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Adaptive features of some species of Lumbricidae

The few-bristled worms is an extremely important taxonomic group in terrestrial ecosystems. These worms did not receive earlier the attention they deserve and now we have some deficiencies in the knowledge about their taxonomy, distribution, biology and ecology. Experiments with species of different morphoecological groups of Lumbricidae were spent. We considered that the differences in amplitude and frequency of gizzard smooth muscles contractions between species of Lumbricidae have adaptive character. The contractive activity of the muscles was studied according to the method of isolated preparations. The greatest amplitude and the least frequency of contractions of visceral muscles was recorded in detritophages worms of mineral soils. The near-surface species showed the smaller amplitude of muscles contractions, and more greater frequencies of contractions. These physiological distinctions support ideas of the ecological heterogeneity of earthworms. The parameters of contractive activity of smooth muscles of gizzard are the specific physiological variable integrated with the morpho-ecological differentiation of earthworms in natural habitats.

Keywords: earthworms, gizzard, isolated smooth muscles, contractive activity, spontaneous activity, induced contractive activity, acetylcholine, atropine.

The best known oligochaete group are earthworms that were one of the first animal group colonizing humus soils. The important role of earthworms has been recognized from the dawn of human history till present. They were known as important factors of soil fertility. Earthworms have been also used in medicine. They have also been used as a model of scientific explanation of our world. In spite of the importance of oligochaetes, there are presently some serious deficiencies in the knowledge about their taxonomy, distribution, biology and ecology, in comparison with other organismal groups.

The process of adaptation to locally-specific habitat conditions often leads to the formation of various life forms exhibited intraspecifically by geographically distant populations [1]. Ecological distinctions between life forms of earthworms can be seen at other organizational levels, for example as adaptive anatomical-morphological and physiological differences. In soil animals, the examination of adaptations to the natural environment through the prism of specificity of soil-forming properties revealed adaptive development trends in digestive, nervous and other organ systems [2, 3].

Ecological distinctions between species and forms of earthworms can be compared to some obviously adaptive anatomical-morphological and physiological distinctions. There are two main morpho-ecological groups of Lumbricidae: the humus formers feeding coarse particulate organic matter near the ground surface and the humus feeders eating soil humus or the actual soil [4]. The features of the digestive systems of different ecological groups of earthworms are connected with their living conditions [5]. The intestine or midgut is investigated in more details since the pharynx, oesophagus, and muscular gizzard are morphologically similar in most species of Lumbricidae.

Two different types of the intestine correspond to two groups of earthworms with different characteristics of feeding. The first group (soil-eaters) is characterized by the cylindrical form of the intestine with a powerful typhlosole. The second group (inhabitants of the uppermost soil horizons) is characterized by the bead-form intestine with a small typhlosole.

However, differences in adaptive characters between two groups of Lumbricidae are not exhausted by the anatomical features of the digestive system. Feeding near the surface is accompanied by loss of some characteristics inherent for soil-dwelling forms. The cuticular cover becomes thinner; the body length decreases; the ability to diapause disappears. At the same time, emersion to the surface is accompanied with many new characteristics: differentiation of the prostomium, a more perfect form of the tail end, plumose type of the longitudinal muscles in the body wall providing greater mobility, more intensive metabolism, and more perfect nervous system regulation.

The ecological groups of Lumbricidae also differ in size of their daily ration and at the time of assimilation of the food. The degree of decomposition and humification of the vegetative remains in their digestive tract differs significantly [6].

The impellent function of the digestive tract is still insufficiently studied in ecologo-physiological relation. It is known that the isolated crop and gizzard of an earthworm are spontaneously active when stretched. However, the contractive activity of the visceral muscles in different earthworm species has not been studied and its parameters have not been established, particularly in a comparative aspect.

The aim of our research was to determine specific features of the contractive activity of smooth muscles of the digestive tract of earthworms, as a specific physiological variable integrated with the morpho-ecological differentiation of species.

In our research, we identified characteristic physiological features of the contractive activity of smooth muscles in the digestive tract of earthworms Aporrectodea caliginosa and Eisenia nordenskioldi integrated them with morpho-ecological differentiation of species. Than we hypothesized that the different reaction properties of this biologically active substance will be different between distinct life forms of A. caliginosa and E. nordenskioldi. We determined the spontaneous and induced contractive activity of crop-gizzard visceral muscles of two life forms of A. caliginosa and E. nordenskioldi. The acetylcholine, is numbered among the main mediators of neuro-muscular transmission in earthworms [7, 8].

