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Distribution of the nematodes of the genus *Eustrongylides* (Nematoda, Dioctophymatidae) in the world

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Eustrongylides spp. are nematodes from the Dioctophymatidae family, potentially dangerous for the health of mammals. The aim of this review is to describe the distribution of the *Eustrongylides* spp. nematode. Eustrongylidosis is a parasitic disease which is common in countries with a continental, tropical or subtropical climate. *Eustrongylides* are biohelminths with a complicated development cycle. The nematode development takes place in the aquatic environment and includes a wide range of intermediate, definitive, and accidental hosts. The purpose of this review is describe the distribution of *Eustrongylides* spp. nematodes in the global regions, describe the prevalence of infection in those regions, and identify intermediate, definitive, and accidental hosts. It was found that *Eustrongylides* spp. nematodes are significantly widespread around the world. In part in North America the agent of eustrongylidosis is registered mostly among birds and fishes, but cases of humans being affected with the disease are noted as well. In South America the given disease was also registered among amphibians and reptiles. In Europe, Asia, Africa, Oceania and countries of the Far East, the disease is registered mostly in fishes, rarely – in birds. The taxonomic identification showed that some nematode species were related to certain geographic areas. For example, *Eustrongylides ignotus* and *Eu. tubifex* were mostly registered in North America, while for Europe (including Ukraine), Near and Middle East, *Eu. excisus* is a dominant species. Analysis of scientific sources showed that continents with warmer climatic conditions (South America, Asia, etc.) are characterized with a wider range of fishes, birds and reptiles which can potentially serve as hosts for the *Eustrongylides* nematodes.

Keywords: eustrongylidosis; distribution; parasitic diseases; zoonotic parasite; hosts.

Introduction

Eustrongylides spp. are the nematodes of the *Eustrongylides* genus, as substantiated by Jägerskiöld in 1909 using the material from the glandular stomach of Ciconiiformes and waterfowls brought by the Swedish expedition from Egypt and Sudan (Jägerskiöld, 1909). Observing the received material Jägerskiöld concluded that this group of nematodes was not studied well enough. In his further research he used the materials from Berlin, Genoa, Greifswald, and Vienna museums as well as the helminths retrieved from birds in Finland. As a result, Jägerskiöld substantiated the new genus of *Eustrongylides*, as well as several new species in the new genus (Jägerskiöld, 1909). According to Jägerskiöld, the new genus *Eustrongylides* included 7 species: *Eu. tubifex*, *Eu. elegans*, *Eu. papillosus*, *Eu. africanus*, *Eu. excisus*, *Eu. ignotus*, *Eu. perpapillatus*. The four latter species were the new ones. All of them, except *Eu. africanus*, had been familiar to the scientists before, but they were mentioned under different species names in such genera as *Srongylus* (Rudolphi), *Eustrongylus* (Diesing) and *Tropidocerca* (Linstow) (Rudolphi, 1802; Diesing, 1861; Linstow, 1899). Cram substantiated *Eu. mergorum* in 1927, which contradicted the species *Eu. elegans*, as it was proven to be the same species (Cram, 1927). In 1960s, according to some researches, the genus *Eustrongylides* included 14 species, mostly found in China, Japan and Australia. *Eu. gadopsis*, *Eu. galaxias*, *Eu. wenrichi* were described on the basis of the larvae form taken from fish, which did not allow their systematic position to be considered as substantiated (Yamaguti, 1961; Karmanova, 1968). At the same time the data of modern molecular taxonomy based on

molecular-genetic research methods show that there are only three species considered basic for the *Eustrongylides* genus: *Eu. tubifex*, *Eu. excisus* and *Eu. ignotus*. The rest are subpopulations of the above-mentioned groups that function in particular biotopes (Muzzall, 1999; Coyner et al., 2002; Menconi et al., 2020).

Distribution of eustrongylidosis in the world

Eustrongylidosis has been reported on every continent and in every climate zone except the arctic and subarctic zones. Overall, the parasite occurs more commonly in the continental, tropical, and subtropical climate zones (Barros et al., 2010; Aydoğdu et al., 2011; Mierzejewska et al., 2012). *Eustrongylides* spp. nematodes are prone to form centers of infection near aquatic areas, mostly in fresh waters, less likely in salt waters and estuaries (Spalding & Forrester, 1993). This nematode can infect a wide range of animals, not only fish and fish-eating birds. The accidental hosts include amphibians (frogs), reptiles (turtles, snakes, caimans), mammals (rabbits, laboratory rats, seals), and humans (Sloboda et al., 2010; Švažas et al., 2011; Shukerova et al., 2011; Eberhard & Ruiz-Tiben, 2014; Ljubojevica et al., 2015). The distribution of the *Eustrongylides* spp. nematode varies between countries and global regions (Table 1).

