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Overview of the Helminth Fauna of Slow Worms of Genus Anguis (Reptilia, Anguidae) in the Western Palearctic

Alexander A. Kirillov[1]*, Nadezhda Yu. Kirillova[1], Alexander B. Ruchin[2]

[1] Institute of Ecology of Volga basin of RAS, Togliatti, Russia.
[2] Joint Directorate of the Mordovia State Nature Reserve and National Park «Smolny», Saransk, Russia.

ABSTRACT

The overview summarizes data on helminths of slowworms of genus Anguis inhabiting the Western Palearctic. The data was collected using all available literature for 180-year period and original data of the authors. The data contain information on 13 countries where slowworms have been studied. 21 parasite species are listed (2 trematodes, 1 cestoda, 17 nematodes and 1 acanthocephalan), each with the location in the host, geographical localities, countries, prevalence, range of infection intensity and literature sources. Most of helminths are «random» slowworms' parasites. There are only 5 common parasites: Entomelas entomelas, Oswaldocruzia filiformis, Oswaldocruzia lisnykiensis, Oxysomatium brevicaudatum and Neoxysomatium caucasicum, all of them nematodes and with direct life cycle. Entomelas entomelas, Oswaldocruzia filiformis and Oxysomatium brevicaudatum are found in most examined legless lizards.

Keywords: *Helminths, Slowworm, Anguis, Western Palearctic*.

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Corresponding author: Alexander A. Kirillov
E-mail ✉ parasitolog@yandex.ru
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INTRODUCTION

The latest molecular research [1-3] shows that genus *Anguis* includes 5 genera of legless lizards, inhabiting Palearctic: *A. fragilis* (Linnaeus 1758) (Western and Central Europe), *A. colchica* (Nordmann 1840) (Eastern Europe and Western Asia), *A. graeca* (Bedriaga 1881) (Southern Balkans), *A. cephallonica* (Werner 1894) (The Peloponnese) and *A. veronensis* (Pollini 1818) (Italy and Southeastern France). In some parts of species of this genus a range of hybridization is observed [4-6]. The northern limit of the spread of *Anguis* almost reaches the Arctic Circle; the eastern limit passes through Tobol River valley in Western Siberia [7-9]. *Anguis* species prefer to live in forest habitats. They use forest floor, rotten stumps, tree trunks, stones and animal burrows as their shelters. Their ratio consists of earthworms, slugs and other soil invertebrates [10-12]. The purpose of this work is to summarize the existing data on helminths of the genus *Anguis* lizards inhabiting Western Palearctic.

MATERIALS AND METHODS

Our overview is based on all available literature sources and on our original data. A number of researchers have been studying genus *Anguis* (more than 220 specimens) in 12 European countries since 1845 till 2018 (Fig. 1). Our study is based on the analysis of helminth fauna of *Anguis* genus collected from several regions of Russia in 2000–2018. In our research, we examined only road-killed slowworms. Animal dissection, fixation and treatment of parasitological material were performed according to standard techniques [13, 14]. Our collected material consisted exclusively of nematodes. Collected parasites were killed by heating in water. Clarification of objects was carried out in lactic acid. The whole mount of nematodes was made by enclosing helminths in Glycerin-Jelly. Helminths were defined according to V.P. Sharpilo (1976) [15].

If the literature sources lacked quantitative indicators, presence of parasite in the region was marked with a "+" sign. Parasite taxonomy is provided according to the Fauna Europaea website (http://www.fauna-eu.org/). For each parasite are given: the number of examined lizards, its locations in the host, localities of detection, country, parasite prevalence (P, % – proportion of infected reptiles), range of intensity of infection (I, specimens) and authors of record.

