Morphological variability of *Oswaldocruzia filiformis* (Nematoda: Molineidae) in amphibians from European Russia

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Abstract. The morphological and morphometric variability of the nematode *Oswaldocruzia filiformis* from ten amphibian species (*Pelophylax ridibundus*, *Pelophylax lessonae*, *Pelophylax esculentus*, *Rana arvalis*, *Rana temporaria*, *Bufo bufo*, *Bufofis viridis*, *Pelobates vespertinus*, *Bombina bombina* and *Lissotriton vulgaris*) was studied. The sampling was performed during the period of 2018–2020 in fifteen localities of European Russia. We examined the following morphological features: the number of crests in mid-body level, the shape of lateral alae, the shape of cephalic vesicle, shape and structure of spicules in males, the shape and structure of male caudal bursa, the shape and structure of the dorsal ray of bursa; and the measurements of nine morphometric characteristics in nematode females and seven characters in males, subjected to variability. Significant differences in the variability of morphometric characteristics of *O. filiformis* of both sexes in different amphibian species and amphibians from various regions were revealed. Likewise, significant differences were revealed for most of morphometric features of *O. filiformis* from amphibians of the same species from different regions of Russia. The type of male caudal bursa and the structure and shape of spicules were identical in all *O. filiformis* males studied. Likewise, we have not found variability in the structure of the reproductive system in *O. filiformis* females. Variability was noted in the shape and size of the cephalic vesicle and lateral alae, in the number at the mid-body level, in the shape and structure of the dorsal rib of male caudal bursa. Differences in morphometric characteristics of *O. filiformis* from amphibians of the same species from different regions of Russia can be explained by the phenotypic plasticity of the species. While variations in the nematode morphology from different amphibian species are caused by the host-induced morphological variability of the parasite. Differences in the size of nematodes and their morphology in different regions of Russia studied may be caused by changes in ecological conditions in amphibian habitats. The broad morphological variability of the nematode *O. filiformis* increases the adaptive capabilities of the helminth and allows it to parasitize a wide range of hosts.

1. Introduction
Parasites are characterized by the same forms and types of variability as free-living organisms. In various host species and geographical regions, parasitic worms can form morphologically different ecomorphs [1–4]. Parasitic worms with a wide species range, parasitizing a broad host spectrum and occurring in different habitats of the same region have the plasticity of morphological characters [1]. The nematode *Oswaldocruzia filiformis* (Goeze, 1782) belongs to such species.
Oswaldocruzia filiformis is a common and widespread parasite of amphibians and reptiles. The obligate hosts of the nematode are anurans and lizards. The life cycle of *O. filiformis* is direct. Animals are infected with *O. filiformis* when they ingest nematode larvae with the food [5]. *Oswaldocruzia* nematodes are also often found in snakes, which are its post-cyclic hosts [6, 7].

Data on the intra- and interpopulational variability of amphibian helminths are contained in a number of papers [8–15]. There are few studies on the population variability of *Oswaldocruzia* nematodes from different localities in European Russia, which showed that only one species *O. filiformis* parasitizes in all amphibian and reptile species studied [19].

The purpose of this research was to study the variability of the morphological and morphometric characters of *O. filiformis* parasitizing amphibians from European Russia depending on the host species and the habitat.

2. Methods
The study of the morphological variability of *O. filiformis* in amphibians was conducted in the territory of European Russia in 2018–2020 in fifteen localities (figure 1). We collected nematodes from ten amphibian species, namely, the European marsh frog *Pelophylax ridibundus* (Pallas, 1771), the pool frog *Pelophylax lessonae* (Camerano, 1882), the edible frog *Pelophylax esculentus* (Linnaeus, 1758), the moor frog *Rana arvalis* Nilsson, 1842, the European common frog *Rana temporaria* Linnaeus, 1758 (Ranidae), the common toad *Bufo bufo*, the European green toad *Bufo toad viridis* (Laurenti, 1768) (Bufonidae), the Pallas’ spadefoot *Pelobates vespertinus* (Pallas, 1771) (Pelobatidae), the European fire-bellied toad *Bombina bombina* (Linnaeus 1761) (Bombinatoridae) and the smooth newt *Lissotriton vulgaris* Linnaeus, 1758 (Salamandridae).

![Figure 1. Schematic map of sampling locations. Red circles – sampling locations of *O. filiformis*; 1 – Zvenigorod Biological Station of Moscow University; 2 – Mordovia Nature Reserve; 3 – vicinity of Pervomaysk (Nizhny Novgorod Oblast); 4 – National Park “Smolny”; 5 – Prisursky Nature Reserve (Republic of Chuvashia); 6 – Togliatti and its surroundings (Samara Oblast); 7 – vicinity of Staryy Buyan village; 8 – Samarskaya Luka (Samara Oblast); 9 – Mekhzavod, suburb of Samara city; 10 – Oktyabrskiy township (Samara Oblast); 11 – South suburb of Volgograd city; 12 – Andra-Ata natural landmark (Republic of Kalmykia); 13 – Verkhnyaya Kvazhva natural landmark (Perm Krai); 14 – vicinity of Kiselevo village (Perm Krai); 15 – vicinity of Aknazarovo village (Republic of Bashkortostan).](image)

A total of 569 specimens of *O. filiformis* were studied: 299 males and 270 females. The morphological measurements were conducted on mature parasites. Nematodes were killed by heating in water, cleared in lactic acid and examined in temporary mounts. A razor blade was used to make
transverse sections of nematodes. Drawings of parasitic worms were made using MBI-9 light microscope and the drawing tube RA-7. Drawings of *O. filiformis* males and females from *Pelophylax ridibundus* & *Bufo bufo* are given by us earlier [19]. The synlophe was studied according to Durette-Desset [21]. The nomenclature of the caudal bursa followed Durette-Desset and Chabaud [22].

The morphological characters studied in *O. filiformis* were: the shape of cephalic vesicle, the shape of lateral alae at mid-oesophagus level, the number of crests in the mid-body level, the shape of spicules in males, the shape and structure of male caudal bursa, the shape and structure of the dorsal ray of bursa. We also examined seven morphometric features in males (body length, width in mid-body level, length of oesophagus, length and width of cephalic vesicle, tail length, spicule length) and nine characters in females (body length, width in mid-body level, length of oesophagus, length and width of cephalic vesicle, tail length, distance from the anterior body end to the vulva, egg length and width).

