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**OVER WORLD DISTRIBUTION OF STEINERNEMATIDAE AND
HETERORHABDITIDAE (NEMATODA, PANAGROLAIMIDA ET RHABDITIDA)
ENTOMOPATHOGENIC NEMATODES**

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The study represents a biogeographic survey over world distribution of the entomopathogenic nematodes (EPN) according to current borders of countries. The distribution of countries where entomopathogenic nematodes were presented including their belonging to biogeographic regions were analyzed. The World Geographical Scheme for Recording Plant Distributions and land area with using of the Bray-Curtis method of cluster analysis were also included. The analysis demonstrates simple of regularities in the EPN distribution. According to the analysis of published data, 120 species of EPN are presented in 72 countries that have the highest number of species in the Palaeartic and Oriental biogeographic regions. Presence of the EPN species in the studied countries and their belonging to the biogeographic regions was inherent for the distribution of countries in the calculated tree. The performed analysis revealed that countries grouped by regions and biogeographic botanical continents have similar fauna of the entomopathogenic nematodes. We assume that finding and character spreading of ENP species depend on the research level in different countries, as well as the biological characteristics of nematodes and certain conditions in different countries.

Keywords: entomopathogenic nematodes, Steinernematidae, Heterorhabditidae, distribution.

INTRODUCTION

The entomopathogenic nematodes (EPN) is an ecological group of invertebrates consisting of nematode parasitoids of insects from Steinernematidae and Heterorhabditidae (Nematoda: Panagrolaimida and Rhabditida) families. The study of EPN is important for developing a perspective biological method [6]. Every year, new species of the entomopathogenic nematodes are described in the arithmetic progression due to a progress of the molecular technique. It is interesting to study the distribution of EPN on the Earth in connection with climatic and biogeographic factors, plant distribution etc. [10, 11].

This study has proved a necessity of fundamental studies in different countries to fill in the gaps in the EPN distribution through the world.

MATERIALS AND METHODS

The study is based on data obtained from publications on distribution of the entomopathogenic nematodes in different countries. Part of the reports on EPN's distribution until 2002 was included in the performed analysis according to Hominick [10].

In a statistical analysis the cluster analysis from PAleontological STatistics v.2.17 program [9] was applied. The Bray–Curtis model was chosen for tree construction. In the analysis the presence/absence of *Steinernema* Travassos, 1927, and *Heterorhabditis* (Poinar, 1976) species were included in the studied countries. The area of each country in square kilometers (five groups, 0–1,000; 1,000–100,000; 100,000–1,000,000; 1,000,000–5,000,000; >5,000,000) belonging to the biogeographic regions (Palearctic: Western and Eastern; Oriental; Afrotropical; Nearctic; Neotropical; Australasian), and botanical continents according to the World Geographical Scheme for Recording Plant Distributions definition (Europe; Asia-Temperate; Asia-Tropical; Africa; Northern America; Southern America; Australasia) were used. For countries with an unidentified state of discovered EPN (e.g., *Steinernema* sp.), only the identified species were accepted as '1' value.

ISO 3166-1 alpha-3 codes [12] were applied for the abbreviated names of the countries (including the updated RUS1 for the European part of Russian Federation and RUS2 – for the Western part).

The world distribution map (Fig. 1) on the high resolution blank map of the world from the Wikimedia [19] was created.

RESULTS AND DISCUSSION

The entomopathogenic nematodes are distributed in all biogeographic regions excluding the Arctic, Antarctic and Subantarctic islands. According to recent studies, 120 species of the entomopathogenic nematodes (*Steinernema* and *Heterorhabditis*) were found in 72 countries (see Table).

The entomopathogenic nematodes are widely spread in the Oriental (46 species from three genera) and Palaeartic regions (32 species of *Steinernema* and 5 species of *Heterorhabditis*) (see Table). EPN are scarcely presented in the Australasian region – 2 species of *Steinernema* and 4 of *Heterorhabditis*.