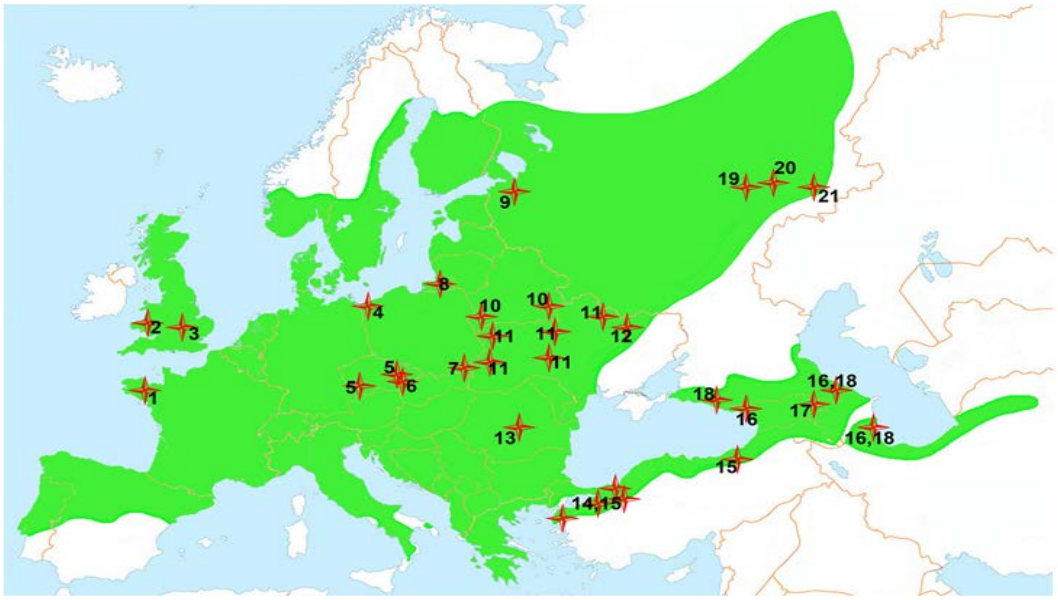

Fig. 1. A map of helminth research sites of slow worms in the Western Palearctic. Legend: stars on the map mark the catching places of lizards. 1 – Dujardin (1845); 2 – Jones et al. (2011); 3 – Baylis (1928); 4 – Markowski (1933); 5 – Moravec (1963); 6 – Borkovcova, Kopriva (2005); 7 – Bertman, Okulewicz (1984, 1987) and Lewin (1990); 8 – Muhling (1898); 9 – Markov (1952); 10 – Shimalov et al. (2000), Shimalov (2010); 11 – Svitin (2017); 12 – Shevchenko (1963); 13 – Mihalca et al. (2007); 14 – Schad et al. (1960) and Dusen et al. (2010); 15 – Sumer et al. (2019); 16 – Sharpilo (2003); 17 – Sharpilo (1962); 18 – Sharpilo (1974); 19 – Kirillov et al. (2015); 20 – Kirillov et al. (2018); 21 – Kirillov (2000). [16-43]

RESULTS AND DISCUSSION

The information on the parasitic worms of European slowworms is short and fractional. As a rule, data on *A. fragilis* parasites were obtained during the study of the overall helminth fauna of reptiles or all vertebrates in general. First information about helminth fauna of *Anguis* genus dates back to the mid-19th century, when F. Dujardin (1845) described a new species of nematodes – *Entomelas entomelas* [16]. P. Muhling (1898) found the nematodes *Oswaldocruzia filiformis* (Goeze 1782) and *Cosmocerca ornata* in the lizards of the Kaliningrad region of Russia (formerly, East Prussia) [17]. *Entomelas entomelas* and *Oxysomatium brevicaudatum* (Zeder 1800) were noted in British slowworms by H.A. Baylis (1928) and Polish lizards by S. Markowski (1933) [18, 19].

Further studies of slowworms' helminths were carried out in Russia [26, 40, 41, 43], Ukraine [15, 30, 31, 38, 44, 45], Georgia [15, 38, 44], Turkey [33, 35, 36], Czech Republic [20, 21] Poland [22-24], Great Britain [25], Belarus [27-29], Romania [32] and Armenia [46]. Works by V.P. Sharpilo (1974, 2003) are devoted to the endemic nematode species of the Caucasus fauna *Neoxysomatium caucasicum*, which first described from slowworm [37, 39].

In total, there are 21 species of parasites in representatives of genus *Anguis* in the Western Palaearctic: 2 trematodes, 1 cestoda, 17 nematodes and 1 acanthocephalan (Table 1).