Statistical analysis was performed using the software packages Microsoft Excel 2003 and Past 2.16 [23]. The following parameters were used: mean, standard deviation (σ) and coefficient of variation (CV) [24]. The significance of differences in the mean values of the morphometric characters studied from different hosts and habitats was evaluated using the Kruskal-Wallis H test. The differences were considered significant at p < 0.05.

### 3. Results

The results of our study showed that the mean body size of *O. filiformis* from different amphibian species and regions ranged from 6.43 to 10.89 mm (body length) and from 0.119 to 0.213 mm (body width) in nematode males; from 9.96 to 19.63 mm (body length) and from 0.161 to 0.266 mm (body width) in nematode females (tables 1–14).

#### Table 1. Morphometry of *Oswaldocruzia filiformis* males from *Rana arvalis*

| Site       | Value  | LB  | WB  | LV  | WV  | LO  | LT  | LS  | NC  |
|------------|--------|-----|-----|-----|-----|-----|-----|-----|-----|
| **4**      | mean   | 10.28 | 0.193 | 0.006 | 0.039 | 0.508 | 0.125 | 0.223 | 40-45 |
| (12*)      | min-max| 8.00-12.85 | 0.165-0.236 | 0.079-0.091 | 0.037-0.040 | 0.457-0.571 | 0.118-0.142 | 0.212-0.234 |
| SD         | 1.24   | 0.02 | 0.005 | 0.002 | 0.04 | 0.01 | 0.005 |
| CV         | 12.06  | 10.36 | 5.81 | 5.13 | 7.87 | 8.00 | 2.24 |
| **9**      | mean   | 8.96 | 0.198 | 0.081 | 0.037 | 0.452 | 0.125 | 0.226 | 37-42 |
| (15)       | min-max| 7.00-10.70 | 0.175-0.221 | 0.079-0.085 | 0.035-0.040 | 0.361-0.535 | 0.118-0.134 | 0.216-0.234 |
| SD         | 1.11   | 0.02 | 0.002 | 0.002 | 0.05 | 0.06 | 0.006 |
| CV         | 12.39  | 5.05 | 2.47 | 5.41 | 11.06 | 4.80 | 2.66 |
| **8**      | mean   | 9.14 | 0.200 | 0.081 | 0.037 | 0.474 | 0.127 | 0.226 | 35-47 |
| (20)       | min-max| 6.65-11.10 | 0.117-0.228 | 0.075-0.087 | 0.035-0.039 | 0.384-0.538 | 0.118-0.138 | 0.214-0.240 |
| SD         | 1.43   | 0.01 | 0.004 | 0.002 | 0.04 | 0.06 | 0.007 |
| CV         | 15.65  | 5.00 | 4.94 | 5.41 | 8.44 | 4.72 | 3.10 |
| **2**      | mean   | 9.42 | 0.178 | 0.075 | 0.032 | 0.452 | 0.126 | 0.215 | 36-51 |
| (21)       | min-max| 7.75-11.25 | 0.154-0.205 | 0.067-0.087 | 0.030-0.035 | 0.413-0.504 | 0.118-0.134 | 0.203-0.228 |
| SD         | 1.10   | 0.02 | 0.006 | 0.002 | 0.03 | 0.01 | 0.01 |
| CV         | 11.68  | 11.23 | 8.00 | 6.25 | 6.64 | 7.94 | 4.65 |
| **7**      | mean   | 10.08 | 0.156 | 0.076 | 0.033 | 0.451 | 0.120 | 0.219 | 39-50 |
| (20)       | min-max| 9.00-11.35 | 0.134-0.189 | 0.069-0.083 | 0.030-0.035 | 0.429-0.472 | 0.114-0.126 | 0.205-0.228 |
| SD         | 0.79   | 0.02 | 0.005 | 0.002 | 0.02 | 0.04 | 0.01 |
| CV         | 7.84   | 12.82 | 6.58 | 6.06 | 4.43 | 3.33 | 4.63 |
| **15**     | mean   | 10.75 | 0.168 | 0.081 | 0.033 | 0.466 | 0.126 | 0.211 | 39-45 |
| (20)       | min-max| 9.15-13.25 | 0.150-0.185 | 0.075-0.087 | 0.031-0.035 | 0.416-0.504 | 0.114-0.134 | 0.197-0.224 |
| SD         | 1.19   | 0.01 | 0.004 | 0.002 | 0.03 | 0.06 | 0.01 |
| CV         | 11.07  | 5.95 | 4.94 | 6.06 | 6.44 | 4.76 | 4.74 |
| **10**     | mean   | 10.18 | 0.138 | 0.083 | 0.037 | 0.438 | 0.129 | 0.224 | 36-44 |
| (20)       | min-max| 8.50-12.65 | 0.122-0.157 | 0.079-0.091 | 0.035-0.039 | 0.409-0.472 | 0.118-0.146 | 0.210-0.238 |
| SD         | 1.17   | 0.01 | 0.004 | 0.002 | 0.02 | 0.01 | 0.01 |
| CV         | 11.49  | 7.25 | 4.82 | 5.41 | 4.57 | 7.75 | 4.46 |

*a* numbering of localities as shown in figure 1: 4 – National Park “Smolny” 9 – Mekhzavod 8 – Samarskaya Luka 2 – Mordovia Nature Reserve 7 – Staryy Buyan village 15 – Aknazarovo village 10 – Oktjabrsky.

*b* number of nematodes studied.

*c* abbreviations: LB – length of body; WB – width of body; LV – length of cephalic vesicle; WV – width of cephalic vesicle; LT – length of tail; LS – length of spicules; NC – number of crests at mid-body; LO – length of oesophagus.
Table 2. Morphometry of *Oswaldocirca filiformis* females from *Rana arvalis*

| Site | Value | LB | WB | LV | LV | WV | WV | LO | LT | AV | LE | WE | NC |
|------|-------|----|----|----|----|----|----|----|----|----|----|----|----|----|
| 4    | mean  | 16.63| 0.219| 0.091| 0.044| 0.536| 0.266| 10.31| 0.082| 0.046 |
|      | (10)  |     |     |     |     |     |     |     |     |     |     |     |     |
| 9    | mean  | 16.19| 0.266| 0.083| 0.042| 0.498| 0.277| 9.88| 0.079| 0.048 |
|      | (4)   |     |     |     |     |     |     |     |     |     |     |     |     |
| 8(12)| mean  | 15.94| 0.256| 0.079| 0.040| 0.447| 0.260| 9.60| 0.075| 0.045 |
|      | max   | 16.50| 0.276| 0.085| 0.043| 0.536| 0.287| 10.20| 0.083| 0.051 |

Designations as in tables 1.

