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APPROACHES TO ECOLOGICAL CLASSIFICATION OF EARTHWORMS: A REVIEW

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Earthworms as critical components of natural communities have traditionally attracted the attention of researchers from various fields of biology and agriculture. From the observations of ancient times and up to our time, the research of earthworms has kept its relevance. One of the most interesting tasks has been the creation of an ecological classification of earthworms and its subsequent use. The purpose of this review is to consider various approaches to identifying ecological groups of earthworms (Oligochaeta, Lumbricidae) and the application of these approaches in scientific research. The article reviews the main types of Russian and world ecological classifications of earthworms and some recent additions to these classifications. Particular attention is paid to scientific research with different approaches to the study of ecological groups of earthworms.

Keywords: *earthworms, life forms, ecological groups, soil ecology, classification*

In most terrestrial ecosystems, earthworms are one of the main soil-forming organisms. They ensure transformation of soil organic matter through decomposition of plant residues, forming a humus horizon and transferring organic compounds into deep soil layers, and also through consumption of humus, thus providing mineralization and migration of C and N compounds in the soil (Giljarov 1951; Kurcheva, 1971; Holdsworth et al., 2008). Earthworms also contribute to soil aeration and uniform distribution of moisture: plants can reach groundwater with their roots using worm passages, and the mucus released through their skin moistens the walls of passages, prevents cracking and subsequent drying of the soil. This helps to create favorable soil conditions not only for plants, but also for microorganisms involved in soil-forming (Gaponov, Hicova, 2005; Lemtiri et al., 2014). Earthworms' habitat is not only the mineral horizons of the soil. They also inhabit forest litter, are abundant in forest deadwood and aggregations of animal feces, contributing to their decomposition, and can also live in swamps or at the bottom of shallow reservoirs (Chekanovskaja, 1962; Perel', 1975). At the same time, in most habitats, for example, in river floodplains and moist forests, earthworms mainly inhabit the soil. In forest ecosystems, however, the species and functional diversity of earthworms can be provided by deadwood to a greater extent (Geraskina, 2016 a, 2016 b; Salomé et al., 2011; Ashwood et al., 2019; Ermolov, 2020 a, 2020 b).

Earthworms have become an interesting object of study for a vast array of researchers. For taxonomists, still are a challenging group with very high variability in many morphological features, as several species are characterized by inherent polymorphism, parthenogenetic and polyploid races; therefore, the study of earthworms required using cytology, genetics, and molecular biology (Briones, 1996; Shekhovcov et al., 2016, 2020, 2020 a). Ecologists and zoologists consider earthworms as zoological indicators for biological diagnostics of various types of soils (Atlavinite, 1960; Paoletti, 1999; Ivask et al., 2006; Zhang et al., 2015). Many studies have clearly shown the viability of the so-called "lumbricidological method" in monitoring of soil and environmental conditions, assessment of soil moisture and acidity as well as decomposition intensity of plant residues (Boeskorov, 2004; Zhukov, 2004; Uvarov, 2019). Earthworms also have a significant impact on other components of soil biota (Tiunov, 2008). A special place in such studies is occupied by the study of complexes of living forms or ecological groups of earthworms. Representatives of each group in this complex perform certain functions, and the absence of a group indicates a change in soil properties or their disturbance (Perel', 1975; Geraskina 2016 a, 2016 b). Therefore, the presence of certain earthworm species and living forms in the biotope, as well as their population density, have become a kind of indicators of soil condition (Chekanovskaja, 1960; Giljarov, 1965; Paoletti, 1999; Akkumuljacija..., 2018). The study of earthworm ecology has received significant application. For example, earthworms are used by humans to restore affected soils, in particular in abandoned quarries and dumps through introduction (Dunger, Voigtländer, 2002; Geraskina, 2016 b, 2019). In agriculture, earthworms are used to increase soil fertility and produce compost, and they are able to maintain soil biological activity for a long time (Igonin, 1995; Titov, 2012; Vorob'eva, Ivanova, 2018). It should be mentioned that certain worm species are sometimes bred for agriculture taking into account their ecological and physiological features, with *Eisenia fetida* serving as an example, which cannot survive in natural biotopes in most regions and therefore inhabits only anthropogenically transformed areas (Meshherjakova, 2011; Titov, 2012).

Currently, comprehensive studies of earthworm biology are carried out both in many regions of Russia and abroad. One of the most popular aspects is the study of earthworm ecology, in particular, their ecological classification. The purpose of this review is to consider various approaches to the identification of ecological groups of earthworms (Oligochaeta, Lumbricidae) and application of these approaches in scientific research.