Phylum Plathelminthes Schneider, 1873
Class Cestoda Rudolphi, 1808
Family Mesocestoididae Perrier, 1897

***Mesocestoides* sp., tetrathyridium.** Cestodes of the genus *Mesocestoides* usually parasitize at the larval stage as a rule in the body cavity of reptiles. Lizards can be intermediate or paratenic (reservoir) host of this parasite. The definitive

hosts of this parasite are birds of prey or mammals. The development cycle of mesocestoides involves 3 levels of hosts: first intermediate (apparently, arthropoda), second intermediate (amphibians, reptiles or rodents) and definitive (birds of prey or mammals) [47, 48].

Other reported reptilian hosts: *Lacerta agilis* [49, 50]; *Lacerta schreiberi* [51]; *Lacerta trilineata* [52]; *Lacerta viridis* [53]; *Apathya cappacocica* [54]; *Phoenicolacerta laevis* [55]; *Anatololacerta danfordi* [56]; *Phrynocephalus mystaceus* [57]; *Podarcis bocagei* [58]; *Podarcis hispanicus* [58]; *Podarcis muralis* [59]; *Podarcis pityusensis* [60]; *Psammodromus hispanicus* [61, 62]; *Eremias arguta* [63]; *Eremias velox* [63]; *Coronella austriaca* [64]; *Zamenis longissimus* [65]; *Psammophis lineolatus* [63].

Class Trematoda Rudolphi, 1808
Family Brachylaimidae Joyeux et Foley, 1930

***Brachylaima* sp.** J. Lewin (1990), according to the figure, noted a young parasite with an undeveloped reproductive system, which may be a consequence of the parasite's development in a non-specific host. All other authors recorded *Brachylaima* sp., metacercariae, in the slowworm and other reptile species. Finding *Brachylaima* sp. in legless lizards should be considered accidental. Terrestrial gastropods are intermediate hosts of trematodes of genus *Brachylaima*, while birds and mammals are the definitive hosts [66]. Parasite infestation occurs when lizards feed on land mollusks, which are intermediate hosts of these trematodes. Apparently, reptiles occur to be abortive hosts for *Brachylaima* spp.

Other reported reptilian hosts: *Lacerta agilis* [49]; *Lacerta trilineata* [52]; *Lacerta strigata* [15, 38]; *Podarcis bocagei* [51]; *Podarcis carbonelli* [67]; *Podarcis lilfordi* [60, 68]; *Podarcis pityusensis* [68], *Chalcides ocellatus* [69].

Family Pleurogenidae Looss, 1899

***Pleurogenoides medians* (Olsson 1876).** It is a common parasite of anurans and caudates. The first intermediate hosts of the trematode are gastropods, the second intermediate hosts are the larvae and adult insects, that live near water (dragonflies, caddisflies, mayflies, alderflies, dipterans), and crustaceans (*Asellus aquaticus,* amphipods) [70]. The invasion of the slowworms by *Pleurogenoides medians*, apparently, happened accidentally by eating additional hosts of the trematode.

Other reported reptilian hosts: *Lacerta agilis* [15, 20, 49, 50]; *Lacerta trilineata* [52]; *Zootoca vivipara* [15]; *Podarcis hispanica* [62, 71].

Phylum Acanthocephala (Rudolphi, 1808)
Class Palaeacanthocephala (Meyer, 1931)
Family Echinorhynchidae Cobbold, 1876

***Acanthocephalus ranae* (Schrank 1788).** It is a common parasite of amphibians, mainly anurans. Crustaceans, such as *Asellus aquaticus* and wood lice [72, 73] serve as intermediate hosts of the genus *Acanthocephalus*. Amphibians become infected by accidental swallowing the intermediate hosts of the parasite.

Other reported reptilian hosts: *Natrix natrix* [27, 31, 74].

Phylum Nematoda Potts, 1932
Class Secernentea Chitwood, 1958
Family Rhabdiasidae Railliet 1916

***Entomelas entomelas* (Dujardin, 1845).** A common parasite of legless lizards of genus *Anguis* and *P. apodus*. As a rule, studies indicate 2 species of the genus *Entomelas* Travassos 1930: *Entomelas dujardini* (Maupas 1916) and *Entomelas entomelas* [75]. M.R. Baker (1980) changed description of *Entomelas* genus and synonymized *Entomelas dujardini* with *E. entomelas*. Life style of the parasite is characterized by heterogony. Invasive larvae are obtained from the free-living generation. Infection of reptiles with invasive larvae occurs both directly from the external environment and through food objects (mollusks and earthworms), which are paratenic hosts of nematodes [76, 77].

