Egyptian Journal of Biological Pest Control

REVIEW ARTICLE Open Access

Global distribution of entomopathogenic nematodes, *Steinernema* and *Heterorhabditis*

Aashaq Hussain Bhat[1], Ashok Kumar Chaubey[1] and Tarique Hassan Askary[2*]

Abstract

Entomopathogenic nematodes (EPNs) in the families' Steinernematidae and Heterorhabditidae are obligate insect parasites. Their easy multiplication, broad host range, compatibility with chemical pesticides, and ease in application has grabbed interest among research practitioners to work on these beneficial microorganisms. Till date, around 100 valid species of *Steinernema* and 21 species of *Heterorhabditis* have been identified from different countries of the world. Extensive surveys have been conducted across the globe to isolate locally adapted EPN species and exploit them to suppress soil-dwelling and foliar insect pests in agricultural fields. Most of the new species have been described from Asia, whereas research in some Asian countries are still at infancy. Some new species have been recorded from Australia but very few surveys have been conducted in New Zealand. Likewise, less information about these tiny creatures is from Central America; however, in North America many new species have been described, some of which have been commercialized for insect pest control, whereas in South America, several native nematode species have been described and exploited as biological control agents. European countries have also been explored for EPN diversity and new species have been reported, exploited under field condition, and commercialized. Many new species and other previously described species have been reported from Africa. Despite frequent surveys in different continents of the world, number of sites touched are low and, therefore, further surveys are still needed to explore untouched geographic areas and climatic conditions, both in plantations and indigenous forests with an aim to identify and exploit additional EPN species.

Keywords: Entomopathogenic nematodes, Distribution, Biocontrol, Insect pests

Background

Steinernematidae Travassos, 1927 and Heterorhabditidae Poinar Jr, 1975 are the two important nematode families, which have drawn attention throughout the world as they have proven promising biocontrol agents of agriculturally important insect pests of soil, foliar, and cryptic habitats (Askary, 2010; Askary and Abd-Elgawad, 2017). The work on entomopathogenic nematodes (EPNs) is believed to have been initiated from Germany where the first species of EPN was described (Steiner, 1923a, b). Later, it spread to New Jersey, USA where a new species was reported that was attacking white grubs and this biocontrol attribute became a turning point for exploration of EPN species from other parts of the world. Extensive studies on EPNs were carried out in the 19th and 20th centuries, which led to a tremendous research on taxonomy and commercialization of steinernematids and heterorhabditids and currently the interest of using them as alternatives to chemical pesticides is paying much attention throughout the world. The use of EPNs in biological control of insect pests brought attention of research practitioners throughout the globe and more researchers became interested in working on EPNs and exploiting them at commercial level.

Surveys have been conducted from almost all parts of the world in order to isolate locally adapted EPN species or isolates with further aim to formulate and commercialize them (Hominick et al., 1996; Hominick, 2002). This led to the increase in described species of

* Correspondence: tariq_askary@rediffmail.com
[2]Division of Entomology, Faculty of Agriculture, Sher-e-Kashmir University of Agricultural Sciences & Technology of Kashmir, Wadura Campus, Sopore, Jammu & Kashmir 193201, India
Full list of author information is available at the end of the article

EPNs from 13 (10 *Steinernema* and 3 *Heterorhabditis*) in the late 1980s (Kaya and Gaugler, 1993) to 66 (55 *Steinernema* and 11 *Heterorhabditis*) in 2007 (Hunt, 2007; Nguyen et al., 2007). Based on molecular data, Hunt and Subbotin (2016) and Hunt and Nguyen (2016) updated the species list of *Steinernema* and *Heterorhabditis* and found several species invalid. Though, surveys to identify local species of EPNs has increased in the past 3 decades, knowledge on the diversity of these beneficial nematodes is still limited, particularly in many forest areas and hilly regions of the developed and developing countries of the world.

In the foregone review, our aim is to highlight the work done on isolation and identification of EPNs in different continents of the world (Tables 1 and 2). Emphasis has been laid for further investigations in this direction in order to identify additional native species and their exploitation for insect pest management programs.

North America

Steinernematids reported from North America include *S. glaseri* (Glazer and Fox, 1930) from *Popillia japonica* (New Jersy); *S. intermedium* (Poinar Jr, 1986) from soil (Charleston, South Carolina, USA); *S. neocurtillae* (Nguyen and Smart Jr, 1992) from *Neocurtilla hexadactyla* (Florida USA); *S. cubanum* (Mráček et al., 1994) from soil samples (Cuba); *S. riobrave* (Cabanillas et al., 1994) from soil (Weslaco,Texas USA); *S. puertoricense* (Román and Figueroa, 1994) from soil (Loiza, Puerto Rico); *S. oregonense* (Liu and Berry, 1996) from soil (Oregon USA); *S. diaprepesi* (Nguyen and Duncan, 2002) from *Diaprepes abbreviates* (Florida); *S. scarabaei* (Stock and Koppenhöfer, 2003) from *Anomala* (= *Exomala*) *orientalis* and *Popillia japonica* (New Jersey, USA); *S. jollieti* (Spiridonov et al., 2004) from soil (Missouri valley near St. Louis, USA); *S. costaricense* (Uribe-Lorío et al., 2007) from soil (Costa Rica); *S. puntauvense* (Uribe-Lorío et al., 2007) from soil (Costa Rica); *S. texanum* (Nguyen et al., 2007) from soil (Texas, USA); *S. phyllophagae* (Nguyen and Buss, 2011) from White grub (*Phyllophaga* sp.) (Florida, USA). Among heterorhabditids, new descriptions include *H. megidis* (Poinar Jr et al., 1987) from *Popillia japonica* (Ohio, USA); *H. hepialius* (Stock et al., 1996), currently synonymized with *H. marelatus*, from *Hepialus californicus* (California); *H. marelatus* (Liu & Berry, 1996) from soil (Oregon); *H. mexicana* (Nguyen et al., 2004a) from soil (Mexico); *H. floridensis* (Nguyen et al., 2006a) from soil (Florida, USA), and *H. georgiana* (Nguyen et al., 2008b) from soil sample (Georgia, USA). In Florida, one more genus of family Steinernematidae, *Neosteinernema longicurvicauda* (Nguyen and Smart Jr, 1994), has been isolated from termite (*Reticulitermes flavipes*), which had not been recorded from anywhere, since its discovery.