1. APPEARANCE THE SCIENTIFIC INTEREST TO EARTHWORM ECOLOGY

Since ancient times, earthworms (Oligochaeta, Lumbricidae) have gained the attention of the first researchers of nature. For example, Aristotle highlighted the important role of earthworms in increasing soil fertility and called them “the intestines of the earth”, while in ancient China earthworms were dubbed “angels of the soil” for the same reason (Geraskina, 2016 b). During the Middle Ages and Modern times, earthworms were often described in the works of philosophers and natural scientists who tried to put together a system of the animal world. Back then, earthworms had been considered to be insects with special anatomical features for a long time, until C. Linnaeus set them apart as a separate class in his system of animals (Class 6 — Worms) in 1735 (Chesnova, Striganova, 1999).

Charles Darwin was the first to give scientific evidence of the lifestyle of earthworms and their soil-forming activity in his famous book, *The Formation of Vegetable Mould, Through the Action of Worms, with Observations on Their Habits*, published in 1881. Prior to that, for 50 years, he had conducted many laboratory experiments and observations in nature, which revealed the features of the burrowing activity, behavior, physiology, food preferences of earthworms and demonstrated their ecological function as decomposers and humus-forming organisms (Charles Darwin..., 1936). It was Darwin who pointed out that earthworms, in fact, change the natural conditions of their habitat, since they transform plant litter not only mechanically, but also chemically, creating humus substances. On the other hand, soil could have passed through the intestines of earthworms many times during its existence, which proves the role and importance of earthworms in soil formation (Charles Darwin..., 1936).

A similar study was conducted by Darwin’s contemporary, the German zoologist V. Hensen, who described in detail the processes of leaf litter decomposition performed by earthworms and studied the structure of their passages. He also discovered that one worm (*Lumbricus terrestris*) releases on average 0.5 g of nitrogen-rich casts per day, ensuring an even distribution of organic substances at different depths of the soil (Chesnova, Striganova, 1999).

These studies paved the way for further research on the role of earthworms in decomposition of plant remains and humification, including in Russia. One of the first Russian works on this topic was an essay by the soil scientist A. I. Polimpsestov (1882), who also argued, however, that, in addition to earthworms, other invertebrates like woodlice and insect larvae also play an important role in soil-forming. This point of view was later developed by other Russian scientists, and new studies of the soil-forming activity of earthworms were reflected in the works of P. E. Muller (1887), P. A. Kostychev (1889), N. A. Dimo (1938) and other researchers. Of great interest are the observations of G. N. Vysockij, who studied the intensive activity and spread of earthworms in the chernozems of southern Russia (Vysockij, 1900).

We would like to mention the works of M. S. Giljarov (1912–1985) who organized and supervised studies of interaction between earthworms and complexes of other soil invertebrates. It was found that mechanical destruction of plant material in the soil is carried out only by animals and not by any other groups of soil organisms (Giljarov, 1951; Giljarov, Striganova, 1978). Through combining morphological and statistical data on earthworms and other invertebrates with the data on soil conditions, Giljarov together with his students created universal methods of zoological diagnostics of soils, which is still used in soil zoological research (Metody..., 1975).

2. FORMATION OF CLASSIFICATION OF EARTHWORMS ECOLOGICAL GROUPS AND LIVING FORMS

Until the late 1920s, earthworms were considered an ecologically homogeneous group. Previously researchers had been more interested in the taxonomy of the described earthworm species, mainly the creation of a generic system for Lumbricidae and other families.

Briefly speaking, a compilation of a taxonomic classification of earthworms started in the late 19th — early 20th century and keeps being updated now. Initially, when distinguishing genera, signs of the external and internal anatomy of earthworms were used, among those the position of setae, shape (section) and color of the body, location of the clitellum and tuberculae pubertatis, number of seminal vesicles, position of spermathecae, and structure of muscle fibers. At different times, there had been several generic systems based on combinations of those features, which gradually replaced each other. We should mention such authors as G. Eisen, D. Rosa, V. Michaelsen, V. Pop, P. Omodeo, and M. Bouche in this regard (Perel', Semenova, 1968; Perel', 1979). Russian researchers who studied earthworm morphology and taxonomy during this period also include the works of P. G. Svetlov and I. I. Malevich. At that time, almost all the proposed classifications had a common principle: genera were identified based on the structure of the reproductive system, whereas species were identified based on external morphological features (Malevich, 1950; Chekanovskaja, 1960). Upon further revision, the generic systems of those authors were abolished. A very good option for the generic earthworm system was created in the 1970s. The American researcher G. Gates was the first to use the shape of nephridial bladders as a taxonomic feature, and the outstanding Soviet and Russian lumbricologist and taxonomist T. S. Vsevolodova-Perel' supplemented his classification with data on the orientation of nephridial bladders relative to the head end of the worm and the change in their shape in different body segments in some species (Perel', 1979; Vsevolodova-Perel', 1997). We should also mention the significant contribution to the taxonomy of earthworms made by the Hungarian zoologist C. Csuzdi. On multiple occasions, he revised the taxonomy on the basis of morpho-anatomical features (which, for example, resulted in identification of an endemic monotypic genus *Rhiphaeodrilus* separated from the genus *Perelia*) and used data from molecular biology studies in taxonomy (as a result, the genus *Dendrodrilus* was included in the genus *Bimastos*) (Csuzdi, Pavlíček, 2005; Csuzdi et al., 2017). Despite the universal character of the proposed generic system, the taxonomy of earthworms continues to change at the present time as well.

