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OSWALDOCRUZIA DUBOISI (NEMATODA, MOLINEIDAE): MORPHOLOGY, HOSTS AND DISTRIBUTION IN UKRAINE

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***Oswaldocruzia duboisi* (Nematoda, Molineidae): Morphology, Hosts and Distribution in Ukraine.** Svitin R. S., Kuzmin Y. I. — *Oswaldocruzia duboisi* Ben Slimane, Durette-Desset et Chabaud, 1993 previously known from France and Bulgaria is reported from Ukraine for the first time. The species was found in the material from 8 amphibian host species, of which *Lissotriton montadoni*, *Triturus cristatus*, *Mesotriton alpestris*, *Pelophylax ridibunda*, *P. lessonae*, and *Hyla arborea* are new host records. Newts (Salamandridae) and green frogs (*Pelophylax*) are considered to be typical hosts for *O. duboisi*. Illustrated morphological redescription of *O. duboisi* based on 141 specimens from various hosts is presented.

Key words: *Oswaldocruzia*, *O. duboisi*, Amphibia, Ukraine, synlophe, cervical alae.

***Oswaldocruzia duboisi* (Nematoda, Molineidae): морфология, хозяева и распространение в Украине.** Свитин Р. С., Кузьмин Ю. И. — Вид *Oswaldocruzia duboisi* Ben Slimane, Durette-Desset et Chabaud, 1993, ранее известный из Франции и Болгарии, впервые обнаружен в Украине. Вид найден в материале от 8 видов амфибий, из которых *Lissotriton montadoni*, *Triturus cristatus*, *Mesotriton alpestris*, *Pelophylax ridibunda*, *P. lessonae* и *Hyla arborea* являются новыми хозяевами *O. duboisi*. Предполагается, что основными хозяевами *O. duboisi* являются тритоны (Salamandridae) и зеленые лягушки (род *Pelophylax*). Представлено иллюстрированное описание *O. duboisi* по 141 изученному экземпляру от разных видов хозяев.

Ключевые слова: *Oswaldocruzia*, *O. duboisi*, Amphibia, Украина, синлоф, латеральные крылья.

Introduction

Nematodes of the genus *Oswaldocruzia* Travassos, 1917 are worldwide distributed intestine parasites of amphibians and reptiles. Presently, more than 80 species are assigned to the genus (Schotthoefer et al., 2009).

In Western Palaearctic, most species of *Oswaldocruzia* are morphologically similar and were often identified as *Oswaldocruzia filiformis* Goeze, 1782 parasitizing amphibians (*Rana temporaria*, *R. arvalis*, *R. ridibunda*, *R. lessonae*, *R. esculenta*, *Bufo bufo*, *B. viridis*, *Hyla arborea*, *Bombina bombina*, *B. variegata*, *Pelobates fuscus*, *Salamandra salamandra*, *Triturus vulgaris*, *T. cristatus*), reptiles of the genera *Anguis*, *Lacerta*, *Natrix*, *Ophisaurus*, *Vipera*, and even fish *Lotta lotta* (Lal, 1944; Ryzhikov et al., 1980; Baker, 1981; Anderson, 2000; Galli et al., 2001; Odnokurtsev and Sedalishchev, 2008; Novokhatskaya, 2008).

Five European species of the genus were described and differentiated using the structure of synlophe and spicules: *O. duboisi* Ben Slimane, Durette-Desset et Chabaud, 1993 from *Rana* sp., *R. dalmatica*, *Triturus vulgaris* in France; *O. guyetanti* Ben Slimane, Durette-Desset et Chabaud, 1993 from *Rana* sp. and *R. temporaria* in France; *O. hispanica* Ben Slimane, Lluch et Durette-Desset, 1995 from *R. temporaria* in Spain; *O. galeanae* Ben Slimane, Lluch et Durette-Desset, 1995 from *Bufo bufo* in Spain; *O. bialata* Molin, 1860 from *R. temporaria* in Italy and from *Bufo* sp. in Bulgaria (Ben Slimane et al., 1993, 1995).

