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Earthworm (Oligochaeta, Lumbricidae) intraspecific genetic variation and polyploidy

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Abstract. Earthworms are known for their intricate systematics and a diverse range of reproduction modes, including outcrossing, self-fertilization, parthenogenesis, and some other modes, which can occasionally coexist in a single species. Moreover, they exhibit considerable intraspecific karyotype diversity, with ploidy levels varying from di- to decaploid, as well as high genetic variation. In some cases, a single species may exhibit significant morphological variation, contain several races of different ploidy, and harbor multiple genetic lineages that display significant divergence in both nuclear and mitochondrial DNA. However, the relationship between ploidy races and genetic lineages in earthworms remains largely unexplored. To address this question, we conducted a comprehensive review of available data on earthworm genetic diversity and karyotypes. Our analysis revealed that in many cases, a single genetic lineage appears to encompass populations with different ploidy levels, indicating recent polyploidization. On the other hand, some other cases like *Octolasion tyrtaeum* and *Dendrobaena schmidti*/*D. tellermanica* demonstrate pronounced genetic boundaries between ploidy races, implying that they diverged long ago. Certain cases like the *Eisenia nordenskioldi* complex represent a complex picture with ancient divergence between lineages and both ancient and recent polyploidization. The comparison of phylogenetic and cytological data suggests that some ploidy races have arisen independently multiple times, which supports the early findings by T.S. Vsevolodova-Perel and T.V. Malinina. The key to such a complex picture is probably the plasticity of reproductive modes in earthworms, which encompass diverse modes of sexual and asexual reproduction; also, it has been demonstrated that even high-ploidy forms can retain amphimixis.

Key words: genetic lineages; karyotypes; phylogeny; species divergence.

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Дождевые черви (Oligochaeta, Lumbricidae): соответствие между внутривидовым генетическим разнообразием и плоидностью

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Аннотация. Дождевые черви известны своей сложной систематикой и разнообразным набором типов размножения, включая амфимиксис, самооплодотворение, партеногенез и некоторые другие способы, которые иногда могут сосуществовать в пределах одного вида. Более того, они демонстрируют значительное внутривидовое разнообразие кариотипов с уровнями плоидности от ди- до декаплоидных и выше, а также высокую генетическую изменчивость. В некоторых случаях один вид может сочетать большую морфологическую изменчивость, несколько рас с разной плоидностью и несколько филогенетических линий со значительными различиями как по ядерной, так и по митохондриальной ДНК. При этом соответствие между расами различной плоидности и генетическими линиями дождевых червей остается в значительной степени неисследованным. В связи с этим мы провели всесторонний обзор имеющихся данных о генетическом разнообразии и кариотипах дождевых червей. Наш анализ показал, что во многих случаях одна генетическая линия включает в себя популяции с разными уровнями плоидности, что указывает на недавнюю полиплоидизацию. С другой стороны, в некоторых случаях, как, например, *Octolasion tyrtaeum* и *Dendrobaena schmidti*/*D. tellermanica*, имеют место выраженные генетические границы между расами, что означает давнюю дивергенцию между ними. Некоторые таксоны, такие как комплекс *Eisenia nordenskioldi*, представляют собой множество давно дивергировавших филогенетических линий со сложными родственными отношениями между ними и как древней, так и недавней полиплоидией. Сопоставление филогенетических и цитологических данных позволяет предположить, что некоторые полиплоидные расы независимо возникали несколько раз, что подтверждает выводы работы Т.С. Всеволодовой-Перель и Т.В. Малининой. Причиной такой сложной картины, вероятно, служит пластичность способов репродукции, которые включают в себя разнообразные виды полового и бесполого размножения; причем даже формы с высокой плоидностью могут размножаться амфимиктически.

Ключевые слова: генетические линии; кариотипы; филогения; дивергенция видов.

Introduction

Polyploidy in animals is relatively rare (Muller, 1925; Orr, 1990). However, certain groups are exceptions to this rule and exhibit a significant incidence of polyploidy (Gregory, Mable, 2005). Earthworms are among these exceptions (Muldal, 1952; Viktorov, 1997): the initial studies demonstrated that polyploidy is observed not only among groups of closely related species, but even within a single species, and often in sympatry (Omodeo, 1952, 1955). Subsequently, this phenomenon was documented in representatives of diverse genera (Vsevolodova-Perel, Bulatova, 2008; Mezhzherin et al., 2018). In addition to that, earthworms demonstrate diverse ways of reproduction (Pavlíček et al., 2023). Although in animals polyploidy is generally associated with parthenogenesis, polyploid earthworms often retain the ability for amphimixis (Viktorov, 1989). While some species comprise a set of races with different ploidy levels, the prevailing view is that this alone is not a sufficient reason to classify them as distinct species (Vsevolodova-Perel, Bulatova, 2008).