North America

In North America the *Eustrongylides* nematodes were reported in the USA and Mexico. The prevalence of infection ranged from 0.5% in *Neo-*

gobius melanostomus in Lake Michigan (Camp et al., 1999) to 95% in *Perca flavescens* (Mitchell, 1814) in Lake Huron (Muzzall, 1999). Eustrongylidosis was also reported among other fishes, such as *Fundulus heteroclitus* (Linnaeus, 1758), *Catostomus commersoni* (Lacepede, 1803), *Lepomis auritus* (Linnaeus, 1758) etc. (Weisberg et al., 1986; Bauer & Whipps, 2013). In the waters of Mexico the eustrongylidosis infection was reported among such intermediate hosts as fishes *Ictalurus balsanus* (Jordan & Snyder, 1899) and *Allophorus robustus* (Bean, 1892); the prevalence of infection ranged from 5.8% to 19.0% (Rosas-Valdez et al., 2009; Martínez-Aquino et al., 2012). Definitive hosts of the *Eustrongylides* nematodes were mostly fish-eating birds of the order Ciconiformes (*Cas-*

merodius albus (Linnaeus, 1758), *Egretta thula* (Molina, 1782), *E. caerulea* (Linnaeus, 1758) etc) and *Ardea herodias* (Linnaeus, 1758). The mean prevalence of infection was 16.5% (Spalding, 1990; Spalding et al., 1993; Ziegler et al., 2000).

Eustrongylidosis was also reported among reptiles as accidental hosts, in part among snakes *Thamnophis sirtalis parietalis* (Say, 1823) (Lichtenfels & Lavies, 1976). Some sources reported on parasitic activity of *Eustrongylides* nematodes in humans in the American states of California, New Jersey, New York, and Maryland, but they included no data about the prevalence of infection (Beaver & Thei, 1979; Guerin et al., 1982; Eberhard et al., 1989; Wittner et al., 1989; Narr et al., 1996).

Table 1
Distribution of the *Eustrongylides* spp. nematodes (Jägerskiöld, 1909) in different global regions and countries