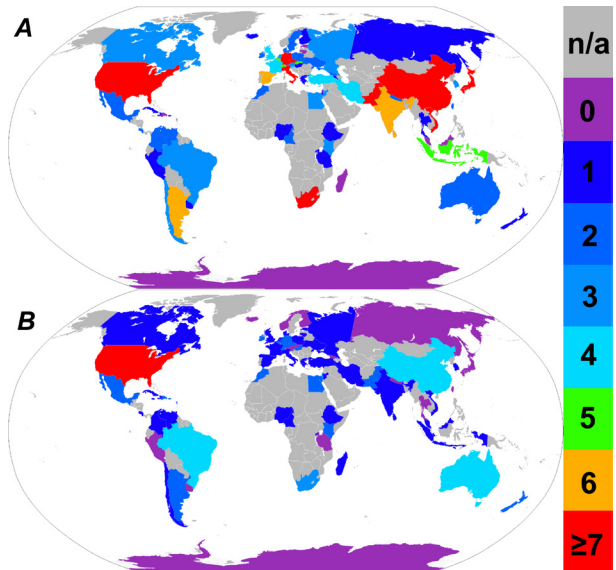
Number of species of the entomopathogenic nematodes in the biogeographic regions Представленість ентомопатогенних нематод у біогеографічних областях

Family	Genus	Number of species in biogeographic regions							
		WP	EP	NA	AT	AU	NT	OL	Number of species
Steinernematidae	<i>Neosteinernema</i>	–	–	1	–	–	–	–	1
	<i>Steinernema</i>	26	8	13	16	2	19	39	123
Heterorhabditidae	<i>Heterorhabditis</i>	5	1	7	6	4	9	5	37
	<i>Heterorhabditoides</i>	–	–	–	–	–	–	2	2
Σ		31	9	21	22	6	28	46	–

Biogeographic regions: AT – Afrotropical; AU – Australasian; EP – East Palaeartic; NA – Nearctic; NT – Neotropical; OL – Oriental; WP – West Palaeartic.

Fig. 1. Data on the distribution of *Steinernema* (A) and *Heterorhabditis* (B) in the world. The right column shows a relation between colors on map and number of species per country; "n/a" meaning: information is not available or research has not been carried out

Рис. 1. Розподіл родів *Steinernema* (A) та *Heterorhabditis* (B) у світі. Колонка справа демонструє зв'язок між кольорами на карті та кількістю видів у країнах, "n/a" означає: інформації немає або дослідження ще не проводили



The highest rate of distribution of *Steinernema* species has been registered in China (19 species) and the highest rate of distribution of *Heterorhabditis* (7 species) – in the United States of America. The highest number of EPN's of both genera has been found in China, that is 23 species in total.

The most common EPN species are: *S. feltiae* (Filipjev, 1934) Wouts, Mráček, Gerdin et Bedding, 1982 (37 countries), *H. bacteriophora* Poinar, 1976 (32 countries) and *S. carpocapsae* (Weiser, 1955) Wouts, Mráček, Gerdin et Bedding, 1982 (31 countries). More rare are *H. indica* Poinar, Karunakar et David, 1992 (20 countries), *H. megidis* Poinar, Jackson et Klein, 1987 (17 countries), *S. affine* (Bovien, 1937) Wouts, Mráček, Gerdin et Bedding, 1982 and *S. kraussei* (Steiner, 1923) Travassos, 1927 (14 and 13 countries). 96 species of *Steinernema* and *Heterorhabditis* have been found only in one country per species.

The distribution of entomopathogenic nematodes depends on different abiotic and biotic factors: temperature [13, 16], density, humidity [18] and chemical composition of substrate [3, 14, 15]; composition of phytocenosis [2, 7]; climatic factors of a region; host finding strategy [4, 8] and climatic preferences of nematodes [5], etc.

Genera's resistance to the influence of all those factors is different [13, 17] and can influence their distribution.

As discussed by Adams, Peat and Dillman [1], such differences in number of *Steinernema* and *Heterorhabditis* species and their distribution can be associated with different time of origin of these species. According to the age of symbiotic organisms *Xenorhabdus* spp., molecular and morphological evidences, the Steinernematidae family had appeared 350 million years ago opposite to the Heterorhabditidae family which is younger and had less time to produce species.

The calculated tree for *Steinernema* and *Heterorhabditis* distribution shows the nominal division of the represented countries into two big clusters A (Fig. 2, A) and B (Fig. 2, B). Cluster A is divided into two sub-clusters: A1, with the European countries in 96 % of cases and A2 with a mixed composition.