Materials and methods

Two representatives of the genus Aporrectodea Örley, 1885, were studied: Aporrectodea caliginosa trapezoides (Dugés, 1828), and Ap. caliginosa caliginosa (Savigny, 1826). Worms were taken from a natural site in the Kazakh Uplands. The ranges are rough with numerous granite intrusions. The floor of every valley or gulley is filled with woody or shrub growth.

The genus Eisenia Malm, 1877 is represented in the Kazakh upland by the species Eisenia nordenskioldi, which is widespread in Asia and might be a complex of diploid and polyploid lineages. Earthworm specimens tested and compared in the project were collected in black alder forests of the Kazakh Uplands and belong to the following two subspecies:

Eisenia nordenskioldi nordenskioldi (Eisen, 1873). Length 60–150 mm, width 4–8 mm. Number of segments 80–130. Prostomium epilobous. The visible dark-purple pigmentation of the body (the pigment cells are localized in the subcuticular muscle layers) is not, in this subspecies, expressed laterally on the 9–11th segments. The dark-purple body with white lateral spots distinguishes this subspecies from other subspecies. However, several polyploid lineages are known in E. n. nordenskioldi. In Kazakhstan, E. n. nordenskioldi of anthropochoric origin has been recorded in soils of forest nurseries, flower beds and lawns. Apart of Kazakhstan, this nominal subspecies is known from the adjacent areas of the Asian part of Russia and from the Urals. This is a surface-living worm feeding on coarse particulate organic matter near the ground surface.

Eisenia nordenskioldi pallida Malevic, 1956. Length 55–116 mm, width 4–6 mm. Number of segments 80–140. The body pigmentation is scarcely noticeable on several anterior segments, the rest of segments are whitish. E. n. pallida is dwelling in the soil mineral layer and feeding on soil humus. This species is autochthonous in the moist pine and deciduous forests in the Kazakh upland**.** Apart of colour and ecology, no other features are known to differentiate between the pair E. n. Nordenskioldi and E. n. pallida. The different morpho-ecological properties of both subspecies allow them to share the same biotop [9].

In our physiological experiments, contractive activity of the muscles was studied according to the method of muscles isolated preparations [10]. The longitudinal tension of isolated muscular crop-gizzard and gut walls preparations from earthworms stimulated spontaneous rhythmic contractions. The common regime of tension of muscle preparations 380–450 mg was adopted as the optimum mode of registration of spontaneous contractions in the two different earthworm taxa.

Acetylcholine-hydrochloride (ACh) ($1\cdot10^{-11}$ – $1\cdot10^{-4}$ M), that stimulates tonic contractions, was used as biologically active substance to study particular features of induced contractile activity of smooth muscles. During the experiment the muscle preparations were superfused with a saline water solution containing: 103 mM NaCl, 3 mM KCl, 1.8 mM $CaCl_2$ and 1 mM $NaHCO_3$. We selected amplitude and frequency of spontaneous and induced contractions of the smooth muscles and constructed dose-response curves of muscle reactions to acetylcholine concentrations in the range from $1\cdot10^{-11}$ up to $1\cdot10^{-4}$ M. Atropine, known as the antagonist of M-holinoreceptors, was applied in concentrations ranging from $1\cdot10^{-6}$ up to $1\cdot10^{-4}$ M in order to identify the nature of receptors.

Reactions of the muscle tissue to the stretching: amplitude of fluctuations of the contraction in percentage of maximal, and their frequency per minute were measured. Presence or absence of spontaneous rhythmic activity was considered. Statistical analysis was performed by using Statistica v. 6.0 (SPSS Inc.). Values

are presented as mean ± SE if the data were normally distributed (normality of data distribution was tested by Kolmogorov-Smirnov test with Lilliefors' correction).

Results and discussion

Force of tension determines expression of spontaneous rhythmics of smooth muscles in the higher and lower vertebrates [11]. The features of longitudinal tension of isolated smooth muscle preparations of two different earthworm taxa were used to establish the common optimum of tension. From the data received a scheme of dependence of frequency and amplitude of spontaneous rhythmic contractions on tension in the visceral muscles of earthworms was constructed.

