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ENTOMOPATHOGENIC NEMATODES (STEINERNEMATIDAE AND HETERORHABDITIDAE): ORIGIN, CLASSIFICATION, SPECIES DIVERSITY, AND PROSPECTS FOR STUDY IN CENTRAL ASIA AND UZBEKISTAN

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Abstract: Entomopathogenic nematodes (EPNs) are soil-dwelling parasitic worms that kill insects within one to two days with the help of symbiotic bacteria. This article examines the origin, phylogeny, species and clade (evolutionary branch) diversity, structure, life cycle and distribution of the families Steinernematidae and Heterorhabditidae on the basis of publications from open sources. By the end of 2023, 113 *Steinernema* and 21 *Heterorhabditis* species had been identified and described, whereas in the late 1980s this number was only 13. The symbiotic bacteria belong to the genera *Xenorhabdus* (32 taxa) and *Photorhabdus* (30 taxa). The two families lie on distant branches within the order Rhabditida: they acquired the habit of parasitizing insects independently of one another, by separate routes (convergence). Data for Central Asia are very scarce: the publications report local isolates only from Northern Kazakhstan, and no confirmed record was found for Uzbekistan. The literature analysis showed that data on classification are reliable, whereas regional data and evidence of efficacy are weak. Drawing on the biological characteristics of families, clades and species, the article proposes possibilities for their use under the conditions of Uzbekistan and a plan for studying the local fauna.

Keywords: entomopathogenic nematodes, *Steinernema*, *Heterorhabditis*, *Xenorhabdus*, *Photorhabdus*, biological control, Central Asia, Uzbekistan.

1. Introduction

For a long time, pest control in agriculture relied mainly on chemical toxicants (insecticides). The drawbacks of this approach are clearly visible today: under the influence of insecticides, pests become habituated (resistant) to them, while natural fauna suffer constant harm (Kaliaskar et al., 2022). The most difficult problem is pests hidden in the soil or inside plant tissue: pupae, beetle larvae, and caterpillars that overwinter in the soil. Entomopathogenic (insect disease-causing) nematodes have been presented as an effective biological control agent against pests in the soil, on leaf surfaces and in concealed places (Bhat et al., 2020).

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The importance of EPNs lies in the fact that they find their prey on their own; they are safe for humans, other vertebrates and plants; in many countries registration is not required; and they can be mass-produced both in insect bodies and in artificial nutrient media (Gülçü et al., 2017). For this reason, they are now produced in factories on a large scale in a number of countries in Europe, North America and Asia (Bhat et al., 2020).

The significance of the topic is evident in two respects. First, from the scientific standpoint: new species are being identified rapidly, classification is being revised on the basis of DNA data, and the partnership between EPNs and bacteria has become a well-known model in evolutionary biology. Second, from the practical standpoint: greenhouse vegetable growing, horticulture, cotton growing and melon cultivation are widespread in Uzbekistan, yet no confirmed publication on the local EPN fauna was found. Local isolates adapted to the local climate (nematode populations isolated from the natural environment) may be more resilient and more virulent than introduced species (Bhat et al., 2020), but this can be learned only by studying the local fauna.

The aim of the article is to summarize the origin, classification and species diversity of the EPN families, to show how they differ from other nematodes, to assess how well they have been studied in Central Asia and Uzbekistan, and to identify future opportunities by family and species.

2. Materials and methods

This work is a review (literature analysis). The data were collected in October 2026 from open journal websites, international databases and university electronic archives using English and Russian keywords (entomopathogenic nematodes, Steinernema, Heterorhabditis, species diversity, Uzbekistan, Kazakhstan, Central Asia). For classification and phylogeny, the reviews by Půža and Machado (2024), Bhat et al. (2020) and Burnell and Stock (2000) were read in full; regional surveys (Shibaeva, Kaliaskar, Kary, Nikdel, Hazir, Özdemir) were examined at the level of abstracts. Each figure and statement was checked against the source in the reference list; statements that did not match were changed or removed. Because access to some older publications in Uzbek and Russian (dissertations, local collections) was limited, they may not have been examined. Therefore, the conclusion for Uzbekistan should be understood as “no confirmed publication was found”, not as “absent in nature”.

3. Origin and historical development

Nematodes (roundworms) are one of the oldest and most numerous groups of animals on Earth. In them, parasitism has arisen not once but repeatedly, independently of one another, on different branches. On the basis of 18S ribosomal genes, Blaxter et al. (1998) constructed a phylogeny of nematodes and showed that the phylum Nematoda contains five major clades (evolutionary branches), and that parasitism of animals arose independently at least four times and parasitism of plants at least three times. Insect-killing nematodes also fall under this general pattern. Dillman et al. (2012) defined the concept of “entomopathogenicity” precisely: a nematode must kill an insect rapidly in partnership with bacteria, that is, in less than 120 hours; it is this trait that separates EPNs from slower associations such as phoresy (the nematode merely being carried on the body of an animal) and necromeny (the nematode waiting for the insect to die).

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The relationship between the two families was long debated. Poinar (1981) proposed that they arose as separate branches in the mid-Paleozoic era, about 375 million years ago, whereas other authors regarded them as "sister" taxa (closest relatives) (Burnell and Stock, 2000). On the basis of 18S rDNA data, Blaxter et al. (1998) showed that Steinernematidae and Heterorhabditidae do not share a common ancestor: *Heterorhabditis* appeared closer to Strongylida, while *Steinernema* appeared closer to Panagrolaimidae and *Strongyloides*. Modern multigene and whole-genome (phylogenomic) analyses confirm this: Heterorhabditidae form the earliest-diverging (basal) group of the superfamily Strongyloidea, whereas Steinernematidae are the earliest-diverging branch of the suborder Tylenchina (Půža and Machado, 2024; Ahmed et al., 2022). Thus, both families arose from distant branches within Rhabditida, and the similarity of their lifestyles is the result of convergence, that is, the independent emergence of a similar trait. Poinar (2011) later estimated both families as belonging to the Permian period (230–252 million years ago) (via Půža and Machado, 2024), which differs from the 1981 estimate by more than 120 million years; this estimate has no fossil (petrified remains) evidence, and it is an inference based on phylogeny. The genus *Heterorhabditis* is evolutionarily younger than *Steinernema* (Adams et al., 2007), so its variability in the usual genetic markers is low.

The history of the bacteria was written separately from that of the nematodes. The first bacterium was isolated from the intestine of *Neoaplectana carpocapsae* (now *S. carpocapsae*) and, on the basis of its structure and biochemical characters, was named *Achromobacter nematophilus* by Poinar and Thomas (1965–1966); this nematode was also referred to as strain DD-136 (Poinar and Thomas, 1966). In 1979, Thomas and Poinar established the genus *Xenorhabdus* for this bacterium and similar strains, but luminescent strains isolated from *Heterorhabditis* were initially also placed in this genus. Only in 1993 did Boemare, Akhurst and Mourant, relying on DNA–DNA hybridization results, separate them into the distinct genus *Photorhabdus* (Půža and Machado, 2024). In the current classification, *Xenorhabdus* comprises 32 and *Photorhabdus* 30 taxa; they are distinguished by whole-genome sequence, average nucleotide identity (ANI) and digital DNA–DNA hybridization (dDDH) values.

