf in the USA, the Japanese beetle, *Popillia japonica* appears to be the most EPN-susceptible species (Grewal et al., 2005b; Klein et al., 2007). The first EPN species that was used for control of scarabs on a widespread basis was Steinernema glaseri. (Gaugler et al., 1992). Its efficacy against scarab larvae, most notably the *P. japonica*, has been documented by several researchers (Gaugler et al., 1992). EPNs that have provided good field control of P. japonica include S. scarabaei (100%), H. bacteriophora (strain GPS11) (34-97%), H. bacteriophora (strain TF) (65-92%), and H. zealandica (strain X1) (73–98%) (Grewal et al., 2005b; Koppenhöfer et al., 2006). Among these, two species, H. bacteriophora and H. zealandica, are commercially available for grub control (Grewal et al., 2005b).

Numerous examples of research and practical use of EPNs for control of *P. japonica* larvae and those of several scarab species are reviewed by Klein (1990), Kaya and Gaugler (1993), Grewal et al., (2005b), Lewis and Clarke (2012), Shapiro, et al. (2002, 2012). The infectivity of Steinernema scarabaei, S. glaseri, Heterorhabditis zealandica, and Heterorhabditis bacteriophora for the Oriental Beetle, Anomala orientalis, and P. japonica was tested in loamy sand, sandy loam, loam, silt loam, clay loam, acidic sand, and an organic potting mix by Koppenhöfer and Fuzy (2006). The two Heterorhabditis spp. were most infective in potting mix, and S. scarabaei was most infective in loamy sand in the greenhouse. In a greenhouse study, S. glaseri was equally infective in all soil types. Acidic sand had a negative effect on

infectivity of all species in laboratory experiments. Persistence of S. scarabaei was highest in all soil types but its recovery declined significantly over time only in clay loam. Cappaert and Koppenhöfer (2003) also demonstrated overwinter persistence in treated field plots.

The combination of EPNs and other control agents has proved to be synergistic and produces higher mortality than either agent alone. For example, Koppenhöfer and Kaya (1997) showed additive and synergistic interaction between EPNs and Bacillus thuringiensis for scarab grub control. Koppenhöfer and Kaya (1998), Koppenhöfer et al. (2000), Polavarapu et al. (2007), and Koppenhöfer and Fuzy (2008), demonstrated synergism between the neonicotinoid insecticide, imidacloprid and EPNs. However, Cappaert and Koppenhöfer (2003) observed antagonism between imidacloprid and S. scarabaei for control of the European chafer, Rhizotrogus majalis (Scarabaeidae). Despite the demonstrated synergistic effect of the combined use of EPNs and other control methods, this strategy has yet to be used on a practical basis for control of scarab larvae.

Successful control of weevils, pests of small fruit crops, ornamentals and turf has been reported by several researchers. One of the most studied pest species is the black vine weevil, Otiorhynchus sulcatus (Curculionidae). Kakouli-Duarte et al. (1997) conducted field trials for control of O. sulcatus larvae in strawberry plants using S. carpocapsae and Heterorhabditis megidis. In field experiments, drip irrigation was used to distribute infective juveniles (IJs) along and across raised strawberry beds. Steinernema carpocapsae treatment in late summer produced 49.5% reduction of early instar O. sulcatus larvae, and late spring application resulted in 65% control of late instar larvae. Whereas spring application of *H. megidis* caused only 26% mortality of late instar larvae. Results of studies by Haukeland and Lola-Luz (2010) in Ireland and Norway demonstrated that H. megidis provided good control of O. sulcatus as long as temperatures were above 10°C.