The beginning of in vitro mass production and field testing of steinernematid nematodes began in North America in the late 1930s by Glaser and his co-workers (Gaugler et al., 1992) and Dutky in the 1950s (Dutky, 1959). In vitro production at commercial level was made possible by producing nematodes monoxenically using a solid-state culture technique (Friedman, 1990; Gaugler and Han, 2002). Bedding developed sponge-based technology, which on one-hand made harvesting of nematodes easy (Friedman, 1990); however, it was labor intensive. Later, liquid fermentation methods of nematode production were introduced (Ehlers, 2001; Friedman, 1990; Gaugler and Han, 2002; Georgis, 2002) but for cottage industries, it was not economically feasible due to requirement of high initial capital investment to purchase and operate bioreactors. Thus, production of nematodes in cottage industries relied on in vivo or in vitro solid-state production scheme developed by Bedding (Gaugler and Han, 2002). In North America, two European companies' *viz*., e-nema and Koppert distribute their nematode products. The commercially used EPNs in North America are *S. carpocapsae* (Weiser), *S. feltiae* (Filipjev), *S. glaseri* (Steiner), *S. kraussei* (Steiner), *S. riobrave* (Cabinillas, Poinar and Raulston), *S. scapterisci* (Nguyen and Smart), *H. bacteriophora* (Poinar), *H. indica* (Poinar, Karunakar and David), *H. megidis* (Poinar, Jackson and Klein), *H. marelatus* (Liu and Berry), and a *Heterorhabditis* species (Georgis et al., 2006).

Central America

The EPN isolates recorded from Central America included *S. carpocapsae* from Chihuahua (Poinar, 1990) and *H. indica* from a subtropical region in Mexico (La Sierra, Tabasco) (Cortez-Madrigal et al., 2003). Many other isolates of *Steinernema* and *Heterorhabditis* were also reported (Diaz-Mederos et al., 2002, Alia et al., 2002, Ruiz-Vega et al., 2003, Cortez-Madrigal et al., 2003; Molina-Ochoa et al., 2003a, b, c; Uribe-Lorio et al., 2005), but their species status needs confirmation. A new species *H. mexicana* Nguyen, Shapiro-Ilan, Stuart, McCoy, James, and Adams has been reported from Tamaulipas (Nguyen et al. 2004a). The biological control traits of this species have been worked out by Shapiro-Ilan et al. (2005).

South America

The work on EPNs has been reported from seven South American countries that included Argentina, Brazil, Chile, Colombia, Peru, Suriname, and Venezuela. The first report of *Heterorhabdits* previously referred as *Rhabditis hambletoni* was reported by Pereira (1937). Pizano et al. (1985) reported *S. glaseri* (originally described from *Popillia japonica* from North America) from the egg of *Migdolus fryanus* (Westwood) obtained

Table 1 List of *Steinernema* species recorded from different countries of the world

