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THE ALTERNATIVE DISTRIBUTION OF RELATED EARTHWORMS *APORRECTODEA CALIGINOSA* AND *A. TRAPEZOIDES* (OLIGOCHAETA, LUMBRICIDAE) IN UKRAINE AS A CASE OF GEOGRAPHICAL PARTHENOGENESIS

S. V. Mezhzherin[1], Yu. Yu. Chayka[2], R. P. Vlasenko[2], E. I. Zhalay[1], O. V. Rostovskaya[1], O. V. Harbar[2]

[1]Schmalhausen Institute of Zoology NAS of Ukraine,
vul. B. Khmelnytskogo, 15, Kyiv, 01030 Ukraine
E-mail: smezhzherin@gmail.com
[2]Zhytomyr Ivan Franko State University Velyka Berdychivska st., 40,
Zhytomyr, 10008 Ukraine
E-mail: o.v.harbar@gmail.com

S. V. Mezhzherin (https://orcid.org/0000-0003-2905-5235)
Yu. Yu. Chayka (https://orcid.org/0000-0002-3965-6088)
R. P. Vlasenko (https://orcid.org/0000-0002-3743-4406)
E. I. Zhalay (https://orcid.org/0000-0003-3637-1156)
O. V. Rostovskaya (https://orcid.org/0000 0002 0712 6365)
O. V. Harbar (https://orcid.org/0000-0003-4357-4525)

The Alternative Distribution of Related Earthworms *Aporrectodea caliginosa and A. trapezoides* (Oligochaeta, Lumbricidae) in Ukraine as a Case of Geographical Parthenogenesis. Mezhzherin, S. V., Chayka, Yu. Yu., Vlasenko, R. P., Zhalay, E. I., Rostovskaya, O. V., Garbar, O. V. — Geographical parthenogenesis describes phenomenon when parthenogenetic hybrid forms or species have larger distribution areas or higher abundance than their amphimictic parental species, especially in climatically unfavorable conditions. This phenomenon was studied in Ukraine for the pair species of earthworms *Aporrectodea caliginosa* (Savigny, 1826) s. l. We found that the hermaphroditic amphimictic *A. caliginosa* clearly predominates in the northern and western regions, and the apomictic parthenogenetic *A. trapezoides* (Duges, 1828) in the southern and eastern regions with a continental arid climate. In the sample sets of *A. caliginosa*–*A. trapezoides* group, usually one of the species sharply predominated, and the equality of their abundance was very rare. The reason for this fact is both the alternative geographical distribution and the ability of *A. trapezoides* to form populations in habitats unfavorable for *A. caliginosa.* In general, the situation in this group agrees with the classical model of geographic parthenogenesis and confirms the high adaptive potential of apomictic organisms. This fact once again raises the question of non-adaptive reasons for the exclusion of the apomictic reproduction in highly organized animals.

Key words: geographic parthenogenesis, earthworms, *Aporrectodea*, amphimixis, apomixis.

Introduction

A special case in the world of wildlife is geographical parthenogenesis, which is a phenomenon of wide but peripheral distribution of apomictic hybrid polyploid forms (species) comparing with the parental amphimictic diploid species. At the same time, the range of the parthenogenetic species falls on the places with unfavorable environmental conditions for amphimictic parental species (Vandel, 1928; Cuellar, 1977; Glesener, Tilman, 1978; Suomalainen et al., 1987; Bierzychudek 1985; Kearney, 2005; Vrijenhoek, Parker, 2009; Hörandl, 2009). Usually parthenogenetic species occur in the regions with extreme continental or cold climate (Grant, 1982; Suomalainen et al., 1987), expanding their range to the north, penetrating into the highlands or arid zones. This phenomenon is typical for plants and animals in terrestrial and freshwater ecosystems that, as a rule, belonged to extratropical zones (Grant, 1982; Cuellar, 1994), first of all, Holarctic (Grant, 1982; Suomalainen et al., 1987; Cuellar, 1994) and desert regions of Australia (Moritz, 1983; Kearney et al., 2003, Kearney, Moussalli, 2003). Among animals, geographic parthenogenesis has been studied in detail in weevils (Suomalainen et al., 1987; Stenberg et al., 2003), stick insects (Morgan-Richards, Trewick, 2010), freshwater snail *Melanoides tuberculata* (Ben-Ami, Heller, 2007), ostracodes (Schmit et al. 2013), lizards of the families Teiidae (Wright et al., 1978) and Gekkonidae (Moritz, 1983; Kearney et al., 2003).