Over time, collected data on the peculiarities of earthworms' lifestyle and the heterogeneity of their role in soil-forming processes led to the conclusion that there are several ecological groups of earthworms.

The first, not very rewarding attempts to define ecological groups of earthworm species were made by V. K. Baluev and D. Wilcke, who mainly took into account the vertical distribution of earthworms in the soil, as well as their pigmentation and ability to diapause (Baluev, 1950; Wilcke, 1953). Further studies have shown that earthworms also differ in their feeding habits: there are the so-called "humus-forming" earthworms feeding on poorly decomposed plant material on the soil surface, and "humus-consuming" ones, which feed on soil humus (Franz, 1950, cit. by: Perel', 1975).

The most complete morpho-ecological classification of the Lumbricidae family, which is still used in the world literature, was proposed by M. Bouche in 1972. He identified three groups of earthworms according to their ecological strategies: *epigeic* earthworms that live in litter and feed on it; large *anecic* earthworms that go deep into the soil using vertical passages but feed on litter on the surface; and *endogeic* earthworms that live directly in the soil and feed on humus in the humus horizon (Bouche, 1972; Fründ et al., 2010; Fierer, 2019).

In the Russian literature, the morpho-ecological classification of earthworms of the Lumbricidae family is used that was developed by T. S. Perel' in 1975 after extensive laboratory research and field observations. This classification is based on the comparison of anatomical, morphological and physiological features (thyphlosole structure, shape of prostomium, body cross-section, etc.) with some environmental features. Besides, the morpho-ecological group of earthworms formed by species from different genera that live in the same environment and have signs of deep convergence, was designated as a *living form* in that classification (Perel', 1975). All representatives of the family were divided into two large morpho-ecological types depending on their feeding habits (on the surface or in the humus horizon), and each of those types included several morpho-ecological groups, distinguished according to their vertical distribution in the soil (epigeic, epi-endogeic earthworms and endogeic earthworms of different soil layers), as well as subgroups of amphibiotic forms, including species whose life cycle is associated with the aquatic environment (Perel', 1975, 1979).

As compared to foreign options, the morpho-ecological classification by T. S. Perel' is more detailed. For the first time, the group of epi-endogeic earthworms was identified, which had previously been combined with epigeic earthworms. Unlike the latter, the epi-endogeic earthworms, although they feed on the surface, live mainly in the upper layers of the soil, rarely going to a depth of more than 15–20 cm. According to their ecological function, epi-endogeic forms of earthworms are sometimes considered equivalent to anecic earthworms, but they differ in the depths of habitat in the soil and the degree of adaptation to different humidity regimes: epi-endogeic species are more moisture-loving and found even in swampy soils, whereas anecic earthworms are better adapted to endure periodic drought (Perel', 1979; Lemtiri et al., 2014; Akkumuljacija..., 2018). Also, this classification found its application in assessing the zonality of earthworms (tundra and northern taiga are inhabited only by epigeic and epi-endogeic earthworms, while steppes are inhabited by endogeic earthworms, and mixed and broad-leaved forests are inhabited by almost all earthworms living forms) and made it possible to identify the main directions of evolution of the Lumbricidae family (Perel', 1975). In 2016, A. P. Geraskina introduced the concept of a *full-fledged complex of earthworms living forms*, implying the presence of all earthworms living forms in a particular biotope (Geraskina, 2016 b).

Over time, world classifications attempted to "split" large ecological groups of earthworms into highly specialized ones. In 1977, based on his own observations and experiments, M. Bouche identified intermediate ecological groups of earthworms: *epi-endogeic*, *epi-anecic*, *endo-anecic*, and *intermediate* (Bouche, 1977). In the late 1990s and early 2000s, an idea started up to identify "subcategories" in the three main ecological groups; for example, *polyhumic*, *mesohumic*, *oligohumic*, and *endo-anecic* subcategories were identified in the endogeic group (Barois et al., 1999; Chan, 2001).