Molecular studies revealed a vast genetic diversity within earthworm species (King et al., 2008; Porco et al., 2013). In most cases, several well-defined clades within a given species were identified, with 15–20 % of nucleotide substitutions between mitochondrial genes (these estimates sometimes vary, because different studies employ various distance measures, like Kimura-2-parameter, etc.). These clades are commonly referred to either as cryptic species or as the so-called genetic lineages (Marchán et al., 2018). The attempts to clarify the issue of genetic divergence on the nuclear level using various molecular methods generally confirmed the existence of significant nucleotide distances between these lineages (Martinsson, Erséus, 2017; Taheri et al., 2018), although in some instances, the data did not demonstrate signs of reproductive isolation of distinct lineages differing on the mitochondrial level (Giska et al., 2015; Martinsson et al., 2017; Martinsson, Erséus, 2018).

Thus, we can see that certain earthworm species have multiple races with different ploidy levels, as well as several genetic lineages with distinct mitochondrial and nuclear genomes. However, the relationship between chromosomal and DNA sequence variation remains unclear. Does each chromosomal race correspond to a particular genetic lineage, or do the boundaries between these entities lie elsewhere?

In this review, we analyzed the patterns of chromosomal and molecular variation in several earthworm species from various genera within the family Lumbricidae. The results provide insight into the relationships between these entities and outline directions for future research.

Materials and methods

The data on the chromosome numbers of the populations of various earthworm species were taken from published materials (Muldal, 1952; Omodeo, 1952, 1955; Vedovini, 1973; Graphodatsky et al., 1982; Bulatova et al., 1984, 1987; Perel, Graphodatsky, 1984; Casellato, 1987; Viktorov, 1989, 1997; Kashmenskaya, Polyakov, 2008; Vsevolodova-Perel, Bulatova, 2008; Vlasenko et al., 2011; Mezhzherin et al., 2018). The information on the number of genetic lineages and on the assignment of particular populations to genetic lineages was extracted from scientific papers (Heethoff et al., 2004; King et al., 2008; Porco et al., 2013; Fernández et al., 2016; Shekhovtsov et al., 2014, 2020a–d; Ermolov et al., 2023), as well as the GenBank database.

For *Dendrobaena octaedra* (Savigny, 1826), we also obtained a sequence dataset for 99 specimens from 24 populations from Russia and adjacent countries (Fig. 1). Briefly, earthworms were fixed in ethanol; DNA was extracted from whole individuals or from parts of the body (ca. 100 mg) using BioSilica columns (Dia-m, Russia) according to the manufacturers' instructions. Fragments of the *cox1* gene were amplified using universal primers and sequenced as described in (Shekhovtsov et al., 2013). Sequences were deposited in GenBank under accession numbers OR366494–OR366522, KJ772497, KJ772504, KX400644, MH755642, MH755644, MH755645, MH755647, MH755649, MH755654, MH755666, MH755670, MH755672. A dataset of 157 full-length 658 bp *cox1* barcodes was taken from GenBank. Unique haplotypes were extracted from these datasets. Sequences of *D. octaedra* L2 were additionally searched in the BOLD database (https://v4.boldsystems.org/). Maximum likelihood trees were constructed using RAxML v. v. 8.2.12 (Stamatakis, 2014) with the GTRCAT substitution model and 1000 bootstrap replicates. Bayesian analysis was performed in MrBayes v. 3.4 (Ronquist et al., 2012). Two simultaneous independent runs were performed with 10 million generations each; 25 % of the generations were discarded as burn-in.