S. no.	Species	Authors & year	Host insect/soil	Location
1	*S. abbasi*	Elawad et al., 1997	Soil	Sultanate of Oman
2	*S. aciari*	Qiu et al., 2005a	Soil	China
3	*S. affine*	(Bovien, 1937) Wouts et al., 1982	*Phyla febrilis* (L.)	Denmark
4	*S. akhursti*	Qiu et al., 2005b	Soil	China
5	*S. anatoliense*	Hazir et al., 2003	Soil	Turkey
6	*S. apuliae*	Triggiani et al., 2004	Soil	Italy
7	*S. arasbaranense*	Nikdel et al., 2011	Soil	Iran
8	*S. arenarium*	(Artyukhovsky et al., 1997) Wouts et al. 1982	Soil	Central Russia
9	*S. ashiuense*	Phan et al., 2006b	Soil	Japan
10	*S. asiaticum*	Anis et al., 2002	Soil	Pakistan
11	*S. australe*	Edgington et al., 2009b	Soil	Chile
12	*S. backanense*	Phan et al., 2006a	Soil	Vietnam
13	*S. beddingi*	Qiu et al., 2005c	Soil	China
14	*S. beitlechemi*	Çimen et al., 2016	Soil	South Africa
15	*S. bicornutum*	Tallosi et al., 1995	Soil	Strazilovo, Serbia
16	*S. biddulphi*	Çimen et al., 2016	Soil	South Africa
17	*S. boemarei*	Lee et al., 2009	Soil	France
18	*S. borjomiense*	Gorgadze et al., 2018	*Oryctes nasicornis*	Georgia
19	*S. brazilense*	Nguyen et al., 2010	Soil	Mato Grosso, Brazil
20	*S. cameroonense*	Kanga et al., 2012	Soil	Cameroon
21	*S. carpocapsae*	(Weiser 1955) Wouts et al. 1982	*Cydia pomonella* (L.)	Czechoslovakia
22	*S. caudatum*	Xu et al., 1991	Soil	China
23	*S. ceratophorum*	Jian et al., 1997	Soil	Jining Province, China
24	*S. changbaiense*	Ma et al., 2012a, b, c	Soil	China
25	*S. cholashanense*	Nguyen et al., 2008a	Soil	China
26	*S. citrae*	Malan et al., 2011	Soil	South Africa
27	*S. colombiense*	Lopez-Nunez et al., 2008	Soil	Colombia
28	*S. costaricense*	Uribe-Lorío et al., 2007	Soil	Costa Rica
29	*S. cubanum*	Mráček et al., 1994	Soil	Western Cuba
30	*S. cumgarense*	Phan et al., 2006a	Soil	Vietnam
31	*S. diaprepesi*	Nguyen and Duncan, 2002	*Diaprepes abbreviates*	Florida
32	*S. eapokense*	Phan et al., 2006a	Soil	Vietnam
33	*S. ethiopiense*	Tamirou et al., 2012	Soil	Ethiopia
34	*S. fabii*	Abate et al., 2016	Soil	South Africa
35	*S. feltiae*	(Filipjev, 1934) Wouts et al. 1982	*Agrotis segetum*	Denmark
36	*S. glaseri*	(Steiner, 1929) Wouts et al., 1982	*Popillia japonica*	New Jersey, USA
37	*S. goweni*	San-Blas et al., 2016	Soil	Venezuela
38	*S. guangdongense*	Qui et al., 2004	Soil	China
39	*S. hebeiense*	Chen et al., 2006	Soil	China
40	*S. hermaphroditum*	Stock et al., 2004	Soil	Indonesia
41	*S. huense*	Phan et al., 2014	Soil	Vietnam
42	*S. ichnusae*	Tarasco et al., 2008	Soil	Sardinia Island, Italy
43	*S. innovationi*	Çimen et al., 2015	Soil	South Africa
44	*S. intermedium*	(Poinar, 1985) Mamiya 1988	Soil	Charleston, South Carolina, USA

Table 1 List of *Steinernema* species recorded from different countries of the world *(Continued)*

S. no.	Species	Authors & year	Host insect/soil	Location
45	*S. jeffreyense*	Malan et al., 2015	Soil	South Africa
46	*S. jollieti*	Spiridonov et al., 2004	Soil	Missouri valley near St. Louis, USA
47	*S. karii*	Waturu et al., 1997	Soil	Kirinyaga, Central Province, Kenya
48	*S. khoisanae*	Nguyen et al., 2006a, b	Soil	South Africa
49	*S. khuongi*	Stock et al., 2019	Soil	Florida
50	*S. kraussei*	(Steiner, 1923a, b) Travassos 1927 = Type species	*Cephaleia abietis* (L.)	Germany
51	*S. kushidai*	Mamiya, 1988	*Anomala cuprea* Hope	Hamikita, Japan
52	*S. lamjungense*	Khatri-Chhetri et al., 2011a	Soil	Nepal
53	*S. leizhouense*	Nguyen et al., 2006b	Soil	Southern China
54	*S. litchii*	Steyn et al., 2017	Soil	South Africa
55	*S. litorale*	Yoshida, 2004	Soil	Japan
56	*S. loci*	Phan et al., 2001c	Soil	Vietnam
57	*S. longicaudum*	Shen & Wang, 1991	Soil	Guangdong, China
58	*S. minutum*	Maneesakorn et al., 2010	Soil	Thailand
59	*S. monticolum*	Stock et al., 1997	Soil	Gyeongnam Province, Republic of Korea
60	*S. neocurtillae*	Nguyen and Smart Jr, 1992	*Neocurtilla hexadactylla* (Perty)	LaCrosse, Florida, USA
61	*S. nepalense*	Khatri-Chhetri et al., 2011b	Soil	Nepal
62	*S. nguyeni*	Malan et al., 2016	Soil	South Africa
63	*S. nyetense*	Kanga et al., 2012	Soil	Cameroon
64	*S. oregonense*	Liu and Berry, 1996	Soil	Oregon, USA
65	*S. pakistanense*	Shahina et al., 2001	Soil	Karachi, Pakistan
66	*S. papillatum*	San-Blas et al., 2015	Soil	Venezuela
67	*S. phyllophagae*	Nguyen and Buss, 2011	*Phyllophaga* sp.	Florida, USA
68	*S. poinari*	Mráček et al., 2014	Soil	Czech Republic
69	*S. puertoricense*	Román and Figueroa, 1994	Soil	Loiza, Puerto Rico
70	*S. pui*	Qiu et al., 2011	Soil	Yunnan, China
71	*S. puntauvense*	Uribe-Lorío et al., 2007	Soil	Costa Rica
72	*S. pwaniensis*	Puza et al., 2017	Soil	Tanzania
73	*S. ralatorei*	Grifaldo-Alcantara et al., 2017	Soil	Mexico
74	*S. rarum*	(de Doucet, 1986) Mamiya, 1988	Soil	Cordoba, Argentina
75	*S. riobrave*	Cabanillas et al., 1994	Soil	Weslaco,Texas, USA
76	*S. riojaense*	Půža et al., 2020	Soil	La Rioja province, Spain
77	*S. ritteri*	de Doucet & Doucet 1990	Soil	Córdoba, Argentina
78	*S. robustispiculum*	Phan et al., 2005	Soil	Vietnam
79	*S. sacchari*	Nthenga et al., 2014	Soil	South Africa
80	*S. sangi*	Phan et al., 2001a	Soil	Vietnam
81	*S. sasonense*	Phan et al., 2006a	Soil	Vietnam
82	*S. scapterisci*	Nguyen and Smart Jr, 1990	*Scapteriscus vicinus* Scudder	Rivera, Uruguay
83	*S. scarabaei*	Stock and Koppenhöfer, 2003	*Anomala* (= *Exomala*) *orientalis* and *Popillia japonica*	New Jersey, USA
84	*S. schliemanni*	Spiridonov et al., 2010	*Osmoderma ceremita*	Germany, Europe
85	*S. siamkayai*	Stock et al., 1998	Soil	Petchabun Province, Thailand
86	*S. sichuanense*	Mráček et al., 2006	Soil	China