The concept of geographical parthenogenesis was introduced as early as the 1920s (Vandel, 1928), nevertheless, the nature of this phenomenon remains not completely clear. Generally, the huge ranges of parthenogenetic forms and species that cover the territories with unsuitable conditions for parental species are explained by the ability of asexual forms to occupy the small areas that are relatively favourable for this species by single specimens, which makes rapid invasions possible (Peck et al., 1998; Suomalainen et al., 1987; Haag, Ebert, 2004; Kearney, 2005; Hörandl, 2009). As a result, in suitable microstations, small populations are formed in one generation, and their members are not affected by inbreeding due to clonal reproduction.

Parthenogenesis is widespread in earthworms and the number of unisexual species of the family Lumbricidae in the Holarctic is not much less than of hermaphroditic ones (Jaenike, Selander, 1979; Viktorov, 1993). They are thriving species with extensive ranges and populations often even more numerous than amphimictic species. (Muldal, 1952; Mezhzherin et al., 2018). Parthenogenetic earthworms are allopolyploids and originated from hybridization of diploid amphimictic species (Viktorov, 1993; Mezhzherin et al., 2018). Genetic studies of populations of parthenogenetic earthworms most often analyze the clonal diversity (Jaenike et al., 1980, 1985; Terhivuo, Saura, 1996, 1997; Terhivuo et al., 2002), and in some works, also the ecological aspects of its maintenance. There is a known tendency for higher concentration of parthenogenetic earthworm species in the Palaearctic regions with environmental conditions that are extreme for earthworms (Perel', 1982).

Earthworms of two species, *Aporrectodea caliginosa* (Savigny, 1826) and *A. trapezoides* (Duges, 1828) that were previously considered as subspecies of *A. caliginosa* auct. (Vsevolodova-Perel, 1997), are a suitable object for studies of geographic parthenogenesis in the family Lumbricidae. The first species is diploid, has amphimic-

Fig. 1. *A. caliginosa–A. trapezoides* sample locations from the territory of Ukraine.

tic reproduction, and is a parental species for the second one. *A. trapezoides* is a unisex hybrid, which is triploid, less often tetraploid, and reproduces by parthenogenesis (Mezhzherin et al., 2018).

Material and methods

The study is based on the sample sets of grey worms *A. caliginosa* and *A.trapezoides*, collected by generally accepted methods of earthworm collecting in agro- and urban landscapes of Ukraine (fig. 1). Totally 120 samples were analyzed, which included 1903 specimens (2–71 specimens in the sample).

Preliminary identification of worms was carried out by morphological criteria. We used the coloration of the anterior part of the body: in most cases in *A. trapezoides* it is noticeably darker than in *A. caliginosa* (Vsevolodova-Perel, 1997; Mezhzherin et al., 2018). In order to increase the reliability of species identification, we carried out allozyme analysis using polyacrylamide gel electrophoresis and a Tris-EDTA-borate buffer system (Peacock et al., 1965). For the analysis, the following enzymes were taken: aspartate aminotransferase (locus Aat-1), malate dehydrogenase (locus Mdh-1) and the spectrum of nonspecific esterases encoded by a series of loci (Es-1, -2, -3, -4), and superoxide dismutase (Sod-1). The electrophoretic variability of the listed enzymes was described earlier (Mezhzherin et al., 2008).

Results

Comparative analysis of the population genetic structure of different species.