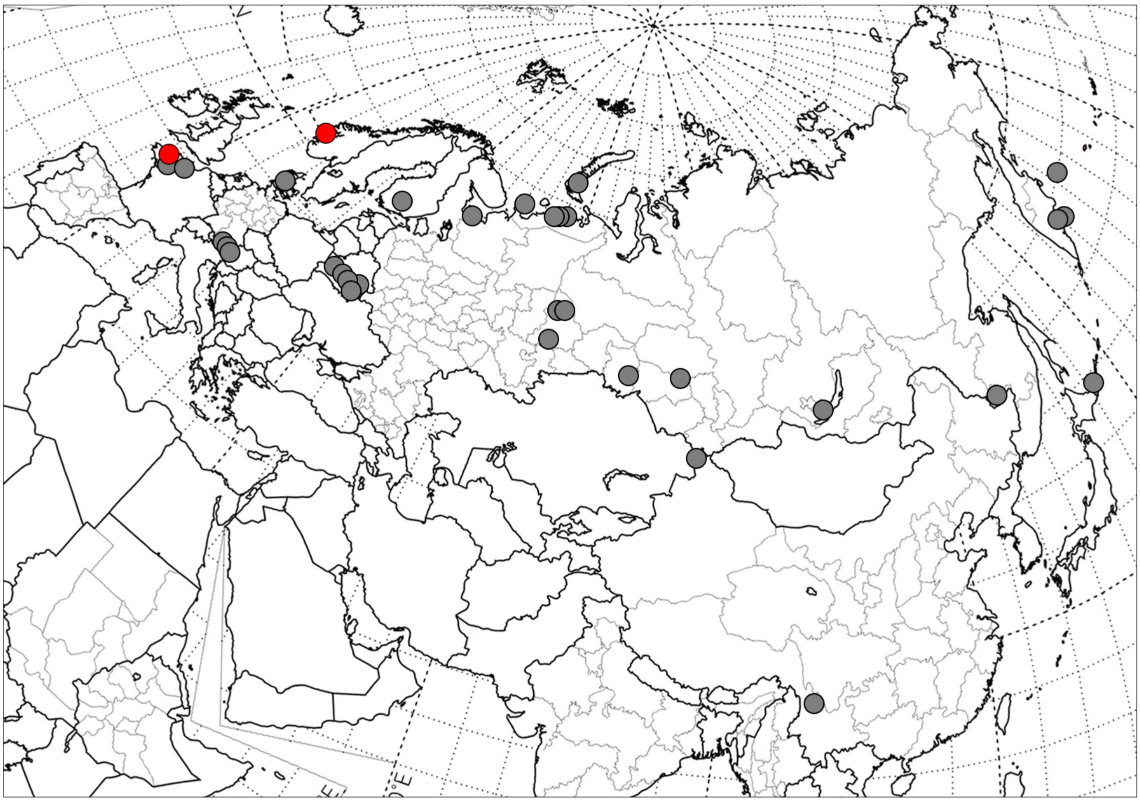

Fig. 1. Sampling locations of the sequenced *D. octaedra* individuals from Eurasia. Russia, Belarus, and Kazakhstan, our data; other countries, GenBank.

Grey dots – lineage 1; red dots – lineage 2.

Results

Dendrobaena octaedra

Among the 99 *D. octaedra* sequences obtained by us, we found 40 unique haplotypes. We also extracted 157 sequences from GenBank with 41 unique haplotypes. We combined these unique haplotypes from the two samples to construct phylogenetic trees (Fig. 2). Our analysis revealed that average genetic diversity within *D. octaedra* is very low compared to other earthworms. The majority of haplotypes belonged to a single group with lower diversity: average p-distance within the group was 2.3 %.

However, two haplotypes from GenBank, MF121744 and MF121754, differed significantly from the rest of the sample with an average p-distance of 19 %. These specimens were designated by the authors as *Dendrobaena octaedra* complex sp. L2. They were collected in the Eawy forest in Normandy (France), near the English Channel. Another three closely related sequences were found in the BOLD database, one from the vicinities of Florelandet (Norway), and the collection points of the other two specimens were undisclosed. These regions were affected by the most recent glaciation, so the local populations of *D. octaedra* were obviously introduced from another region relatively recently (ca. 10 kya). There are too few data on these specimens; since there are no associated papers with morphological descriptions, there is a chance that they might belong to another yet unknown species.

Four chromosomal races are known within *D. octaedra*, $4n = 72$, $5n = 90$, $6n = 108$, and $8n = 144$ (Casellato, 1987; Viktorov, 1993; Mezhzherin et al., 2018). Since the predominant majority of *D. octaedra* populations belong to a single genetic lineage, we can suggest that these three chromosomal races coexist within this lineage.