Structure of the synlophe is unknown in other European *Oswaldocruzia* spp.: *O. ukrainae* Ivanitzky, 1940; *O. ivanizkii* Sudarikov, 1951, *O. fulleborni* Iwanitzky, 1940, *O. problematica* Ivanitsky, 1940, *O. molge-*

ta Lewis, 1928, though they were included as valid species in the list of Palaearctic species of the genus *Oswaldocruzia* by Ben Slimane et al. (1995).

Of 10 species of *Oswaldocruzia* found in Western Palaearctic, 5 were previously reported from Ukraine: *O. filiformis*, *O. ukraineae*, *O. ivanizkii*, *O. fulleborni*, and *O. problematica* (Skrjabin et al., 1954; Ryzhikov et al., 1980). At least some species described in Western Europe after 1980 presumably occur in Ukraine as well, since their hosts are widespread in Western Palaearctic.

During the investigation of the helminthological material stored in the collection of the Department of Parasitology of the Institute of Zoology, NAS of Ukraine we found several *Oswaldocruzia* species from amphibian hosts, including *O. duboisi* from various newts and frogs from Ukraine. This species was identified based on characteristic synophe structure. It was first found in France and described based on several specimens; the host range of the species was not exactly identified (*Rana* sp., *R. dalmatina* and *Triturus vulgaris*) (Ben Slimane et al., 1993). Thereafter, the species was reported only once as parasite of *Rana esculenta* in Bulgaria (Durette-Desset et al., 1993). Our studies of more than 100 specimens of *O. duboisi* from various host species added some information to the morphology, distribution and specificity of the species. This information is presented herein.

Material and methods

Material from the collection of the Department of Parasitology of the Institute of Zoology, NAS of Ukraine was investigated. Totally, 141 specimens of *O. duboisi* were studied, of which 43 males and 41 females were measured: 7 males and 3 females from *P. ridibunda*, 4 males and 8 females from *P. lessonae*, 3 males and 2 females from *P. esculenta*, 4 males and 12 females from *M. alpestris*, 10 males and 7 females from *L. montadoni*, 13 males and 11 females from *L. vulgaris*, 2 males from *T. cristatus*.

All specimens were fixed and stored in 4% solution of formalin in saline. Prior to examination, nematodes were cleared in phenol-glycerine solution (2 : 1 ratio). After the studies, all nematodes were placed in 70% alcohol for further storage.

Morphology of nematodes was studied under the light microscope Zeiss Axio Lab. All measurements in the text are given in micrometers unless otherwise indicated. Figures were made using the drawing tube RA-7. Photomicrographs were made using Zeiss Axio Imager M1 system.

The study of the synophe is based on the method of Durette-Desset (1985). The nomenclature of the synophe in the oesophageal region follows that of Ben-Slimane et al. (1993). The nomenclature of the caudal bursa follows Durette-Desset and Chabaud (1981). Nomenclature of amphibians follows Pisanets (2007).

Results

Oswaldocruzia duboisi Ben-Slimane, Durette-Desset et Chabaud, 1993

Hosts. Salamandridae: *Lissotriton vulgaris*, *L. montadoni*, *Triturus cristatus*, *Mesotriton alpestris*; Ranidae: *Pelophylax ridibunda*, *P. lessonae*, *P. kl. esculenta*; Hylidae: *Hyla arborea*.

Site: intestine, stomach.

Distribution in Ukraine: Ivano-Frankivska oblast (8 localities), Kyivska oblast (2 localities), and Crimea (2 localities) (fig. 1).

Description. General. In both sexes, body thin, elongated, with maximum width near midlength. Anterior end rounded. Oral opening triangular; 4 externo-labial papillae, 4 cephalic papillae and 2 amphids present (fig. 2, 4). Body cuticle thin. On anterior end, cuticle forming cephalic vesicle. Vesicle undivided (fig. 2, 1) or consisting of two parts: anterior part rounded and smooth; posterior part less inflated, smooth or with transverse folds (fig. 2, 2, 3). Only divided cephalic vesicle was observed in specimens from *L. vulgaris* (tables 3, 4).

Oesophagus club-shaped, cylindrical in anterior half, then widening posteriorly, with oval posterior bulb (fig. 2, 1). Position of excretory pore variable, but not beyond level of posterior third of oesophagus. Two excretory glands dissimilar in size, both glands somewhat longer than oesophagus. Nerve ring encircling oesophagus near its midlength, often closer to its anterior third. Minute deirids situated at level of oesophageal-intestinal junction.