In this case, the allocation of subcategories is based on the ability of earthworms to inhabit the soil horizon that is, to some extent, enriched with organic matter which they feed on. In 2020, all variants of the Bouche's classification were revised using an original method (Bottinelli et al., 2020): first, a review of publications was conducted, which mentioned earthworms ecological groups proposed by Bouche, both basic and intermediate. It turned out that different researchers could classify one and the same species of earthworms as belonging to different ecological groups: for example, *Lumbricus terrestris* was described both as *anecic* and *epi-anecic*, while *Lumbricus rubellus* was described as *epigeic*, *epi-endogeic* and even *epi-anecic*. Subsequently, using mathematical modeling, a scheme based on 13 morpho-anatomical features was drawn up, which distributed earthworms into ecological groups. A new classification version of earthworms ecological groups followed: for example, *Octolasion lacteum* (commonly considered to be *endogeic*) was assigned to the endo-anecic group, *Lumbricus terrestris* (*anecic*) was described as *epi-anecic*, and *Allolobophora chlorotica* was described as *epi-endo-anecic* (Bottinelli et al., 2020). That study has, once again, shown that the question of ecological groups and earthworms living forms is yet open to be discussed.

3. APPLICATION OF ECOLOGICAL CLASSIFICATION OF EARTHWORMS IN RESEARCH

3.1. Earthworms living forms in ecological research

After taxonomic and morpho-ecological classifications of earthworms had been created, new approaches to their study appeared. Early environmental studies mainly described the influence of earthworms on soil properties. For example, G. F. Kurcheva experimented with the rate of plant litter neutralization by earthworms at control sites (Kurcheva, 1971); P. U. Bahtin and M. N. Pol'skij investigated the activity of earthworms in sod-podzolic soils (Bahtin, Pol'skij, 1950); K. I. Gavrilov studied the role of earthworms in enriching the soil with biologically active substances (Gavrilov, 1963). At the same time, the participation of certain species and living forms of earthworms in these processes was not evaluated separately.

In further studies, data on the proportions of earthworms living forms started to be used to characterize ecological conditions of biotopes. One of the followers of T. S. Vsevolodova-Perel', I. B. Rapoport, shows in her works focusing on the landscape distribution of earthworms of the Caucasus how the diversity of earthworms living forms in different biotopes varies depending on the altitudinal zonality (Rapoport, 2010, 2015). She also provides a comparison of the chorological and morpho-ecological groups of earthworms (Rapoport, 2015).

Studies conducted in the Komi Republic in the 1970s–2000s have shown how the species composition and complexes of earthworms living forms change with changing zones from the southern to extreme northern taiga. Approximately nine species of three living forms were found in the southern and middle taiga subzones, while only two species representing one living form live in the subzone of the extreme northern taiga (Krylova et al., 2011). In the taiga zone, M. Ja. Vojtehov investigated the soil-forming activity of earthworms through a series of experiments with food preferences. It was found that, in acidic soils and litter formed by taiga vegetation, different earthworms living forms support each other's existence: for example, endogeic earthworms can consume decomposition products of coniferous plant litter only when they are enriched with casts of epi-endogeic earthworms (Vojtehov, 2018).

Despite the mutually beneficial existence, a number of experiments have shown that competition between earthworms of different species is possible within the same living form. For example, when epi-endogeic species were kept in mesocosms, competition for food resources was observed between *L. rubellus* and *Eisenia nordenskioldi nordenskioldi* (Golovanova et al., 2018). In endogeic species, competition occurs mainly in limited spaces with high population density. It has been shown that once a certain population density level is reached, *Al. chlorotica* and *Aporrectodea caliginosa* stop reproducing and lose weight (Uvarov, 2019). However, this is true only for experiments under artificial conditions, and the probability of actual competition among earthworms in the natural environment may be extremely low.

Earthworms can provide for the existence of other representatives of the soil fauna as well. In a number of experiments, it has been shown that casts of anecic and endogeic earthworms are an available food source for Enchytraeidae, which release C and N compounds and ensure their transport within the soil. Also, they are able to significantly affect soil fertility and increase microbial biomass in the soil only in combination with earthworms (Sandor, Schrader, 2012). The gastrointestinal tract of an earthworm with its complex chemical and microbiological processes is actually similar to a bioreactor (Brown et al., 2000). In each part of it, specific stages of the nitrogen and carbon cycle take place. Some soil bacteria, protozoa and fungal spores are digested, while others pass through earthworm's intestines undamaged and are dispersed in the soil, and some others are activated only after passing through earthworm's intestines, eventually reaching favorable conditions for further development (Moody et al., 1995; Lemtiri et al., 2014).