Other reported reptilian hosts: *Pseudopus apodus* [78].

***Rhabdias bufonis* (Schrank 1788).** It is a common parasite of amphibians. The development of nematodes of the family Rhabdiasidae occurs without the participation of intermediate hosts and is characterized by the alternation of free-living and parasitic generations. In most species of rhabdiasids, invasive larvae develop in the free-living generation [77]. Infection of amphibians occurs through percutaneous penetration of invasive parasite larvae from the soil.

No other reported reptilian hosts.

***Rhabdias fuscovenosa* (Railliet 1899).** It is a common parasite of colubrid snakes. Invasive larvae infect snakes orally. Unlike nematodes of amphibians, invasive larvae from *Rhabdias* species, that parasitize on reptiles, develop from parasitic eggs [79]. Eggs, which are laid by female parasites, enter the digestive tract through the trachea and excrete outside, where larvae reach the invasive stage [80]. Reptile infection with nematodes happens orally, so paratenic hosts may be involved [77, 80].
Other reported reptilian hosts: *Lacerta viridis* [21]; *Natrix natrix* [15, 20, 31, 32, 40, 42, 43, 63, 78, 81-85]; *Natrix tessellata* [15, 20, 32, 38, 42, 43, 63, 81, 84, 85]; *Coronella austriaca* [15], *Elaphe dione* [15], *Zamenis longissimus* [34]; *Eryx tataricus* [15], *Vipera ursinii* [15], *Vipera berus* [15, 32, 40, 86].

***Rhabdias* sp.** Nematodes from slowworms in Ukraine were not identified to the species level [31].
Other reported reptilian hosts: *Coronella austriaca* [31].

Family Rhabditidae Oerley 1880
Rhabditidae sp. Nematodes of this family are common parasites among insects and mollusks. According to R. Jones et al. (2011), the finding of this parasite in the slowworms' faeces may indicate post-cyclic parasitism (the parasite lives in the slowworm's body because of its food objects - soil invertebrates) [25]. We assume that the record of data on nematodes as an *Anguis*' parasite is a mistake. Other researchers weren't able to detect this parasite during dissections of slowworms.
No other reported reptilian hosts.

Family Molineidae Skrjabin et Schulz, 1937
***Oswaldocruzia filiformis* (Goeze 1782).** It is a common parasite of Palaearctic amphibians and reptiles. The development of the parasite occurs without the participation of intermediate hosts. Invasion of the hosts happens orally through the contact with invasive parasite larvae on land [87].
Apparently, all information about *Oswaldocruzia filiformis* in reptiles must be reviewed. In recent studies, new species were described and identification key for genus *Oswaldocruzia* Travassos 1917 was created. Three species of this genus were also reviewed: *Oswaldocruzia filiformis* (Goeze 1782), *Oswaldocruzia bialata* (Molin 1860) and *Oswaldocruzia skrjabini* Travassos, 1937 [87-95]. R.S. Svitin (2017) described new species for reptiles: *Oswaldocruzia lacertica* (sand lizard) and *Oswaldocruzia lisnykiensis* (*Anguis*) [30]. Still, mostly, parasitological studies of amphibians and reptiles name *Oswaldocruzia filiformis* species.
Svitin and Gorobchishin (2015) assume that all *Oswaldocruzia* spp. in snakes should be considered to be cases of post-cyclic parasitism [96].
Other reported reptilian hosts: *Lacerta agilis* [15, 20, 28, 32, 40, 42, 43, 50, 65, 86, 97]; *Lacerta viridis* [20, 21, 33, 53, 59, 98]; *Podarcis tauricus* [33]; *Darevskia rudis* [99]; *Pseudopus apodus* [15]; *Takydromus amurensis* [15]; *Zootoca vivipara* [20, 26, 28, 40, 43, 100]; *Coronella austriaca* [15, 31]; *Natrix natrix* [20, 23, 27, 31, 49, 63, 64, 96, 101]; *Natrix tessellata* [15, 63]; *Telescopus fallax* [15]; *Vipera ammodytes* [15]; *Vipera berus* [20, 26, 27, 40, 43, 96, 102, 103].