A. caliginosa is a diploid amphimictic species. Genetic marking shows its homogeneity at loci *Aat*-1, *Es*-4, *Mdh*-1, *Sod*-1. There is an ambiguous variability in the loci of nonspecific esterases (*Es*-1, *Es*-2), encoding products with high electrophoretic mobility. This variability defies traditional genetic interpretation and is probably caused by peculiarities of gene regulation or null alleles. Maybe, this is an intraspecific variability or the result of microevolutionary differentiation. The latter is indirectly confirmed by the fact that populations tend to fix different types of electromorphs. Nevertheless, the expected and observed genotype distributions of polyallelic system in *Es*-4 locus do not differ for individuals with alternative electromorphs of *Es*-1 and *Es*-2 loci. This fact can be an evidence that evolutionarily significant genetic differentiation are absent within this species. Among the individuals, primarily identified as *A. caliginosa*, there were also specimens evading by electrophoretic spectra, in particular, with trigheterozygous spectra that are unusual for diploid organisms (fig. 2).

Ultimately, at the modern level of knowledge, the studied specimens identified by morphological characteristics as *A. caliginosa* can be considered the representatives of a single biological species; possible exceptions, if any, are less than 1 %.

The analysis of genotype distribution in the Es-4 locus, carried out in the largest sample sets, confirmed the panmicticity of the species populations. The only exception is the population from Fedorivka village vicinity (Kyiv Region), with a shortage of heterozygotes in the samples (table 1). This case is most likely associated with the possibility of optional self-fertilization, caused by the peculiarities of the habitat.

A. trapezoides is a triploid parthenogenetic species with a clonal population structure. By three enzyme systems, within Ukraine there were identified

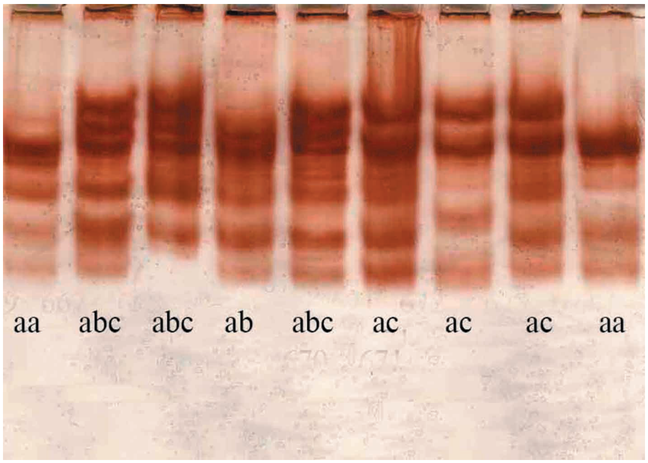

Fig. 2. Electrophoretic spectrum variability of nonspecific esterases in *A. caliginosa* population (Sloboda-Selets village, Zhytomyr Region). Note: “aa” is homozygote, “ab” and “ac” are standard heterozygotes, “abc” is threeheterozygote.

Table 1. A sharp deficit of heterozygotes in *A. caliginosa* population from Fedorivka village (Kyiv Region)

Genotypes *Es*-4						χ^2	d. f.
aa	ab	ac	bb	bc	cc		
8 (4,5)	1 (3,8)	2 (6,2)	3 (0,8)	1 (2,6)	5(2,1)	15,9	1

Note. In parentheses, the expected values based on the Hardy-Weinberg formula.

at least 20 clones (Mezhzherin et al., 2008) with a certain geographic localization. In the sample sets, up to 5 clones were found, usually 1–2.

Distribution on the territory of Ukraine. The range of *A. caliginosa* covers the forest and forest-steppe Palaearctic zones, while *A. trapezoides* inhabit farther south territories (Vsevolodova-Perel, 1997), it occurs in forest-steppe, steppe and Mediterranean climatic regions. The ranges of these species intergrade in south forest, forest-steppe and north steppe zones.