Ansari et al. (2008) observed that application of the fungus, Metarhizium anisopliae (Hypocreales), following 1 or 2 weeks later by either *Heterorhabditis bacteriophora*, *S. feltiae* or *Steinernema kraussei* provided 100% control of third-instar *O. sulcatus*. The authors suggest that EPN and *M. anisopliae* act synergistically for control of the weevil in potted winter creeper, *Euonymus fortune*, under greenhouse conditions. Other examples of weevil control are provided by: Klein (1990), Simser and Roberts (1994), Booth et al. (2002), van Tol and Raupp (2005), Georgis et al. (2006), and McGraw and Koppenhöfer (2008). See below *EPN application for control of insects in soil surface habitats*.

Continued prospection for new EPN species or races that are infective for scarabs and weevils is highly warranted. For example, Cappaert and Koppenhöfer (2003) and Koppenhöfer and Fuzy (2003) demonstrated elevated pathogenicity of S. scarabaei against P. japonica, A. orientalis, R. majalis, northern masked chafer, Cyclocephala borealis, and Asian garden beetle, Maladera castanea compared to other EPNs. Additionally, this species can persist in the environment for considerable periods (Cappaert and Koppenhöfer, 2003; Koppenhöfer and Fuzy, 2009). Experimental evaluations of several species for scarab control in turf and lawn include H. bacteriophora, H. megidis, and new isolates of Heterorhabditis spp. and Steinernema kushidai and Steinernema spp. (Shapiro-Ilan et al., 2002; Grewal et al. 2004).

Fungus gnats, Lycoriella spp. and Bradysia spp. (Diptera: Sciaridae) are significant subterranean pests in mushroom production and cultivation of greenhouse plants, respectively. Steinernema feltiae and Heterorhabditis spp. have demonstrated good efficacy for control of L. auripilla, L. mali, L. solani, B. coprophila and B. difformis (Scheepmaker et al., 1998a, 1998b; Jagdale et al., 2004, 2007; Jess et al. 2005; Tomalak et al., 2005; Grewal, 2007). Application rates of 1.0 to 1.5 x 10⁶ of S. feltiae IJs/m² provide affordable and effective control of Lycoriella spp. that is comparable to or better than that of insecticides commonly used in mushroom production (Jagdale et al., 2004; Grewal, 2007). Also, because S. feltiae recycles in gnat larvae, it maintains its effectiveness longer than diflubenzuron and methoprene (Grewal and Richardson, 1993). Commercially produced S. feltiae are now routinely used for control of Lycoriella spp. in the United States and Europe (Grewal and Georgis, 1998; Georgis et al., 2006; Grewal, 2007).

Foliar application: Arthurs et al. (2004), analyzed data from dozens of field trials in which EPNs were applied for control of insect pests in above ground habitats. The lowest efficacy was reported for foliar habitats. The major limiting factor of foliar application of EPNs to leaf surfaces is the rapid desiccation of the IJs, although anti-desiccants have been shown to increase the effectiveness of EPNs against certain pest species. Steinernema carpocapsae, is the most commonly applied species for control of foliar and other above-ground pests. Due to

its ambusher host-finding strategy, they are ideal candidates for pest insects that are encountered on the surface soil when they descend from foliage.

Treatment of diamondback moth larvae, *Plutella xy*lostella (Lepidoptera:Plutellidae), on watercress with B. thuringiensis and S. carpocapsae, both at half rate, resulted in 58% control, significantly higher than that of each applied at full rate (Baur et al., 1998). These authors concluded that repeated applications of EPNs alone would probably be ineffective in attaining control. However, they suggested that EPNs could serve as components of IPM of P. xylostella if efficacy can be increased and they could help manage resistance to B. thuringiensis. Baur et al. (1997) demonstrated that additives generally improved EPN persistence and efficacy on watercress, but the improvement was probably not sufficient to increase the feasibility of foliar applications of EPNs against P. xylostella. Similar results were reported by Schroer and Ehlers (2005) and Schroer et al. (2005) for S. carpocapsae and combination of the nematode and B. thuringiensis with a polymer. Other researchers have reported on the efficacy of EPNs for control of P. xylostella with similar results, i.e less than 50% of targeted populations were controlled with high concentrations of EPNs (Somvanshi et al., 2006; Nyasani et al., 2008). However, Lello et al. (1996) reported that high output hydraulic nozzles deposited the greatest number of IJs onto foliage and produced up to 98% mortality.