***Oswaldocruzia lisnykiensis* Svitin 2017.** It is a common parasite of lizards of genus *Anguis* [30]. V.P. Sharpilo (1976) thinks that the phenomenon of host-specificity among the parasitic worms of reptiles is extremely rare. Apparently, as other *Oswaldocruzia* spp., they have direct life cycle without the participation of intermediate hosts.
No other reported reptilian hosts.

Family Cosmocercidae Railliet, 1916
***Oxysomatium brevicaudatum* (Zeder 1800).** It is a common parasite of amphibians and, less commonly, reptiles. It seems that, as other cosmocercid species, they have direct development cycle, without the participation of intermediate hosts. Eggs develop in the environment. Infection of hosts with invasive larvae most likely happens orally.
Other reported reptilian hosts: *Natrix natrix* [15, 33]; *Vipera berus* [15]; *Zamenis longissimus* [34].

***Oxysomatium* sp.** Nematodes of the genus *Oxysomatium* (not identified to the species) were

found in only one of the examined slowworms in Armenia [46].
No other reported reptilian hosts.

***Neoxysomatium caucasicum* Sharpilo, 1974**. It is a common parasite of lizards of genus *Anguis*. Life cycle has not been studied, but should be direct. Infection of slowworms with invasive larvae happens orally from the environment.
No other reported reptilian hosts.

***Cosmocerca ornata* (Dujardin, 1845)**. It is a common parasite of amphibians. As other nematodes of *Cosmocercidae* family, they have direct development cycle, without the participation of intermediate hosts [77].
Our studies have shown that invasive larvae (L3) penetrate the amphibians through the eyes, in the near-surface layer of water. On the conjunctiva of the lower eyelid, they survive third and fourth moltings. Young nematodes migrate to third part of posterior intestine through the oropharyngeal cavity and gastrointestinal tract [104]. Therefore, we consider the finding of *Cosmocerca ornata* in slowworms to be a mistake. The researchers probably dealt with the *Cosmocerca commutata* (Diesing 1851), a parasite of terrestrial amphibians.
No other reported reptilian hosts.

***Aplectana acuminata* (Schrank 1788)**. A common parasite of anurans. It seems that, as other cosmocercid species, they have direct life cycle, without the participation of intermediate hosts. Infection of hosts with invasive larvae happens orally from the environment.
Other reported reptilian hosts: *Natrix natrix* [15].

Family Protostrongylidae Leiper, 1926
Protostrongylidae sp. Nematodes of *Protostrongylidae* family have an indirect life cycle. The development of parasites requires participation of intermediate hosts, terrestrial molluscs, in which larvae become invasive [105, 106]. Infection of slowworms with protostrongylids occurs by consuming molluscs.
No other reported reptilian hosts.

Family Spirocercidae Chitwood et Wehr, 1932

***Ascarops strongylina* (Rudolphi 1819), juv.** It is a widespread parasite of pigs, boars and livestock [15]. The parasite has an indirect life cycle. Nematode eggs fall into the environment with host's faeces. Coprophagous beetles are intermediate hosts of the parasite. After that, the larvae become infectious, and infect pigs when they ingest infected dung beetles [107]. Reptiles serve as paratenic hosts of the parasite.
Other reported reptilian hosts*: Lacerta agilis* [15, 27, 50]; *Zootoca vivipara* [15, 28]; *Dolichophis jugularis* [108]; *Platyceps najadum* [108]; *Dolichophis caspius* [15]; *Coronella austriaca* [27]; *Gloydius halys* [109]; *Malpolon monspessulanus* [108]; *Natrix tessellata* [15], *Natrix natrix* [15, 27]; *Coronella austriaca* [15], *Vipera aspis* [110]; *Vipera berus* [15, 27]; *Vipera latastei* [110]; *Emys orbicularis* [15].