The ratio of *A. caliginosa* and *A. trapezoides* specimens within the sample sets at the territory of Ukraine is the following (fig. 3). From 120 sample sets, in 62 only *A. caliginosa* specimens were found, in 10 only *A. trapezoides* specimens, and in 47 both *A. caliginosa* and *A. trapezoides* were present. Homogeneous sample sets were noted both in the southern and northern parts of Ukraine, but with a clear predominance of *A. caliginosa* in the northern and western regions, and *A. trapezoides* in the southern. The frequency of *A. caliginosa* in the samples from the southern regions was low, and on the contrary, of *A. trapezoides* it was the largest. In the northern and western regions of Ukraine, the situation was the opposite.

Correlation analysis confirmed the increased frequency of parthenogenetic species in the samples from the southern and eastern areas. Thus, there was a highly reliable negative correlation ($r = -0.46$; $p < 0.001$; d.f. = 119) between the latitude of the sample location and *A. trapezoides* frequency in it (fig. 4). A highly reliable, but in this case, positive correlation ($r = 0.39$; $p < 0.001$; d.f. = 119) was also registered between longitude and *A. trapezoides*

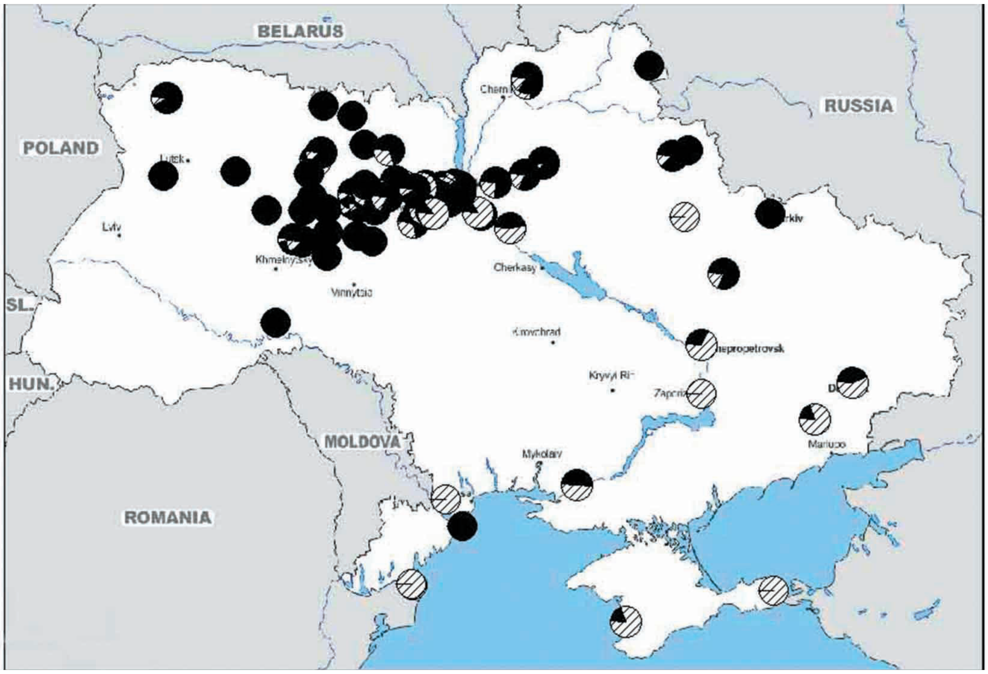

Fig. 3. *A. caliginosa–A. trapezoides* specimens ratio in *A. caliginosa* s. l. sample sets. Black filling — *A. caliginosa*, cross-hatching — *A. trapezoids*.