Along with the transfer of microorganisms and decomposition of organic residues, earthworms can accumulate various chemical elements when feeding, in particular heavy metals (Usmani, Kumar, 2015). This made it possible to use earthworms as bioindicator organisms to assess soil pollution. For example, the epi-endogeic earthworm *E. nordenskioldi* and the endogeic *O. lacteum* proved to be suitable indicators in the study of the content of heavy metals, especially Pb, in soils near roadsides, clearly showing the detrimental effect heavy metals have on soil biota (Golovanova, 2003). Similar work was carried out to assess the impact of emissions from iron and steel plants: the Ural epi-endogeic endemic *Rhiphaeodrilus diplotetratheca* (formerly *Perelia diplotetratheca*) showed significant differences in the size and weight of earthworms depending on the degree of soil pollution (Reznichenko, 2017). It was also found that the anecic earthworm *L. terrestris* can not only accumulate compounds of As, Cu, Pb, and Zn in its body but also include them in its casts ejected on the soil surface, thereby ensuring the removal of heavy metals from the soil (Sizmur et al., 2011). Some researchers plan to use *L. terrestris* and *E. fetida* for detecting and eliminating oil pollution due to the ability of earthworms to accumulate and remove various pollutants (Hanna, Weaver, 2002).

Isotope analysis is one of the modern methods used in the study of the ecological functions of animals. This method is often used when studying trophic relationships of various invertebrates and enables the identification of their feeding features and them being a part of a certain ecological group (Tiunov, 2007; Goncharov, 2016). Using isotope analysis in studying the ecology of earthworms made it possible to assess the features of their feeding and food preferences. For example, when a pasture is converted into a cornfield, the same species of epigeic and epi-endogeic earthworms prefer to use "fresh" organic residues of C4 plants rather than "old" organic matter of the soil formed mainly by C3 plants, which they fed on earlier (Briones et al., 1999). Isotope analysis helps us understand the trophic features of earthworms during the decomposition of organic matter: the content of accumulated nitrogen in the tissues of earthworms proved that, when feeding, epigeic and anecic earthworms prefer to use organic material less susceptible to microbial decomposition than endogeic earthworms. Adding crushed oat flakes with isotopic labels to feed substrates showed that the endogeic earthworms *A. caliginosa* are more inclined to absorb small food particles in large quantities, unlike the anecic *L. terrestris* (Heiner et al., 2011). Isotope analysis methods are also applicable to the study of the chemical composition of earthworm casts, which are complex stable sets of organomineral matter and microbial communities. Using the example of anecic *L. terrestris*, such studies help us trace the “path of the casts”: what kind of consumed litter they consist of, which microbial communities developed there over time, and how further consumption of casts by plants or other soil animals occurs (Vidal et al., 2019). It is believed that isotope analysis can enable further revision of the ecological classification of earthworms (Briones et al., 1999).

A large number of studies showed that in some biotopes the earthworms species diversity is represented by a certain living form. For example, northern dark coniferous forests had been considered a virtually unsuitable habitat for earthworms and extremely poor in terms of their species for a long time (Perel’, 1958, 1979). Later it was found that in the dark coniferous forests (especially green moss and blueberry-green moss) of the middle and northern taiga, most of the earthworm population may be found in deadwood, not soil (Geraskina, 2016 c, 2016 d). The main inhabitants of deadwood are epigeic and epi-endogeic earthworms with a relatively high species diversity; at the same time, deadwood is sometimes also inhabited by endogeic earthworms that use it as a temporary habitat during unfavorable conditions. Similar conclusions were made for other types of forest. Initially, these studies were limited only to the sorting of deadwood accidentally discovered in forest habitats. Later, calculations of the worm population density per unit volume began, and deadwood has been recognized as a specific microsite inhabited by earthworms (Kooch, 2012; Geraskina, 2016 d; Ermolov, 2018 a, 2018 b, 2020 a; Vorobejchik et al., 2020). In habitats with disturbed or heavily polluted soil, deadwood often becomes the only habitat for earthworms (Vorobejchik et al., 2018, 2020). In 2019, a new method of site sampling for earthworms in forest communities was developed, which made it possible to give the most accurate assessment when comparing the population of earthworms in soil and deadwood (Ashwood et al., 2019). Conversely, in anthropogenic habitats, in particular agricultural land and fallows, the major part of earthworms population consists of endogeic earthworms, especially middle-soil-layer ones, which can make up to

100% of the entire population (Geraskina, 2009; Shashkov et al., 2016). As the overgrowth progresses, abandoned fields are gradually populated first by epi-endogeic, and then by epigeic earthworms, while endogeic earthworms, for example, *A. caliginosa*, live even in fields actively used in agriculture (Geraskina, 2009, 2016 a). Therefore, the introduction of earthworms to various anthropogenic areas where earthworms are completely absent is started with representatives of this living form because they are able to survive and show ecological plasticity in relation to various environmental factors (Ansari, Ismail, 2012; Geraskina, 2019).