Country, area, year (author)	Nematode species	Host species	Prevalence, %	Site of infection
North America				
<i>Intermediate hosts</i>				
The USA, Maryland, Chesapeake Bay, 1983 (Weisberg et al., 1986)	<i>Eustrongylides</i> spp.	<i>Fundulus heteroclitus</i> (Linnaeus, 1766)	41.3	Abdominal cavity, intestines
The USA, Lake Michigan, Lake Huron, Saginaw Bay 1991–1996 (Muzzall, 1999)	<i>Eu. tubifex</i>	<i>Perca flavescens</i> (Mitchell, 1814)	3.0–95.0	Abdominal cavity, intestines, muscle tissue
The USA, Indiana, Southern Lake Michigan, 1995–1997 (Camp et al., 1999)	<i>Eustrongylides</i> spp.	<i>Neogobius melanostomus</i> (Pallas, 1814)	0.5	Encysted in mesenteries
Mexico, Balsas River, 2007 (Rosas-Valdez et al., 2009)	<i>Eustrongylides</i> sp.	<i>Ictalurus balsanus</i> (Jordan & Snyder, 1899)	14.2–19.0	Mesentery, muscle tissue
Central Mexico Plateau, Zacapu Lake, Michoacán, 2012 (Martínez-Aquino et al., 2012)	<i>Eustrongylides</i> spp.	<i>Allophorus robustus</i> (Bean, 1892)	5.9	Mesentery
The USA, New York, Wolf Lake, 2013 (Bauer & Whipps, 2013)	<i>Eustrongylides</i> spp.	<i>Catostomus commersoni</i> (Lacepede, 1803)	5.1	Muscle tissue and visceral cavities
The USA, Saginaw Bay, Lake Huron, Michigan, 2015 (Muzzall & Hessenauer, 2018)	<i>Eu. tubifex</i>	<i>Lepomis auritus</i> (Linnaeus, 1758) <i>Sander vitreus</i> (Mitchill, 1818)	53.3 7.1	Mesentery, muscle tissue
<i>Definitive hosts</i>				
The USA., Florida, 1990 (Spalding, 1990; Spalding & Forrester 1993)	<i>Eu. ignotus</i>	Ciconiformes: <i>Casmerodius albus</i> (Linnaeus, 1758) <i>Egretta thula</i> (Molina, 1803) <i>Eu. caerulea</i> (Linnaeus, 1758) <i>Nyctanassa violacea</i> (Linnaeus, 1758) <i>Butorides striatus</i> (Linnaeus, 1758)	16.5	Esophagus wall, intestinal wall, under the stomach mucosa, abdominal cavity
<i>Accidental hosts</i>				
The USA, 1976 (Lichtenfels & Lavies, 1976)	<i>Eustrongylides</i> spp.	<i>Thamnophis sirtalis parietalis</i> (Say, 1823)	80.0	Subcutaneous granulomas, muscle tissue, abdominal cavity
South America				
<i>Intermediate hosts</i>				
Brazil, Upper Parana River, 2000–2001 (De Carvalho et al., 2003)	<i>Eustrongylides</i> spp.	<i>Acestrorhynchus lacustris</i> (Lutken, 1875)	3.9	Abdominal cavity, intestine
Brazil, Santo Antonio do Leverger, Mato Grosso 2003 (Barros et al., 2007)	<i>Eustrongylides</i> spp.	<i>Hoplias malabaricus</i> (Bloch, 1875)	33.0	Mesentery, muscle tissue
Brazil, the Cuiabá River, 2010 (Barros et al., 2010)	<i>Eustrongylides</i> spp.	<i>Pygocentrus nattereri</i> (Kner, 1875)	64.6	Abdominal cavity, muscle tissue, maw
Brazil, Pantanal basin in Mato Grosso do Sul, 2016 (Ventura et al., 2016)	<i>Eustrongylides</i> spp.	<i>Gymnotus</i> spp.	17.1	Abdominal cavity
Brazil, Jari River, 2019 (Oliveira et al., 2019)	<i>Eustrongylides</i> spp.	<i>Hoplerhynchus unitaeniatus</i> (Spix & Agossiz, 1829) <i>Osteoglossum bicirrhosum</i> (Cuvier, 1829)	7.1–50.0 8.3	Mesentery Liver, muscle tissue
Brazil, Rio de Janeiro, 2020 (Kuraieim et al., 2020)	<i>Eustrongylides</i> spp.	<i>Hoplias malabaricus</i> (Bloch, 1794)	44.4	Muscle tissue, visceral cavities, parenchymal organs
Brazil, Tapajós River in the municipality of Santarém, 2020 (Correa et al., 2021)	<i>Eustrongylides</i> sp.	<i>Hoplias aff. Malabaricus</i> (Bloch, 1794)	62.9	Muscle tissue, visceral cavities
Brazil, Federal District, 2021 (Ferreira et al., 2021)	<i>Eustrongylides</i> sp.	<i>Simpsonichthys boitonei</i> (A.L. de Carvalha, 1959)	Not available	Muscle tissue, visceral cavities
<i>Definitive hosts</i>				
Brazil, State of Rio Grande do Sul, 2011 (Monteiro et al., 2011)	<i>Eustrongylides</i> spp.	<i>Phalacrocorax brasilianus</i> (Gmelin, 1789)	2.1	Esophagus
<i>Accidental hosts</i>				
Paraguay, 1991 (Goldberg et al., 1991)	<i>Eustrongylides</i> spp.	<i>Caiman yacare</i> (Daudin, 1802)	3.0	Stomach wall
Europe				
<i>Intermediate hosts</i>				
Georgia, Lake Paleostomi, 1975 (Chernova, 1975)	<i>Eu. excisus</i>	<i>Rutilus rutilus</i> (Linnaeus, 1758)	15.3	Mesentery, intestines
The UK, Fernworthy Reservoir, Devon (1976) (Kennedy & Lie, 1976)	<i>Eustrongylides</i> spp.	<i>Salmo trutta</i> (Linnaeus, 1758)	6.8	Mesentery, intestines
Russian Federation, the Caspian Sea, 1992. (Mikailov et al., 1992)	<i>Eu. excisus</i>	<i>Acipenser nudiiventris</i> (Lovetcky, 1828) <i>Acipenser persicus natio kurenensis</i> (Belyaeff, 1932)	62.2 33.1	Esophagus, intestines