Upon the increase in background tension of smooth muscles' preparation from 150 mg up to 250 mg, the amplitude of spontaneous contractions increased to 54 ± 2.03 %, and their frequency to 3 ± 0.4 %. Tensions 360–430 mg revealed the maximum amplitude of spontaneous contractions (85–100 ± 4.05 %) and were accompanied by acceleration of the rhythm to 39 ± 0.4 %. The even greater tension of an isolated smooth muscles' preparation led to a fast increase in frequency and reduction of amplitude of contractions.

The fast-dosed outstretching of a preparation at loadings 360–420 mg did not change the contractive reaction authentically. At the reduction of background loading down to 260 mg the tone of a preparation diminished, the amplitude of spontaneous contractions decreased for 20 % and the frequency for 25 % ($p<0.01$).

Thus, at a tension of 360–430 mg the most expressed rhythmic contractions of smooth muscles were noted. The maximal amplitudes of rhythmic contractions in this regime were registered in 92.8 % of experiments ($p<0.01$) for individuals of both subspecies. Such loading allows keeping rhythmic activity of the isolated smooth muscle tissue preparations for soil-dwelling Ap. c. caliginosa up to 30 hours. The other litter-dwelling subspecies of earthworms is characterized by a shorter time of activity of the similar preparations (up to 4–5 hours). On the results we accept the force of tension of smooth muscles preparation 380–450 mg as the common and optimum mode of registration of spontaneous contractions for two subspecies of Ap. caliginosa.

The rhythmic contractions with subspecies-specific frequencies and amplitudes (phase) were the basic form of spontaneous contractive activity of the gizzard muscles. In the 10 % of experiments ($p<0.01$), spontaneous contractive activity was expressed as slow tonic (phase-tonic) waves. Harmonious (transitive) fluctuations of varying amplitude were observed also in 10 % of experiments ($p<0.01$).

The more elaborated definition of parameters of spontaneous contractive activity of visceral muscles revealed an essential difference of average amplitude and frequency of contractions in two life forms of Ap. caliginosa. The biggest amplitude of contractions was registered for the soil-dwelling subspecies Ap. c. caliginosa (86.71 ± 3.66 mg). The frequency of contractions of visceral muscles was 2.46 ± 0.58 a minute.

Gizzard muscles of the litter-dwelling subspecies Ap. c. trapezoides contracted with less force, but faster. The average amplitude of force was 49.58 ± 2.56 mg and the frequency 4.89 ± 0.37 contractions/min.

The rhythmic contractions with specific frequencies and amplitudes (phase) constituted the basis for determining the spontaneous contractive activity of isolated crop-gizzard and gut walls in E. n. nordenskioldi and E. n. pallida. A thorough analysis of spontaneous contractive activity in muscle preparations revealed essential differences in average amplitude and frequency of contractions between E. n. nordenskioldi and E. n. pallida. The biggest amplitude of contractions was registered in the soil-dwelling subspecies E. n. pallida (68.23 ± 3.25 mg). The frequency of contractions of smooth muscles was 3.23 ± 0.53/minute. Visceral muscles of the digestive tract of the litter-dwelling subspecies E. n. nordenskioldi contracted with less force, but faster. The average amplitude of force was 46.06 ± 4.05 mg and the frequency 4.21 ± 0.44 contractions/min.

We found that the Ach application to several regions of the earthworm gut causes a rapid increase in tension, accompanied by an abolition of rhythmic movements. In our experiment, ACh induced the contractions of gut and isolated smooth muscles crop-gizzard preparations in a dose-dependent amplitude and frequency (tonic induced contractile activity). The induced contractions were persistent for several minutes after Ach application and were accompanied by an increase in the amplitude. We observed that if the spontaneous contractions of smooth muscles were absent the application of Ach caused also contractive activity of smooth muscles.

We estimated the sensitivity of the earthworm smooth muscles at different concentrations of ACh from the established concentration-response curves. The minimum concentration inducing the changes in the

spontaneous contraction activity in the visceral muscles is approximately $1 \cdot 10^{-10}$ M ACh. The maximum effective doses of acetylcholine in the studied subspecies are: $1 \cdot 10^{-5}$ M in E. n. nordenskioldi and Ap. c. trapezoides and $1 \cdot 10^{-4}$ M in E. n. pallid and Ap. c. caliginosa.