***Physocephalus sexalatus* (Molin, 1860), juv.** It is a widespread parasite of domestic pigs and boars [77]. The life cycle is the same with that of *Ascarops strongylina*. At larval stage, it is a widespread parasite of reptiles, birds, insectivores, bats and rodents, which serve as paratenic hosts of the parasite. Infection of reptiles with this parasite occurs after eating intermediate hosts of the parasite – coprophagous beetles [107].
Other reported reptilian hosts: *Laudakia caucasia* [15, 38], *Laudakia erythrogastra* [109], *Laudakia lehmanni* [109], *Phrynocephalus mystaceus* [109], *Pseudopus apodus* [15], *Eremias velox* [15, 38], *Lacerta strigata* [15, 38], *Zootoca vivipara* [15], *Lacerta agilis* [15, 38], *Lacerta saxicola* [15, 38], *Telescopus fallax* [15], *Natrix natrix* [15], *Natrix tessellata* [15], *Podarcis tauricus* [15], *Dolichophis caspius* [15, 38], *Platyceps najadum* [15], *Zamenis longissimus* [15], *Coronella austriaca* [15], *Vipera berus* [15], *Emys orbicularis* [15], *Agrionemys horsfieldii* [15].

Family Physalopteridae Railliet, 1893
***Abbreviata* sp.** Nematodes of genus *Abbreviata Travassos* (1919) parasitize the digestive tract of reptiles. These parasites have an indirect life cycle. The intermediate hosts of physalopterids are arthropods [77]. Infection of reptiles occurs by arthropods consumption.
Other reported reptilian hosts: *Lacerta agilis* [21]; *Lacerta viridis* [21]; *Coronella austriaca* [21].

Unidentified larvae of suborder Spirurina Railliet et Henry, 1915

***Agamospirura minuta* (Sharpilo 1963), juv.** Intermediate hosts, arthropods [77], are involved in the life cycle of spiruride nematodes. Reptiles are paratenic hosts. J. Lewin (1990) considers erroneous defining of *Agamospirura* larvae, found in slowworms by V.P. Sharpilo (1964, 1976), as Spirurina. J. Lewin thinks that the larvae of *Protostrongylidae* sp. are similar to *Agamospirura* spp., which was found in reptiles by V.P. Sharpilo.

Other reported reptilian hosts: *Lacerta viridis*, *Coronella austriaca*, *Natrix natrix*, *Natrix tessellata*, *Vipera berus* [15, 38, 44].

***Agamospirura* sp., juv.** Larvae of spirurian nematodes, found in slowworms in Ukraine, were not identified to the species level [31].

Other reported reptilian hosts: *Lacerta agilis* [31], *Natrix natrix* [31]; *Coronella austriaca* [31], *Vipera berus* [31].

Out of 21 parasites that were found in legless lizards, the majority of helminths are «random» parasites of slowworms (10 species): *Brachylaima* sp., *Pleurogenoides medians*, *Acanthocephalus ranae*, *Cosmocerca ornata*, *Aplectana acuminata*, *Rhabdias bufonis*, *Rhabdias fuscovenosa*, *Rhabdias* sp., *Abbreviata* sp., and Rhabditidae sp. These helminth species are common parasites of other vertebrates (mainly, amphibians and snakes).

Most of parasites (15 species) of genus *Anguis* were discovered in adult form. Six species of helminthes parasitize legless lizards in larval stage. The finding of larval form of parasites in slowworms involves that they are paratenic hosts of these helminthes.

Relatively high rates of invasion were noted in slowworms with such parasites: *Neoxysomatium caucasicum*, *Oxysomatium* sp., *Cosmocerca ornata*, *Aplectana acuminata*, *Physocephalus sexalatus*, juv., *Rhabdias fuscovenosa*, *Rhabdias bufonis*, *Rhabdias* sp., *Rhabditidae* sp., *Protostrongylidae* sp., juv. Low rates of invasion and occasional discoveries were recorded in slowworms with such parasites: *Mesocestoides* sp., tetrathyridium, *Brachylaima* sp., *Pleurogenoides medians*, *Acanthocephalus ranae*, *Abbreviata* sp., *Ascarops strongylina*, juv., *Agamospirura minuta*, juv., *Agamospirura* sp., juv.

Nematodes predominate in helminth fauna of slowworms. Cestodes, trematodes, and acanthocephalans are rarely found in legless lizards. Helminth fauna of lizards of the genus *Anguis* characterizes the ecology of these reptiles. Infection of legless lizards with helminths happens, firstly, because of slowworms living in a damp forest floor (favorable environment for the development of nematodes' eggs and larvae with a direct development cycle), and secondly, because of lizards feeding on terrestrial invertebrates, which are intermediate and/or paratenic hosts of parasites.