Synophe symmetrical. Lateral cervical alae present, each beginning slightly posterior to cephalic vesicle and transforming into one simple crest posterior to level of oesophageal-intestinal junction. On transverse sections (fig. 2, 5, 6; 3, 3, 4), alae tri-



Fig. 1. Finds of *O. duboisi* in Ukraine.

Рис. 1. Находки *O. duboisi* на территории Украины.

angular, with rounded top, longer dorsal side and shorter, often concave ventral side. Struts in alae present, but usually poorly visible. Two crests present on dorsal side of each ala closer to its base. Crest situated at base of ala more prominent, other one sometimes indistinct. Maximum height of cervical alae at level of oesophageal-intestinal junction. Ventral crests always present on sections at mid-oesophagus level. Number of crests in oesophageal region varying depending on distance from anterior end: from 22 to 33 crests including cervical alae. Seventy-one equal crests present at mid-body level (fig. 2, 7).

Males (fig. 2, 10–12; 3, 1, 2; tables 1, 3). Cervical alae about 530 long, 10 height, beginning at about 180 from anterior end of body. Testis extending along entire trophicogenital part of body. Caudal bursa (fig. 2, 12; 3, 2) of type II. Rays 2 and 3 joined along their whole length, ray 4 joined to ray 5 in its proximal half, rays 5 and 6 joined along their whole length, rays 6 and 8 jointed in region of midlength. Dorsal ray (fig. 2, 11) bifurcated into two rays 10 posterior to base of rays 9.

Spicules (fig. 2, 10) equal, with three branches: distally sharpened blade, fork divided in two branches at level of posterior third, and shoe with thin process. All branches of same length and without extra branches. Spicule length varying significantly in sample studied (table 1).

We did not observe obvious correlation between the length of spicules and the body size, or between the length of spicules and host species. However, we found 5 males from *P. ridibunda* in Crimea possessing markedly larger spicules (225–250 long) than other studied males (spicules 155–210 long).

Females (fig. 2, 1, 8, 9; tables 2, 4). Larger than males. Posterior end sharpened. Cervical alae about 648 long, 25 height, beginning at about 197 from anterior end of body.