The scientific history begins in Germany: in 1923, Steiner described *Aplectana kraussei* from a sawfly (*Lyda* sp.) larva, which is now *S. kraussei*, regarded as the type species of the genus *Steinernema* (the species to which the genus name was originally attached) (Burnell and Stock, 2000). In 1927, Travassos established the genus *Steinernema* for this species. In 1929 in the USA, Steiner described *Neoaplectana glaseri* (now *S. glaseri*) from the Japanese beetle (*Popillia japonica*); in 1930 Glazer and Fox recorded its parasitism on the larvae of this beetle, and in the late 1930s Glaser and colleagues tested it under field conditions, opening the way to the practical use of EPNs (Bhat et al., 2020). In 1955, Weiser described *S. carpocapsae* from the codling moth, a species that later became the most studied and most widely used. The year 1976 is remembered for two independent works: Poinar established the genus *Heterorhabditis* and a new family, while Khan, Brooks and Hirschmann described *Chromonema heliothidis* from *Heliothis zea* larvae, which was later transferred to *Heterorhabditis* (Burnell and Stock, 2000). The genus *Neoaplectana* was eventually merged with *Steinernema* (Wouts et al., 1982). Work on EPNs in Europe began in the early 1980s, and large-scale production was established from 1986 (Bhat et al., 2020).

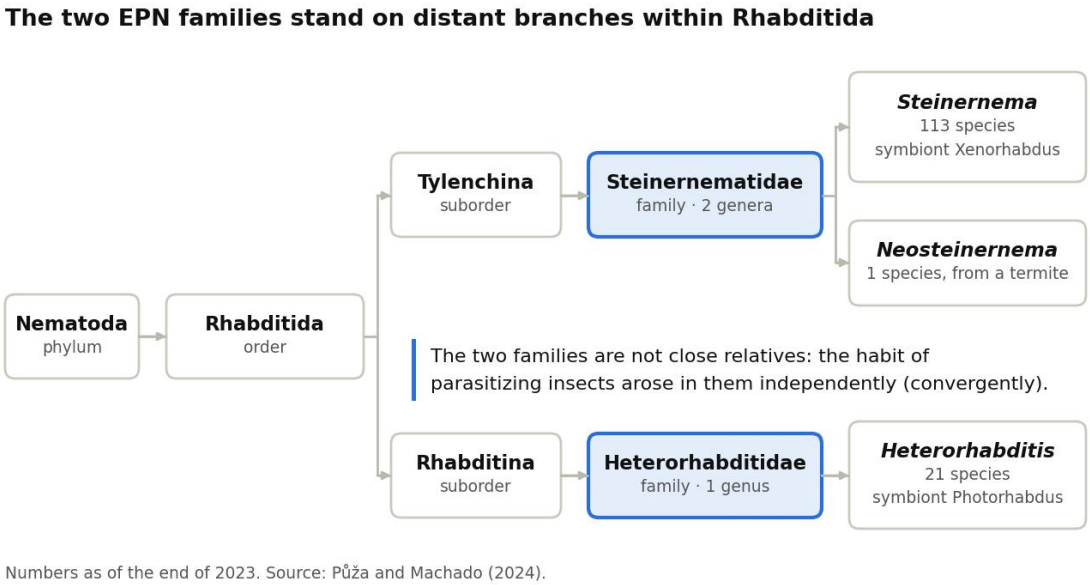
The number of described species grew rapidly: 13 in the late 1980s (10 *Steinernema*, 3 *Heterorhabditis*; Kaya and Gaugler, 1993), 22 in 1995, 35 in 2000 (25 *Steinernema*, one

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Neosteinernema and 9 *Heterorhabditis*; Burnell and Stock, 2000), 66 in 2007 (55 and 11; Bhat et al., 2020), 108 in 2015, and 113 *Steinernema* and 21 *Heterorhabditis* at the end of 2023 (Půža and Machado, 2024). The growth was not uniform: Hunt and Subbotin (2016) found that more than ten species names, for which DNA evidence was insufficient, were synonyms (redundant names) of other species. For this reason, the differences among the figures in various sources (95 and 16 in Özdemir et al., 2020; 100 and 17 in Gülçü et al., 2017; 100 and 21 in Bhat et al., 2020; 113 and 21 in the most recent count) reflect not only new discoveries but also the cleaning-up of the list. Most new species have been described from Asia, but in a number of Asian countries this research is still at an initial stage (Bhat et al., 2020).

4. Classification and species diversity

EPNs belong to the order Rhabditida. The classification ranks, from top to bottom, are: phylum, order, family, genus, species (intermediate ranks omitted). There are two families of practical importance: Steinernematidae (genera *Steinernema* Travassos, 1927 and *Neosteinernema* Nguyen and Smart, 1994) and Heterorhabditidae (the single genus *Heterorhabditis* Poinar, 1976). The genus *Neosteinernema* contains one species (*N. longicurvicauda*), which was described from a termite in Florida and has not been found elsewhere since (Bhat et al., 2020). Figure 1 shows the path from the phylum Nematoda to the genera in the form of a tree; it is immediately apparent that the two families within Rhabditida belong to separate branches rather than to a common close ancestor. Their symbiotic bacteria belong to the genera *Xenorhabdus* (32 taxa) and *Photorhabdus* (30 taxa). Typically, each *Steinernema* species forms a pair with one *Xenorhabdus* species, whereas *Heterorhabditis* species may occur together with several *Photorhabdus* species (Půža and Machado, 2024).