The parasites with a direct life cycle prevail in helminth fauna of slowworms (12 species). The remaining 9 parasitic species are characterized by an indirect life cycle with intermediate hosts. Helminths of slowworms are better studied in Ukraine (9 recorded species), Belarus (8), Russia and Turkey (7 in each) and Poland (6). Helminth fauna of legless lizards in Czech Republic (5), Georgia (4), and Great Britain (3) is proven to be less diverse. Only one species was found in slowworms in Spain, Armenia, Azerbaijan, Romania and France. That is probably due to the small number of examined legless lizards.

There are only 5 common parasites for the lizards of genus *Anguis*: *Entomelas entomelas, Oswaldocruzia filiformis, Oswaldocruzia lisnykiensis, Oxysomatium brevicaudatum* and *Neoxysomatium caucasicum*. All of them are nematodes with a direct life cycle. *Entomelas entomelas, Oswaldocruzia filiformis* and *Oxysomatium brevicaudatum* are found in lizards in most studies. Most of the helminth species recorded in legless lizards are parasites of other vertebrates (mainly amphibians and snakes).

Overview has shown the need for further helminthological studies of slowworms in Palearctic, since these studies should expand list of parasite-host for legless lizards.

Table 1. Checklist of parasites of slow worm *Anguis fragilis*

Parasite	Infection site	Locality	Country	n	P (%)	I	Author of record
Mesocestoides sp., tetrathyridium	sw	Bieszczady Mountains	Poland	44	2,3	1	[24]
Brachylaima sp.	i	Bieszczady Mountains	Poland	44	4,6	1	[24]
		Trabzon, Bursa provinces	Turkey	15	6,7	1	[36]
Pleurogenoides medians	i	Kharkov region	Ukraine	17	5,9	25	[31]
Acanthocephalus ranae	i	Brest and Gomel regions	Belarus	19	21,1	1–3	[28]
Entomelas entomelas	bc	Pomerania	Poland	4	–	1–6	[19]
	l, p	Leningrad region	Russia	20	70,0	1–25	[26]
	l, p	–	Turkey	9	66,7	–	[33]
	l	Lagodekhi	Georgia	2	1 of 2	4	[38]
	l	Bohemia (Sumava)	Czech Republic	2	1 of 2	3	[20]
	o, p	Moravia	Czech Republic	10	90,0	1–50	[20]
	o, p	Kharkov region	Ukraine	17	52,9	1–17	[31]
	l	Bieszczady Mountains	Poland	1	+	8	[22]
	l, o, p, nc	Bieszczady Mountains	Poland	44	92,3	1–22	[24]
	l, o	–	Spain	+			[111]
	l, o, p	Samarskaya Luka	Russia	2	100	1–6	[43]
		Brest and Gomel regions	Belarus	30	36,7	1–10	[28; 29]
	–	–	Romania	2	1 of 2	3	[32]
	l	alıkesir, Bursa, Duzce Sakarya provinces	Turkey	18	44,4	1–9	[35]
	l, o, p	Mordovia Nature Reserve	Russia	3	3 of 3	2–15	[40]
	l, o, p	«Smolny» National Park, Mordovia	Russia	24	91,7	1–16	[41]
	l, o	Trabzon, Bursa provinces	Turkey	15	93,3	1–15	[36]
Rhabdias bufonis	l	alıkesir, Bursa, Duzce Sakarya provinces	Turkey	18	44,4	1–9	[35]
Rhabdias fuscovenosa	l	Southern Moravia	Czech Republic	7	28,6	>350	[21]
Rhabdias sp.	l	Kharkov region	Ukraine	17	64,7	1–10	[31]
Rhabditidae sp.	i	Wales	UK	100	83,0	1–2000*	[25]
Oswaldocruzia filiformis	i	–	Turkey	9	11,1	–	[33]
		Lagodekhi	Georgia	2	2 of 2	3–8	[33]
		Bohemia (Sumava)	Czech Republic	2	1 of 2	1	[20]
		Moravia	Czech Republic	10	20,0	1–6	[20]
		Kharkov region	Ukraine	17	52,9	1–10	[31]
		Krasnodar region	Russia	4	75,0	1–2	[112]
		Bieszczady Mountains	Poland	2	2 of 2	9–12	[23]
	d, s	Bieszczady Moun-	Poland	44	89,7	1–53	[24]