3.2. Polymorphism and molecular-biological studies of earthworms living forms

It's worth noting that representatives of various earthworms living forms can be found not only within the same genus, but also within a species or subspecies. Currently, the study of polymorphism in earthworms started to use methods of molecular biology, one of them being variability analysis of the gene of cytochrome c oxidase subunit 1 (*cox1*) along with morphometric analysis (Voronova et al., 2012).

G. N. Ganin (1959–2019) had studied the Far Eastern endemic *Drawida ghilarovi* Gates, 1969 (fam. Moniligastridae) and revealed that individuals of this species form two morpho ecological groups that differ in their color and ecological features. Earthworms inhabiting meadows and swamps are epi-endogeic, black-colored and have an optional diapause; forest earthworms are anecic, have a brownish color and an obligate diapause (Ganin, 2013 a, 2013 b; Ganin, 2014). However, upon further study of the identified forms, especially the study of their phylogeny using molecular biology methods, it was found that forest anecic earthworms *Drawida ghilarovi* consist of ten separate genetic lineages, which hypothetically can be different species, whereas the black epi-endogeic meadow and swamp morph represents a new species (Zhang et al., 2020).

It has been repeatedly suggested that there are two living forms in the Asian subspecies *E. n. nordenskioldi*, which is characterized by pronounced polymorphism (Perel', Grafodatskij, 1983). V. S. Boeskorov, who studied the ecology of *E. n. nordenskioldi* in permafrost soils of Yakutia, identified two morpho-ecological groups of these earthworms (epi-endogeic and anecic) and defined their range (Boeskorov, 2004). Large individuals of *E. n. nordenskioldi* were also classified as anecic earthworms by T. S. Vsevolodova-Perel' during the study of earthworms in the forests of the Western Sayan (Perel', 1994). Ju. B. Byzova, who experimented on the intensity of *Oligochaeta* respiration in the soil, when describing the collected samples from different regions of Russia, often reported differences in size and weight as well as in physiological features in individuals of this subspecies, classifying them as different living forms (Byzova, 1965, 2007). She classified large individuals of *E. n. nordenskioldi* collected in Western Siberia (in particular, in the Novosibirsk area) as anecic earthworms (Byzova, 2007). This statement is confirmed by a recent study conducted in the forests of the forest-steppe Ob region in the Novosibirsk area, where morphometric analysis revealed size groups of *E. n. nordenskioldi* with earthworms having different habitat conditions (Ermolov, 2020 b). An attempt was made to confirm that large-sized earthworms *E. n. nordenskioldi* are anecic earthworms on the basis of their morphological similarity with a typical representative of anecic earthworms *L. terrestris* (Ermolov, 2020 b). Most of the works on molecular biology of *E. n. nordenskioldi* were performed by S. V. Shekhovcov. Within this subspecies on the territory of Russia, he managed to identify nine different genetic lineages (Shekhovcov et al., 2016, 2018). However, no analysis of the relationship between morpho-anatomical and molecular-genetic differences of individuals of this subspecies was performed; this is planned for future works (Shekhovcov, Berman, 2018). Nevertheless, it was found that earthworms of some genetic lineages differ in cold resistance: there are moderately resistant lineages (−10… −12 °C) and lineages that tolerate low temperatures (−28… −34 °C) (Berman et al., 2019).

The Caucasian species *Dendrobaena schmidti* Michaelsen, 1907 is also polymorphic. There is an assumption that epigeic, epi-endogeic and endogeic earthworms living forms can be identified within the species (Rapoport, 2009), since individuals of this species collected in different parts of the Caucasus significantly differ in body size, pigmentation intensity, development of glandular fields and vertical distribution in the soil (Shekhovcov et al., 2020b). Two genetic lineages have also been identified for *D. schmidti*, individuals in which significantly differ in size and degree of pigmentation. However, these differences may overlap in some cases, and the main taxonomic features of the species within the lineages do not differ (Shekhovcov et al., 2020 b).