The concentrations of ACh (pD_2) inducing a half-maximal contractive response were estimated from the logistic curve. For E. n. nordenskioldi $pD_2 = 1 \cdot 10^{-7}$ M, for Ap. c. trapezoides pD_2 — $3 \cdot 10^{-7}$ while the half-maximal response for the soil-dwelling form E. n. pallida and Ap. c. caliginosa is higher ($pD_2 = 6 \cdot 10^{-7}$ M and $pD_2 = 1{,}2 \cdot 10^{-6}$ M). The isolated smooth crop-gizzard and gut muscles in the surface-living form are of higher reactivity and affinity to acetylcholine. In general, there is asimilarity of the half-maximal response on acetylcholine in smooth muscles of earthworms and primitive vertebrates [12].

We examined the role of the cholinergic antagonist atropine on the ACh-induced response of muscles. Atropine has excitatory effect on crop-gizzard of some species of genera Lumbricus and Allolobophora, but not on the crop-gizzard of Eisenia fetida. Other researchers have shown that the effect of Ach on somatic and visceral muscles is partially blocked by atropine.

We have not found expressed contractile effect of atropine on isolated crop-gizzard and gut preparations of E. nordenskioldi and Ap. caliginosa. Atropine in concentrations $1 \cdot 10^{-6} – 1 \cdot 10^{-5}$ M acted on earthworm muscles within 10 minutes. Three ACh applications ($1 \cdot 10^{-9} – 1 \cdot 10^{-8}$ M) on the background of atropine were used for determining the degree of receptors blockade of muscles. Blockade was complete if the phasic contractions of muscles had not changed. The ACh ($1 \cdot 10^{-7} – 1 \cdot 10^{-5}$ M) induced response (in the presence of atropine) consisted of series of suppressive phasic contractions. Thus atropine moved concentration-response curves on acetylcholine for about 70 % of experiments. But atropine reversibly reduced the ACh-induced response. We observed an increase in spontaneous contractions and a significant increase in ACh-induced contractions after a 10 min. washout time, between the termination of atropine treatment and the last exposure to ACh. Atropine in a concentration of $1 \cdot 10^{-4}$ M completely eliminated ACh-induced responses. Receptors of smooth muscles of earthworm might be similar to muscarinic receptors of vertebrates. However, atropine is a muscarinic antagonist in vertebrates. It is therefore difficult to extrapolate the obtained results to invertebrates [13].

We assume that the occurrence of the observed rhythmic contractions with subspecies-specific frequencies and amplitudes are the basic form of spontaneous contractive activity of earthworms smooth muscles of the digestive system. A higher amplitude of contractions was registered in the soil-dwelling subspecies E. n. pallida and A. c. caliginosa than in the surface dwelling supspecies. This is consistent with our results, obtained earlier for different life forms of earthworms. This means that the life forms of species differs not only in spontaneous but also in induced contractive activity of crop-gizzard and gut-visceral muscles, mediated by muscarinic acetylcholine receptors. Furthermore, the smooth muscles of the surface-living form are characterized by a high sensitivity to small doses ($1 \cdot 10^{-10} – 1 \cdot 10^{-8}$ M) of acetylcholine and by a more pronounced reactivity. We can suppose that the distinctions between parameters of inducedcontractive activity of smooth muscles in life forms are related to the metabolic features and particular nervous regulation.

According to histological researches, the gizzard of earthworms has very powerful muscular walls [14] consisting of three layers: two external longitudinal muscle layers from which the inner one has huge cells, and a thick internal layer of circular muscles with very large cells. The circular muscle layer has species-specific characters. For example, muscular rings of Ap. c. caliginosa are very thin and numerous.

The food mass taken from the intestine of Ap. c. caliginosa and studied under a preparation microscope was composed of fine mineral grains mixed with very fine vegetative rests. No large particles were observed in the intestine. This species feeds on much decayed vegetative material, which apparently does not grind in the stomach [15]. Besides, the intestine of Ap. c. caliginosa is represented by an almost regular cylindrical tube with a round typhlosole bearing deep folds. The intestine can be stretched no more than 1.2–1.5 times. Such a structure of the intestine has much adaptive value for feeding by organic particles dispersed in the soil. The large absorbing surface of the intestine allows using soils poor in organic substances. According to our experiments, the gizzard of this detritophage vigorously pushes the dense food mass, but its contractions occur not more often than 2–3 times a minute, therefore, the food mass passes to the intestine pretty passively. Subsoil species of earthworms processing large amounts of soil promote preservation of water, air permeability of soil, enrichment of the bottom horizons and formation of the soil's particulate structure.