Table 3. Morphometry of *Oswaldocirca filiformis* males from *Bufo bufo*

| Site | Value | LB | WB | LV | LV | WV | WV | LO | LT | AV | LE | WE | NC |
|------|-------|----|----|----|----|----|----|----|----|----|----|----|----|
| 4    | mean  | 10.89| 0.213| 0.096| 0.043| 0.527| 0.130| 0.213 |
|      | (10)  |     |     |     |     |     |     |     |     |     |     |     |     |
| 9    | mean  | 18.73| 0.223| 0.086| 0.035| 0.517| 0.227| 11.88| 0.070| 0.035 |
|      | (5-8) |     |     |     |     |     |     |     |     |     |     |     |     |
| 7    | mean  | 14.46| 0.197| 0.079| 0.032| 0.492| 0.209| 9.25| 0.063| 0.032 |
|      | (24)  |     |     |     |     |     |     |     |     |     |     |     |     |
| 15   | mean  | 21.50| 0.244| 0.089| 0.036| 0.524| 0.272| 14.00| 0.083| 0.039 |
|      | (20)  |     |     |     |     |     |     |     |     |     |     |     |     |
| 10   | mean  | 10.50| 0.196| 0.084| 0.037| 0.518| 0.281| 10.67| 0.071| 0.039 |
|      | (20)  |     |     |     |     |     |     |     |     |     |     |     |     |

Designations as in tables 1 and 2.

Table 4. Morphometry of *Oswaldocirca filiformis* females *Bufo bufo*

| Site | Value | LB | WB | LV | LV | WV | WV | LO | LT | AV | LE | WE | NC |
|------|-------|----|----|----|----|----|----|----|----|----|----|----|----|
| 4    | mean  | 19.63| 0.254| 0.109| 0.055| 0.586| 0.306| 12.98| 0.087| 0.046 |
|      | (12)  |     |     |     |     |     |     |     |     |     |     |     |     |
| 9    | mean  | 14.80| 0.231| 0.093| 0.043| 0.503| 0.232| 9.95| 0.078| 0.046 |
|      | (25)  |     |     |     |     |     |     |     |     |     |     |     |     |
| 3    | mean  | 15.74| 0.235| 0.101| 0.039| 0.518| 0.246| 10.33| 0.082| 0.038 |
|      | (20)  |     |     |     |     |     |     |     |     |     |     |     |     |

Designations as in tables 1 and 2.

* localities: 4 – National Park “Smolny” 2 – Mordovia Nature Reserve 3 – vicinity of Pervomaysk.
### Table 5. Morphometry of Oswaldocruzia filiformis males from Pelophylax ridibundus

| Site          | Value | LB    | WB    | LV    | WV    | LO    | LT    | AV    | LE    | WE    | NC    |
|---------------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|
| Mordovia Nature Reserve | mean  | 18.00 | 0.288 | 0.114 | 0.047 | 0.551 | 0.283 | 11.25 | 0.094 | 0.041 | 0.041 |
| SD            | 0.82  | 0.02  | 0.007 | 0.005 | 0.02  | 0.01  | 0.067 | 0.007 | 0.003 | 0.003 | 0.003 |
| CV            | 5.21  | 8.51  | 6.93  | 12.82 | 3.86  | 4.07  | 6.49  | 8.54  | 7.89  | 7.89  | 7.89  |
| (2)           |       |       |       |       |       |       |       |       |       |       |       |
| Descriptions  | as in tables 1, 2 and 3. |

### Table 6. Morphometry of Oswaldocruzia filiformis females Pelophylax ridibundus

| Site          | Value | LB    | WB    | LV    | WV    | LO    | LT    | AV    | LE    | WE    | NC    |
|---------------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|
| Togliatti     | mean  | 18.53 | 0.216 | 0.093 | 0.055 | 0.222 | 0.280 | 11.67 | 0.083 | 0.044 | 0.044 |
| SD            | 4.25  | 0.02  | 0.005 | 0.005 | 0.03  | 0.05  | 0.03  | 0.01  | 0.004 | 0.004 | 0.004 |
| CV            | 10.00 | 8.77  | 5.32  | 10.97 | 5.80  | 16.03 | 23.42 | 11.63 | 6.33  | 6.33  | 6.33  |
| (15)          |       |       |       |       |       |       |       |       |       |       |       |
| Descriptions  | as in tables 1 and 2. |

### Table 7. Morphometry of Oswaldocruzia filiformis males from Pelobates vespertinus

| Site          | Value | LB    | WB    | LV    | WV    | LO    | LT    | AV    | LE    | WE    | NC    |
|---------------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|
| Togliatti     | mean  | 18.50 | 0.256 | 0.087 | 0.039 | 0.532 | 0.244 | 6.38  | 4.07  | 6.76  | 6.76  |
| SD            | 18.30 | 0.116 | 0.079 | 0.035 | 0.217 | 0.492 | 0.213 | 12.75 | 4.48  | 4.48  | 4.48  |
| CV            | 10.50 | 18.63 | 6.33  | 5.26  | 13.76 | 7.46  | 4.48  | 4.48  | 4.48  | 4.48  | 4.48  |
| (13)          |       |       |       |       |       |       |       |       |       |       |       |
| Descriptions  | as in tables 1 and 2. |

### Table 8. Morphometry of Oswaldocruzia filiformis females from Pelobates vespertinus

| Site          | Value | LB    | WB    | LV    | WV    | LO    | LT    | AV    | LE    | WE    | NC    |
|---------------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|
| Togliatti     | mean  | 18.50 | 0.256 | 0.087 | 0.039 | 0.532 | 0.244 | 6.38  | 4.07  | 6.76  | 6.76  |
| SD            | 18.30 | 0.116 | 0.079 | 0.035 | 0.217 | 0.492 | 0.213 | 12.75 | 4.48  | 4.48  | 4.48  |
| CV            | 10.50 | 18.63 | 6.33  | 5.26  | 13.76 | 7.46  | 4.48  | 4.48  | 4.48  | 4.48  | 4.48  |
| (1)           |       |       |       |       |       |       |       |       |       |       |       |
| Descriptions  | as in tables 1 and 2. |
Table 9. Morphometry of Oswaldocruzia filiformis males from Rana temporaria.

| Site      | Value | LB   | WB   | LV   | WV   | LO  | LT   | LS   | NC  |
|-----------|-------|------|------|------|------|-----|------|------|-----|
| 1* (6)    | mean  | 8.72 | 0.154| 0.091| 0.039| 0.479| 0.122| 0.212| 34-39|
|           | min-max| 7.60-9.85 | 0.141-0.165 | 0.087-0.094 | 0.037-0.041 | 0.464-0.496 | 0.118-0.130 | 0.201-0.220
| 14        | mean  | 9.96 | 0.133| 0.089| 0.035| 0.443| 0.125| 0.210| 38-44|
|           | min-max| 9.25-11.10 | 0.126-0.142 | 0.087-0.091 | 0.031-0.039 | 0.429-0.457 | 0.118-0.130 | 0.205-0.213
| 2 (6)     | mean  | 7.98 | 0.135| 0.075| 0.031| 0.436| 0.122| 0.189| 35-45|
|           | min-max| 7.60-8.25 | 0.126-0.146 | 0.071-0.077 | 0.028-0.034 | 0.394-0.480 | 0.118-0.126 | 0.177-0.201

Designations as in tables 1 and 2.