Polymorphism is also revealed in the endogeic *O. lacteum* (synonym of *O. tyrtaeum*). Studies conducted in Belarus and Western Siberia have shown that within this species there are one small and two large-sized earthworms that have different ecological conditions of their habitat. Large-sized earthworms are more common in wetter soils with a well-developed humus horizon, whereas smaller ones predominate in dry soils with low humus content (Shekhovcov et al., 2020; Ermolov, unpublished data). It is noteworthy that large-sized earthworms have not previously been found in Western Siberia (Shekhovtsov et al., 2014). In Belarus and in the Novosibirsk area, a relationship was found between a certain genetic lineage of individuals and their dimensional characteristics within the species (Shekhovcov et al., 2020 a).

Pronounced polymorphism discovered in the endogeic cosmopolitan *A. caliginosa* when studying the populations of this species in Ukraine and Belarus was unexpected. It turned out that earthworms from different populations have significant differences in size of adult individuals, as well as various variations in body and clitellum pigmentation, from light gray and pink to brown and yellow-orange (Mezhzherin et al., 2018). It is noteworthy that polymorphism in *A. caliginosa* was not observed in Siberia and the Urals; only sometimes it was reported in some regions of Central Russia (Shekhovcov et al., 2016 a; Ermolov, unpublished data). S. V. Shehovtsov and colleagues also studied the genetic diversity of *A. caliginosa* in Russia and the Republic of Belarus (Shekhovtsov et al., 2016; Shekhovcov et al., 2017). In the course of this study, several genetic lineages of this species were identified in Russia, and the morphological diversity of Belarusian earthworms is partly explained by them being part of a certain genetic lineage. However, it is impossible to clearly distinguish genetic lineages based on differences in external morphology, since some signs overlap and may be associated with some ecological features of the habitat of the species (Shekhovtsov et al., 2021).

Sometimes it turns out that there may be several genetic lineages within one species that have few if any, morphological differences. For example, when the genetics of the European cosmopolitans *Aporrectodea longa*, *Aporrectodea rosea*, *Al. chlorotica*, and *L. rubellus* was studied in the UK, a high divergence (more than 14%) of the nucleotide sequences of the mitochondrial gene *cox1* was found in some of them. In the species *Al. chlorotica*, represented by two forms differing in color, 35 haplotypes were identified for the form with pink pigmentation and 20 haplotypes for the form with green pigmentation (King et al., 2008). Later it became necessary to use not only mitochondrial, but also nuclear markers, since only five strongly divergent lineages were identified within this species for the 16S rRNA gene (King et al., 2008). Similar results in difference of data on different genes were also found by Polish researchers in *L. rubellus* (Giska et al., 2015). At the same time, in the former USSR countries, these species are represented by only one line (Shekhovcov, spoken communication).

3.3. Classification of earthworms by habitat conditions

In addition to the classification of the living forms of Lumbricidae mentioned above, researchers have also suggested other options for the identification of earthworm ecological groups based on their relationship with some abiotic factors.

One of the good examples is the classification of earthworms by cold resistance developed by D. I. Berman, A. N. Lejrih and E. N. Meshherjakova (Meshherjakova, 2011; Lejrih, 2012). The earthworms under study (sampled in different regions of Russia) were divided into three groups: species resistant to below-freezing temperatures in the worm and cocoon phase; species resistant to below-freezing temperatures only in the cocoon phase; and species not resistant to temperatures below –1 °C at any of the phases of ontogenesis. However, each group includes representatives of different living forms, and no connection was found between the cold resistance of earthworms and they are belonging to a particular living form since everything depends on physiological characteristics of a particular species (Berman, Lejrih, 1985; Meshherjakova, 2011).

A very interesting classification of earthworms based on their relation to soil moisture was first proposed by O. V. Zhukov et al., which identifies groups of mesophiles, hygrophiles and ultragygrophiles (Zhukov et al., 2007; Kunah et al., 2010). However, this classification is also only partially consistent with the system of living forms by Vsevolodova-Perel' or Bouche: for example, all subgroups of amphibiotic earthworms can be attributed to ultrahygrophiles, whereas species belonging to other living forms are classified as either hygrophiles or mesophiles. Nevertheless, Zhukov showed that the system he proposed can be used in zooindication to assess the degree of soil moisture with the help of a complex of earthworms (Zhukov, 2004).