classification tree · from the phylum Nematoda to genera

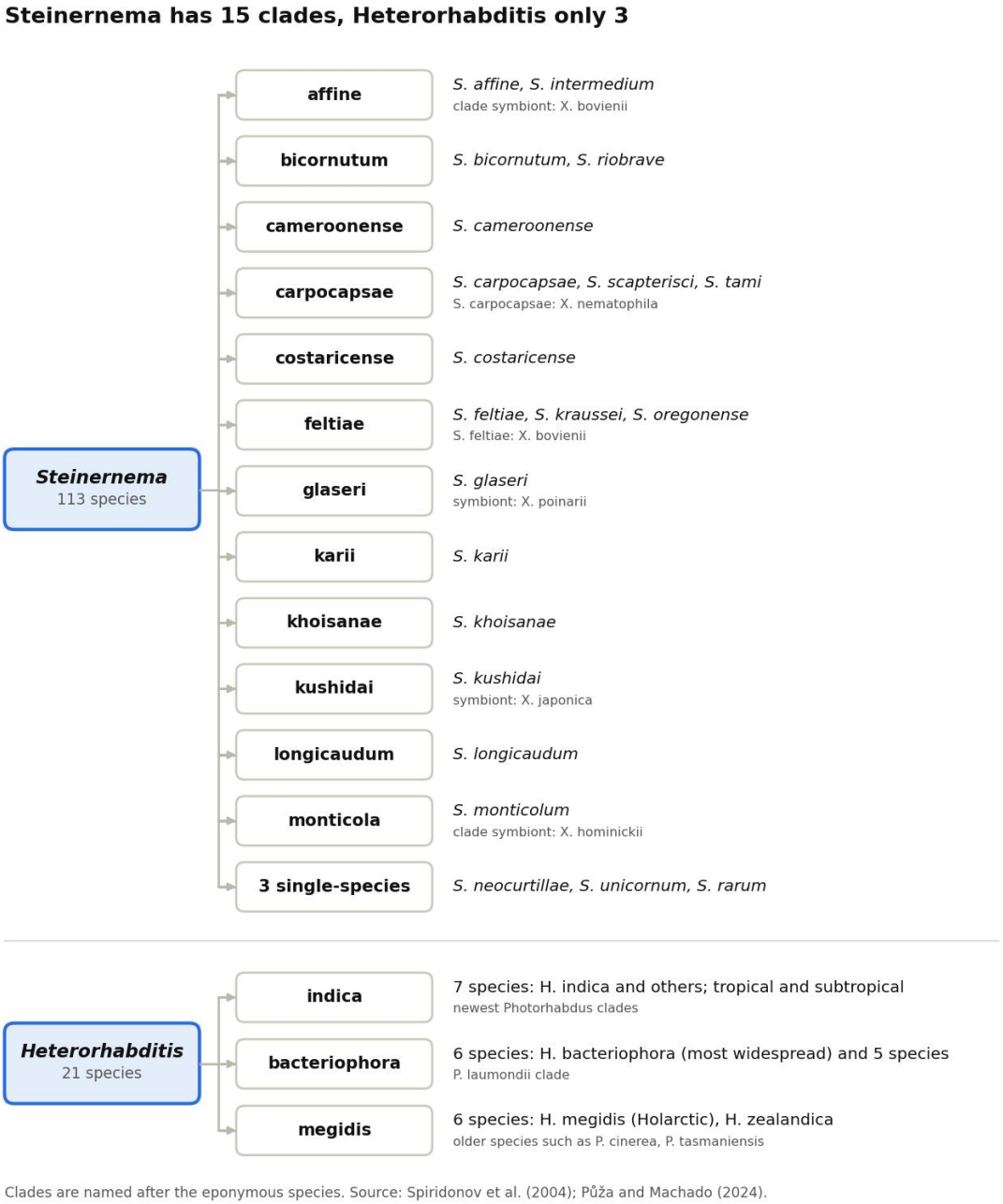
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Figure 1. Classification tree of entomopathogenic nematodes: from phylum to genus. The two families stand on separate branches, and the similarity of their lifestyles is the result of convergence (the independent emergence of a similar trait).

Species are distinguished using external structure (morphology: structure of males, dimensions of the infective juvenile (IJ; see Section 5)), cross-breeding and DNA characters together. The main character is the ITS region of rDNA: in *Steinernema* this region is the most effective for separating closely related species, but in some species ITS sequences differ within a single individual, which complicates the work. The D2D3 region is mandatory in describing a species, but it varies too little to distinguish closely related species; therefore mitochondrial COI and 12S rRNA are also being reported in new descriptions. In *Heterorhabditis* these characters vary even less, so in recent years new species such as *H. ruandica*, *H. zacatecana* and *H. casmirica* have been described using multigene analysis (Půža and Machado, 2024). The delimitation of species remains contested: Adams (1998) preferred to rely on unique character states and Spiridonov et al. (2004) on sequence divergence, while Adams et al. (2007) considered sequence divergence arbitrary; at present a mixture of both approaches is used. EPNs are easy to isolate from soil by the baiting method using insect larvae (Burnell and Stock, 2000); *Galleria mellonella* larvae were also used in the surveys in Iran and Northern Kazakhstan (Kary et al., 2009; Shibaeva et al., 2022).

The tree continues to branch among the species themselves: species are grouped into clades, that is, groups of species sharing a common ancestor. A clade is a branch of the tree consisting of a single common ancestor and all of its descendants. Within *Steinernema*, five major clades were first distinguished on the basis of ITS sequences: affine-intermedium, carpocapsae-scapterisci-tami, feltiae-kraussei-oregonense, bicornutum-ceratophorum-riobrave and arenarium-glaseri-karii-longicaudum (Spiridonov et al., 2004). Subsequent analysis divided the genus into twelve clades consisting of several species each and three clades consisting of a single species each (*S. neocurtillae*, *S. unicornum*, *S. rarum*). *Heterorhabditis*, in turn, is divided into three clades: “Indica” (7 species), living in the tropics and subtropics; “Bacteriophora” (6 species), headed by the most widespread *H. bacteriophora*; and “Megidis” (6 species), distributed in the Holarctic (Půža and Machado, 2024). Thus, *Steinernema* is considerably more diverse both in species and in clades, whereas *Heterorhabditis* is a smaller and evolutionarily younger group. When a local isolate is found, determining which clade it falls into is the first step in comparing it with known species.

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clade (branch) tree · *Steinernema* and *Heterorhabditis*

Figure 2. Clades (evolutionary branches) of *Steinernema* and *Heterorhabditis* and their main species.

Table 1. Main differences between the families Steinernematidae and Heterorhabditidae (Burnell and Stock, 2000; ICAR-NBAIR; Půža and Machado, 2024)

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Character	Steinernematidae	Heterorhabditidae
Genera	*Steinernema*, *Neosteinernema*	*Heterorhabditis*
Number of described species (2023)	113 (*Steinernema*)	21
Symbiotic bacterium (partner)	*Xenorhabdus*	*Photorhabdus*
Adult form of the first generation	males and females (two-sex reproduction)	hermaphroditic female (one individual has organs of both sexes)
Entry into the insect	natural openings (mouth, anus, spiracles)	natural openings, and by piercing the cuticle with the help of the dorsal tooth
Site of bacterial storage	in a special vesicle in the anterior part of the intestine	no special vesicle; in the anterior part of the intestine
Second-stage cuticle (sheath)	easily shed	well retained
Colour of the infected insect cadaver	yellowish-brown, light brown	red, brick-coloured, purple, sometimes other colours
Position in the phylogeny	earliest-diverging branch of the suborder Tylenchina	earliest-diverging (basal) group of the superfamily Strongyloidea

Symbiotic bacteria partly, but not completely, mirror the phylogeny of the nematodes. According to the review by Půža and Machado (2024), the principle "one nematode species — one *Xenorhabdus* species" generally applies in *Steinernema* species, but some "multi-host" bacteria occur in several nematode species. The single broad analysis covering all Steinernematidae showed 12 cases of cospeciation (parallel splitting of two partner species into new species) among 30 pairs, and at least 17 host switches. In *Heterorhabditis–Photorhabdus* pairs, the dependence of the bacterium on its own nematode (host specificity) is high, but widespread species such as *H. indica* and *H. bacteriophora* occur with many bacterial species. In more than one third of Steinernematidae species, the symbiotic bacterium has not yet been identified, that is, the classification is incomplete here as well.