* localities: 1 – Zvenigorod.14 – Kiselevo village. 2 – Mordovia Nature Reserve.

Table 10. Morphometry of Oswaldocruzia filiformis females Rana temporaria

| Site      | Value | LB   | WB   | LV   | WV   | LO  | LT   | LS   | NC  |
|-----------|-------|------|------|------|------|-----|------|------|-----|
| 1* (12)   | mean  | 15.39| 0.230| 0.090| 0.042| 0.516| 0.264| 9.81 | 0.083| 0.042|
|           | min-max| 12.75 | 0.213 | 0.080 | 0.039 | 0.484 | 0.224 | 7.25 | 0.075 | 0.039|
|           | max    | 19.25 | 0.244 | 0.106 | 0.047 | 0.551 | 0.311 | 12.50 | 0.091 | 0.047|

Designations as in tables 1 and 2.

* localities: 1 – Zvenigorod. 14 – Kiselevo village. 2 – Mordovia Nature Reserve.

Table 11. Morphometry of Oswaldocruzia filiformis males from Pelophylax lessonae.

| Site      | Value | LB   | WB   | LV   | WV   | LO  | LT   | LS   | NC  |
|-----------|-------|------|------|------|------|-----|------|------|-----|
| 9* (5)    | mean  | 7.33 | 0.155| 0.086| 0.036| 0.401| 0.130| 0.207| 41-43|
|           | min-max| 6.75-7.70 | 0.134-0.173 | 0.079-0.091 | 0.035-0.037 | 0.394-0.406 | 0.126-0.134 | 0.185-0.228
| 4 (5)     | mean  | 7.13 | 0.167| 0.077| 0.032| 0.440| 0.129| 0.197| 35-40|
|           | min-max| 6.50-7.70 | 0.157-0.177 | 0.071-0.079 | 0.030-0.035 | 0.394-0.472 | 0.120-0.134 | 0.185-0.209
| 6 (3)     | mean  | 8.62 | 0.146| 0.093| 0.044| 0.470| 0.126| 0.186| 35-40|
|           | min-max| 7.50-9.40 | 0.126-0.177 | 0.091-0.094 | 0.043-0.045 | 0.445-0.492 | 0.120-0.132 | 0.177-0.193
| 5 (2)     | mean  | 6.43 | 0.125| 0.081| 0.035| 0.388| 0.116| 0.193| 38-40|
|           | min-max| 6.25-6.60 | 0.120-0.130 | 0.079-0.083 | 0.031-0.039 | 0.374-0.402 | 0.114-0.118 | 0.181-0.205

Designations as in tables 1 and 2.

* localities: 9 – Mezhkavod. 4 – National Park “Smolny”.6 – Togliatti. 5 – Prurskiy Nature Reserve.

Table 12. Morphometry of Oswaldocruzia filiformis females from Pelophylax lessonae

| Site      | Value | LB   | WB   | LV   | WV   | LO  | LT   | AV  | LE | WE | NC  |
|-----------|-------|------|------|------|------|-----|------|-----|----|----|-----|
| 9 (1)     | mean  | 11.90| 0.193| 0.091| 0.035| 0.440| 0.224| 7.94 | 0.077| 0.037| 54  |
|           | min-max| 12.33 | 0.205 | 0.089 | 0.038 | 0.463 | 0.232 | 7.93 | 0.076| 0.036| 56-58|
| 4 (2)     | mean  | 12.00-12.65 | 0.201-0.209 | 0.087-0.091 | 0.037-0.043 | 0.457-0.515 | 0.228-0.250 | 10.20 | 0.071| 0.035| 66-72|
|           | min-max| 16.18 | 0.224 | 0.093 | 0.044 | 0.518 | 0.222 | 10.28 | 0.073| 0.034| 66-72|
| 6 (2)     | mean  | 10.93 | 0.181| 0.084| 0.038| 0.438| 0.200| 7.19 | 0.073| 0.035| 49-52|
|           | min-max| 10.00-11.75 | 0.170-0.189 | 0.085-0.093 | 0.037-0.042 | 0.421-0.430 | 0.190-0.210 | 6.63 | 0.071| 0.034| 49-52|

Designations as in Tables 1, 2 and 11.
Table 13. Morphometry of Oswaladocruzia filiformis males from Pelophylax esculenta, Bufotes viridis and Triturus vulgaris

| Site    | Value | LB     | WB     | LV     | WV     | LO     | LT     | LS     | NC    |
|---------|-------|--------|--------|--------|--------|--------|--------|--------|-------|
| 8       | mean  | 8.00   | 0.155  | 0.083  | 0.040  | 0.458  | 0.127  | 0.220  | 36-45 |
| (7)     |       |        |        |        |        |        |        |        |       |
| 6       | mean  | 7.92   | 0.149  | 0.079  | 0.037  | 0.431  | 0.134  | 0.215  | 33-40 |
|         | min-max | 6.70-9.25 | 0.130-0.181 | 0.075-0.083 | 0.035-0.039 | 0.378-0.488 | 0.126-0.146 | 0.192-0.236 |       |
| SD     | 0.84  | 0.01   | 0.003  | 0.002  | 0.04   | 0.01   | 0.01   |        |       |
| CV     | 10.60 | 6.71   | 3.56   | 4.74   | 8.82   | 7.46   | 4.65   |        |       |
| 9       | mean  | 6.90   | 0.119  | 0.074  | 0.028  | 0.425  | 0.113  | 0.185  | 36-44 |
| (4)     |       |        |        |        |        |        |        |        |       |
| 13      | mean  | 7.50   | 0.126  | 0.079  | 0.035  | 0.402  | 0.114  | 0.208  | 44    |
| (1)     |       |        |        |        |        |        |        |        |       |

Designations as in tables 1 and 2.