		tains					
	i	Samarskaya Luka	Russia	2	1 of 2	11	[43]
		Brest and Gomel regions	Belarus	19	10,5	1	[28]
		South Moravia	Czech Republic	7	14,3	2	[21]
		alıkesir, Bursa, Duzce Sakarya provinces	Turkey	18	22,2	1–14	[35]
		Mordovia Nature Reserve	Russia	3	3 of 3	1–3	[40]
		«Smolny» National Park, Mordovia	Russia	24	20,8	1–2	[41]
		Trabzon, Bursa provinces	Turkey	15	6,7	1–2	[36]
Oswaldocruzia lisnykiensis	i	Kyiv, Chernivtsi, Volyn, Sumy, Lviv, Khmelnytskyi regions	Ukraine	+			[30]
Oxysomatium brevicaudatum	i	Pomerania	Poland	4	100	1–6	[19]
		–	Turkey	9	11,1	–	[33]
		Bohemia (Sumava)	Czech Republic	2	2 of 2	5–18	[20]
		Moravia	Czech Republic	10	90,0	1–67	[20]
		Kharkov region	Ukraine	17	58,8	1–7	[31]
	c	Bieszczady Mountains	Poland	44	61,5	1–42	[24]
	i	alıkesir, Bursa, Duzce Sakarya provinces	Turkey	18	83,3	1–8	[35]
		Southern Moravia	Czech Republic	7	42,9	3–10	[21]
		Brest and Gomel regions	Belarus	30	20,0	1–8	[28; 29]
		Samarskaya Luka	Russia	2	2 of 2	8–27	[43]
		«Smolny» National Park, Mordovia	Russia	24	100,0	1–41	[41]
		Trabzon, Bursa provinces	Turkey	15	93,3	1–60	[36]
		Wales	UK	100	38,0	1–686*	[25]
Oxysomatium sp.	i	–	Armenia	1	+	14	[45]
Neoxysomatium caucasicum	i	Lagodekhi	Georgia	2	2 of 2	10–13	[33; 37]
		Krasnodar region	Russia	4	75,0	28–29	[112]
		Suhumi, Chiatura	Georgia	+			[37]
		Lankaran and Astara regions	Azerbaijan	+			[37]
		Dagestan	Russia	12	–	10–35	[39]
Cosmocerca ornata	i	Kharkov region	Ukraine	17	5,9	1	[31]
		Brest and Gomel regions	Belarus	30	3,3	1	[28; 29]
		alıkesir, Bursa, Duzce Sakarya provinces	Turkey	18	50,0	1–6	[35]
Aplectana acuminata	i	Leningrad region	Russia	20	95,0	1–43	[26]
		Kharkov region	Ukraine	17	5,9	2	[31]

Protostrongylidae sp., juv.	hp, sw, dw	Bieszczady Mountains	Poland	44	9,1	1–25	[24]
Ascarops strongylina, juv.	–	Brest and Gomel regions	Belarus	30	3,3	15	[28; 29]
Physocephalus sexalatus, juv.	–	Brest and Gomel regions	Belarus	19	21,1	4–112	[28]
Abbreviata sp.	–	Southern Moravia	Czech Republic	7	28,6	1–3	[21]
Agamospirura minuta, juv.	iw	Volyn, Khmelnytskyi regions	Ukraine	9	16,3	1–8	[44]
		Lagodekhi	Georgia	2	2 of 2	1–8	[15]
		Brest and Gomel regions	Belarus	19	5,3	1	[28]
Agamospirura sp., juv.		Kharkov region	Ukraine	17	11,8	2–3	[31]

* – Jones et al. (2011) examined faecal samples of slow worms

bc – body cavity; c – colon; d – duodenum; dw – duodenum wall; hp – hepatic parenchyma; i – intestine; iw – intestine wall; l – lung; nc – nasal cavity; o – oesophagus; p – pharynx; s – stomach; sw – stomach wall; juv. – third-stage juvenile

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