The circular muscular layer of gizzard in the litter-dwelling subspecies Ap. c. trapezoides is thick and precisely distinguishable. This subspecies basically consumes decaying vegetative remains entering the intestine as a loose mass completely accessible for digestion. The amount of mineral particles is small. There is no special crushing and grating of this food in the gizzard, even as large particles of plants come across to the

hindmost part of the intestine. The bead-like form is providing an extension of the intestine during the passage of more viscous food mass containing less mineral particles. The food is more easily forced along the intestine. More frequent contractions provide faster promotion of food in the intestine.

We assume that the parameters of contractions of visceral muscles are connected with morpho-functional features of the digestive system of different ecological groups of Lumbricidae. The higher amplitude of contractions of the gizzard in the actual soil-dwellers is probably connected with large volume and dense structure of the ingested food. These worms swallow vegetative fragments together with mineral soil particles, and slow contractions of the digestive tract promote slow passage of food along the typhlosole, assisting the more complete assimilation of organic substances from soil.

We consider the observed parameters of the activity of digestive tract in Ap. caliginosa as stable characteristics of the forms adapted to consumption of certain types of food resources. These physiological distinctions support ideas of the ecological heterogeneity of Lumbricidae and validity of distinguishing the life forms in this group according to characteristics of feeding.

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В.С. Абукенова

Люмбрицидтердің кейбір түрлерінің адаптивтік ерекшеліктері

Азқылтанақты құрттар — жер беті экожүйесінің өте маңызды таксономиялық тобы әлі күнге дейін жеткілікті зерттелмеген. Қазіргі таңда олардың таксономиясы, биоценозда таралуы, биология және экологиясы жайлы деректер аз. Бұл эксперименттік зерттеулер Lumbricidae тұқымдасының әртүрлі морфоэкологиялық топтарына жүргізілді. Lumbricidae туысының түрлері мен түрше аралығында асқазан бұлшық етінің жиырылғыш жиілігінің белсенділігі мен амплитуда айырмашылығы бейімделеу сипат алады деп топшыладық. Бұлшық еттің жиырылғыш белсенділігі оқшауланған препарат әдісіне сүйеніп жасалды. Жоғарғы амплитуда мен асқазан бұлшық етінің ең төменгі

жиырылу жиілігі детритофагтарда — топырақтың минералды қабатындағы құрттарда байқалды. Жер бетіне таяу түрлер мен түршелерде бұлшықет жиырылу белсенділігінің аз амплитудасы мен жиырылу жиілігінің жоғары көрсеткіші анықталды. Түрлердің биоценоздағы экологиялық дифференциациясы, Lumbricidae висцеральді бұлшық еттерінің өзіндік жиырылу белсенділігінің ерекшеліктері зерттелген. Бұл физиологиялық өзгерістер Lumbricidae экологиялық әртүрлілігін береді. Люмбрицидтер әр түрлері мен формаларының морфоэкологиялық дифференциациясы үйреншікті сипат алатын асқазан бұлшық етінің функционалды белсенділігі өзгерістерімен сипатталды.

Кілт сөздер: жауын құрты, асқазан, оқшауланған бұлшықет препараты, жиырылғыш белсенділігі, қауырт белсенділік, индуцирленген жиырылғыш белсенділігі, ацетилхолин, атропин.

В.С. Абукенова

Адаптивные особенности некоторых видов люмбрицид

Малощетинковые черви — эта чрезвычайно важная таксономическая группа в наземных экосистемах, которая до сих пор остается недостаточно изученной. В настоящее время получено еще мало данных об их таксономии, распределении в биоценозах, биологии и экологии. Были проведены эксперименты с видами семейства Lumbricidae различных морфо-экологических групп. Мы предположили, что различия в амплитуде и частоте сократительной активности гладких мышц кишечника между видами и подвидами Lumbricidae носят адаптивный характер. Сократительная активность гладких мышц была изучена согласно методу изолированных препаратов. Наибольшая амплитуда и наименьшая частота сокращений мышц кишечника были зарегистрированы у детритофагов, червей минеральных слоев почв. Для поверхностнообитающих видов и подвидов определена меньшая амплитуда сократительной активности мышц и большая частота сокращений. Эти физиологические различия подтверждают существование экологической разнородности Lumbricidae. Параметры сократительной активности гладких мышц кишечника — определенная физиологическая переменная, связанная с морфо-экологической дифференциацией дождевых червей в природных местообитаниях.

Ключевые слова: дождевые черви, кишечник, изолированный мышечный препарат, сократительная активность, спонтанная активность, вызванная сократительная активность, ацетилхолин, атропин.

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