Species: 8 – Pelophylax esculenta (Samarskaya Luka), 6 – Bufotes viridis (Togliatti), 9 – Triturus vulgaris (Mekhzavod), 13 – Triturus vulgaris (Verkhnyaya Kvazhva).

Table 14. Morphometry of Oswaladocruzia filiformis females from Pelophylax esculenta, Bufotes viridis, Triturus vulgaris and Bombina bombina

| Site    | Value | LB     | WB     | LV     | WV     | LO     | LT     | AV     | LE     | WE     | NC    |
|---------|-------|--------|--------|--------|--------|--------|--------|--------|--------|--------|-------|
| 8       | mean  | 16.50  | 0.236  | 0.094  | 0.051  | 0.508  | 0.227  | 10.33  | 0.083  | 0.045  | 61    |
| (1)     |       |        |        |        |        |        |        |        |        |        |       |
| 6       | mean  | 16.88  | 0.248  | 0.096  | 0.049  | 0.573  | 0.287  | 11.18  | 0.084  | 0.044  | 49-52 |
| (2)     |       |        |        |        |        |        |        |        |        |        |       |
| 9       | mean  | 16.55  | 0.240- 0.094- 0.047- 0.559- 0.276- 11.06- 0.079- 0.039- |        |        |        |        |        |        |        |        |       |
| (3)     |       |        |        |        |        |        |        |        |        |        |       |
| 10      | mean  | 12.75  | 0.181  | 0.079  | 0.031  | 0.427  | 0.193  | 6.30   | 0.070  | 0.037  |        |
| (1)     |       |        |        |        |        |        |        |        |        |        |       |

Designations as in tables 1 and 2.

Species: 8 – Pelophylax esculenta (Samarskaya Luka), 6 – Bufotes viridis (Togliatti), 9 – Triturus vulgaris (Mekhzavod), 10 – Bombina bombina (Oktyabrskiy).

Comparison of the body size of O. filiformis from amphibians in different regions of European Russia revealed that the largest nematode females and males were found in Bufo bufo from the National Park “Smolny”, the smallest nematode females were found in Triturus vulgaris from Mekhzavod, and males in P. lessonae from the Prirsksy Nature Reserve (tables 3, 4, 11, 14). The coefficient of variation (CV) of body length varied from 6.44 to 17.37%, CV of body width – from 4.70 to 18.63% in Oswaladocruzia males; CV of body length 4.48 to 24.62% and body width 4.33 to 11.81% in nematode females. Comparison of the mean body sizes of nematodes of both sexes from different amphibian species, various regions studied according to the Kruskal-Wallis test revealed significant differences in both males (body length, H = 91.8; body width H = 181.8) and females (body length H = 86.1; body width H = 65.2) at p < 0.001.

One of the most variable characters was the shape of nematode cephalic vesicle. It could be whole or consist of two parts, a wider anterior part and a narrow posterior part. A posterior part could be smooth or with transverse folds (figure 2). Vesicle shape is variable even in nematodes from one amphibian individual.

The mean values of the length and width of the nematode cephalic vesicle from different amphibian species varied from 0.073 to 0.102 mm (length) and from 0.031 to 0.044 mm (width) in males; in females – from 0.078 to 0.109 mm (length) and from 0.031 to 0.055 mm (width) (tables 1–14). The CV values of the length and width of the head vesicle varied in males from 2.47 to 10.42% (length) and from 4.74 to 9.30% (width); in females from 2.35 to 11.90% and from 2.86 to 12.82%, respectively. Statistical analysis using the Kruskal-Wallis test revealed significant differences in the cephalic vesicle size of O. filiformis of both sexes from different amphibian species and regions, both
in male nematodes (length, H = 144.7; width H = 189.5) and in females (length, H = 137.0; width, H = 165.5) at p < 0.001.

Figure 2. Variability of cephalic vesicle of *O. filiformis*: a – male from *Pelophylax lessonae*; b – male from *Pelophylax esculentus*, c – female from *Pelophylax esculentus*; d – female from *Rana arvalis*, e – female from *Bufoes viridis*, f – male from *Bufo viridis*, g – female from *Pelobates vespertinus*, h – female from *Bombina bombina*, i – female from *Lissotriton vulgaris*. Scale bars: 0.1 mm.

The mean values of oesophagus length varied in nematodes of both sexes from different hosts and regions studied. Thus, in nematode males, the length of oesophagus varied from 0.388 to 0.527 mm, in females – from 0.427 to 0.586 mm (tables 1–14). The longest oesophagus was observed in the largest nematodes in *Bufo bufo* from the National Park “Smolny”; the shortest oesophagus was observed in nematode males in *Pelophylax ridibundus* from the Samarskaya Luka, in females – in *Rana temporaria* from the Mordovia Nature Reserve (tables 3, 4, 5, 10). The length of oesophagus is more variable in *O. filiformis* males (CV = 2.32–13.76%), less variable in nematode females (3.83–6.38%) (tables 1–14). Comparison of nematodes in the length of the oesophagus from amphibians showed differences in males (H = 99.7) and in females (H = 101.3) at p < 0.001.

The tail length varied in nematode males from 0.116 to 0.134 mm, in females from 0.200 to 0.312 mm (tables 1–14). The largest tail length was observed in large *O. filiformis* males in *Bufo bufo* from the National Park “Smolny” and females in *P. ridibundus* from the Samarskaya Luka. The shortest tails were observed in nematode males in *L. vulgaris* from Mekhzavod and in females in *Bufo bufo* from the Mordovia Nature Reserve (tables 3, 4, 6, 13). The tail length is more variable in nematode females (CV = 4.07–16.03%), less variable in males (3.33–8.00%). Significant differences were revealed in the tail length in males (H = 69.9) and females (133.4) of nematodes according to the Kruskal-Wallis test at p < 0.001.