Earthworms are most often used as indicators in the studies of soil acidity (Giljarov, 1965). For example, the experiments of A. I. Zrazhevskij proved the effect of an anion of a certain acid that forms the pH of the soil on earthworms (Zrazhevskij, 1957). The works of O. P. Atlavinite looked into correlations between the population and occurrence of individual earthworm species, on the one hand, and soil pH, on the other hand (Atlavinite, 1960). It was shown that some earthworm species are very resistant to a wide pH range, for example, *A. caliginosa*, while others are most commonly found in acidic soils (*D. octaedra*) or prefer neutral and slightly alkaline soils (*E. fetida*). Earlier studies by R. Baltzer showed that soils of different types with different pH values are inhabited by certain species and complexes of earthworms living forms (Baltzer, 1955). This study implied that, based on the predominance of a particular earthworm species, soil pH can be determined: for example, *L. rubellus* inhabits acidic and slightly acidic soils, *A. caliginosa* and *A. rosea* prefer slightly acidic and neutral soils, whereas *O. lacteum* inhabit neutral and alkaline soils. However, pH value is by no means the only feature that determines the suitability of soil as a habitat of earthworms. In addition to pH, there are many other physical and chemical soil properties that significantly affect earthworms: for example, a study of earthworms in Western Siberia revealed *L. rubellus* in acidic (pH = 5.42), slightly acidic (pH = 5.72) and neutral (pH = 7.49) soils, but its greatest population was found in neutral floodplain soils (149 ± 31 individuals/m^2) due to the highest moisture content (Ermolov, 2020 b). Therefore, when studying the relationship of earthworms with soil acidity, it is important to take into account other soil factors as well, such as humidity, content of organic matter, nitrogen, calcium and other macro- and micronutrients (Ivask et al., 2006). However, soil pH, changed by anthropogenic impact, often becomes a limiting factor for earthworms. For example, experiments conducted in China showed that in areas with frequent acid rains, earthworm populations are at risk of complete extinction, since earthworms are not able to survive in soil with pH of 2 and below (Zhang et al., 2015).

It is known that earthworms are calciphilic organisms that have special organs for alkalizing acidic food, i. e. *calciferous glands* (Chekanovskaja, 1960; Vsevolodova-Perel', 1997; Gaponov, Hicova, 2005). Previously, it was believed that calcareous glands can be of only three types and have no significance as a taxonomic feature (Vsevolodova-Perel', 1997). Recent studies have shown, however, that the anatomy of calcareous glands is very diverse: a detailed analysis of 13 genera of earthworms identified seven groups of species with different structure of calcareous glands (Briones, Piearce, 2011; cit. by: Biology of Earthworms, 2011). Moreover, the same types of gland structure were often found among different genera. This suggests that the taxonomic position of some species still remains ambiguous. The structure of calcareous glands also makes it possible to indirectly assess the acidity of the habitat of earthworms and their food preferences (Briones, Piearce, 2011; cit. by: Biology of Earthworms, 2011).

CONCLUSION

Studies of the ecology of earthworms originate from ancient times and still remain relevant. First simple observations of ancient thinkers and medieval naturalists gradually began to be generalized by naturalists of modern times, who gave them a scientific justification and thereby proved the significant role of earthworms in soil formation.

Later, earthworm classification became a relevant issue. For many decades, various taxonomic systems of earthworms have been developed, but the question of taxonomy remains open even today. In addition to taxonomy, there has been great interest to ecological classification of earthworms, the “classic variants” of which were created in the 1970s in France and Russia. Since the end of the last century, various researchers have been trying to expand the proposed classifications, supplementing the main ecological groups with intermediate groups and subcategories.

The ecological classification of earthworms has found ample applications in various studies. By analyzing the structure and species composition of complexes of earthworms living forms and the ability of individual representatives to live under certain environmental conditions, researchers obtained a unique tool to diagnose soils in different biotopes. Between earthworms of different living forms and other soil organisms trophic and functional connections have been identified that ensure the flow of substances and the maintenance of biodiversity in ecosystems. When studying the polymorphism of earthworms, it was found that there can be different living forms even within the same species, which, based on the evidence from molecular biology, are later often classified as new species.

However, there are still a lot of unanswered questions that arise when studying the ecology of earthworms. For example, can all different genetic lineages be considered different species and how can this be proven in terms of ecological and genetic concepts? Are some earthworm species invasive to a number of regions or have they always lived there? What are the limiting factors for endemic species and cosmopolitans; is their cohabitation possible? What environmental factors can cause polymorphism in earthworms and what is the reason for the transition to parthenogenesis?

These and other issues require further development of methods to study the features of earthworm ecology, and mainly enhancing the experimental component. It is especially important to conduct comprehensive studies at the confluence of ecology and genetics, taxonomy and zoogeography, climatology and soil science. This will help us find answers to the questions posed and lay the foundation for further research.

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