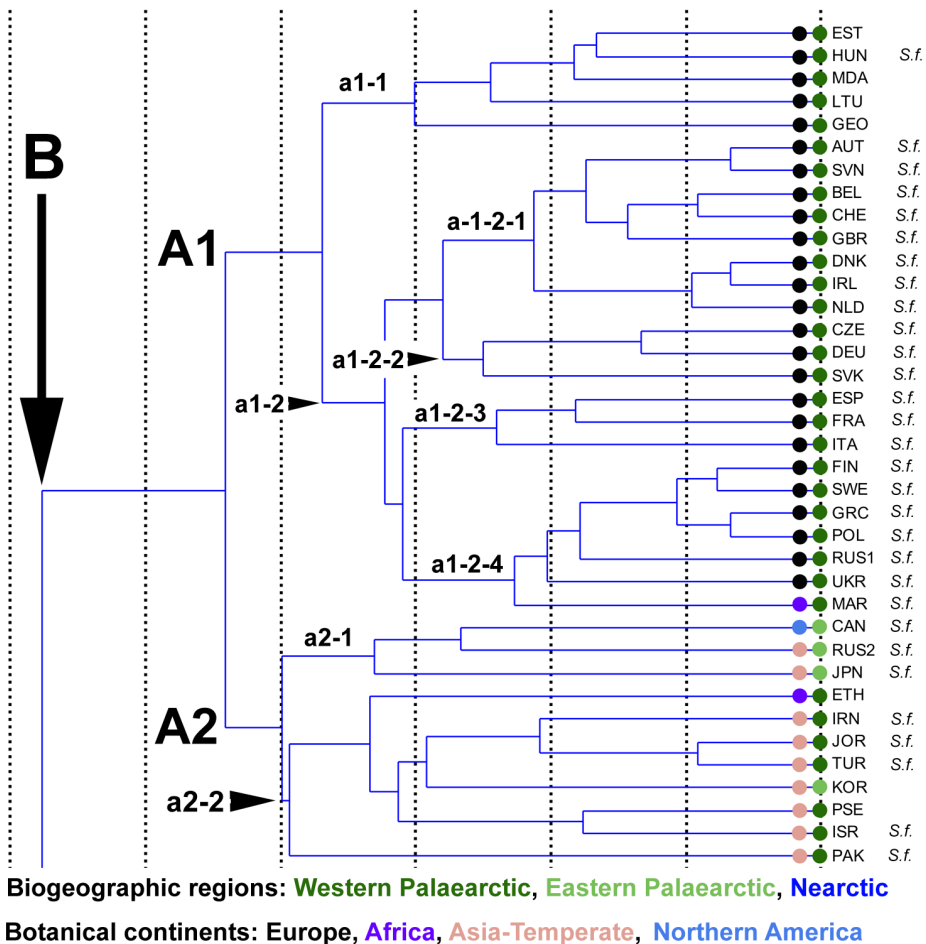


Fig. 2, A. The calculated tree for the distribution of countries with presence of *Steinernema* and *Heterorhabditis*. The grid shows the level of similarity with a step of 10 %. In the right column, the presence of *S. feltiae* was noticed (abbreviated as 'S.f.')

Рис. 2, А. Обчислене дерево представленості країн із наявністю родів *Steinernema* та *Heterorhabditis*. Сітка зображує рівень подібності з кроком у 10 %. У правій колонці відмічено наявність виду *S. feltiae* (скорочено як 'S.f.')

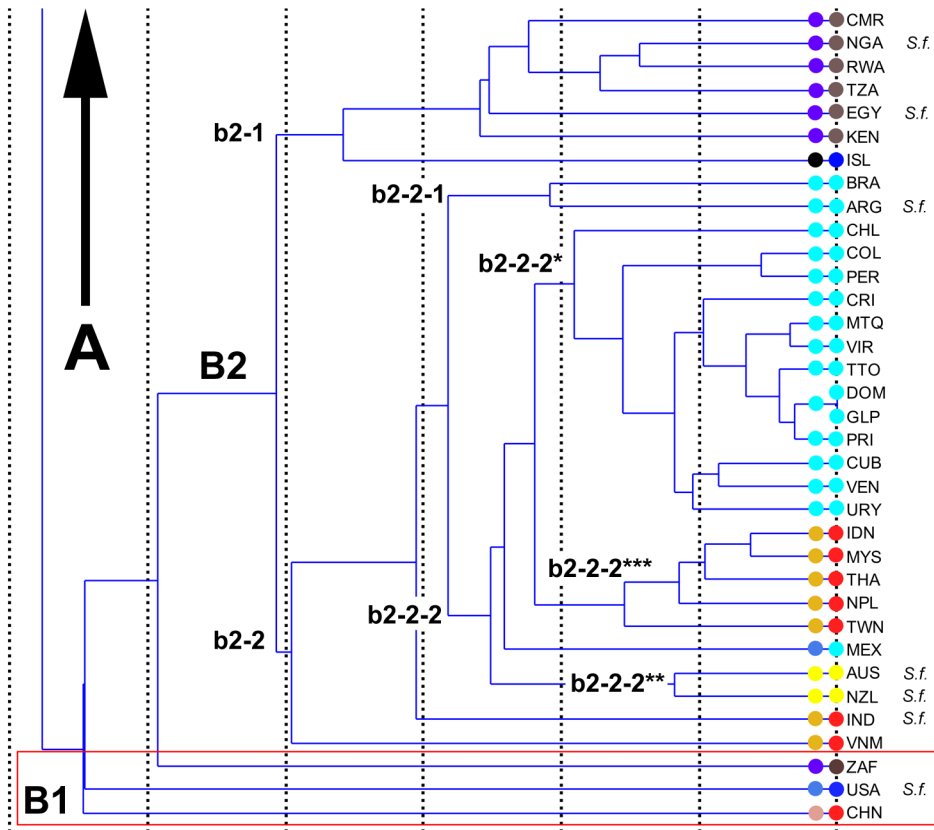
A1 sub-cluster is divided into two groups:

- **a1-1**: Western Palaearctic countries and Europe with pure EPN fauna, in some countries the general presence of *H. bacteriophora* and *H. megidis* is shown.
- **a1-2**, divided into four sub-groups:
 - **a1-2-1**: most common species are *H. megidis* and *S. affine*;
 - **a1-2-2**: common species are *S. affine*, *S. carpocapsae*, *S. intermedium* (Poinar, 1986) Mamiya, 1988 and *S. weiseri* Mráček, Sturhan et Reid, 2003. Besides, in Czech Republic and Germany, *S. krausseii*, *S. silvaticum* Sturhan, Spiridonov et Mráček, 2005, *H. bacteriophora* and *H. megidis* normally occur. *S. feltiae* is general for the whole sub-group.

- **a1-2-3** with common species of *H. bacteriophora*, *S. affine* and *S. carpocapsae*, and **a1-2-4** in the most of medium-sized countries. The medium size of countries and the presence of *S. feltiae* are general for both sub-groups.

A2 sub-cluster is divided into two groups, both with countries of the Palearctic region and Asia-Temperate botanical continent:

- **a2-1**, with *S. feltiae*, in Canada and Japan, the presence of *S. carpocapsae* and *S. krausseii* is similar;
- **a2-2**, with most common species of *H. bacteriophora*, *S. carpocapsae*, and rarely – *H. indica* and *S. feltiae*.



Biogeographic regions: **Afrotropical**, **Oriental**, **Nearctic**, **Neotropical**, **Australasian**

Botanical continents: **Europe**, **Africa**, **Asia-Temperate**, **Asia-Tropical**, **Northern America**, **Southern America**, **Australasia**

Fig. 2, B. The calculated tree for the distribution of countries with presence of *Steinernema* and *Heterorhabditis*. The grid shows the level of similarity with a step of 10 %. In the right column the presence of *S. feltiae* was noticed (abbreviated as 'S.f.')

Рис. 2, B. Обчислене дерево представленості країн із наявністю родів *Steinernema* та *Heterorhabditis*. Сітка зображує рівень подібності з кроком у 10 %. У правій колонці відмічено наявність виду *S. feltiae* (скорочено як 'S.f.')

Cluster **B** is divided into two sub-clusters, **B1** and **B2**. **B1** sub-cluster has countries with big territory and highly endemic EPN fauna.

B2 sub-cluster is characterized by a spread of *H. indica* and is divided into the following parts:

- **b2-1**, mostly for countries of the Afrotropical region. *H. bacteriophora*, *H. indica* and *S. carpocapsae* are distributed here almost equally.
- **b2-2**, a mixed group which is also divided into two sub-groups and Indonesia and Vietnam:
 - **b2-2-1**, consists of Brazil and Argentina with similar *S. carpocapsae*, *S. glaseri* (Steiner, 1929) Wouts, Mráček, Gerdin et Bedding, 1982, *H. bacteriophora*.
 - **b2-2-2** sub-group, consists of **b2-2-2***–**b2-2-2***** and Mexico.
 - **b2-2-2***, contains only countries of the Neotropical region. The core of the group has similarities *H. indica* in fauna; other countries have similar *H. bacteriophora*.
 - **b2-2-2****, consists of Australia and New Zealand which have mostly similar fauna of EPN and common *H. bacteriophora*, and *H. zealandica* Poinar, 1990.
 - **b2-2-2*****, contains only countries of the Oriental region.