The spicules of nematode males did not differ in structure and shape in amphibians of different species and regions and agreed with the descriptions of *O. filiformis* given earlier [19, 20]. Differences were noted only in the size of the spicules (figure 3), the length of which varied from 0.185 to 0.234 mm (tables 1, 3, 5, 7, 9, 11, 13). The longest spicules were observed in the nematode male in *Pelophylax ridibundus* from the Republic of Kalmykia, while the shortest spicules – in *Pelophylax lessonae* from Togliatti, *Rana temporaria* and *Bufo bufo* from the Mordovia Nature Reserve (tables 3, 5, 9, 11). We noted low values CV of the spicule length (1.73–5.05%). This indicates a low level of spicule length variability in nematodes from the same host species, different hosts and regions studied. Comparison of the spicule length in nematode males from different amphibian species and regions showed significant differences (H = 179.5, p < 0.001).
The structure and shape of the male caudal bursa remained relatively constant in comparison with other morphological features of *O. filiformis* (figure 4). Caudal bursa of males was symmetrical, three-lobed, and belongs to type II according to Durette-Desset and Chabaud [22]. The shape and structure of the dorsal rib formed by 9th and 10th rays of caudal bursa, are variable both in nematodes from the same host species, and from different hosts and regions studied. All nematode males in our research had an extra branch on the 10th ray of variable shape and size (figure 5). We have not observed significant variability in the structure of the reproductive system of *O. filiformis* females.
Figure 5. Variability of dorsal ray of *O. filiformis* caudal bursa; *a* – male from *Pelophylax lessonae*, *b, c, d, e* – males from *Rana arvalis*, *f, g* – males from *Rana temporaria*, *i* – male from *Bufoes viridis*, *j, k, l, m, n, o* – males from *Pelobatus vespertinus*. Scale bars: 0.05 mm

The distance from the anterior body end to the vulva in nematode females varied widely (7.19–12.98 mm) and depended on the female body length (tables 2, 4, 6, 8, 10, 12, 14). The lowest parameter was observed in females in *L. vulgaris* from Samara city, which body length was the smallest. The greatest distance to the vulva was noted in the largest female nematodes in *Bufo bufo* from the National Park “Smolny” (table 4). A high level of variability of distance from the anterior end to the vulva were recorded (CV = 4.88–23.42%). The lowest CV values were observed in nematodes in *Pelophylax ridibundus* from Republic of Kalmykia, and the highest CV values of the distance to the vulva were recorded in nematodes in *P. ridibundus* from the Samarskaya Luka, as for the body length of *O. filiformis* females (table 6). Differences in this character were found in nematode females (*H = 74.5, p < 0.001*).

Egg sizes in nematode females varied from 0.070 to 0.087 mm (length) and from 0.034 to 0.048 mm (width) (tables 2, 4, 6, 8, 10, 12, 14). The largest eggs were recorded in the largest females in *Bufo bufo* from the National Park “Smolny” and in *Pelophylax ridibundus* from the Samarskaya Luka. The smallest eggs were found in *O. filiformis* females in *Rana arvalis* from Starvy Buyan (tables 2, 4, 6). We observed a relatively low level of variability in egg size – 3.61–11.63% (length) and 4.55–9.52% (width). Differences in egg sizes in nematode females from different amphibian species and regions are significant (egg length *H* = 129.1; width *H* = 182.6, *p < 0.001*).

In our study, the shape and development degree of the lateral alae in nematodes varied from one host species, various hosts and region studied (figure 6).

We noted the variability of the number of crests in the mid-body level. The drawings of transverse sections at mid-body of *O. filiformis* are presented in figure 7. The number of crests is variable in nematodes of the same sex, even from a single host individual. In males the number of crests is always less than in females and ranges from 33 to 58 (tables 1–14). The number of crests in the mid-body level ranges from 39 to 78 in *O. filiformis* females (tables 1–14). The smallest number of crests in the mid-body was observed in nematode males in *Bufo bufo* from the Mordovia Nature Reserve and Pervomaysk, the largest – in *Pelobates vespertinus* from the Mordovia Nature Reserve (tables 3, 7). The smallest number of crests in females was found in *Pelophylax ridibundus* from Samarskaya Luka, the largest – in *P. ridibundus* from the Republic of Kalmykia (table 6).
Figure 6. Variability of lateral alae of *O. filiformis* at the middle of oesophagus; *a*, *b*, *c* – females from *Pelophylax lessonae*; *d* – female from *Pelophylax esculentus*; *e* – male from *Rana arvalis*; *f* – male from *Bufoes viridis*, *g*, *h* – males from *Pelobates vespertinus*. Scale bars: 0.05 mm

Differences in the variability range of morphological characteristics of *O. filiformis* males and females in various amphibian species and amphibians from different regions were revealed. Thus, the most variable morphological features are both in nematode males and females in *Pelophylax ridibundus* from the Samarskaya Luka, the least variable are in *O. filiformis* males in *Bufo bufo* from the Mordovia Nature Reserve and in nematode females in *Pelophylax ridibundus* from the Republic of Kalmykia (tables 3, 6). Comparison of the mean values of morphometric characters of *O. filiformis* in different amphibian species and regions according to the Kruskal-Wallis test revealed significant differences in seven features in nematode males and nine characters in females (*p* < 0.001).

We analyzed the morphometric variability of male and female nematodes from amphibians of the same species from different regions of Russia using the examples of *Rana arvalis*, *Bufo bufo*, and *Pelophylax ridibundus*. Comparative analysis of the mean values of morphological features in nematode males and females in *Rana arvalis* from seven regions studied according to the Kruskal-Wallis test revealed significant differences for all the considered characteristics (*p* < 0.001). The greatest range of variability of the considered characteristics of *O. filiformis* from *Rana arvalis* from different regions in nematode males was noted for the body length (7.8–15.7%) and width (5.0–12.8%), the smallest – for the spicule length (2.2–4.7%) and the width of the cephalic vesicle (5.1–6.3%) (tables 1, 2). The tail length (4.2–14.2%), the distance from the anterior body end to the vulva (7.7–17.3%) and the length of the cephalic vesicle (2.4–11.9%) are the most variable in nematode females; the least variable in females is the length of the oesophagus (3.9–5.8%) (tables 1, 2).

Comparison of the mean values of morphological characteristics of *O. filiformis* males and females in *Bufo bufo* from three regions revealed significant differences in all the considered characteristics (*p* < 0.05), except for differences in body width in nematode females (*p* > 0.05). Nematode males in *Bufo bufo* from different regions have the most variable length of the cephalic vesicle (2.5–10.4%); the least variable feature is the spicule length (4.5–5.1%) (tables 3, 4). Nematode females have the most variable body length (5.2–19.5%), the least variable the length of the oesophagus (3.4–4.0%) and egg width (7.9–8.7%) (tables 3, 4).
Figure 7. Transverse sections of *O. filiformis* at mid-body level: 
(a) – male from *Pelophylax lessonae*, 39 crests; 
(b) – female from *Pelophylax lessonae*, 58 crests; 
(c) – male from *Pelophylax esculentus*, 36 crests; 
(d) – female from *Pelophylax esculentus*, 62 crests; 
e – male from *Rana arvalis*, 46 crests; 
f – female from *Rana arvalis*, 72 crests; 
g – male from *Rana temporaria*, 38 crests; 
h – female from *Rana temporaria*, 41 crests; 
i – male from *Bufo* *tes virid*is, 37 crests; 
j – female from *Bufo* *tes virid*is, 49 crests; 
k – male from *Pelobates vespertinus*, 56 crests; 
l – female from *Pelobates vespertinus*, 69 crests; 
m – male from *Lissotriton vulgaris*, 40 crests; 
n – female from *Lissotriton vulgaris*, 59 crests; 
o – female from *Bombina bombina*, 66 crests. Scale bars: 0.1 mm.