Country, area, year (author)	Nematode species	Host species	Prevalence, %	Site of infection
		<i>Huso huso caspicus natio kurensis</i> (Babushkin, 1942)	38.9	
Romania, Lake Sinoe, Histria, Constanta County, 2007 (Sloboda et al., 2010)	<i>Eu. excisus</i>	<i>Neogobius eurycephalus</i> (Kessler, 1874)	29.6	Abdominal cavity, muscle tissue
		<i>N. syman</i> (Nordmann, 1840)	23.3	
		<i>N. melanostomus</i> (Pallas, 1814)	25.0	
		<i>Natrix tessellate</i> (Laurenti, 1768)	Not available	
Norway, River Otra, 2008 (Haugen et al., 2008)	<i>Eu. tubifex</i>	<i>Salmo trutta</i> (Linnaeus, 1758)	90.3–100.0	Intestine
Bulgaria, Srebarna Lake, 2005–2006, (Shukerova et al., 2011)	<i>Eu. excisus</i> <i>Eu. tubifex</i>	<i>Perca fluviatilis</i> (Linnaeus, 1758)	13.9 0.6	Mesentery, skin, muscle tissue, surface of internal organs
Poland, the Włocławek Reservoir on the lower Vistula River, 2012 (Mierzejewska et al., 2012)	<i>Eu. excisus</i> <i>Eu. tubifex</i>	<i>Perccottus glenii</i> (Dybowski, 1877)	2.4 12.5	Mesentery
Serbia, Danube-Tisa-Danube Canal, 2013 (Bjeli-Cabrilo et al., 2013)	<i>Eu. excisus</i>	<i>Sander lucioperca</i> (Linnaeus, 1758)	14.0	Abdominal wall muscles
Ukraine, the Zaporizhzhya Reservoir, 2013 (Yesipova, 2013)	<i>Eu. excisus</i>	<i>Silurus glanis</i> (Linnaeus, 1758)	12.0	Muscle tissue, visceral cavities
		<i>Perca fluviatilis</i> (Linnaeus, 1758)	65.0	
		<i>Sander lucioperca</i> (Linnaeus, 1758)	25.0	
Moldova, Prut-Dniester interriveran, 2014 (Moshu, 2014)	<i>Eu. excisus</i>	<i>Silurus glanis</i> (Linnaeus, 1758)	100.0	Muscle tissue, visceral cavities
		<i>Esox lucius</i> (Linnaeus, 1758)	94.0–100.0	
		<i>Perca fluviatilis</i> (Linnaeus, 1758)	94.0–100.0	
		<i>Perca fluviatilis</i> (Linnaeus, 1758)	72.0–100.0	Abdominal wall muscles
Ukraine, the Zaporizhzhya Reservoir, 2014 (Sinyava, 2014)	<i>Eu. excisus</i>	<i>Perca fluviatilis</i> (Linnaeus, 1758)	6.8	Abdominal wall muscles
Italy, Trasimeno Lake, 2016 (Branciani et al., 2016)	<i>Eustrongylides</i> spp.	<i>Micropterus salmoides</i> (Linnaeus, 1758)	1.9	
		<i>Atherina boyeri</i> (Risso, 1810)	0.1	
Ukraine, the Dnipro-Buh estuary, 2016–2019 (Goncharov et al., 2018; Honcharov, 2020)	<i>Eu. excisus</i>	<i>Perca fluviatilis</i> (Linnaeus, 1758)	85.1	Abdominal cavity, Mesentery, muscle tissue
		<i>Sander lucioperca</i> (Linnaeus, 1758)	58.1	
		<i>Esox lucius</i> (Linnaeus, 1758)	58.9	
		<i>Rutilus rutilus</i> (Linnaeus, 1758)	17.4	
		<i>Atherina boyeri</i> (Risso, 1810)	2.3	Muscle tissue
Italy, Northwest Tuscany, Lake Massaciuccoli, 2019 (Guardone et al., 2021)	<i>Eustrongylides</i> spp.	<i>Lepomis gibbosus</i> (Linnaeus, 1758)	18.3	Muscle tissue, visceral cavities
Italy, Lake San Michele, 2020 (Menconi et al., 2020)	<i>Eustrongylides</i> spp.	<i>Micropterus salmoides</i> (Lacepede, 1802)	16.7	