It is clear that presence of the EPN species in the studied countries and their belonging to biogeographic regions were inherent for the tree construction. In the cases of low diversity of EPN fauna, the belonging to botanical continents and land area is of prime importance. For example, Spain, France and Italy are classified as medium-sized countries in the Western Palaearctic region, all belonging to the European botanical continent. All these countries have similar species of EPN in fauna: obvious *S. affine*, *S. carpocapsae*, *S. feltiae*, *H. bacteriophora* and partly *S. arenarium* (Artyukhovskiy, 1967) Wouts, Mráček, Gerdin et Bedding, 1982. Besides, forming of mutual diversity of EPN species contributes to France bordering with Spain and Italy overland.

Since some countries possess huge land areas, the intensive process of describing new species stands apart (Republic of China, South Africa, United States of America, India and Vietnam).

Unfortunately, the analysis is indirectly related to national borders, temperature and moisture conditions, landscape relief and the level of studying of EPN, and, thus cannot be claimed as completely objective. However, it was shown indirectly by the land size (which could be a perspective for complete study) of countries and their belonging to the botanical continents and biogeographic regions (depending on climatic features, phytocenose compositions and indirectly to fauna of insect hosts).

According to current study, the level of investigation of EPN presence on different territories is of great importance. Information about the distribution of EPN's or related studies in 127 countries are not available. High number of gaps in distribution of the main genera of EPN's nearby or within the densely populated countries was noted.

Taking into consideration all studied countries having EPN according to the grouping factor, it might be concluded that most of countries in the same biogeographic regions show similar distribution of the entomopathogenic nematodes.

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ЩОДО ПОШИРЕННЯ ЕНТОМОПАТОГЕННИХ НЕМАТОД РОДИН STEINERNEMATIDAE ТА HETERORHABDITIDAE (NEMATODA, PANAGROLAIMIDA ET RHABDITIDA) У СВІТІ

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У статті досліджено біогеографічне поширення ентомопатогенних нематод (ЕПН) у світі відповідно до сучасних меж країн. Ми проаналізували за допомогою клас-

терного аналізу (метод Брея–Кьортиса) розподіл країн, де були виявлені ентомопатогенні нематоди, за приналежністю до біогеографічних областей, Світової географічної схеми запису поширення рослин і площі їх суходолу. Дослідження демонструє простий аналіз закономірностей поширення ЕПН. Згідно з аналізом літературних даних, 120 видів ЕПН поширені у 72 країнах світу з найбільшою кількістю видів у Палеоарктичній та Індо-Малазійській біогеографічній областях. Наявність видів ЕПН у досліджених країнах та їх приналежність до біогеографічних областей визначальні для розподілу країн у вичисленому дереві. Аналізом з'ясовано, що країни, згруповані за біогеографічними областями та ботанічними континентами, мають схожу фауну ентомопатогенних нематод. Ми припускаємо, що виявлення та характер поширення видів ЕПН залежать від дослідженості різних країн нарівні з біологічними особливостями нематод і окремими умовами у різних країнах.

Ключові слова: ентомопатогенні нематоди, Steinernematidae, Heterorhabditidae, поширення.

К РАСПРОСТРАНЕНИЮ ЭНТОМОПАТОГЕННЫХ НЕМАТОД СЕМЕЙСТВ STEINERNEMATIDAE И HETERORHABDITIDAE (NEMATODA, PANAGROLAIMIDA ET RHABDITIDA) В МИРЕ

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В статье исследовано биogeографическое распространение энтомопатогенных нематод (ЭПН) в мире в соответствии с современными границами стран. Мы проанализировали с помощью кластерного анализа (метод Брея–Кёртиса) распределение стран, где были обнаружены энтомопатогенные нематоды, по принадлежности к биogeографическим областям, Мировой географической схеме записи распространения растений и площади их сухопутной части. Исследование показывает простой анализ закономерностей распространения ЭПН. Согласно анализу литературных данных, 120 видов ЭПН представлены в 72 странах мира с наибольшим количеством видов в Палеоарктической и Индо-Малазийской биogeографических областях. Наличие видов ЭПН в исследованных странах и их принадлежность к биogeографическим областям являются определяющими для распределения стран в вычисленном дереве. Анализ показал, что страны, сгруппированные по биogeографическим областям и ботаническим континентам, имеют сходную фауну энтомопатогенных нематод. Мы предполагаем, что обнаружение и характер распространения видов ЭПН зависят от исследованности разных стран наравне с биологическими особенностями нематод и отдельными условиями в разных странах.

Ключевые слова: энтомопатогенные нематоды, Steinernematidae, Heterorhabditidae, распространение.

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