Control of other pest species with EPNs on foliar surfaces has been variable (Georgis et al., 2006). For example, Bélair et al. (2003) demonstrated that foliar applications of *S. carpocapsae* did not provide an acceptable level of control of imported cabbageworm *Artogeia rapae* (Lepidoptera: Pieridae) under environmental conditions in Québec. On the other hand, research on *S. carpocapsae* and *S. feltiae* demonstrated their potential for control of the leafminers (Diptera: Agromyzidae): *Liriomyza trifolii* (Hara et al., 1993; LeBeck et al., 1993; Sher et al., 2000; Tomalak et al., 2005) *Liriomyza huidobrensis* (Williams and Walters, 2000), and *Tuta absoluta* (Batalla-Carrera et al., 2010) and other leafminer species.

EPN application for control of insects in epigeal (soil surface) habitats: The most successful use of EPNs above ground involves soil surface treatment of insects while they are transiting over or through the soil surface. One of the best examples of successful control of an insect pest at the soil surface is that of EPNs for control of Diaprepes root weevil, Diaprepes abbreviatus (Coleoptera: Cucurlionidae) in citrus. The weevil is a major pest in Florida citrus since its introduction from Caribbean islands in the 1960s. Its subterranean grubs can severely damage roots and heavy persistent infestation can result in tree mortality. The eggs of the weevil are laid on leaves and after hatching, larvae drop to the ground, and enter the soil. Because neonate D. abbreviatus larvae

are highly susceptible to EPNs, surface application of IJs while they are entering the soil provides an effective means for their control. In Florida, EPNs have been marketed for weevil control for nearly 20 years. Two commercially produced species, Steinernema riobrave and Heterorhabditis indica have been used for effective control. These nematodes appear to be most effective at high temperatures $(27 \pm 2^{\circ}C)$ in coarse sandy soils. Larval mortality of over 90% has been reported for field trials with *S. riobrave* when applied at 1.2×10^{10} IJs/ha (McCoy et al. 2002, 2007; Shapiro-Ilan et al, 2002; Stuart et al., 2008). The use of irrigation systems for application of EPNs has been effective in delivering IJs into the zone below trees where larvae enter the

Cutworms (Lepidoptera: Noctuidae) (Agrotis, Amathes, Noctua, Peridroma, Prodenia spp.) are leaf, bud, and stem feeders and some species feed on roots. They spend some or all of their feeding stages in contact with the soil. Many species overwinter as penultimate or last instar larvae or pupae in the soil or under fallen leaves and other debris at the soil surface. During their feeding or resting activity on the surface of the soil they are good targets for ambusher EPNs when soil moisture is sufficient for IJ survival and infectivity. Although several studies have demonstrated good control of cutworms in crops and turf (Capinera et al., 1988; Buhler and Gibb 1994; West and Vrain, 1997; Shapiro-Ilan et al., 2002; Ebssa and Koppenhöfer, 2011) they are not yet implemented on a large scale.

Steinernema spp. and Heterorhabditis spp. have also been used with varying degrees of success in field trials for pest insects that exit fruit and enter the soil to pupate. For example, plum curculio, Conotrachelus nenuphar, (Coleoptera:Curculionidae) (Shapiro-Ilan, 2004, 2008; Alston et al., 2005; Kim and Alston 2008; Pereault et al., 2009), fruit flies (Rhagoletis indifferens, Anastrepha ludens; Diptera: Tephritidae) (Yee and Lacey, 2003; Toledo et al., 2005) and several other species reviewed by Georgis et al. (2006) and Dolinski and Lacey (2007).