Table 2. Selected nematode–bacterium pairs

Nematode	Symbiotic bacterium (partner)	Note
S. carpocapsae	*X. nematophila*	partner of the first described EPN (mid-1960s)

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Nematode	Symbiotic bacterium (partner)	Note
S. feltiae	*X. bovienii*	bacterial strains have changed together with nematode populations
S. glaseri	*X. poinarii*	this bacterium also occurs in *S. cubanum*
S. kushidai	*X. japonica*	pair described from Japan
affine clade	*X. bovienii*	linked at the clade level
monticola clade	*X. hominickii*	linked at the clade level
H. bacteriophora (bacteriophora clade)	*P. laumondii* clade	linked at the clade level
megidis clade	older species such as *P. cinerea* and *P. tasmaniensis*	linked at the clade level
indica clade (except *H. indica*)	the newest *Photorhabdus* clades	linked at the clade level

5. Morphology (structure) and differences from other nematodes

First of all, we must define what the infective juvenile (IJ) is, because the rest of the article is built around this stage. The IJ is the third-stage, developmentally arrested “dauer” (resistant) juvenile of the nematode (Burnell and Stock, 2000). It is the only free-living stage in the life cycle; all other stages are passed only inside the host’s body (Dillman et al., 2012; Tofangsazi et al., 2012). The IJ does not feed, carries the symbiotic bacterium in its intestine, moves freely in the soil searching for a host, and, once it finds one, enters its body and releases the bacterium (Půža and Machado, 2024). For this reason, the IJ is precisely the active component of a biopreparation applied to the soil: the rate recommended in the USA is 1–3 billion IJ per acre (Berry, 1998).

EPNs are roundworms of the order Rhabditida. Their free-living juvenile (IJ) is transparent and in *S. carpocapsae* is 438–650 µm long (Berry, 1998). The IJ does not feed and carries the symbiotic bacterium in its intestine. In *Steinernema* the bacterium is kept in a special vesicle in the anterior part of the intestine, whereas in *Heterorhabditis* there is no special vesicle and the bacterial cells lie in the anterior part of the intestine (Burnell and Stock, 2000). The IJ of *Heterorhabditis* has a dorsal tooth on its head, which helps to pierce the outer covering (cuticle) of the insect (Berry, 1998; Burnell and Stock, 2000). Another difference: the *Steinernema* IJ easily sheds the second-stage cuticle, whereas *Heterorhabditis* retains it well (ICAR-NBAIR).

The main difference from other nematodes lies in the partnership between nematode and bacterium. In the opinion of Burnell and Stock (2000), EPNs are the only group among the rhabditids that live

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together with a gut bacterium (forming a symbiosis). The parasites in the order Rhabditida originated from free-living, bacteria-feeding nematodes; in some representatives necromeny is observed, that is, the nematode waits until the host dies and develops at the expense of saprophytic (decay-causing) bacteria in its body. In Sudhaus's (1993) opinion, *Heterorhabditis* and *Steinernema* arose precisely from necromenic nematodes, once these began to cooperate with a harmful (entomopathogenic) bacterium (Burnell and Stock, 2000). As Blaxter et al. (1998) showed, parasitism arose independently several times in nematodes; therefore, in separating EPNs from other parasite groups, the host type (insect) and the partnership with bacteria are the key characters.

6. Biology and life cycle (developmental cycle)

Having found a host in the soil, the IJ enters the body through natural openings, while *Heterorhabditis*, with its dorsal tooth, can also penetrate the thin membrane between body segments (the intersegmental membrane). After passing into the insect's blood fluid (haemolymph), the IJ releases the bacterial cells from its intestine. The insect usually dies within 24–48 hours (Půža and Machado, 2024; Burnell and Stock, 2000). The bacterium converts the insect's tissues into food for the nematode, and with its secondary metabolites (antibiotics and toxins) protects the cadaver from other microbes and from animals that devour dead insects (for example, ants) (Půža and Machado, 2024). The nematodes develop by feeding on bacterial cells: in *Steinernema* males and females develop from the IJ, whereas in *Heterorhabditis* a hermaphroditic female matures first, after which in both genera several generations alternate through males and females. In *Galleria* larvae at 23 °C, *S. carpocapsae* reached adulthood in 2 days and *H. bacteriophora* in 3 days (Burnell and Stock, 2000). When the food in the cadaver runs out, the nematodes switch again to the "dauer" form, the bacterium resettles in their intestine, and the new IJs usually leave the cadaver for the soil 7–14 days after infection; this period depends on host size and temperature. In this way, the IJ completes the life cycle and sets out to search for a new host.

Foraging strategies differ among species: *Steinernema* species usually search for prey near the soil surface, whereas *Heterorhabditis* species often penetrate deeper soil layers and actively seek prey (Berry, 1998). Adaptation to temperature also differs among species and isolates: for example, an isolate of *S. feltiae* obtained from Turkey was better adapted at 32 °C than *Heterorhabditis* strains (Susurluk et al., 2001); therefore, it is important to test local isolates separately.

7. Distribution: the world, Central Asia and Uzbekistan

EPNs have been found on all continents except Antarctica (Gülçü et al., 2017; Bhat et al., 2020). Most new species have been described from Asia, but in some Asian countries this research is still at an initial stage (Bhat et al., 2020). *S. carpocapsae* and *S. feltiae* are widespread worldwide, and among *Heterorhabditis* the most widespread is *H. bacteriophora* (Burnell and Stock, 2000).

The situation in Central Asia is different. The most precise data from the region come from Northern Kazakhstan: 15 isolates were obtained in the Akmola and Pavlodar regions (13 from coniferous and mixed forests and 2 from field soil: one a potato field, one a field sown with perennial grasses). On the basis of the colour of the *Galleria* larval cadaver and the structure of males, they were identified as belonging to the family Steinernematidae; the species level was not determined. Of the 15 isolates, 12 caused approximately 50–70% mortality in wireworm (*Agriotes obscurus*) in the laboratory, and

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isolates AF29, AF57 and KP76 were found to be the best for further work (Shibaeva et al., 2022). The same group conducted another experiment with local isolates from the semi-arid zone of Northern Kazakhstan: when two local and two commercial isolates (*S. feltiae* and *S. carpocapsae*) were tested on larvae of darkling beetles (Tenebrionidae), local isolate AF29 caused 67% mortality at a dose of 100 IJ/cm². The authors regard this as the first evidence of the efficacy of local EPNs in this zone and emphasize that commercial biopreparations are expensive for Central Asian farmers (Kaliaskar et al., 2022). In one Russian-language study, *S. carpocapsae*, *S. feltiae* and *S. glaseri* were tested on cotton pests (*Spodoptera littoralis*, *Pectinophora gossypiella*); the highest efficacy against larvae was observed with *S. feltiae*, while pupae were generally less susceptible (El Deeb, 2010). This is not a local finding but a test result.