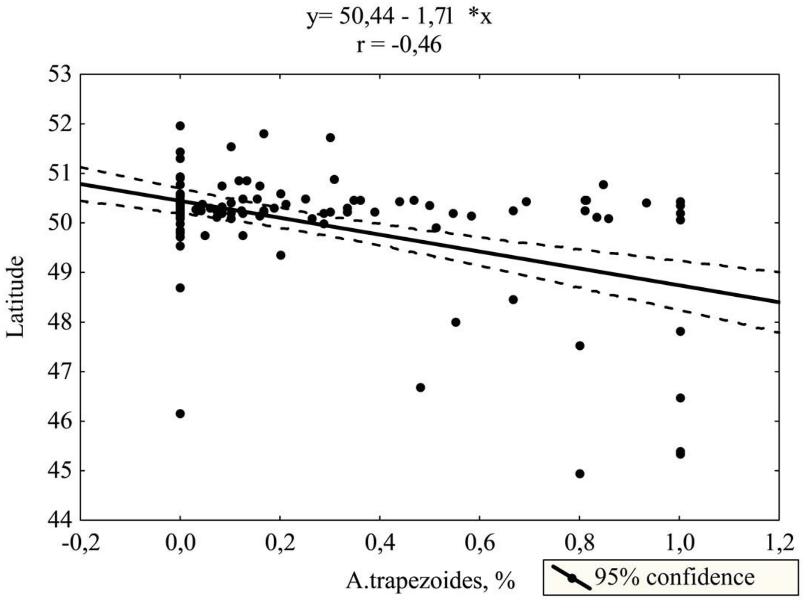

Fig. 4. Changes in the proportion of *A. trapezoides* in *A. caliginosa* s. l. sample sets depending on geographical latitude.

frequency in the sample (fig. 5). This means that the highest *A. trapezoides* frequency is in the southern and eastern areas of Ukraine, while *A. caliginosa* prevails in the northern and western regions. Based on the tendencies obtained, we may conclude that the increase of *A. trapezoides* abundance takes place in areas with a dry and continental climate.

The alternative geographical distribution of *A. caliginosa* and *A. trapezoides*, revealed by correlation analysis, was also confirmed for the samples combined according to the administrative zoning of Ukraine and natural climatic zones (table 2). Thus, the average frequency of *A. trapezoides* in the forest zone was only 0.11 ± 0.01, in the forest-steppe, it was 0.30 ± 0.02, and in the steppe zone, A. *trapezoides* completely prevailed over *A. caliginosa*; its frequency in the samples was 0.93 ± 0.02.

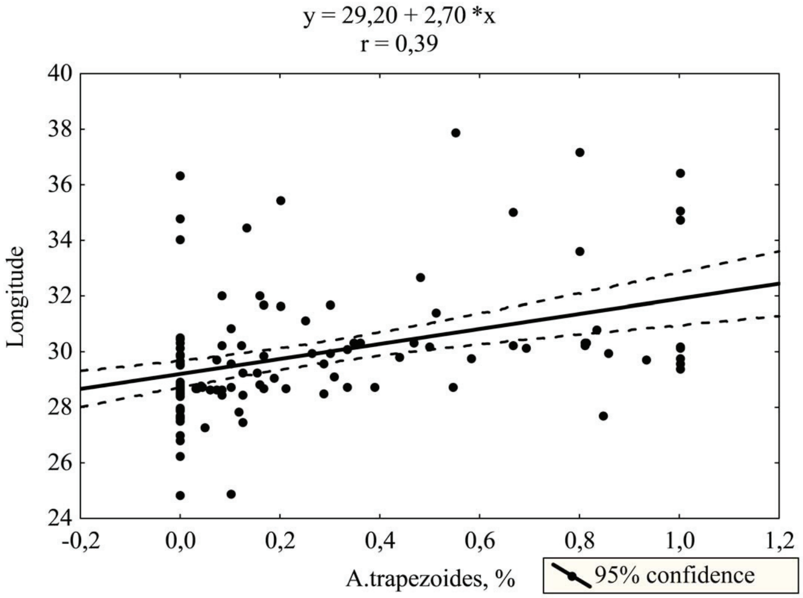

Fig. 5. Changes in the proportion of *A. trapezoides* in *A. caliginosa* s. l. sample sets depending on geographical longitude.