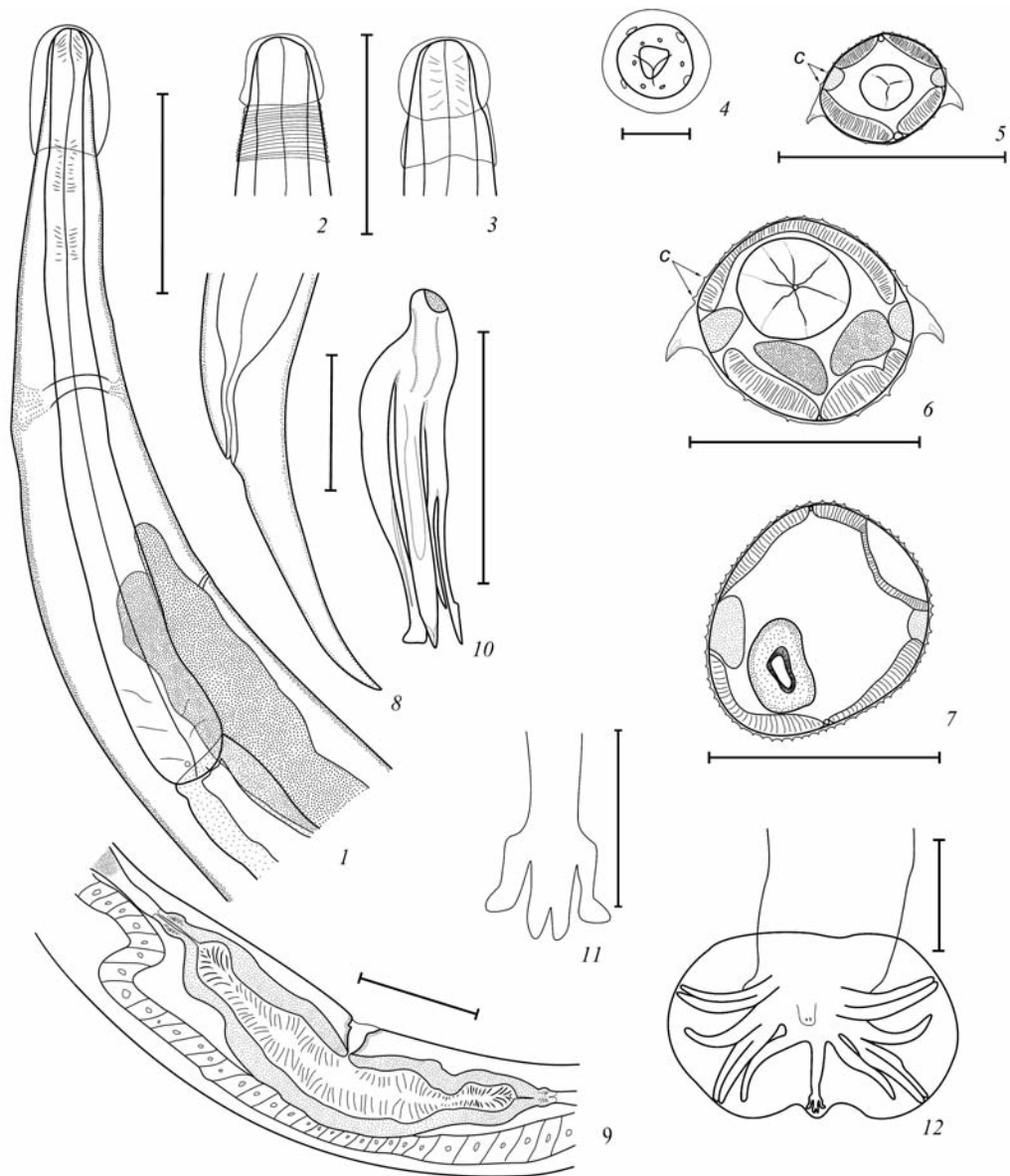


Fig. 2. *Oswaldocruzia duboisi*: 1 — anterior part of the body, female from *L. montadoni*, right lateral view (cephalic vesicle of type I); 2, 3 — variations of cephalic vesicle shape (types II and III), males from *L. vulgaris* and *L. montadoni*, respectively; 4 — anterior end, apical view, male from *P. lessonae*; 5 — transverse section at mid-oesophagus level, male from *L. vulgaris* (*c* — crests on dorsal side of cervical ala); 6 — transverse section at posterior part of oesophagus, female from *P. lessonae*; 7 — transverse section at mid-body, female from *P. ridibunda*; 8 — posterior end, female from *P. ridibunda*, left lateral view; 9 — ovejector and vulva, right lateral view, female from *P. ridibunda*; 10 — right spicule, left lateral view, male from *L. vulgaris*; 11 — dorsal ray of the caudal bursa, male from *L. vulgaris*; 12 — caudal bursa, ventral view, male from *L. vulgaris*. Scale bars: 1–3, 5–10, 12 — 0.1 mm; 4, 11 — 0.05 mm.

Рис. 2. *Oswaldocruzia duboisi*: 1 — передняя часть тела самки из *L. montadoni*, латерально (головная везикула типа I); 2, 3 — различия в строении головной везикулы, самцы из *L. vulgaris* и *L. montadoni* соответственно (головная везикула типа II и III); 4 — передний конец, апикально, самец из *P. lessonae*; 5 — поперечный срез тела на уровне середины длины пищевода, самец из *L. vulgaris* (*c* — гребни на дорсальной стороне латерального крыла); 6 — поперечный срез тела на уровне заднего конца пищевода, самка из *P. lessonae*; 7 — поперечный срез на уровне середины тела, самка из *P. ridibunda*; 8 — хвост самки из *P. ridibunda*, латерально; 9 — яйцесет и вульва, латерально, самка из *P. ridibunda*; 10 — правая спикула, вид слева, самец из *L. vulgaris*; 11 — дорсальная ветвь половой бursы, самец из *L. vulgaris*; 12 — половая бурса, самец из *L. vulgaris*. Масштаб: 1–3, 5–10, 12 — 0,1 мм; 4, 11 — 0,05 мм.