Table 1 List of *Steinernema* species recorded from different countries of the world *(Continued)*

S. no.	Species	Authors & year	Host insect/soil	Location
87	*S. silvaticum*	Sturhan et al., 2005	Soil	Berlin Germany, Europe
88	*S. surkhetense*	Khatri-Chhetri et al., 2011b	Soil	Nepal
89	*S. tami*	Luc et al., 2000	Soil	Vietnam
90	*S. taiwanensis*	Tseng et al., 2018	Soil	Taiwan
91	*S. texanum*	Nguyen et al., 2007	Soil	Texas, USA
92	*S. thanhi*	Phan et al., 2001b	Soil	Vietnam
93	*S. tielingense*	Ma et al., 2012	Soil	China
94	*S. tophus*	Çimen et al., 2014	Soil	South Africa
95	*S. unicornum*	Edgington et al., 2009a	Soil	Chile
96	*S. xinbinense*	Ma et al., 2012	Soil	China
97	*S. xueshanense*	Mráček et al., 2009	Soil	China
98	*S. weiseri*	Mráček et al., 2003	Soil	Czech Republic, Europe
99	*S. yirgalemense*	Nguyen et al., 2004b	Soil	Yirgalem, Ethiopia
100	*S. bertusi*	Katumanyane et al., 2019	Soil	Tito, Mpumalanga, and Port Edward, Kwa Zulu Natal, South Africa

*Species considered as junior synonym, species *inquirendae* and *nomun nudum* are mentioned in the text

from a field in the State of São Paulo, Brazil. Some territories of South America are still unexplored for EPNs; however, some of the new species of steinernematids described from here include *S. rarum* {(de Doucet, 1986) Mamiya, 1988} from Argentina, *S. ritteri* (de Doucet and Doucet, 1990) from Argentina, *S. scapterisci* (Nguyen and Smart Jr, 1990) from Uruguay, *S. colombiense* (Lopez-Nunez et al., 2008) from Colombia, *S. unicornum* (Edgington et al., 2009a) and *S. australe* (Edgington et al., 2009b) from Chile, *S. brazilense* (Nguyen et al., 2010) from Brazil, and *S. papillatum* (San-Blas et al., 2015) *S. goweni* (San-Blas, 2016) from Venezuela. Among *Heterorhabditis*, two new species *H. amazonensis* (Andaló et al., 2006) and *H. atacamensis* (Edgington et al., 2011) were reported from Brazil and Chile, respectively. Few already described species reported from South America included *S. carpocapsae*, *S.*

Table 2 List of *Heterorhabditis* species recorded from different countries of the world

S. no.	Species	Authors & year	Host insect/ soil	Location
1	*H. amazonensis*	Andaló et al., 2006	Soil	Brazil
2	*H. atacamensis*	Edgington et al., 2011	Soil	Chile
3	*H. bacteriophora*	Poinar, 1976	*Heliothis punctigera* Wallengren	Brecon, South Australia
4	*H. baujardi*	Phan et al., 2003	Soil	Vietnam
5	*H. beicherriana*	Li et al., 2012	Soil	China
6	*H. downesi*	Stock et al., 2002	Soil	Ireland
7	*H. floridensis*	Nguyen et al., 2006a	Soil	Florida, USA
8	*H. georgiana*	Nguyen et al., 2008b	-	Georgia
9	*H. indica*	Poinar Jr et al., 1992	Soil (Soil baited with *Scirpophaga excerptalis* Walker, larvae)	Coimbatore, India
10	*H. marelatus*	Liu & Berry, 1996	Soil	Seaside, Oregon, USA
11	*H. megidis*	Poinar Jr et al., 1987	*Popillia japonica* Newman	Jeromesville, Ohio, USA
12	*H. mexicana*	Nguyen et al., 2004a	Soil	Mexico
13	*H. noenieputensis*	Malan et al., 2014	Soil	South Africa
14	*H. safricana*	Malan et al., 2008	Soil	South Africa
15	*H. taysearae*	Shamseldean et al., 1996	Soil	Egypt
16	*H. zealandica*	Poinar, 1990	*Heteronychus arator* F.	Auckland, New Zealand

*Species considered as junior synonym, species *inquirendae* and *nomun nudum* are mentioned in the text

feltiae, *S. scapterisci*, and *H. bacteriophora* (Rosales and Suarez, 1998; Saenz, 1999; Fan et al., 2000).