Table 2. *A. caliginosa–A. trapezoides* specimens ratio in the earthworm sample sets divided by natural-climatic zones and administrative units of Ukraine

Zones	Region	Species frequencies		N	n
		A. caliginosa	*A. trapezoides*		
Forest	Volyn	0.96	0.04	2	25
	Rivne	1	0	1	12
	Zhytomyr	0.89	0.11	49	889
	Chernihiv	0.87	0.14	5	76
	Sumy	0.90	0.10	4	48
	Generally	0.89	0.11	60	1028
Forest-Steppe	Khemlnitsky	0.96	0.04	5	50
	Vinnytsia	1	0	3	30
	Kyiv	0.63	0.37	36	559
	Cherkasy	0.49	0.51	1	41
	Poltava, Kharkiv, Dnipro	0.39	0.61	4	18
	Generally	0.70	0.30	49	698
Steppe	Zaporizhzhia	0	1	1	9
	Kherson	0.14	0.86	1	25
	Odesa	0.11	0.89	4	56
	AR of Crimea	0.05	0.95	2	40
	Generally	0.07	0.93	8	130

The excluding type of *A. caliginosa* and *A. trapezoides* geographical distribution from north-west to south and east was evident within the forest and forest-steppe zones (table 2). In the northwestern part of Polissia in the Volyn and Rivne Region, the share of *A. trapezoides* in the samples accounted for only 0.03 ± 0.03. In the central part of the forest zone (Zhytomyr Region), the frequency of this species was almost four times higher (0.11 ± 0.01). The same was the frequency in the left-bank part of the forest zone (0.125 ± 0.03). A similar trend takes place in the forest-steppe zone. In the west, the share of *A. trapezoides* was only 0.02 ± 0.02, in the Central forest-steppe zone (Kyiv and Cherkassy Regions) it increased 20 times (0.41 ± 0.02). In the east of the forest-steppe zone in the Poltava, Kharkiv and Dnipropetrovsk Regions, the parthenogenetic species outnumbered the amphimictic one with a frequency of 0.61 ± 0.11.

Community structure. *A. caliginosa* and *A. trapezoides*, as befits the parent species and hybrid, do not have significant differences in environmental preferences. They are vicarious species with a similar biotopic distribution, and habitat in open landscapes and dry soils. The distribution of these species in the samples has clearly alternative nature, which is manifested in two poles of concentration values (fig. 6). In one of them there are samples with a predominance of *A. caliginosa*, in the other, with a predominance of *A. trapezoides*. *A. caliginosa* frequency of more than 80 % occurred in 65 % of the samples, and the sharp *A. trapezoides* predominance in 13 % of the samples. Samples with equal frequency of the species were extremely rare. Only 7 samples fall within the range of 40–60 %, which is only 6 % of the total number of samples.

At first glance, the reason for the mutually exclusive species distribution in the samples is a vicarious geographic distribution of these species. The amphimictic species is concentrated in the northern and western regions of Ukraine, and the parthenogenetic species in the southern and eastern regions. In the central regions, both species are often found in equal proportions. Therefore, the bipolar form of distribution can be explained by the lack of samples from the Northern Steppe and Southern Forest-Steppe. However, this is not entirely true, since homogeneous settlements are also observed in regions with pessimal conditions for each of the species: in the northwestern regions of Ukraine for *A. trapezoides*, and in the southern and eastern regions for *A. caliginosa*. Obviously, “antagonism”