Table 1. Morphometry of *O. duboisi* males, 43 specimens (SD — standard deviation, CV — coefficient of variation)

Таблица 1. Морфометрия *O. duboisi*, самцы, 43 экз. (SD — стандартное отклонение, CV — коэффициент вариации)

Characters	mean	min.	max.	SD	CV
Length of body	5626	3540	7280	843.0	14.98
Width of body	168	90	530	110.2	65.51
Length of cephalic vesicle	64	53	83	8.98	14.10
Width of cephalic vesicle	38	28	48	4.81	12.69
Length of oesophagus	396	283	583	58.13	14.69
Length of oesophagus in % of body length	7.11	4.76	9.89	1.09	15.37
Width of anterior end of oesophagus	24	19	28	2.02	8.42
Width of oesophagus at midlength	24	20	28	1.73	7.22
Width of oesophageal bulb	50	33	58	7.19	14.50
Distance to nerve ring from anterior end of oesophagus	178	115	268	30.74	17.28
Distance to nerve ring in % of oesophagus length	45.05	35.40	57.75	5.31	11.79
Distance to excretory pore from anterior end of oesophagus	260	198	348	36.47	14.04
Distance to excretory pore in % of esophagus length	66.08	49.07	87.42	9.49	14.36
Length of tail	118	98	168	17.57	14.88
Length of spicules	176	155	250	27.27	14.70
Length of spicules in % of body length	3.18	2.13	4.59	0.55	17.2

Table 2. Morphometry of *O. duboisi* females, 41 specimens

Таблица 2. Морфометрия *O. duboisi*, самки, 41 экз.

Characters	mean	min.	max.	SD	CV
Length of body	8887	2290	13620	2114	23.79
Width of body at midlength	173	100	250	28.38	16.43
Length of cephalic vesicle	71	50	95	10.24	14.49
Width of cephalic vesicle	44	38	50	3.61	8.27
Length of oesophagus	437	375	508	32.74	7.49
Length of oesophagus in % of body length	5.21	3.47	17.69	2.52	48.46
Width of anterior end of oesophagus	27	25	33	2.01	7.41
Width of oesophagus at midlength	27	23	33	2.24	8.46
Width of oesophageal bulb	206	148	273	32.44	15.74
Distance to nerve ring from anterior end of oesophagus	189	160	245	21.70	11.47
Distance to nerve ring in % of oesophagus length	43.29	37.36	51.16	3.80	8.78
Distance to excretory pore from anterior end of oesophagus	270	190	433	48.81	18.09
Distance to excretory pore in % of oesophagus length	61.50	46.55	86.10	8.49	13.81
Distance from anterior end to vulva	5619	2760	8400	1102	19.61
Distance to vulva in % of body length	62.31	43.95	68.55	4.61	7.40
Length of tail	206	148	273	32.44	15.73
Length of tail in % of body length	2.42	1.67	7.42	1.03	42.68

Vulva wide, post-equatorial in position. Anterior ovary beginning near posterior end of excretory glands and forming from 2 to 16 loops and bends depending on size (age) of female*. Posterior ovary beginning anterior to vulva and forming 2–10 loops and bends. Anterior and posterior uteri containing 4–59 and 0–52 eggs, respectively. All eggs observed in uteri and ovejectors on morula stage. Length of anterior infundibula 95–428, maximum width closer to uterus 68–95, minimum width closer to sphinc-

* Details of genital system shape and measurements are given based on 10 females studied.