Europe

Steinernematids isolated from European countries include *S. affine* (Bovien, 1937) Wouts et al., 1982 from Denmark, *S. kraussei* (Steiner, 1923a, b) from Germany, *S. carpocapsae* (Weiser, 1955) from Czechoslovakia, *S. bicornutum* (Tallosi et al., 1995) from Serbia (formerly Yugoslavia), *S. weiseri* (Mráček, et al., 2003) from Czech Republic, *S. apuliae* (Triggiani et al., 2004) from Italy, *S. silvaticum* (Sturhan et al., 2005) from Germany, *S. ichnusae* (Tarasco et al., 2008) from Italy, *S. boemarei* (Lee et al., 2009) from France, *S. schliemanni* (Spiridonov et al., 2010) from Germany, *S. poinari* (Mráček et al., 2014) from Czech Republic and *S. riojaense* (Půža et al., 2020) from Spain. Among new species of *Heterorhabditis*, *H. downesi* has been reported from here. Other indigenous species reported from Europe are *H. bacteriophora*, *H. indica*, *H. megidis*, *S. feltiae, S. vulcanicum, S. arenarium*, and several undescribed species (Tarasco et al., 2015).

In Europe, the work on EPNs began since early 1980s and the large-scale production of these nematodes started in the year 1986. Currently, three large-scale companies are in operation producing nematodes by in vitro methods, which includes Becker Underwood (UK), e-nema (Germany), and Koppert (The Netherlands). There are also some small-scale producers like Andermatt Biocontrol (Switzerland), Bionema (Swansea, Wales), and Owiplant (Poland). The nematode products commercially used in Europe for insect pest suppression include *H. megidis*, *H. bacteriophora*, *S. feltiae*, *S. carpocapsae*, and *S. kraussei*. All these products were based on clay, vermiculite or polymer formulations.

Turkey

Özer et al. (1995) reported *S. carpocapsae* from the Black Sea region, but later, A.P Reid re-identified this isolate as *S. feltiae* (Hominick et al., 1996). Among *Heterorhabditis*, the first nematode species described from Turkey was *H. bacteriophora* detected by Kepenekci et al. (1999) in *Aelia* population (*Aelia rostrata* Boh.) collected from Ekecik (Aksaray) winter quarters. Other species of EPNs reported from Turkey included *S. feltiae*, *S. carpocapsae*, *S. affine*, *S. websteri*, *S. anatoliense*, *S. weiseri*, *S. bicornutum*, *S. kraussei*, and some undescribed *Steinernema* species, while among heterohabditids, 3 species viz., *H. bacteriophora*, *H. marelatus*, and *H. megidis* were reported (Kepenekci and Susurluk, 2000; Hazir et al., 2003; Yılmaz et al., 2007; Ünlü et al., 2007; Kepenekci, 2002, 2014; Ertürk et al., 2014; Gökçe et al., 2015; Canhilal et al., 2016, 2017). Hazir et al. (2003) described a new species of *Steinernema*, *S. anatoliense,* which was isolated from soil samples collected in the locality of Kars, East Anatolia, and was later synonymized with *S. carpocapsae*. However, there is still paucity of information on the diversity of EPN species in Turkey.

Russia

Ivan N. Filipjev, who is regarded as the founder of modern nematology in Russia was the first to describe *S. feltiae* (Filipjev, 1934). Galina V. Veremchuk later initiated applied research in EPNs in the All-Union Plant Protection Institute, St.-Petersburg-Pushkin and described several steinernematid species, which are considered now as junior synonyms of other steinernematid species (Nguyen and Hunt, 2007). Moreover, other species described from Russia are *S. arenarium*, *S. bicornutum*, *S. kraussei*, *S. feltiae*, *S. carpocapsae*, *S. krussie*, *S. kushidai*, *H. zealandica*, *H. megidis*, and *H. bacteriophora* (Ivanova et al., 2000).

The two products of EPNs that are currently marketed in Russia are 'Nemabact' and 'Entonem F', which are suspensions of *S. carpocapsae* and *S. feltiae*, respectively. Their production and commercialization is regulated by 'Biodan' company in Sankt-Petersburg and 'Biometodika' company in Moscow region.

Africa

Surveys for isolation of EPNs in Africa include Egypt, Kenya, Ethiopia, Tanzania, Benin, Morocco, South Africa, Rwanda, Algeria, Cameroon, and Nigeria. The species of steinernematids and heterorhabditids described in the past 2 decades are *H. bacteriophora, S. arenarium, S. glaseri, S. karii*, *S. yirgalemense*, *S. weiserii*, *H. taysearae*, and *H. indica* (Waturu et al., 1997; Waturu, 1998; Mwaniki et al., 2008; Stack et al., 2000) from Kenya; *S. yirgalemense*, *S. ethiopiense*, and *H. bacteriophora* (Nguyen et al., 2004b; Mekete et al., 2005; Tamirou et al., 2012) from Ethiopia; *S. cameroonense*, *S. nyetense, H. baujardi*, and *H. amazoniensis* from Cameroon (Kanga et al., 2012); *S. khoisanae*, *S. citrae*, *S. sacchari*, *S. tophus*, *S. innovationi*, *S. jeffreyense*, *S. beitlechemi*, *S. fabii*, *S. nguyeni*, *S. biddulphi*, *S. litchii*, *S. yirgalemense*, *H. bacteriophora, H. safricana*, and *H. noenieputensis* (Nguyen et al., 2006a, b; Malan et al., 2011; Nthenga et al., 2014; Çimen et al., 2014; Çimen et al., 2015; Malan et al., 2015; Çimen et al., 2016; Hatting et al., 2009; Abate et al., 2016; Malan et al., 2016; Steyn et al., 2017; Malan et al., 2008; Malan et al., 2014) from South Africa; *S. feltiae* and *H. bacteriophora* (Tarasco et al., 2009; Zamoum et al., 2011) from Algeria; *Steinernema* sp, *H. sonorensis,* and *H. indica* (Zadji et al., 2013; Houssou et al., 2014) from Benin; *S. feltiae* from Morocco (Akalach and Wright, 1995) and Nigeria (Akyazi et al., 2012); *S. carpocapsae* and *H.*

bacteriophora from Rwanda (Yan et al., 2016) and *S. pwaniensis* (Puza et al., 2017) from Tanzania.