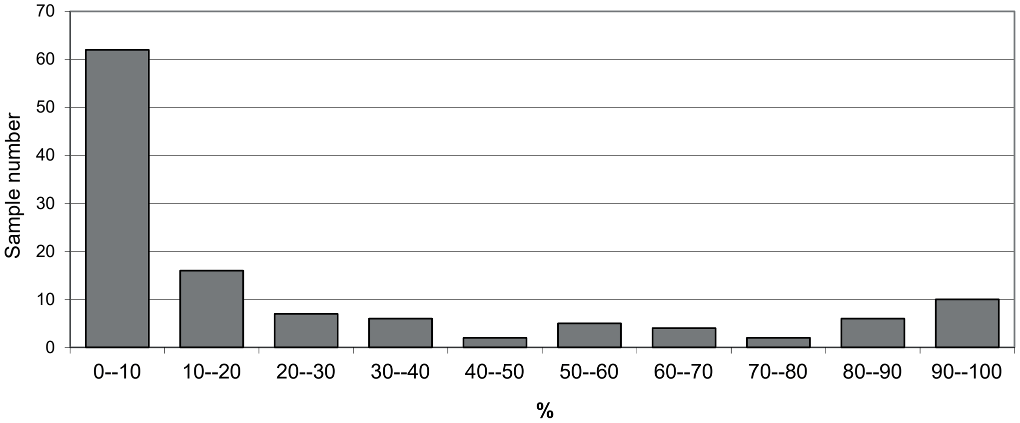

Fig. 6. Distribution of *A. trapezoides* proportion in the sample sets of *A. caliginosa* s. l. earthworms within the Ukraine.

of the two species may be due to their ecological preferences, or the founder effect is very important for them.

In Zhytomyr Region, the distribution of *A. trapezoides* is also of alternative type (fig. 7), despite the fact that in most samples there were only few or no specimens of this species. Only in a few cases, *A. trapezoides* prevailed over *A. caliginosa* or formed the homogeneous settlements. The dominance of *A. trapezoides* over *A. caliginosa* that is extremely rare for Ukrainian northern regions may be an accident, but the standard deviation of *A. trapezoides* distribution exceeded the mean by almost two times (M = 0.1; SD = 0.17), suggesting that empirical distribution did not correspond to the theoretical one described as a set of random rare events. This is confirmed by the statistical reliability of the difference between the empirical and the theoretical distribution according to the Poisson formula ($\chi 2 = 5.03$; df = 1; $p < 0.05$). Thus the presence of few samples with *A. trapezoides* predominance in the Zhytomyr Region, where this species is quite rare, is natural.

An analysis of abiotic characteristics of *A. trapezoides* habitats in northern Ukraine (Zhytomyr and Kyiv Regions) shows that, as a rule, this species inhabits poor sandy soils. Earthworm density in these places was very low and other earthworm species were not found there. Thus, at the northern limits of *A. trapezoides* range, homogeneous settlements are formed only when environmental conditions are pessimal for earthworms. It remains

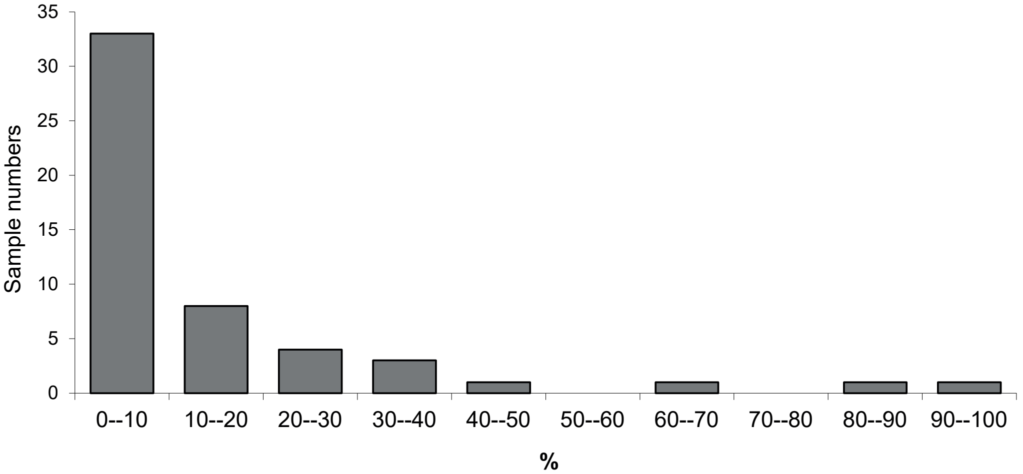

Fig. 7. Distribution of *A. trapezoides* proportion in the sample sets of *A. caliginosa* s. l. earthworms in the northern part of the range (Zhytomyr Region).

unclear whether the colonization of these places is passive or *A. trapezoides* actively choose such habitats. The first assumption is supported by the fact that in the poor soils, *A. trapezoides* abundance was insignificant and not higher than in the optimum soils for *A. caliginosa* s. l. Obviously, the parthenogenetic species evenly but with a low density inhabits the northern areas of Ukraine, and sandy soils are a neutral factor for it. The latter may be explained by the fact that, owing to parthenogenesis, this species can reproduce by single specimens and do not require dense reproductive groups, as for amphimixis.