Differences between the mean values of the morphological characters studied in nematodes in *Pelophylax ridibundus* from the three regions according to the Kruskal-Wallis test are significant in most cases (*p* < 0.05). Differences in the body width and tail length of nematode males from different regions are not reliable; in females – in the length of the oesophagus (*p* > 0.05). The greatest range of variability of nematode characters in *P. ridibundus* from different regions was noted for body length (8.3–17.4%), the smallest – for tail length (7.5–7.6%) in nematode males (tables 5, 6). The body length (4.5–24.6%) and the distance from the anterior end of the body to the vulva (4.9–23.4%) are the most variable, and the length of the cephalic vesicle is the least variable (4.3–5.3%) in nematode females (tables 5, 6).

4. Discussion
The analysis of *O. filiformis* variability in ten amphibian species from fifteen regions showed significant changes in the size and morphology of nematodes both from one host species and from different hosts. Among all eleven characters of nematode males and females, none of them had CV greater than 25%, which may indicate the homogeneity of *O. filiformis* infrapopulations in different
amphibian species and regions. The values of CV indicate a relatively low individual variability of morphological characteristics of nematodes in amphibians from the same host species, as well as from different host species and regions of European Russia. The degree of variability of individual nematode characters varies between host species and amphibians from different regions.

We noted a broad variability in four morphometric characters (female body length, male body width, distance from the anterior end to the vulva in females, and tail length in females). The smallest feature subject to variability in our studies is the length of the male spicules. The structure and shape of the spicules and caudal bursa of males were relatively constant in comparison with other morphological features of the nematode. The most variable morphological characters in shape were the cephalic vesicle in nematodes of both sexes and the dorsal rib of the male bursa.

We noted earlier and in this study that the number of crests varies not only in *O. filiformis* males and females but also in nematodes of the same sex from one host species and even from one host individual [19, 20]. We have noted a tendency for the number of crests in the mid-body level to depend on the size (age) of nematodes. In smaller (young) males and females, the number of crests in the middle of the body was usually less than in large (adult) parasites. Differences in the number of crests in *Oswaldocruzia* males and females were noted earlier by several authors [25–30].

General patterns in the change of certain morphological features of nematodes from different hosts and regions of Russia were not revealed. In our opinion, probably due to the influence of a number of biotic (host species, host population structure, the number of nematodes in the host intestine, the impact of other parasites, etc.) and abiotic (seasonality, environment temperature and humidity, etc.) factors on the development of nematodes in the host. These factors determine the infestation degree of the host, the morphological features and the nature of the nematode variability. Intrapopulational variability of nematodes from vertebrates and, amphibians, in particular, was noted by us and other authors (12–14, 16, 31). They showed that the body size of nematodes varied under the influence of such factors as sex, age, phenotype and host species, number of parasites in the host and seasonal changes.

The interspecific variability of *O. filiformis* is determined by differences in the biology and physiology of different amphibian hosts, as well as their size. The largest nematodes in our study were recorded in the individuals of *Bufo bufo*, the greatest amphibians in our study (tables 3, 4). The influence of the host size, i.e., the spatial niche, on the body size of *O. filiformis* nematodes is shown in Tarasovskaya and Zhumadilov [18]. On the other hand, the larger size of the nematodes in *Bufo bufo* may be due, in our opinion, to the more favorable conditions for the development of nematodes that develop in this amphibian species. This fact suggests that *Bufo bufo* is an older, possibly primary host of *O. filiformis*.

Differences in the body size of nematodes and their morphology in various regions of Russia are related with different environmental conditions of amphibian habitats, where abiotic factors mainly influence. The impact of host species and ecological conditions in different localities on the variability of morphometric features in amphibian nematodes is shown by several authors [15, 18, 32, 33].

5. Conclusion

The results of our study showed a broad morphological variability of *O. filiformis* of both sexes from amphibians in different regions of European Russia. Significant differences were observed in the body size and a number nematode organs. Variability was noted in the shape and size of the cephalic vesicle and lateral alae, in the number at the mid-body level, in the shape and structure of 9th and 10th rays of the male caudal bursa. The type of caudal bursa and the structure and shape of spicules were identical in all *O. filiformis* males studied. Likewise, we have not found variability in the structure of the reproductive system in *O. filiformis* females.

The degree of variability of different characters of *O. filiformis* is not identical and is due to the influence of a combination of many biotic and abiotic factors on nematodes in the host. The marked significant differences in morphometric characteristics of nematodes from amphibians of the same species from different regions studied are related with the phenotypic plasticity of the species.
Differences in the morphology of nematodes from various amphibian species are caused by the host-induced morphological variability of the parasite. Variation in the size of nematodes and their morphology in different regions of Russia studied may be caused by changes of ecological conditions in amphibian habitats. The broad morphological variability of the nematode *O. filiformis* increases the adaptive capabilities of the helminth and allows it to parasitize a wide range of hosts.

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**References**

[1] Roytman V A and Kazakov B 1977 Some aspects of morphological variability of helminths *Proceeding of the Helminthological Laboratory of Academy of Sciences of the USSR* **27** 110–128

[2] Anikieva L V 1992 Population morphology of *Proteocephalus torulosus* (Cestoda: Proteocephalidea) from cyprinids of the Karelian lakes *Ecological parasitology* **1** (2) 135–149

[3] Anikieva L V 2004 Variability and phenotypic structure of *Proteocephalus torulosus* (Cestoda: Proteocephalidea) – a parasite of cyprinid fishes *Parazitologiya* **38** (2) 171–179

[4] Kirillov A A and Kirillova N Yu 2010 Morphological variability of *Plagiorchis elegans* (Rudolphi, 1802) (Trematoda: Plagiorchiidae) *Proceedings of Samara Scientific Centre of RAS* **12** (1) 138–141

[5] Svitin R 2016 Nematodes of the Genus Oswaldocruzia Travassos, 1917 of Western Palaearctic *The author’s abstract dis…. Cand. Sc.* (Kyiv: Institute of Zoology)