Aporrectodea rosea (Savigny, 1826)

Races with $2n = 36$, $3n = 54$, $4n = 72$, $5n = 90$, $6n = 108$, $8n = 144$, and $10n = {\sim}180$ were described for *A. rosea* (Muldal, 1952; Casellato, Rodighiero, 1972; Casellato, 1987; Vsevolodova-Perel, Bulatova, 2008; Vlasenko et al., 2011). The initial barcoding studied uncovered the existence of several genetic lineages within this species: R.A. King et al. (2008) detected three lineages, whereas D. Porco et al. (2013) discovered four. R. Fernández et al. (2016) performed a detailed phylogeographic analysis of *A. rosea* in Western Europe, demonstrating that it can be divided into two major clades: the Eurosiberian and the Mediterranean. The former has a cosmopolitan distribution and includes the four lineages identified by R.A. King et al. (2008) and D. Porco et al. (2013), while the latter is confined to the Mediterranean region. Subsequently, additional genetic lineages were found in Russia and adjacent countries, all belonging to the Eurosiberian clade (Shekhovtsov et al., 2020a).

Therefore, many genetic lineages and ploidy races coexist within *A. rosea*. Detailed data on the relationships between them are currently not available. However, there is a single example that can shed light on this issue: S.V. Mezhzherin et al. (2018) reported a case of four chromosomal races ($2n$, $3n$, $6n$, and $8n$) in the A.V. Fomin Botanical Garden (Kyiv).