Discussion

Thus, within Ukraine, two genetically close species of *A. caliginosa* s. l. replace each other in latitudinal and longitudinal directions and have a wide intergradation zone. The amphimictic parental species *A. caliginosa* dominates by abundance over the hybrid apomictic species *A. trapezoides* in the northern and western regions, sharply yielding to it in the southern and eastern regions with dry and continental climate. In general, the situation corresponds to geographic parthenogenesis, which key feature is a marginal distribution of the alloploid species, which range should fall on the territory with pessimal environmental conditions for the parental species. The obvious mechanism that ensures the stable existence of a parthenogenetic species under extreme conditions and low population density is ameiotic gametogenesis, which allows single individuals to find microstations that are suitable for their existence, and eventually establish populations. This gives the ability to exist sustainably in unfavorable conditions, to increase an abundance rapidly, avoiding inbreeding, and then expand into new habitats. All of the above is true for the apomictic species *A. trapezoides*, which mainly inhabit dry and continental areas of Ukraine.

Geographical parthenogenesis is the reason for the shift of parthenogenetic species range to the Palaearctic arid steppe regions, but we cannot so clearly explain *A. trapezoides* lack in northern latitudes with favorable conditions for earthworms. Genetic marking of gray worms carried out in the European part of Russia (Shekhovtsov et al., 2017) shows that within the Western Palaearctic, *A. trapezoides* was not found north than the forest-steppe, although *A. caliginosa* is quite common in the forest zone (Vsevolodova-Perel, 1997). We may assume that *A. trapezoides* distribution to the north is limited because this hybrid form either has antagonistic interactions with the parental species, or originated in the southern borders of *A. caliginosa* range, since it is quite possible that the second parental species had a southern range.

The reason for ploidy level increase of *A. trapezoides* in the southernmost range limits is another problem related to geographic parthenogenesis in *A. caliginosa* s. l. group. While in the northern part of the range *A. trapezoides* specimens are triploid only, in the Crimea (Mezhzherin et al., 2018) and in the south of France (Casellato, 1987), tetraploids are common. In such a situation, the cause of tetraploidy should be the hybridization of the triploid form with a genetically similar amphimictic species. Ploidy level increase symptomatically occurs in another parthenogenetic species, *Octolasion tyrtaeum*, for which only diploids are found at the northern range limits, and in the south, they are replaced by triploids (Mezhzherin et al., 2018). Ploidy level increase in regions with the most unfavorable conditions has an analogy in the world of plants, where in the northern polar latitudes only polyploid forms grow (Grant, 1982).

Carried out on earthworms research confirms that avoiding amphimixis and recombinations gives clonal organisms a number of advantages. In *A. trapezoides* case, it gives a possibility not only to expand the range, but also to inhabit unsuitable places within the zone of A. *caliginosa* dominance, creating low-density settlements. In addition, parthenogenetic organisms are not "wasted" on males. This raises the question of the reasons why the most highly organized animal groups transit to an exclusively amphimictic reproduction. A selective advantage over apomixis as the reason for the evolutionary predominance of amphimixis has been repeatedly discussed (Maynard Smith, 1978; Lewis, 1987; West et al., 1999; Mogie et al., 2007), but a consensus has not yet been formed. Moreover, an explanation based on selective evolutionary concepts, which postulates that amphimixis and recombination have important adaptive significance, is not confirmed in the case of geographic parthenogenesis. It is obvious that amphimixis and bisexuality are a consequence of evolutionary specialization, which has no direct adaptive function.

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