Neighbouring regions are important for comparison, because soil samples there have been systematically examined. In northwestern Iran in 2002–2004, 833 soil samples were examined by the insect-bait method, of which 27 (3.2%) were positive (EPN found): *H. bacteriophora* was isolated from 17 sites, *S. feltiae* from 8, and *S. carpocapsae* and *S. bicornutum* from one site each; Steinernematidae were found mainly in orchards and pastures, and Heterorhabditidae in pastures and alfalfa fields (Kary et al., 2009). In the forests and pastures of Arasbaran, 21 of 691 samples (3%) were positive, and *S. glaseri*, *S. kraussei* and three undescribed *Steinernema* species were additionally identified (Nikdel et al., 2010). In a survey in Turkey in 1999–2000, 22 of 1080 sites (2%) were positive: *S. feltiae* was found at 10 sites, *H. bacteriophora* at 7, *S. affine* at 4, and a new *Steinernema* species at one site; the authors note that EPNs are widespread in the country but that their frequency of occurrence is lower than in other parts of the world (Hazir et al., 2003). In total, 12 species have been recorded in Turkey, and in 2020 *S. litorale* was found for the first time for Turkey and the Middle East (in 1 of 67 samples) (Özdemir et al., 2020). In Russia, *S. arenarium*, *S. bicornutum*, *S. kraussei*, *S. feltiae*, *S. carpocapsae* and three *Heterorhabditis* species have been recorded, and liquid suspensions of *S. carpocapsae* (“Nemabact”) and *S. feltiae* (“Entonem F”) are sold on the market (Bhat et al., 2020). These figures offer a practical lesson for Uzbekistan: the share of positive samples may be around 2–3%, so hundreds of samples must be collected in order to draw reliable conclusions about the local fauna.

Table 3. EPNs recorded in Central Asia and neighbouring regions

Region	Recorded	Source
Northern Kazakhstan (Akmola, Pavlodar)	15 isolates, family Steinernematidae, species not identified	Shibaeva et al., 2022
Northern Kazakhstan (semi-arid zone)	local isolates (AF29 and others), laboratory test	Kaliaskar et al., 2022
Uzbekistan	no confirmed publication found	this article
Iran (northwest), 833 samples	27 positive (3.2%): *H. bacteriophora*, *S. feltiae*, *S.*	Kary et al., 2009

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Region	Recorded	Source
	carpocapsae, *S. bicornutum*	
Iran (Arasbaran), 691 samples	21 positive (3%): *H. bacteriophora*, *S. carpocapsae*, *S. bicornutum*, *S. feltiae*, *S. glaseri*, *S. kraussei* and 3 undescribed *Steinernema* species	Nikdel et al., 2010
Turkey, 1999–2000, 1080 sites	22 positive (2%): *S. feltiae*, *H. bacteriophora*, *S. affine*, new *Steinernema* sp.	Hazir et al., 2003
Turkey	12 species; *S. litorale* first record (1 of 67 samples)	Özdemir et al., 2020
Russia	*S. arenarium*, *S. bicornutum*, *S. kraussei*, *S. feltiae*, *S. carpocapsae*, *H. zealandica*, *H. megidis*, *H. bacteriophora*	Ivanova et al., 2000 (via Bhat et al., 2020)

8. Literature analysis: what is certain and what remains uncertain

The conclusions of the review rest on how well the sources agree with one another. For this reason, the main statements were compared across sources and their level of reliability was assessed.

Table 4. Main claims and their sources

Question	Sources	Result	Reliability
Number of species	Půža and Machado, 2024; Bhat et al., 2020; Gülçü et al., 2017; Burnell and Stock, 2000	2023: 113 and 21; 2020: about 100 and 21; 2017: 100 and 17; 2000: 25+1 and 9. The difference depends on the year of the count and on the removal of redundant names (synonyms)	high
Evolutionary origin	Blaxter et al., 1998; Burnell and Stock, 2000; Ahmed et al., 2022; Půža and	two independent branches; in older works also regarded as "sister" taxa	high for branching, low for age

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Question	Sources	Result	Reliability
	Machado, 2024	(closest relatives); age estimates 375 and 230–252 million years	
Species boundaries	Adams, 1998; Spiridonov et al., 2004; Adams et al., 2007	approaches differ; the main criterion is divergence in DNA sequence; the ITS and D2D3 markers may prove insufficient in the future	moderate
Symbiotic (partner) pairs	Půža and Machado, 2024; Gülçü et al., 2017	in *Steinernema* mainly "one nematode — one bacterium", in *Heterorhabditis* with several bacteria; in one third the partner bacterium is unknown	moderate
Central Asian fauna	Shibaeva et al., 2022; Kaliaskar et al., 2022	only Northern Kazakhstan, species not identified	low
Neighbouring regions	Kary et al., 2009; Nikdel et al., 2010; Hazir et al., 2003; Özdemir et al., 2020	species identified in Iran and Turkey; share of positive samples 2–3%	high
Efficacy	Shibaeva et al., 2022; Kaliaskar et al., 2022; El Deeb, 2010	50–70% mortality in the laboratory, 67% (AF29); pupae less susceptible; no field trials	low
Temperature and foraging strategy	Berry, 1998; Susurluk et al., 2001	differences exist at the genus level, and differences among isolates are also large	moderate

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Three conclusions follow from the analysis. First, data on classification are recent and reliable, but species delimitation remains contested; therefore, the number of species should always be given together with its year. Second, the ancient dates differ from one another by more than 120 million years (375 and 230–252 million years), and both rest on an inference based on phylogeny; therefore, it is appropriate for the article to write "independent, ancient origin" instead of an exact age. Third, data on Central Asia are limited to the northern part of a single country, are not identified to species level, and rely mainly on laboratory testing. It is precisely this weakness that justifies the research plan in the following sections. Because access to some older publications in Uzbek and Russian was not possible, the assessment of regional data should be regarded as incomplete.

8.1. Review of sources

Below, each source used in the article is presented separately, with its link and the specific data taken from it. Sources without a link are classic printed publications whose bibliographic details were checked against the reference lists of Burnell and Stock (2000) and Bhat et al. (2020).