The invasive mole cricket, Scapteriscus vicinus (Orthoptera:Gryllotalpidae), from South America, is a serious pest of lawn and turf in the Southern United States. Successful classical biological control of the cricket with Steinernema scapterisci, an EPN collected in the putative center of origin of the cricket in Uruguay, is documented by Hudson et al. (1988), Parkman and Smart (1996), and Parkman et al. (1996). The nematode was successfully established after introduction of S. scapterisci-infested cadavers and applications in small plots at a rate equivalent to 2 x 10⁹ IJs/ha (Hudson et al., 1988; Parkman et al., 1993; Parkman and Smart, 1996). In addition, S. scapterisci was auto-dispersed by infected mole crickets to create new foci of infection (Parkman et al., 1993). Due to the territoriality of S. vicinus, Parkman and Frank (1992) developed a unique method of treatment using sound traps to

attract and infect the crickets. Three years after the initial introduction of S. scapterisci, mole cricket populations at release sites were reduced by up to 98%. Application of S. scapterisci to untreated sites and augmentative applications have been facilitated by commercial production of the nematode (Grewal et al., 2005b).

Cryptic habitats: Cryptic habitats include but are not limited to: under bark and leaf litter, in prop piles, fruit bins, nut shells, and pruning wounds. The use of EPNs for successful control of a number of orchard insect pests in cryptic habitats has been reported in several reviews (Cross et al., 1999; Shapiro et al. 2005; Lacey et al. 2007; Lacey and Shapiro, 2008).

Codling moth, Cydia pomonella (Lepidoptera:Tortricidae), a worldwide pest of apple and other pome fruit, provides an excellent example of the successful use of EPNs for control in cryptic habitats. Diapausing full grown larvae overwinter in hibernacula under bark and in other cryptic habitats. After harvest, they account for 100% of the codling moth population. Control of these larvae would result in reduced emergence of adult moths the following spring. The most evaluated species for codling moth control are S. carpocapsae, S. feltiae, H. bacteriophora, and H. zealandica. The abiotic factors that have the greatest influence on their larvicidal activity against C. pomonella are temperature, moisture, and type of habitat (Kaya et al., 1984; Lacey and Unruh, 1998; Unruh and Lacey, 2001; Lacey et al., 2006a; Navaneethan et al., 2010; de Waal et al., 2011). Application of IJs of S. carpocapsae or S. feltiae at 2.5×10^6 IJs/tree or 1-2.5 x 10⁹/ha under optimal conditions of temperature and moisture (20-25°C, saturated humidity) can provide up to 90% reduction of overwintering larvae (Unruh and Lacey, 2001; Lacey et al. 2006a). Although both species are efficacious, S. feltiae is more temperature tolerant and can be applied later in the fall when temperatures are too low (10°C) for S. carpocapsae. Larvicidal activity has been improved by the addition of humectants to IJ suspensions, supplemental application of water and through the use of mulches in orchards with few above ground cryptic habitats (Unruh and Lacey, 2001; Lacey et al. 2005, 2006a, 2006b, 2010; de Waal et al., 2011).

Fruit bins that are in the orchard during the time when diapause-destined larvae are seeking cryptic habitats, can also provide overwintering sites. These larvae withstand storage conditions (0-4 °C, high N₂, low O_2) and may emerge in orchards the following year when bins are placed in the orchard. EPNs have been evaluated against cocooned larvae in fruit bins by drenching and immersing the bins in water containing IJs (Lacey and Chauvin, 1999; Cossentine et al., 2002; Lacey et al., 2005; de Waal et al., 2010). Although interest in the use of EPNs for codling moth control has been expressed by orchardists, particularly those in organic fruit production, EPNs are not currently implemented for control of overwintering larvae.

Several studies and field trials of EPNs for control of other insect pests of orchards in cryptic habitats have been reported. These include the filbertmoth, *Melissopus latiferreanus* (Tortricidae), (Chambers et al., 2010); navel orangeworm, *Amyelois transitella* (Lepidoptera: Pyralidae), (Siegel et al., 2004, 2006); Oriental fruitmoth, *Grapholita molesta* (Tortricidae), (Riga et al., 2006); peachtree borer, *Synanthedon pictipes* (Lepidoptera: Sesiidae), (Shapiro-Ilan et al., 2010), and additional species reviewed by Shapiro-Ilan et al. (2005, 2012). Lacey et al. (2007) and Lacey and Shapiro-Ilan (2008).