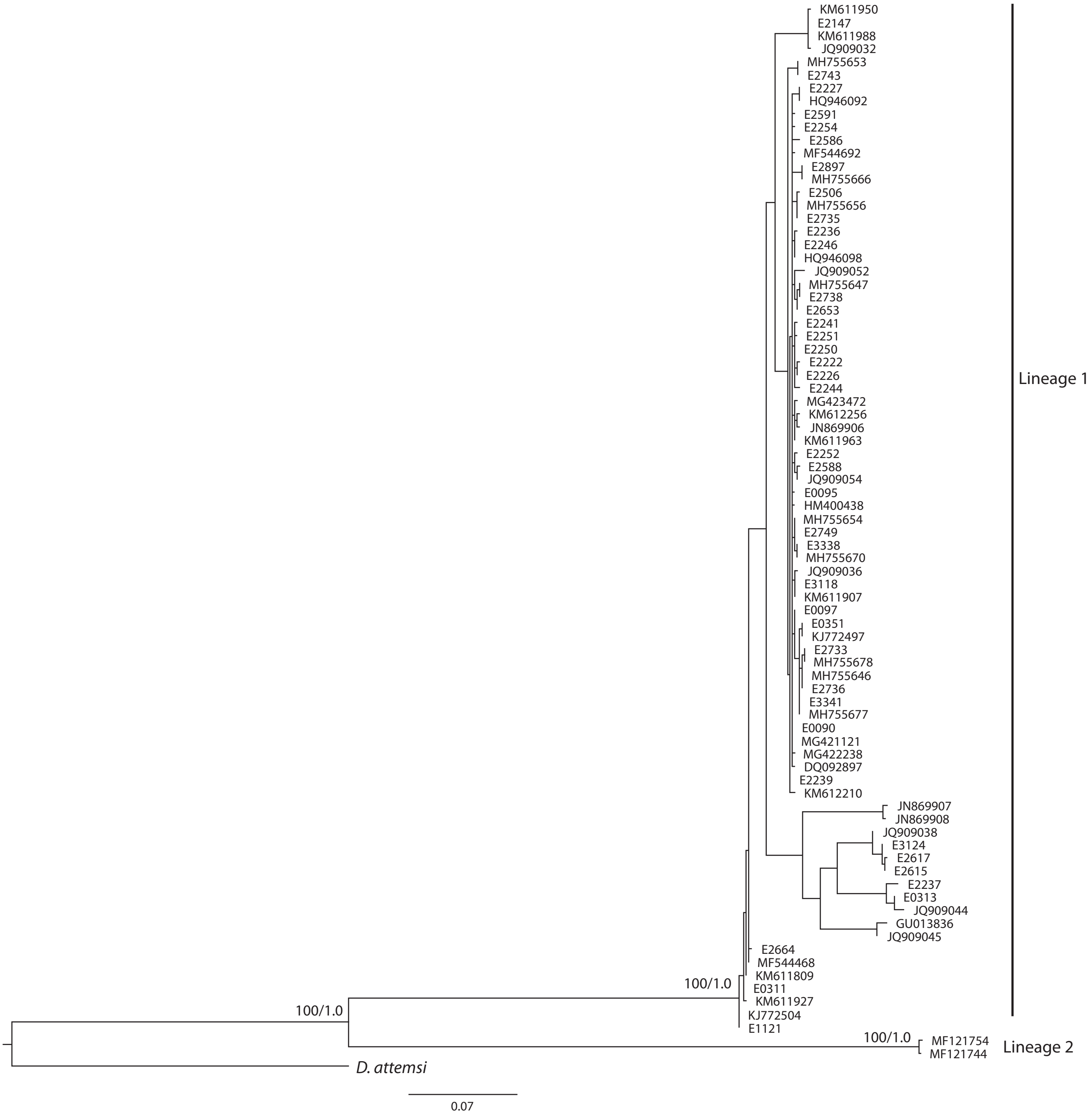

Fig. 2. The phylogenetic tree built for the *D. octaedra* haplotypes using the maximum likelihood method.
Numbers near branches indicate bootstrap support/Bayesian posterior probabilities.

According to phylogeographic studies (King et al., 2008; Shekhovtsov et al., 2020a), three lineages are rarely found in sympatry, and four have never been reported. Therefore, it is plausible that in this case, several chromosomal races coexist within a single lineage. Sure, this cannot be called hard evidence, but we don't have better data so far.

It is worth noting that body size does not correlate with chromosome number in *A. rosea* (Vlasenko et al., 2011). It is presumed that the races with $2n = 36$, as well as at least some populations with $4n = 72$ and $6n = 108$ are amphimictic (Vsevolodova-Perel, Bulatova, 2008).

Bimastos rubidus (Eisen, 1874)

B. rubidus (formerly known as *Dendrodrilus rubidus*) is a rare species containing only a single genetic lineage (Ermolov et al., 2023) despite the fact that it has considerable intraspecific diversity and was until recently considered to contain four subspecies (Holmstrup, Simonsen, 1996; Vsevolodova-Perel, 1997; Sims, Gerard, 1999; Csuzdi et al., 2017). Chromosomal studies reported the presence of six ploidy races within the species: $2n = 34$, $3n = 51$, $4n = 68$, $5n = 85$, $6n = 102$, and $8n = 136$ (Muldal, 1952; Omodeo, 1952; Vedovini, 1973; Casellato, 1987; Mezhzherin et al., 2018). Thus, similar to

D. octaedra, multiple ploidy races are encompassed within a single genetic lineage.

Octolasion tyrtaeum (*lacteum*) (Örley, 1881)

O. tyrtaeum is generally believed to comprise two discrete size groups, referred to as “small” (body length 4–8 cm) and “big” (10–14 cm) (Meinhardt, 1974; Heethoff et al., 2004). Molecular studies demonstrated that mitochondrial and nuclear gene sequences of these two groups are significantly different and belong to two distinct genetic lineages (Heethoff et al., 2004; Shekhovtsov et al., 2014). These two lineages were reported to differ in ploidy: the “small” one is diploid, while the “big” one is triploid (Mezhzherin et al., 2018). Thus, in this case we can observe that a ploidy race corresponds to a single lineage. *O. tyrtaeum* is also a rare example of the dependence of body size on ploidy in earthworms (Mezhzherin et al., 2018).

It should be noted that this division of *O. tyrtaeum* into two groups is not straightforward. A third genetic lineage with body size similar to the “small” lineage but with different body proportions was found (Shekhovtsov et al., 2014, 2020b). Its ploidy is unknown. Moreover, body size may also differ between populations of different lineages (Shekhovtsov et al., 2020b).

Dendrobaena schmidti (Michaelsen, 1907)

D. schmidti is widespread in the Caucasus and adjacent regions. It exhibits a wide range of pigmentation intensity, from unpigmented to deep purple coloration, and body size, ranging from 35 to 160 mm. Due to this variation, many subspecies were isolated from *D. schmidti*, some of them later recognized as distinct species (Perel, 1966; Kvavadze, 1985; Vsevolodova-Perel, 2003). However, not all these subspecies were widely accepted by researchers due to the lack of clear boundaries between them (Vsevolodova-Perel, 2003).