Table 4a. Review of sources

No.	Source and link	What was studied	Specific data	Section
1	Půža and Machado, 2024	Classification and phylogeny of EPNs and their symbiotic bacteria (Zoological Letters, review)	113 *Steinernema* and 21 *Heterorhabditis* at the end of 2023; from 22 (1995) to 108 (2015); *Xenorhabdus* 32 and *Photorhabdus* 30 taxa; *Steinernema* 12 multi-species and 3 single-species clades, *Heterorhabditis* 3 clades (7, 6 and 6 species); 12 cospeciation events and at least 17 host switches in 30 pairs; the symbiotic	3, 4, 5, 8, 9

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No.	Source and link	What was studied	Specific data	Section
			bacterium is unknown in more than one third of Steinernematidae species	
2	Bhat et al., 2020	Worldwide distribution of EPNs (Egyptian J. Biol. Pest Control, review)	about 100 *Steinernema* and 21 *Heterorhabditis*; number of species from 13 (late 1980s) to 66 (2007); most new species from Asia; *Neosteinernema longicurvicauda* only from a termite in Florida; "Nemabact" (*S. carpocapsae*) and "Entonem F" (*S. feltiae*) in Russia; EPNs on all continents except Antarctica	3, 7, 9
3	Burnell and Stock, 2000	Biology, distribution and phylogeny of EPNs (Nematology, review)	in 2000, 25 *Steinernema*, 1 *Neosteinernema*, 9 *Heterorhabditis*; the insect dies in 24–48 hours; *Steinernema* stores the bacterium in an	3, 5, 6

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No.	Source and link	What was studied	Specific data	Section
			intestinal vesicle, *Heterorhabditis* has no vesicle; *Heterorhabditis* also enters by means of the dorsal tooth; Poinar's (1981) estimate of 375 million years; conflicting evidence on the relationship between the two families	
4	Gülçü et al., 2017	Ecology and use of EPNs (Biopesticides International, review)	100 *Steinernema* and 17 *Heterorhabditis*; 20 *Xenorhabdus* and 4 *Photorhabdus*; EPNs are safe for humans, vertebrates and plants, and registration is not required in many countries	1, 3
5	Blaxter et al., 1998	DNA-based phylogeny of nematodes (Nature)	53 18S rDNA sequences; 5 clades in the phylum; parasitism of animals arose independently at least 4 times, and parasitism of plants at least 3	3, 5

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No.	Source and link	What was studied	Specific data	Section
			times	
6	Dillman et al., 2012	the concept of "entomopathogenic" (PLoS Pathogens)	EPNs kill the host in partnership with bacteria in less than 120 hours; the IJ is the only free-living stage	3, 5
7	Tofangsazi et al., 2012	General description of EPNs (UF/IFAS EENY-530)	the IJ is the only free-living stage; enters through the spiracle (breathing pore), mouth, anus or cuticle	5
8	Berry, 1998	Short guide to EPNs (Oregon State University)	*S. carpocapsae* IJ transparent, 438–650 µm; *Heterorhabditis* pierces the cuticle with the dorsal tooth; *Steinernema* searches near the soil surface, *Heterorhabditis* deeper; 1–3 billion IJ per acre in the USA	5, 6, 9
9	ICAR-NBAIR	Biology and classification of EPNs (database)	insect cadavers killed by Steinernematidae are brownish-ochre, those killed by Heterorhabditidae are red, brick-coloured or	4

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No.	Source and link	What was studied	Specific data	Section
			purple; *Steinernema* stores the bacterium in a vesicle in the anterior part of the intestine; in *Heterorhabditis* the first generation is hermaphroditic	
10	Kary et al., 2009	Soil survey in northwestern Iran (Nematology)	833 samples in 2002–2004, 27 positive (3.2%); 17 (2.0%) *Heterorhabditis*, 10 (1.2%) *Steinernema*; *H. bacteriophora* from 17 sites, *S. feltiae* from 8 sites, *S. carpocapsae* and *S. bicornutum* from one site each	7, 9
11	Nikdel et al., 2010	Arasbaran forests and pastures, Iran (Nematology)	691 samples in 2006–2008, 21 positive (3%); 9 (1.3%) Heterorhabditidae, 12 (1.7%) Steinernematidae; *S. kraussei*, *S. glaseri* and 3 undescribed species	7
12	Hazir et al.,	Soil survey in	1080 sites in	7

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No.	Source and link	What was studied	Specific data	Section
	2003	Turkey (Biodiversity and Conservation)	1999–2000, 22 positive (2%); 15 Steinernematidae and 7 Heterorhabditidae isolates; 4 species; *S. feltiae* from 10 sites	
13	Özdemir et al., 2020	First record of *S. litorale* in Turkey (Insects)	1 of 67 samples (Ankara, Çamkoru), symbiotic bacterium *X. bovienii*; 12 species in Turkey; LC50 in *Galleria* 153.4, 51.0 and 15.4 IJ at 48, 72 and 96 hours	7
14	Shibaeva et al., 2022	EPN isolates from Northern Kazakhstan	15 isolates (13 forest, 2 field), family Steinernematidae; 12 of them caused 50–70% mortality in wireworm; AF29, AF57 and KP76 were the best	7, 10
15	Kaliaskar et al., 2022	Efficacy of local and commercial isolates (AGRIVITA)	doses of 100–400 IJ/cm²; AF29 caused 67% mortality at 100 IJ/cm²;	7, 9

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No.	Source and link	What was studied	Specific data	Section
			commercial preparations are expensive for Central Asian farmers	
16	El Deeb, 2010	three *Steinernema* species against cotton pests (RUDN)	*S. feltiae* was the most effective against larvae of *Spodoptera littoralis* and *Pectinophora gossypiella*; pupae were less susceptible	7, 9
17	Susurluk et al., 2001	Three nematode–bacterium complexes from Turkey (Nematology)	*S. feltiae* was better adapted to 32 °C than the *Heterorhabditis* strains	6, 9
18	Wouts et al., 1982; Steiner, 1923; Weiser, 1955 (no link was found for the last two)	species and genus names	Wouts: *Neoaplectana* — a synonym (redundant name) of *Steinernema*; Steiner: *Aplectana kraussei* from a sawfly (*Lyda* sp.) (now *S. kraussei*); Weiser: *S. carpocapsae* from the codling moth	3
19	Thomas and Poinar, 1979;	history of the symbiotic	genus *Xenorhabdus*	3

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No.	Source and link	What was studied	Specific data	Section
	Boemare et al., 1993; Poinar and Thomas, 1966 (no link found)	bacteria	(1979), genus *Photorhabdus* (1993), *Achromobacter nematophilus* (Poinar and Thomas, 1965) and the nematode DD-136	
20	Khan et al., 1976; Nguyen and Smart, 1994; Steiner, 1929; Glazer and Fox, 1930	earliest species	*Chromonema heliothidis*: first generation hermaphroditic, cadaver brick-coloured and glowing in the dark; *Neosteinernema longicurvicauda* from a termite; *Neoaplectana glaseri* from the Japanese beetle	3, 4
21	Adams, 1998; Spiridonov et al., 2004; Ahmed et al., 2022; Adams et al., 2007; Hunt and Subbotin, 2016 (no link was found for the last two)	species delimitation, clades and whole-genome analysis (phylogenomics)	Adams: a mixture of the evolutionary and phylogenetic species concepts; Spiridonov: 84 new ITS sequences from 24 nominal species, ITS is useful within clades and of little use between clades;	3, 4