COMMERCIALIZATION

Advances in mass-production and formulation technology of EPNs, the discovery of numerous efficacious isolates/strains and the desirability of reducing pesticide usage have resulted in a surge of scientific and commercial interest in these nematodes. The lessons learned from earlier problems have encouraged scientists and companies to increase their effort toward improving cost efficiency and better products positioning in the market within the confines of product capabilities. At present, EPNs are produced and marketed by few companies and as a result these companies are making reasonable profits which is critical to continued commercial production. From the producer's point of view, marketing nematodes is a success. However, from the global point of view, the revenues and the market share has been limited to certain markets with little

opportunities to expand to new markets. Although the demand for biopesticide products has increased significantly since 2003 (Table 2), the global revenues of the nematodes have been flat, whereas significant increase in the revenues and market share of many of other biopesticide products have been realized (Table 2). Factors such as cost, shelf life, handling, mixing, coverage, new caution signal- based pesticides, compatibility and profit margins to manufacturers and distributors have contributed to the failure of EPNs to penetrate many markets or gain significant market share in the current markets (Table 3).

Genetic improvements through traditional selection regimes and changes in bacterial payload may be the solution to develop stable formulations, improve nematode searching abilities, producing more virulent nematodes, and increasing tolerance to environmental extremes. However, it is important to carefully assess the return of investment when newer technologies are used for genetic modifications that could result in the loss of organic approval and registration exemption status from the registration requirements in many countries. Nevertheless, genetic improvements will play major roles in strengthening and expanding the market share of EPNs in the current crops-pest complex. However, the fact will remain that other advancements are needed to strengthen the efficacy and the field host range beyond the current target insects, crops and environment (examples: root maggots, flea beetles, corn rootworms, cucumber beetles and wireworms)

TABLE 2. Biopesticide and entomopathogenic nematode market size compared to chemical pesticides at the distributor level (\$US million) (CPL Business Consultant report, 2008, BBC Research report, 2009).

Product Type	2003	2005	2007	2009
Chemical pesticides	29,144	31,076	33,390	37,315
Biopesticides total (product details listed below)	265.8	367.7	619.6	794.2
Essential and industrial oils, plant extracts, others	61.2	134.4	347.6	539.1
Bacillus thuringiensis	166.3	159.6	163.6	153.7
Bacillus subtilis	17.4	30.1	57.4	63.2
Trichoderma spp.	9.3	15.2	16.4	22.7
Beauveria spp.	7.4	13.8	16.2	21.7
Entomopathogenic nematodes	16.2	14.6	18.7	13.8

Table 3. Factors affecting market expansion of entomopathogenic nematodes (modified from Georgis 2004, Georgis et al., 2006).

Markets, crops and target insects	Field efficacy is limited to few selected insects and environment.		
	Certain product labels list unsuitable target insects.		
	Efficacy against certain insects is significantly lower than competitive products.		
	Certain product labels recommend suboptimum application rates.Limited data on cost effectiveness in IPM programs.		
Formulation and shelf life	Refrigeration requirements and limited room temperature shelf life.		
	Certain formulations require time for mixing and preparing spray solution.		
	Suboptimum storage by the distributors, dealers and growers.		
Usage directions	Certain product labels lack proper application directions.		
	Application requirements such as temperature, moisture, irrigation, timing and product coverage are impractical in certain applications.		
	Improper handling, mixing and application by end users.		
Technical support	Limited experience and knowledge of farm advisors and extension personnel		
Cost and gross margins	In general, products are more expensive than competitive products.		
	Gross margins are generally lower for the distributors than competitive products.		

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