Egypt

In Egypt, the initial research on EPN began in the 1970s when Dr. El-Kifl worked on the biological control potential of *Neoaplectana* (= *Steinernema*) *carpocapsae* against the cotton leaf worm, *Spodoptera littoralis*, one of the most economically important insect pests in Egypt. The surveys carried out in Egyptian soils revealed that species of heterorhabditids were more prevalent than steinernematids; however, research regarding their use to control other insect species was done as well. Steinernematids recorded from Egypt included *S. abbasi*, *S. carpocapsae*, *S. arenarium*, *S. kushidai*, and *S. glaseri* (Abd-Elbary et al., 2012), whereas heterorhabditids included *H. bacteriophora*, *H. indica* (Abd-Elgawad and Nguyen, 2007), *H. baujardi* (Abd El-Rahman, 2006), and *H. egyptii* (Abd-Elgawad and Ameen, 2005). *H. taysearae* is a new species from the soils of Egypt; however, *H. egyptii* is currently included in species *inquirendae* (Subbortin and Hunt, 2007). Many other heterorhabditids and some steinernematids have been isolated from Egyptian soils but yet to be identified (Abd-Elgawad et al., 2013).

Asia

India

In India, the initial research on EPN was conducted primarily with exotic species/strains of *S. carpocapsae*, *S. glaseri*, *S. feltiae*, and *H. bacteriophora* imported by researchers. However, when applied in field conditions for control of insect pests, inconsistent results were observed probably due to their poor adaptability to the local agro-climatic conditions. Apart from this, it was also believed that exotic EPN introduction may lead to a negative impact on non-target organisms (Kaya et al., 2006), which will be commeriorated (commercialized) by the isolation of indigenous nematode isolates which serve as a valuable resource, not only from a biodiversity perspective but also from an environmental perspective due to their adaptability and utility in biological control. Therefore, a search for indigenous species/strains resulted in a number of nematode isolates from different parts of India (Ganguly, 2003). Fifteen species including 12 steinernematids and 3 heterorhabditids have been reported from India, of which only one new species, *Heterorhabditis indica* (Poinar Jr et al., 1992), was described. Among steinernematids, no new species have been reported till date, but the three previously described new species have been synonymized with existing ones *viz*., *Steinernema thermophilum* (Ganguly and Singh, 2000) synonymized with *S. abbasi* (Elawad et al., 1997), *S. meghalayense* (Ganguly et al., 2011) synonymized with *S. carpocapsae* (Weiser, 1955) Wouts et al., 1982, and *S. dharanai* (Kulkarni et al., 2012) was recognized as a junior synonym of *S. hermaphroditum* Stock et al., 2004 (Hunt, 2007). The other steinernematid species reported from India are *S. bicornutum* Tallosi, Peters and Ehlers (Hussaini et al., 2001), *S. riobrave* Cabanillas, Poinar and Raulston (Ganguly et al., 2002), *S. glaseri* Steiner (Kadav and Lalramliana, 2012), *S. carpocapsae* Weiser (Hussaini et al., 2001), *S. tami* Luc, Nguyen, Reid and Spiridonov (Hussaini et al., 2001), *S. siamkayai* Stock, Somsook and Reid (Ganguly et al., 2002), *S. feltiae* (Filipjev, 1934) Wouts et al., 1982 (Ganguly and Sosamma, unpublished data), *S. sangi* Phan, Nguyen and Moens (Lalramnghaki et al., 2017), *S. surkhetense* Khatri-Chhetri,Waeyenberge, Spiridonov, Manadhar and Moens (Bhat et al., 2017), *S. pakistanense* Shahina, Anis, Reid, Rowe and Maqbool (Bhat et al., 2018), *S. cholashanense* Nguyen et al., 2008a (Mhatre et al., 2018), and *S. hermaphroditum* (Bhat et al., 2019). Other indigenous isolates described from India included *S. feltiae* and *S. riobrave* but there is no authentic data of these two and they are simply described on few morphometrical characters which are not valid proof of their existence in India. Few others were previously described as new species like *S. masoodi*, *S. seemae*, *S. qazi*, and *S. sayeedae* (Ali et al., 2005, 2009, 2010 and Ali and Azra, 2011) but all these provide poor and inaccurate descriptions and hence were regarded as *species inquirendae* by Hunt (2007). Ali et al. (2010), provided molecular sequencing data of *S. masoodi* and *S. seemae* which when analyzed revealed that these sequences do not belong to entomoparasitic nematodes (Hunt and Subbotin, 2016). From these data, it is clear that *S. masoodi* and *S. seemae* are still not molecularly characterized and remain as *species inquirendae*.

Among *Heterorhabditis*, three indigenous nematode species have been reported of which *H. indica* Poinar Jr et al. (1992) only new species is described from India till date. The other two indigenous species from India include *H. bacteriophora* Poinar (Bhat et al., 2020) and *H. baujardi* Phan, Subbotin, Nguyen and Moens (Vanlalhlimpuia and Lalramnghaki, 2018).