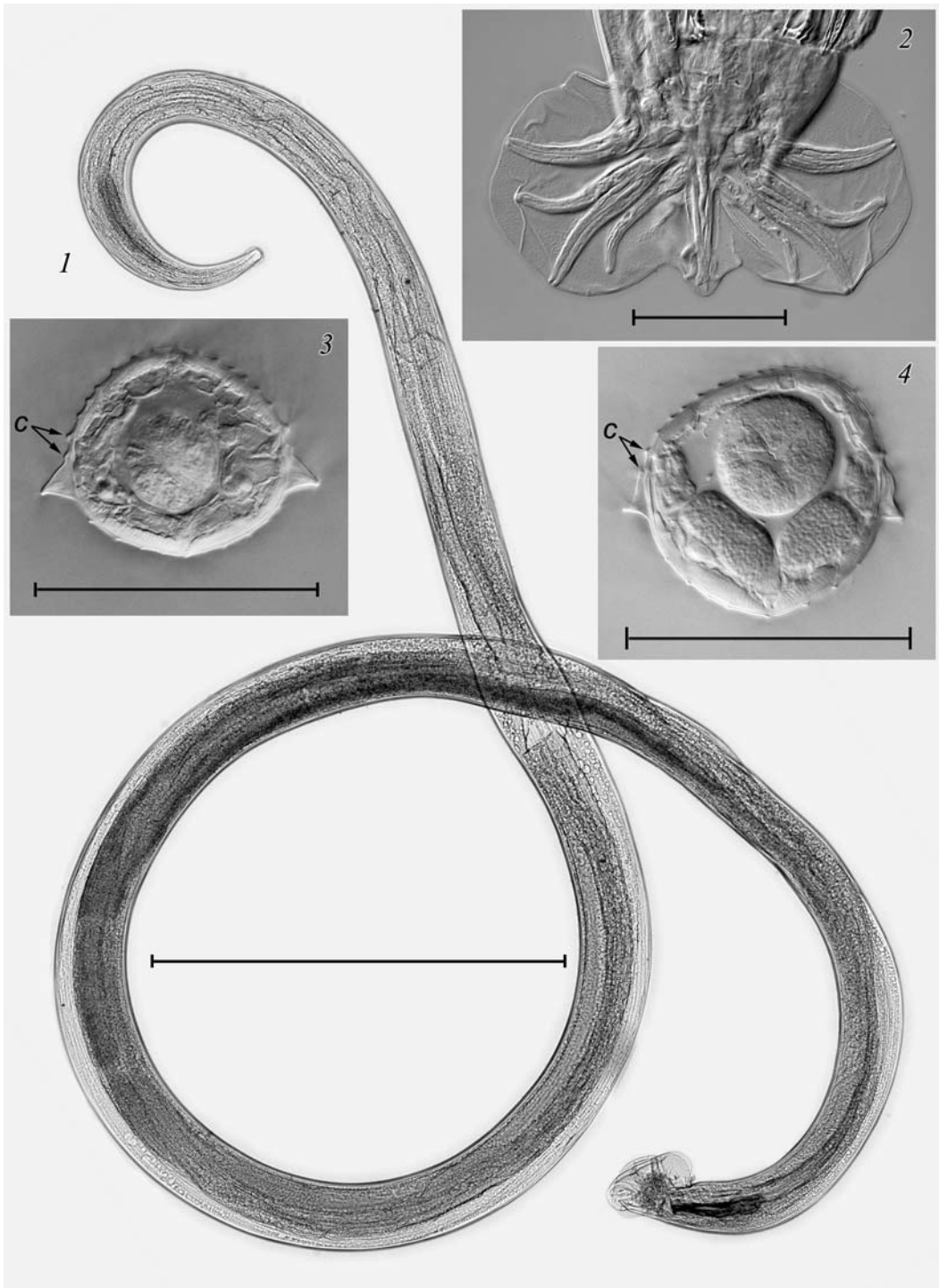


Fig. 3. *Oswaldocruzia duboisi*, photomicrographs: 1 — male, general view; 2 — caudal bursa, ventral view; 3 — transverse section at mid-oesophagus level; 4 — transverse section at posterior part of oesophagus (c — crests on dorsal side of cervical ala). Scale bars: 1 — 1 mm; 2–4 — 0.1 mm.

Рис. 3. *Oswaldocruzia duboisi*: 1 — общий вид самца; 2 — половая бурса, вентрально; 3 — поперечный срез тела на уровне середины длины пищевода; 4 — поперечный срез тела на уровне заднего конца пищевода (c — гребни на дорсальной стороне латерального крыла). Масштаб: 1 — 1 мм; 2–4 — 0,1 мм.

ter 36–77. Length of posterior infundibula 189–446, maximum width 63–117, minimum width 41–72. Anterior sphincter 36–77 long, 63–77 wide; posterior one 45–77 long and 59–90 wide. Length of anterior ovejector 248–338, maximum width 99–180, minimum width 63–144. Length of posterior ovejector 212–324, maximum width 90–189, minimum width 59–171. Ovejectors with well-developed musculature. Vagina 81–95 long and 5–9 in diameter. Egg size 95–117×157–162 (N = 21).