Chromosomal studies demonstrated that all the subspecies of *D. schmidti* distinguished in the book of E.S. Kvavadze (1985) exhibit the same chromosome number of $2n = 36$ (Bakhtadze et al., 2003, 2005). On the other hand, *D. tellermanica*, originally described as *D. s. tellermanica* in 1966 (Perel, 1966) and subsequently elevated to the species rank (Vsevolodova-Perel, 2003), is tetraploid ($4n = 72$) (Bakhtadze et al., 2003, 2005). *D. tellermanica* was distinguished from *D. schmidti* based on the lack of pigmentation, the start of the clitellum on the 25th segment (vs. 26th in *D. schmidti*), and wider distribution beyond the Caucasus region. Initially, it was believed to be strictly parthenogenetic, but later studies revealed the presence of populations with mature spermatozoa and spermatophores (Vsevolodova-Perel, 2003).

Recent molecular studies (Shekhovtsov et al., 2020c, 2023) showed that while *D. schmidti* and *D. tellermanica* are related, they exhibit significant differences in terms of nucleotide substitutions. This implies relatively ancient polyploidization, similar to *O. tyrtaeum*.

Eisenia nordenskioldi (Eisen, 1879) complex

E. nordenskioldi has a vast distribution in Northern Asia and adjacent areas and is known for its high morphological diversity (Malevich, 1956; Vsevolodova-Perel, 1997). Thus it is not surprising that it was found to have extensive genetic diversity (Blakemore, 2013; Shekhovtsov et al., 2013, 2016, 2018; Hong, Csuzdi, 2016). Molecular studies revealed that *E. nordenskioldi* consists of multiple genetic lineages divided into two large clades (Shekhovtsov et al., 2020d). These lineages strongly differ in mitochondrial and nuclear genome sequences (Shekhovtsov et al., 2020c), as well as genome size (Shekhovtsov et al., 2021). Therefore, *E. nordenskioldi* should be regarded as a species complex. Preliminary, this complex was divided into two large clades, referred to as *E. nordenskioldi* s. str. (genetic lineages 6, 7, and 9) and *Eisenia* sp. 1 aff. *E. nordenskioldi* (all other lineages) (Shekhovtsov et al., 2020d).

E. nordenskioldi is probably the best studied model of karyotype diversity among earthworms (Graphodatsky et al., 1982; Bulatova et al., 1984, 1987; Perel, Graphodatsky, 1984; Viktorov, 1989, 1997; Kashmenskaya, Polyakov, 2008; Vsevolodova-Perel, Bulatova, 2008). Races with $2n = 36$, $4n = 72$, $6n = 96–102$, and $8n = 142–152$ were identified (Viktorov, 1997). However, it is not yet clear how the division into genetic lineages correlates with the different ploidy races. Although no direct studies are available, published data allow one to attribute certain populations of *E. nordenskioldi* to specific lineages and races. For example, the population from Magadan with $8n = 152$ chromosomes (Viktorov, 1989) belongs to lineage 9: individuals collected from the same locations were sent to A.G. Viktorov and the authors of this paper by D.I. Berman. Furthermore, extensive studies failed to find other lineages of the pigmented form of *E. nordenskioldi* in this region (Shekhovtsov et al., 2020d).

M.N. Kashmenskaya and A.V. Polyakov (2008) conducted a study on the chromosome set of two individuals identified as *E. n. nordenskioldi* and *E. atlavyniteae*, a closely related species isolated from *E. nordenskioldi* (Perel, Graphodatsky, 1984), from the Central Siberian Botanical Garden in Novosibirsk. Both individuals were found to be diploid ($2n = 36$). A later study of earthworms from the same location found lineages 1, 2, and 3 of the pigmented form of *E. nordenskioldi* (Shekhovtsov et al., 2013). Although we cannot attribute the specimens from the study of M.N. Kashmenskaya and A.V. Polyakov (2008) to a precise lineage, we know that this location does not harbor any lineage of *E. nordenskioldi* s. str. Therefore, these diploid populations belong to *Eisenia* sp. 1 aff. *E. nordenskioldi*.

Tetra- and octoploid races of *E. nordenskioldi* were reported from the Taymyr Autonomous Okrug, located in the north of West Siberia (Bulatova et al., 1984; Viktorov, 1989; Vsevolodova-Perel, Leirikh, 2014). Molecular studies identified genetic lineages 1 and 9 of the pigmented form of *E. nordenskioldi* from the same region (Shekhovtsov et al., 2020d). T.V. Malinina and T.S. Perel (1984) used allozyme data to demonstrate that the octoploid population from Taymyr is related to those from the south of West Siberia compared to other regions, suggesting that it likely belongs to lineage 1.