[6] Svitin R and Gorobchishin V 2015 Postcyclic parasitism of the nematodes of genus Oswaldocruzia Travassos, 1917 in some reptilian species on the territory of Ukraine *Proceedings of the Kiev National University* **1** (18) 68–70

[7] Kirillov A A and Kirillova N Yu 2018 Overview of helminths in reptiles from the National Park “Samarskaya Luka” (Russia) *Nature Conservation Research* **3** (1) 73–82

[8] Hartwich G 1972 Uber *Rhabdias bufonis* (Schrank, 1788) und die Abtrennung von *Rhabdias dossei* nov. spec. (Nematoda: Rhabdiasidae) *Mitteilungen aus dem Zoologischen Museum Berlin* **48** (2) 401–404

[9] Procopic J and Krivanek K 1974 Trematodes of the genus *Haematoloechus* Looss, and their variability *Helminthologia* **15** 779–802

[10] Grabda-Kazubska B and Combes C 1981 Morphological variability of *Haplolometra cylindracea* (Zeder, 1800) (Trematoda, Plagiorchiidae) in populational and geographic aspects *Acta Parasitologica Polonica* **28** 39–65

[11] Tarasovskaya N E 2011 Morphometric analysis of trematodes *Pleurogenes intermedius* from the moor frog in the aspect of the influence of intraspecific interactions on the helminth sizes *Experimental biology* **4** (50) 103–105

[12] Tarasovskaya N E 2012 To the studying on the interspecific interactions of lung nematode *Rhabdias bufonis* from the moor frog (*Rana arvalis*) *Experimental biology* **3** (55) 90–97

[13] Tarasovskaya N E and Pashkevich V I 2011 To the helminthofauna of *Rana arvalis* in Akmola region *Biological sciences of Kazakhstan* **1** 87–94

[14] Kirillov A A and Kirillova N Yu 2015 Variability and determining factors of the body size structure of the infrapopulation of *Cosmocerca ornata* (Nematoda: Cosmocercidae) in marsh frogs *Parazitologiya* **49** (2) 104–118

[15] Gonzalez C E, Gomez V I and Hamann M I 2019 Morphological variation of Aplectana hylambatis (Nematoda: Cosmocercidae) from different anuran hosts and localities in
Argentine Annals of the Brazilian Academy of Sciences 91 (3) e20171028
[16] Tarasovskaya N E 2009 Intraspécific interactions of the nematode Oswaldocruzia filiformis from Rana arvalis and their influence on the helminth body sizes Gylm zhene bilim 3 (16) 97–104
[17] Aralkhanova A E 2010 Features of morphology of nematodes Oswaldocruzia filiformis from the East Kazakhstan area Hygiene, epidemiology and immunology 1 (43) 113–115
[18] Tarasovskaya N E and Zhumadilov B Z 2019 Morphological peculiarities of nematodes Oswaldocruzia filiformis quantity in moor frog in northern regions of Kazakhstan as the indicator of herbal cover Experimental biology 3 (80) 148–167
[19] Kirillova N Yu, Kirillov A A, Shchenkov S V and Chikhlyaev I V 2020 Oswaldocruzia filiformis sensu lato (Nematoda: Molineidae) from amphibians and reptiles in European Russia: morphological and molecular data Nature Conservation Research 5 (2) 41–56
[20] Kirillova N Yu and Kirillov A A 2020 Morphological variability of Oswaldocruzia filiformis (Nematoda: Molineidae) in reptiles inhabiting the protected areas of the Republic of Mordovia (Russia) IOP Conference Series: Earth and Environmental Science 607 012007
[21] Durette-Desset M C 1985 Trichostrongyloid nematodes and their vertebrate hosts: reconstruction of the phylogeny of a parasitic group Advances in Parasitology 24 239–306
[22] Durette-Desset M C and Chabaud A G 1981 Nouvel essai de classification des Nématodes Trichostrongyloidea Annales De Parasitologie Humaine et Comparée 56 297–312
[23] Hammer O, Harper D A T and Ryan P D 2001 PAST: paleontological statistics software package for education and data analysis. Palaeontologia Electronica 4 (1) 9 Version 2.16. Available from: http://palaeo-electronica.org/2001_1/past/issue1_01.htm
[24] Rokitskii P F 1961 Essentials of variation statistics for biologists (Minsk: Belarus State University Press)
[25] Ben Slimane B, Durette-Desset M C and Chabaud A G 1993 Oswaldocruzia (Trichostrongyloidea) Parasites d’amphibiens des collections du Muséum de Paris Annales De Parasitologie Humaine et Comparée 2 88–100
[26] Ben Slimane B and Durette-Desset M C 1996 New Oswaldocruzia (Nematoda, Trichostrongylina, Molineoidae) parasites of amphibians from French Guyana and Ecuador Miscellânia Zoológica 19 55–66
[27] Ben Slimane B, Chabaud A G and Durette-Desset M C 1996a Les nématodes Trichostrongylina parasites d’amphibiens et de reptiles: problèmes taxonomiques, phylétiques et biogéographiques Systematic Parasitology 35 179–206
[28] Ben Slimane B, Guerrero R and Durette-Desset M C 1996b Oswaldocruzia venezuelensis sp. n. (Nematoda, Trichostrongylina, Molineoidae), a parasite of Bufo marinus from Venezuela Folia Parasitologica 43 297–300
[29] Durette-Desset M C, Alves dos Anjos L and Vrcibradic D 2006 Three new species of the genus Oswaldocruzia Travassos, 1917 (Nematoda: Trichostrongylina, Molineoidae) parasites of Enyalius spp. (Iguanidae) from Brazil Parasite 13 115–125
[30] Guerrero R 2013 Two new species of Oswaldocruzia (Nematoda: Trichostrongylina: Molineoidae) parasites of the cane toad Rhinella marina (Amphibia: Anura) from Peru Acta Parasitologica 58 (1) 30–36
[31] Vakker V G 2018 The parasitic system of the nematode Oswaldocruzia filiformis (Strongylida: Molineidae) in Kazakhstan Principles of ecology 4 44–64
[32] Roden H R and Bolek M G 2011 Distribution and reproductive strategies of Gyrinicol a batrachiensis (Oxyuroida: Pharyngodonidae) in larvae of eight species of amphibians from Nebraska Journal of Parasitology 97 629–635
[33] Vhora M S and Bolek M G 2013 New host and distribution records for Aplectana hamatospicula (Ascaridida: Cosmocercidae) in Gastrophyne olivacea (Anura: Microhylidae) from the Great Plains U.S.A. Journal of Parasitology 99 417–420