Tail (fig. 2, 8) tapering, elongated, with or without sharp cuticular needle on tip.

Discussion

In the present study, we found *O. duboisi* in 3 distant localities on the territory of Ukraine: Ivano-Frankivska oblast in western Ukraine, Kyivska oblast in northern central Ukraine, and Crimea, southern Ukraine. We suppose that real distribution of the species in Ukraine is not so scattered, and it will be found in other localities in the further studies. Previously *O. duboisi* was reported from France (Ben Slimane et al., 1993) and Bulgaria (Durette-Desset et al., 1993). Its occurrence in Ukraine means that the species is rather widely distributed in Western Palaearctic. In our opinion, distribution area of the species may be outlined by further studies and correct identification of *Oswaldocruzia* from newts and green frogs.

Our studies confirmed that *O. duboisi* parasitize two distantly related groups of hosts: newts *L. vulgaris*, *L. montadoni*, *T. cristatus*, *M. alpestris* (Caudata: Salamandridae) and frogs *Pelophylax* spp. and *Rana dalmatina* (Anura: Ranidae). *Lissotriton montadoni*, *T. cristatus*, and *M. alpestris* are new salamandrid hosts for *O. duboisi*. Apparently, the observed specificity of *O. duboisi* is an example of ecological fitting (Brooks et al., 2006), since its hosts from the both groups commonly share the same fresh-water habitats (Shcherbak and Shcherban, 1980).

We also found *O. duboisi* in the material from 2 *H. arborea* (1 parasite specimen in each host). Twelve other samples of parasites collected from *H. arborea* contained other species of *Oswaldocruzia* clearly different from *O. duboisi*. In our opinion, *H. arborea* is not a specific host of *O. duboisi*, though it may be occasionally infected by this nematode.

Oswaldocruzia duboisi is morphologically similar and closely related to *O. filiformis* (Ben Slimane et al., 1995). The latter species was reported from a wide range of hosts in Western Palaearctic, including newts (Salamandridae) and green frogs (*Pelophylax*, Ranidae) (Ryzhikov et al., 1980; Odnokurtsev and Sedalishchev, 2008; Yildirimhan, 2008). In our opinion, some records might be results of misidentification, and the authors in fact dealt with *O. duboisi*. In our studies, we did not find *O. filiformis* in the material from newts and green frogs from Ukraine. The species was found only in the material collected from *Bufo bufo* (Bufonidae) in various parts of the country.

Morphological examination of *O. duboisi* and *O. filiformis* confirmed the characters proposed by Ben Slimane et al. (1995) for differentiation of these two species: the cervical alae in *O. duboisi* are triangular on transverse sections and bear two small crests on the dorsal side, whereas in *O. filiformis* the alae consist of two increased crests and one smaller crest between them. Other morphological characters including metrical ones are very similar in both species.

Use of some characters for differentiation of *Oswaldocruzia* is complicated by high degree of their variability. We observed similar variations in shape of cephalic vesicle in the specimens from separate hosts of *O. duboisi*: all three types of the vesicle were observed in specimens from *Pelophylax* spp., *M. alpestris* and *L. montadoni* (tables 3, 4). On the other hand, all studied specimens from *L. vulgaris* possessed divided cephalic vesicle (types II and III), though all other characters in those specimens were close to the characters of specimens from other hosts (tables 3, 4).