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No.	Source and link	What was studied	Specific data	Section
			Ahmed: analysis of Tylenchina and Rhabditina based on 286 genomes and transcriptomes	
22	Kaya and Gaugler, 1993	Classic review of EPNs (Annual Review of Entomology)	13 species in the late 1980s (10 *Steinernema* and 3 *Heterorhabditis*; via Bhat et al., 2020)	3

9. Future prospects by family and species

Knowing the clade structure helps to define the prospects more precisely. The "Indica" clade of *Heterorhabditis* occurs mainly in the tropics and subtropics, whereas the "Megidis" clade occurs in the Holarctic (in the temperate and cold regions of the Northern Hemisphere); therefore, the local representatives of these clades are expected to differ between the hot southern and the cooler foothill regions of Uzbekistan (Půža and Machado, 2024). Adaptation to temperature depends on isolates even within a species: for example, an isolate of *S. feltiae* obtained from Turkey was better adapted at 32 °C than *Heterorhabditis* strains (Susurluk et al., 2001); therefore, local isolates must be tested separately rather than relying on the species alone. These considerations must be tested experimentally under the conditions of Uzbekistan.

The species diversity itself is the greatest asset: each species has its own temperature range, foraging strategy and prey range, that is, one can select "its own" nematode for a specific pest and specific conditions. Therefore, we consider the prospects at the family and species level.

Steinernematidae. With 113 species and 15 clades, this family is rich in species, so the likelihood of finding new isolates in the local fauna is high. Because *Steinernema* species search for prey near the soil surface (Berry, 1998), they may be tested against pests near the soil surface and in concealed places. In Iran, Steinernematidae were isolated mainly from orchards and pastures (Kary et al., 2009), and in Russia preparations based on *S. carpocapsae* and *S. feltiae* are sold commercially (Bhat et al., 2020).

Heterorhabditidae. The number of species is small (21, in 3 clades), but members of this family search actively in deeper soil layers and, thanks to the dorsal tooth, can also penetrate the cuticle (Berry, 1998; Burnell and Stock, 2000); therefore, they are candidates against larvae inside the soil. *H. bacteriophora* was the most frequently found species in Iran (Kary et al., 2009). The bacteria

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Photorhabdus and *Xenorhabdus* remain a separate research direction as a source of antibiotics and other substances against human, veterinary and plant pathogens (Gülçü et al., 2017).

Table 5. Known characteristics of groups and directions for testing in Uzbekistan

Group	Known characteristic (source)	Direction for testing
Steinernema (in general)	searches near the soil surface (Berry, 1998)	pests near the soil surface and in concealed places
Heterorhabditis (in general)	searches in deeper soil layers, pierces the cuticle (Berry, 1998; Burnell and Stock, 2000)	larvae inside the soil
S. feltiae	the most frequently found Steinernematidae species in Iran and Turkey (Kary et al., 2009; Hazir et al., 2003); the Turkish isolate is adapted to 32 °C (Susurluk et al., 2001); the most effective in the laboratory against larvae of cotton moths (El Deeb, 2010)	larvae of cotton and vegetable pests
S. carpocapsae	basis of the "Nemabact" preparation in Russia; found in Iran and Turkey (Bhat et al., 2020)	mobile larvae
S. kraussei	occurs in forests and pastures (Burnell and Stock, 2000); found in Arasbaran, Iran (Nikdel et al., 2010)	forest and foothill regions
H. bacteriophora	the most frequently found species in Iran, 17 sites (Kary et al., 2009); the most widespread Heterorhabditidae species (Burnell and Stock, 2000)	soils of pasture and alfalfa fields
Indica clade (*H. indica*)	tropical and subtropical (Půža and Machado, 2024)	hot southern regions
Megidis clade	Holarctic (Půža and	cooler, foothill regions

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Group	Known characteristic (source)	Direction for testing
	Machado, 2024)	

Overall, the results that may be achieved in the future can be seen in five directions. The first is to create a database of local isolates: in Kazakhstan local isolates were compared with commercial isolates and one local isolate gave the best result (Kaliaskar et al., 2022); creating such a database in Uzbekistan could also provide an alternative to imported preparations. The second is local production: multiplication in *Galleria* larvae and on solid (dense) nutrient media is suitable for small enterprises, whereas liquid fermentation requires a large bioreactor and high initial investment (Bhat et al., 2020). The third is to move variants that proved effective in the laboratory to field trials and to choose the target stage correctly: larvae of cotton pests are susceptible, whereas pupae are less susceptible (El Deeb, 2010). The fourth is to adapt application technology (rate, soil moisture, application timing) to local conditions. The fifth is to obtain new compounds from the symbiotic bacteria (Gülçü et al., 2017).

10. Research plan (roadmap) for Uzbekistan

The first stage is to identify the local fauna. It is necessary to take samples systematically from forest, orchard, vegetable and cotton field soils in regions with different climates, such as Samarkand, Tashkent, Fergana, Surkhandarya, Khorezm and Karakalpakstan, to examine them by the *Galleria* baiting method, to identify the isolated nematodes by external structure and by the ITS, D2D3 and COI genes, and to submit the sequences to an international database. The second stage is to test selected isolates in the laboratory against local pests and at various temperatures (LC50, speed of kill), followed by closed greenhouse and small field trials. The third stage is to multiply the best strains cheaply under local conditions and to develop application recommendations for farmers. At every stage, cooperation with the countries of the region (the experience of Kazakhstan) is important for documentation and for comparing results.

11. Conclusion

Entomopathogenic nematodes belong to two families of independent origin, and at present 134 species (113 *Steinernema* and 21 *Heterorhabditis*) are known, a number that continues to grow. The phylogeny places them on distant branches within the order Rhabditida; at the clade level, *Steinernema* divides into 15 and *Heterorhabditis* into 3 clades. Their strength lies in the joint work of the nematode and its symbiotic bacterium, and their importance in being a safe alternative to chemical agents that is effective against pests in the soil and in concealed places. In Central Asia the EPN fauna is almost unstudied: information on local isolates exists only from Northern Kazakhstan, no confirmed publication was found for Uzbekistan, and evidence of efficacy remains at the laboratory level. This gap is both a problem and an opportunity: systematic soil sampling, selection of suitable species by clade, and the creation of local biopreparations could turn Uzbekistan into a centre of EPN research in Central Asia.