China

In China, the work on EPNs started during mid-1980s and early 1990s in collaboration with some institutes of Australia and Guangzhou (Bedding, 1990). Some new species of steinernematids described from China include *S. caudatum* (Xu et al., 1991), *S. longicaudum* (Shen and Wang, 1992), *S. ceratophorum* (Jian et al., 1997), *S. guangdongense* (Qiu et al. 2004), *S. aciari* (Qiu et al., 2005a), *S. akhursti* (Qiu et al., 2005b), *S. beddingi* (Qiu et al., 2005c), *S. leizhouense* (Nguyen et al., 2006b), *S. sichuanense* (Mráček et al., 2006), *S.*

hebeiense (Chen et al., 2006), *S. cholashanense* (Nguyen et al., 2008a), *S. xueshanense* (Mráček et al., 2009), *S. pui* (Qiu et al., 2011), *S. changbaiense* (Ma et al., 2012a), *S. tielingense* (Ma et al., 2012b) and *S. xinbinense* (Ma et al., 2012a, b, c). Among heterorhabditids, one new species, *H. beicherriana* (Li et al., 2012) were recorded. Some other already described species of Steinernematidae identified from China include *S. litorale*, *S. silvaticum*, *S. feltiae*, *S. bicornutum*, *S. affine*, *S. riobrave*, *S. yirgalemense*, *S. kushidai*, *S. scapterisci*, *S. carpocapsae*, *S. ritteri*, *S. tami*, *S. rarum*, and *S. sasonense* and those of Heterorhabditidae are *H. megidis*, *H. zealandica*, *H. brevicaudis*, *H. indica*, and *H. baujardi* (Wang et al., 2014).

China has also made advances in in vitro solid production of EPNs and produced several species of EPNs using solid cultures which were based on the lower labor cost, improved media and mechanization process (Han et al., 1995; Han and Ehlers, 1988). Century Horse Development Ltd. named company under the guidance of Guangdong Entomological Institute currently is involved in EPN commercialization for field trials in China and for internal and international markets. The work on EPN for controlling quarantine pests is still in progress.

Pakistan

In Pakistan, the research studies on EPNs was started by Shahina and Maqool in 1996. The intense interest in the use of EPNs for biological control resulted in exploration for new species. Two new species *S. pakistanense* (Shahina et al., 2001) and *S. asiaticum* (Anis et al., 2002) have been described from Pakistan. Among *Heterorhabditis*, *H. pakistanense* (Shahina et al., 2016) was described new species from Pakistan which was later synonymized with *H. indica* (Hunt and Subbotin, 2016). The other already described species reported from the country include *S. abbasi*, *S. siamkayai*, *S. feltiae*, *S. cholashanense*, *S.* affine, *S. carpocapsae*, *S. litorale*, *H. bacteriophora*, and *H. indica* (Shahina and Salma, 2010; Tabassum et al., 2017).

Iran

Initial surveys conducted for the isolation of EPNs led to the discovery of several known or new species. Parvizi et al. (unpublished) reported *S. arenarium* and *H. bacteriophora* as natural pathogens of *Agrotis ipsilon* from West Azerbaijan province. Tanha maafi et al. (2006) isolated *S. feltiae* from soils of Mazandaran and Tehran provinces. A new species *S. arasbaranense* (Nikdel et al., 2011) was described from East Azerbaijan province. Other surveys resulted in some already described species *viz*., *S. glaseri*, *S. carpocapsae*, *S. bicornutum*, *S. kraussei* (Karimi et al., 2009; Kary et al., 2009; Nikdel et al., 2008, 2010; Ebrahimi and Niknam, 2011; Nikdel and Niknam, 2015; Rahatkhah et al., 2015).

Thailand

Surveys conducted in Thailand have revealed some new and already described species of both steinernematids and heterorhabditids. Some of the newly described species from agricultural soils are *S. siamkayai* (Stock et al., 1998) and *S. minutum* (Maneesakorn et al., 2010). The other already described species reported from the country are *H. bacteriophora*, *H. baujardi*, *H. indica*, *S. khoisanae*, and *S. websteri* (Thanwisai et al., 2012). Species of EPNs including *S. siamkayai*, *S. minutum*, S. *khoisanae*, *S. scrabaei*, *S. kushidai*, *H. indica*, *H. bacteriophora*, *H. baujardi*, *H. somsookae* (synonymized with *H. baujardi*), *H. gerradi* (synonymized with *H. indica*), and *H. zealandica* are commonly found species of entomopathogenic nematodes in Thailand (Thanwisai, et al., 2012; Maneesakorn et al., 2015; Yooyangket et al., 2018).

Japan

S. kushidai (Mamiya, 1988), *S. litorale* (Yoshida, 2005), and *S. ashiuense* (Phan et al., 2006b) are new species first described from Japan. Some of the already described species reported from Japan are *H. indica*, *H. megidis*, *S. carpocapsae*, *S. feltiae*, and several undescribed steinernematids (Yoshida et al., 1998).

Vietnam

Surveys carried out in Vietnam revealed the presence of already described and some new species. *S. tami* (Luc et al., 2000), *S. loci* (Phan et al., 2001a), *S. sangi* (Phan et al., 2001a), *S. thanhi* (Phan et al., 2001b), *S. robustispiculum* (Phan et al., 2005), *S. backanense* (Phan et al., 2006a, b), *S. cumgarense* (Phan et al., 2006a, b), *S. eapokense* (Phan et al., 2006a, b), *S. sasonense* (Phan et al., 2006a, b), and *S. huense* (Phan et al., 2014) are some species of Steinernematids recorded from Vietnam. Among heterorhabditids, *H. baujardi* (Phan et al., 2003) has been found new to this country. The other locally described species include *S. siamkayai*, *H. bacteriophora*, *H. indica*, and *H. megidis* (Phan et al., 2003).