Table 3. Main measurements and types of cephalic vesicle of *O. duboisi* males from separate host species
Таблица 3. Основные мерные признаки и тип головной везикулы у самцов *O. duboisi* из разных видов хозяев

Characters	<i>Pelophylax</i> spp.	<i>M. alpestris</i>	<i>L. montadoni</i>	<i>L. vulgaris</i>	<i>T. cristatus</i>
	N = 14	N = 4	N = 10	N = 13	N = 2
Length of body, mm	5.7–9.0	5.3–7.3	3.5–6.1	4.7–7.2	5.0–5.1
Width of body	110–190	130–180	90–170	120–180	450–530
Length of cephalic vesicle	58–83	78–83	53–68	53–78	70–78
Width of cephalic vesicle	40–48	38–43	35–45	28–75	28–45
Length of oesophagus	370–433	408–583	283–430	368–433	375–380
Length of oesophagus, in % of body length	4.72–7.11	7.11–8.00	4.76–9.89	5.97–8.28	7.41–7.58
Width of anterior end of oesophagus	23–29	25–25	23–25	23–28	25–25
Width of oesophagus at midlength	20–28	23–28	23–25	23–25	23–23
Width of oesophageal bulb	45–63	53–58	38–58	43–58	45–48
Distance to nerve ring from anterior end of oesophagus	150–200	165–268	115–205	143–203	205–208
Distance to nerve ring, in % of oesophagus length	37.65–51.61	39.2–45.9	37.8–57.8	35.4–47.9	54.6–54.7
Distance to excretory pore from anterior end of oesophagus	223–333	210–328	233–303	198–348	248–248
Distance to excretory pore, in % of oesophagus length	56.8–83.0	51.5–65.1	56.4–86.8	49.1–87.4	65.1–66.0
Length of tail	95–133	118–168	98–130	103–155	103–115
Length of spicules	160–258	155–180	158–205	165–203	158–163
Length of spicules in % of body length	2.50–4.59	2.13–3.0	3.32–4.50	2.82–3.50	3.12–3.22
Type of cephalic vesicle	I, II, III	II, III	I, II, III	II, III	II

Table 4. Main measurements and types of cephalic vesicle of *O. duboisi* females from separate host species
Таблица 4. Основные мерные признаки и тип головной везикулы у самок *O. duboisi* из разных видов хозяев

Characters	<i>Pelophylax</i> spp.	<i>M. alpestris</i>	<i>L. montadoni</i>	<i>L. vulgaris</i>
	N = 13	N = 12	N = 7	N = 11
Length of body, mm	6.3–13.6	6.8–8.8	8.7–11.4	2.3–13.6
Width of body at midlength	100–250	120–180	150–190	140–250
Length of cephalic vesicle	50–95	63–95	60–78	50–80
Width of cephalic vesicle	38–50	43–48	40–50	38–50
Length of oesophagus	375–508	403–483	423–508	378–490
Length of oesophagus, in % of body length	3.47–6.17	5.50–5.90	4.41–5.70	3.6–5.7
Width of anterior end of oesophagus	25–33	25–30	25–33	25–32
Width of oesophagus at midlength	23–33	23–28	25–28	25–33
Width of oesophageal bulb	43–65	50–65	50–63	43–65
Distance to nerve ring from anterior end of oesophagus	160–245	163–238	163–238	160–245
Distance to nerve ring, in % of oesophagus length	37.4–51.2	38.3–50.3	37.4–47.0	38.5–51.2
Distance to excretory pore from anterior end of oesophagus	190–433	203–303	235–325	190–338
Distance to excretory pore, in % of oesophagus length	46.6–86.1	46.6–69.5	55.3–68.8	49.0–71.4
Distance from anterior end to vulva, mm	2.8–8.4	3.9–5.8	5.5–7.3	2.8–8.4
Distance to vulva, in % of body length	43.9–68.6	51.8–67.2	62.1–65.2	43.9–51.1
Length of tail	148–273	175–223	178–248	148–255
Length of tail, in % of body length	1.67–2.95	2.21–2.75	1.87–2.57	1.67–7.42
Type of cephalic vesicle	I, II, III	I, II, III	I, II, III	II, III

Metrical characters also varied significantly in the studied samples, except for the width of oesophagus in its anterior and middle parts (tables 1, 2). Spicule length varied within a wide range, from 155 up to 255 μm ; this variation corresponds with range of spicule length given in the first description of the species — 155–250 μm (Ben Slimane et al., 1993). We found no correlation between the variations of metrical characters in *O. duboisi* and its host species or geographic locality (see tables 3 and 4). The only exception was observed in 5 males with comparatively larger spicules, all collected from 2 specimens of *P. ridibunda* in Crimea. This sample may represent a separated lineage within the species *O. duboisi*, or may belong to a separate cryptic species.

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