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Glossary

English / Latin term	Uzbek term	Russian	Definition
phylum	Tip	тип	the largest group in classification; all nematodes belong to the phylum Nematoda
order	Tartib	отряд	EPNs belong to the order Rhabditida
suborder	Kenja tartib	подотряд	Tylenchina, Rhabditina
superfamily	Superoila	надсемейство	a union of families, for example Strongyloidea
family	Oila	семейство	Steinernematidae, Heterorhabditidae
genus	Turkum	род	*Steinernema*, *Heterorhabditis*, *Neosteinernema*
species	Tur	вид	the basic unit of classification, for example *S. feltiae*
taxon	Takson	таксон	any group in classification: species, genus, family, and so on
type species	Tip tur	типовой вид	the species to which a genus name was originally attached and which defines the genus
clade	Klada	клада	a branch of the tree consisting of a single common ancestor and all of its descendants

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English / Latin term	Uzbek term	Russian	Definition
phylogeny	Filogeniya (qarindoshlik shajarasi)	филогения	the evolutionary relatedness of organisms and the tree diagram that shows it
phylogenomics	Filogenomika	филогеномика	construction of a phylogeny on the basis of whole-genome (all DNA) data
taxonomy, systematics	Taksonomiya (sistematika)	таксономия, систематика	the science of naming, grouping and determining the relatedness of organisms
synonym	Sinonim	синоним	a redundant name given later to a species; the case in which a species name is found to be invalid
convergent evolution	Konvergensiya (o'xshash belgilarning mustaqil paydo bo'lishi)	конвергентная эволюция	the independent emergence, in groups descended from different ancestors, of a similar character or lifestyle, unrelated to one another
cospeciation	Kospeksiya	коспециация	parallel splitting of two partner species into new species
entomopathogenic nematode	Entomopatogen nematoda (EPN)	энтомопатогенная нематода	a soil nematode that rapidly kills an insect with the help of a symbiotic bacterium; by the criterion of Dillman et al. (2012), killing occurs in less

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English / Latin term	Uzbek term	Russian	Definition
			than 120 hours
infective juvenile (IJ)	Infektsion (yuqtiruvchi) lichinka, IJ	инвазионная личинка	a third-stage, developmentally arrested "dauer" juvenile and the only free-living stage in the life cycle; does not feed, carries the symbiotic bacterium in its intestine, searches for a host in the soil; in *S. carpocapsae* 438–650 µm long; the active component of a biopreparation
dauer juvenile	Dauer (chidamli) lichinka	дауэр-личинка	a developmentally arrested juvenile stage resistant to unfavourable conditions; in EPNs the IJ corresponds to this form
symbiosis	Simbioz (birga yashash)	симбиоз	the living together of two organisms
mutualism	Mutualizm (o'zaro foydali hamkorlik)	мутуализм	a symbiosis in which both partners benefit; between EPNs and bacteria it is obligate in nature
symbiont	Simbiont (hamkor organizm)	симбионт	a partner living together with another; here, the bacterium *Xenorhabdus* or *Photorhabdus*
host	Xo'jayin	хозяин	an organism in which a parasite or pathogen

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English / Latin term	Uzbek term	Russian	Definition
			lives; for EPNs, an insect
parasite	Parazit	паразит	an organism that lives at the expense of a host
necromeny	Nekromeniya	некромения	the nematode waits until the host dies and develops at the expense of saprophytic (decay-causing) bacteria in the cadaver
phoresy	Forez	форезия	the nematode merely being carried on the body of another animal
amphimixis	Amfimiktik (ikki jinsli) ko'payish	амфимиксис	reproduction through males and females
hermaphrodite	Germafrodit	гермафродит	the presence of organs of both sexes in one individual; the first generation of *Heterorhabditis*
haemolymph	Gemolimfa	гемолимфа	the fluid that takes the place of blood in an insect
septicaemia	Septitsemiya	септицемия	general poisoning of the organism caused by microbes that have entered the blood
cuticle	Kutikula	кутикула	the outer protective covering of the body of a nematode or insect
dorsal tooth	Dorsal (orqa) tishcha	дорсальный зубец	the tooth on the head of a *Heterorhabditis*

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English / Latin term	Uzbek term	Russian	Definition
			IJ that helps to pierce the insect cuticle
ambusher	Pistirmachi	засадная стратегия	a foraging strategy in which the predator waits in place and catches its prey
cruiser	Izquvar	активный поиск	a foraging strategy in which the predator actively searches for prey within the soil
virulence	Virulentlik (zaharlilik darajasi)	вирулентность	the ability of a disease-causing agent (pathogen) to cause disease in or kill a host
scavenger	Skavenjer (o'liksoz)	падальщик	an animal that devours dead insects, for example an ant
secondary metabolite	Ikkilamchi metabolit	вторичный метаболит	antibiotics and toxins produced by a bacterium
bioluminescence	Bioyarqirash	биолюминесценция	emission of light by a living organism; a characteristic of *Photorhabdus*
isolate	Izolyat	изолят	a nematode or bacterial population isolated from a natural sample
strain	Shtamm	штамм	an isolate that is maintained and studied in the laboratory
native (indigenous) isolate	Mahalliy (aborigen) izolyat	местный изолят	an isolate obtained from the given region and adapted to the

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English / Latin term	Uzbek term	Russian	Definition
			local climate
insect baiting (*Galleria* baiting)	Hasharot-tuzoq usuli	метод ловушек-приманок	isolating EPNs from soil with the help of insect larvae such as *Galleria*
soil survey	Survey (tuproq namunalarini tizimli tekshirish)	обследование	determining the EPN fauna by taking many samples from a region
median lethal concentration	LC50 (yarim o'ldiruvchi konsentratsiya)	средняя летальная концентрация	the concentration that kills 50% of the test organisms
rDNA, 18S rDNA	rDNK, 18S rDNK	рДНК	DNA encoding ribosomal RNA; used in constructing the phylogeny of nematodes
ITS, D2D3, COI	ITS, D2D3, COI	ITS, D2D3, COI	DNA regions used to distinguish species: the internal spacer region of rDNA (ITS), the D2D3 segment of 28S rDNA and the mitochondrial cytochrome oxidase I gene (COI)
ANI, dDDH	ANI, dDDH	ANI, dDDH	similarity indices used to separate bacterial species on the basis of the genome: average nucleotide identity and digital DNA–DNA hybridization
biological control	Biologik nazorat	биологический	suppression of pests with the help of

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English / Latin term	Uzbek term	Russian	Definition
	(biologik kurash)	контроль	living organisms
biopesticide, bioproduct	Biopreparat	биопрепарат	a pest-control agent based on living organisms
pest	Zararkunanda	вредитель	an insect that causes damage to crops
liquid fermentation, solid-state culture	Suyuq fermentatsiya, qattiq muhitda ko'paytirish	жидкая ферментация, твёрдофазное культивирование	methods of mass production of EPNs on an industrial scale; the liquid method requires a bioreactor (Bhat et al., 2020)

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