The population of *E. nordenskioldi* from the Dzhanybek experimental station of the Institute of Forest Science RAS, located in the steppe zone of European Russia in Volgograd Oblast, has been reported to have $4n = 72$ (Malinina, Perel, 1984; Viktorov, 1989). This population was artificially introduced from the floodplain of the Eruslan River in Saratov Oblast, Russia (Vsevolodova-Perel, Bulatova, 2008). According to our data, only lineage 7 of *E. nordenskioldi* is found in

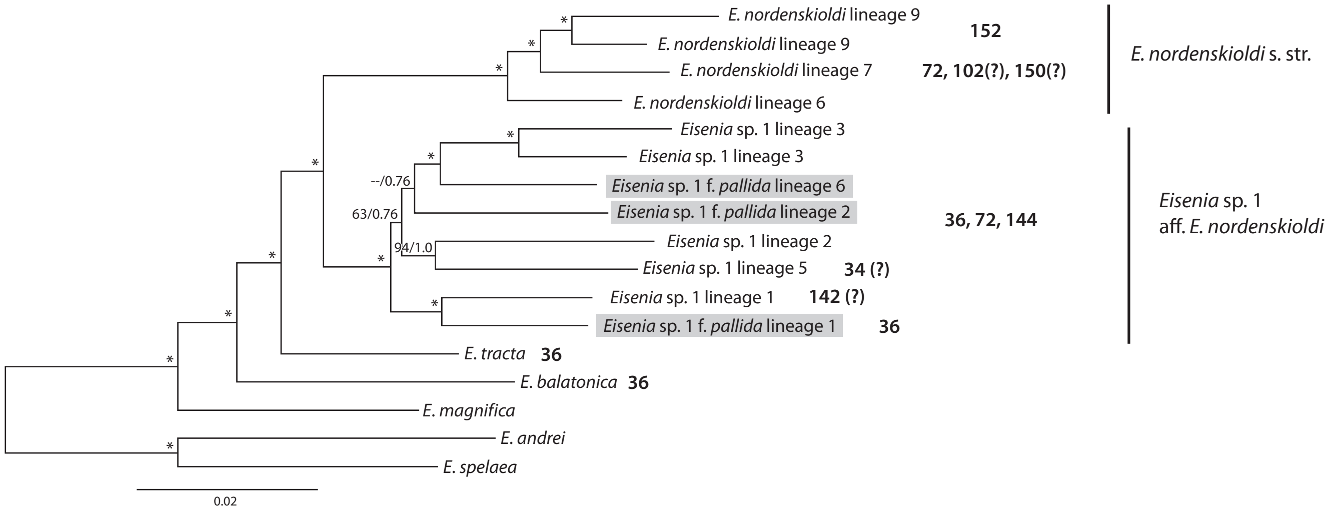

Fig. 3. The position of chromosomal races of *E. nordenskioldi* on the phylogenetic tree of the species according to published data. The tree was taken from (Shekhovtsov et al., 2020d) built using transcriptomic data of various genetic lineages of *E. nordenskioldi* and outgroup species using the maximum likelihood algorithm.

Grey boxes around lineage names indicate that these lineages belong to the *pallida* (unpigmented) form. Bold numbers indicate chromosome numbers; question signs indicate that karyotype assignment is tentative. Numbers near branches indicate bootstrap support/Bayesian posterior probabilities. * Refers to 100/1.0.

this region. The population from the Prioksko-Terrasny Nature Reserve in Moscow Oblast is also within the distribution range of lineage 7. Moreover, T.V. Malinina and T.S. Perel (1984) suggested that it is related to the Dzhanybek population based on allozyme data, so we could also attribute it to lineage 7. The same can be hypothesized for the Kursk population, which has $6n = 102$ chromosomes (Viktorov, 1989).

A.G. Viktorov (1989) reported that *E. nana* from East Kazakhstan Oblast has 34 chromosomes. It has since been discovered that this species is actually a synonym of lineage 5 of the pigmented form of *E. nordenskioldi* (Shekhovtsov et al., 2020d; Golovanova et al., 2021). As the individuals used for both genetic and chromosomal analyses were collected from the same region, it is reasonable to hypothesize that they belong to the same lineage.