Korea

Extensive surveys by research workers led to the isolation of several steinernematids and heterorhabditids viz., *S. carpocapsae*, *S. glaseri*, *S. longicaudum*, *S. intermedia*, *S. feltiae*, *H. bacteriophora*, and *H. megidis* (Choo et al., 1995; Hang et al., 2007; Lee et al., 2002). Moreover, one new species *S. monticolum* was isolated from soils of Gyeongnam Province (Stock et al., 1997).

Nepal

Surveys conducted for determining the EPN diversity from Nepal resulted in isolation of *S. abbasi*, *S.*

cholashanense, *S. feltiae*, *S. siamkayai*, and *H. indica* (Khatri-Chhetri et al., 2010). Some new species reported from Nepal are *S. nepalense*, *S. surkhetense*, *S. lamjungense*, and *S. everestense* (Khatri-Chhetri et al., 2011a, b).

Jordan

The first survey to record the presence and distribution of steinernematids and heterorhabditids and their associated bacteria in Jordan was done by Stock et al. (2008). Four EPN species including three *Steinernema* and one *Heterorhabditis* were recovered. These include *S. anatoliense*, *S. carpocapsae*, *S. feltiae*, and *H. bacteriophora*.

Sultanate of Oman

There is no available data regarding diversity of EPNs from Oman except S. *abbasi* (Elawad et al., 1997), which was identified and described as a new species from this country. This species was isolated by Dr. Mohamed S. Abbas (Elawad et al., 1996) from soil of alfalfa fields located at Agricultural Research Station near Salalah in the south of the Sultanate of Oman.

United Arab Emirates

Surveys carried out in United Arab Emirates (UAE) revealed the isolation of *S. abbasi* and *H. bacteriophora* from adults of the red palm weevil, *Rhynchophorus ferrugineus* and from the soil of a palm orchard and a clover field (Abbas et al., 2001a), *S. riobrave* from larvae of *Spodoptera exigua* infesting clover and *H. bacteriophora* from the soil of a clover field (Abbas et al., 2001b).

Kingdom of Saudi Arabia

Saleh and Alheji (2003) isolated *H. indica* from the soil in the Eastern province of Saudi Arabia.

Australia

Surveys were conducted for about 10 years in all states and territories of Australia for isolation of EPNs (Akhurst and Bedding, 1986). Steinernematids recorded during the survey were *S. bibionis* (synonymized with *S. feltiae*), *S. feltiae*, *S. glaseri*, *S. kraussei*, and *S. longicaudum* and those of heterorhabditids were *H. zealandica* and *H. bacteriophora* (Wouts et al. 1982; Akhurst and Bedding, 1986). All these species were described by Akhurst and Bedding (1986) using morphological examination and cross-breeding studies. Some of the species previously reported have either been synonymized or included as *species inquirendae*.

New Zealand

Very few surveys have been conducted for predicting the EPN biodiversity in New Zealand and therefore not much information is available from this country. Ali and Wharton (2017) carried out investigation for the presence of entomopathogenic nematode in Otago region in the South Island of New Zealand and reported the occurrence of *S. kraussei* and *S. feltiae*. *H. zealandica* has also been reported from soils of Waikato pasture.

Conclusions

Entomopathogenic nematodes (EPNs) have been searched from almost all the continents with the exception of Antarctica. Further surveys are required to include additional geographic areas and climatic conditions, both in plantations and forest areas with an aim to identify native additional EPN species. The native species and populations of EPNs may prove a valuable resource, not only from a biodiversity perspective but also from an environmental perspective because of their adaptability to local environmental conditions. Besides, their virulence and recycling potential within the host may also be higher. Utilization of native EPN species would serve as an alternative to chemical pesticides and fit well in integrated pest management program.

Acknowledgements

This study was supported by Department of Zoology, Chaudhary Charan Singh University, Meerut, India and Division of Entomology, Faculty of Agriculture, Sher-e-Kashmir University of Agricultural Sciences & Technology of Kashmir (SKUAST-K), Wadura Campus, Sopore, Jammu & Kashmir, India.

Availability of data and materials

Data collected from different sources during this study are included in this article.

Authors' contributions

The first author, AHB collected the information mentioned in the tables, under subheadings of the manuscript and summarized the data related to different countries under various subheadings. The second author, AKC edited the paper and removed errors and grammatical mistakes. The third author, THA prepared abstract and introduction part of the manuscript and made necessary corrections. All authors read and approved the final manuscript.

Authors' information

Aashaq Hussain Bhat is DST Inspire Fellow and Guest Faculty at Department of Zoology, Chaudhary Charan Singh University, Meerut, India. Ashok Kumar Chaubey is Professor at Department of Zoology, Chaudhary Charan Singh University, Meerut, India. Tarique Hassan Askary is Assistant Professor at Division of Entomology, Faculty of Agriculture, Sher-e-Kashmir University of Agricultural Sciences & Technology of Kashmir (SKUAST-K), Wadura Campus, Sopore, Jammu & Kashmir, India.

Funding

AHB is thankful to Department of Science and Technology, New Delhi, India for providing finiancial assistance through DST Inspire Fellowship/2014/76.

Ethics approval and consent to participate

Not applicable

Consent for publication

Not applicable

Competing interests

The authors declare that they have no competing interests.

Author details
[1]Nematology Laboratory, Department of Zoology, Chaudhary Charan Singh University, Meerut 250004, India. [2]Division of Entomology, Faculty of Agriculture, Sher-e-Kashmir University of Agricultural Sciences & Technology of Kashmir, Wadura Campus, Sopore, Jammu & Kashmir 193201, India.

Received: 7 October 2019 Accepted: 26 January 2020
Published online: 23 March 2020

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