The unpigmented *pallida* form of *E. nordenskioldi* is considered to be diploid (Vsevolodova-Perel, Leirikh, 2014). These data were obtained for the population from the Novosibirsk Akademgorodok (Malinina, Perel, 1984; Viktorov, 1989). However, the *pallida* form is distributed throughout Siberia and the Far East and also contains many genetic lineages with different distributions (Shekhovtsov et al., 2016). The *pallida* form from Akademgorodok belongs to lineage 6 (Shekhovtsov et al., 2020d). It has a small genome size (ca. 270 Mb) (Shekhovtsov et al., 2021), while lineage 1 of the *pallida* form has a big genome (ca. 2500 Mb), suggesting that it may be polyploid.

We summarized the obtained data in Fig. 3, which includes chromosome numbers and the phylogenetic tree constructed using 212 nuclear genes (Shekhovtsov et al., 2020d). However, it is important to note that the chromosome numbers displayed are representative of certain populations and may not apply to the entire lineage.

Eisenia tracta, the sister species of the *E. nordenskioldi* complex, has $2n = 36$ chromosomes, as does its relative *E. balatonica* (Fig. 3). Therefore, it is reasonable to suggest that the ancestors of the two clades of *E. nordenskioldi* were also diploid with 36 chromosomes, and that polyploidy arose independently in both clades. This hypothesis on the independent origin of polyploid races in *E. nordenskioldi* was proposed by T.V. Malinina and T.S. Perel (1984) based on allozyme data. The authors concluded that octoploid populations arose independently at least twice. Our data supports this position, as octoploid races appear to have arisen independently in the two large clades of *E. nordenskioldi* (Fig. 3).

It is worth noting that published papers (Viktorov, 1997; Vsevolodova-Perel, Bulatova, 2008) and our unpublished data indicate that all studied populations of *E. nordenskioldi* have well-developed testes and normal spermatogenesis. According to A.G. Viktorov (1997), the evidence for parthenogenesis was only observed for the *acystis* form from Central Asia, which was subsequently isolated into a separate species (Vsevolodova-Perel, 1997). Additionally, octoploid individuals of lineage 9 from Magadan were observed copulating (D.I. Berman, personal communication). Thus, the available evidence suggests that polyploidy does not result in the loss of sexual reproduction in the *E. nordenskioldi* complex in most cases.

Discussion

Based on the data presented above, it is apparent that the relationships between ploidy races and genetic lineages are rarely straightforward. This was only observed in the cases of *O. tyrtaeum* and the *D. schmidti* – *D. tellermanica* pair. For many species, multiple ploidy races were found to belong to the same genetic lineage. In all these cases, races of different ploidy do not have any apparent differences on the level of mitochondrial or nuclear DNA, suggesting that polyploidization events in these cases may be recent. However, in other cases, such as the *E. nordenskioldi* complex, the age of the polyploidization events is unknown, but is likely to be significant, 1–3 Mya as estimated in (Shekhovtsov et al., 2013).

Although the precision of molecular clock dating using only mitochondrial data and no fossils is limited (Kodandaramaiah, 2011), deep divergence between these taxa is obvious.

Earthworms exhibit a high degree of plasticity in their modes of reproduction: most species are reported to have either amphimixis or parthenogenesis, as well as less common modes such as autogamy or restitutional automixis (Pavlíček et al., 2023). Although it is generally considered that polyploidy in animals should be associated with parthenogenesis, there is no obvious association between these modes in earthworms: many polyploid races retain the ability to reproduce sexually. Furthermore, populations with sexual reproduction or partial degeneration of the sexual system were found in species that are considered parthenogenetic (Fernández et al., 2010). In other parthenogenetic species, there are genetic clues to possible sexual reproduction (Simonsen, Holmstrup, 2008). This flexibility in reproduction modes may contribute to the widespread occurrence of polyploidy in earthworms.

Some researchers suggested that polyploid races may have arisen as a result of allopolyploidization (Mezhzherin et al., 2018). However, it is important to note that none of the available molecular studies have yet provided evidence to support this hypothesis.

Conclusion

Based on the available data, we can conclude that the most frequent case in earthworms is "one genetic lineage – several ploidy races", implying that this polyploidy is recent. However, in some instances, polyploid populations can survive for prolonged periods of time, giving rise to new genetic lineages.

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