		<i>Perca fluviatilis</i> (Linnaeus, 1758)	10.0	
<i>Definitive hosts</i>				
Lithuania, the Baltic Sea, the Curonian Lagoon 2009 (Švažas et al., 2011)	<i>Eustrongylides</i> spp.	<i>Phalacrocorax carbo sinensis</i> (Shaw & Nodder, 1801)	7.1	Abdominal cavity, intestine
North-Western Poland, 1999–2010 (Kavetska et al., 2012)	<i>Eu. mergorum</i>	Wild ducks (Anseriformes: Anatidae)	3.7	Mesentery, intestine, stomach
<i>Accidental hosts</i>				
Russian Federation, the Caspian Sea, Makhachkala (Shchupakov, 1936; Kurochkin, 1958)	<i>Eu. excisus</i>	<i>Phoca caspica</i> (Gmelin, 1788)	40.0	Stomach wall
<i>Middle East</i>				
<i>Intermediate hosts</i>				
Turkey, Lake Uluabat, 1998–1999 (Ozturk et al., 2002)	<i>Eu. excisus</i>	<i>Neogobius fluviatilis</i> (Pallas, 1814)	29.8	Abdominal cavity
Iran, the Caspian Sea and its basin, 2005 (Sattari et al., 2005)	<i>Eu. excisus</i>	<i>Esox Lucius</i> (Linnaeus, 1758)	24.0	Muscles, gonads, body cavities, liver
		<i>Perca fluviatilis</i> (Linnaeus, 1758)	2.6–6.0	
		<i>Neogobius fluviatilis</i> (Pallas, 1814)	16.3	
		<i>N. kessleri</i> (Gunter, 1861)	50.0	
		<i>N. caspius</i> (Eichwald, 1831)	18.2	
		<i>Aspius aspius</i> (Linnaeus, 1758)	20.0	
		<i>Barbus capito</i> (Kessler, 1872)	40.0	
		<i>Abramis brama</i> (Linnaeus, 1758)	37.3	Mesentery, muscle tissue
Turkey, Lake Durusu (Terkos) 2001–2002, (Karatoy & Soylu, 2006)	<i>Eu. excisus</i>	<i>Carassius carassius</i> (Linnaeus, 1758)	1.0	Intestine
Iran, Aras Dam, 2007 (Pazooki et al., 2007)	<i>Eu. excisus</i>	<i>Blicca bjoerkna</i> (Linnaeus, 1758)	8.3	Abdominal cavity, muscle tissue
Turkey, the Bursa province, Kocadere Stream, Gölbaşı Lake, 2005–2006 (Selver et al., 2010; Aydogdu et al., 2008; Selver et al., 2009)	<i>Eustrongylides</i> spp.	<i>Rutilus rutilus</i> (Linnaeus, 1758)	3.5	
		<i>Scardinius erythrophthalmus</i> (Bean, 1903)	20.0	
Turkey, Antalya, Antalya Bay, 2009 (Aydoğdu et al., 2011)	<i>Eu. excisus</i>	<i>Aphanius mento</i> (Heckel, 1843)	6.9	Abdominal cavity, muscle tissue
Turkey, Lake Sığirci, Ipsala (Soylu, 2013)	<i>Eu. excisus</i>	<i>Perca fluviatilis</i> (Linnaeus, 1758)	94.2	Abdominal wall muscles
Turkey, Lake Eğirdir (Metin et al., 2014)	<i>Eu. excisus</i>	<i>Sander lucioperca</i> (Linnaeus, 1758)	100.0	Abdominal cavity, peritoneum, muscle tissue, adipose tissue, liver, spleen, swim bladder and stomach
Iran, the Caspian Sea, 2012 (Noei et al., 2015)	<i>Eu. excisus</i>	<i>Acipenser persicus</i> (Borodin, 1897)	7.7	Abdominal cavity, intestinal
Turkey, Marmara Lake, Turkey, 2016 (Demir & Karakişi, 2016)	<i>Eu. excisus</i>	<i>Carassius gibelio</i> (Bloch, 1782)	19.5	Abdominal cavity
Turkey, Samsun City Derbent, Dam Lake, 2020 (Pekmezci & Bolukbas, 2021)	<i>Eu. excisus</i>	<i>Sander lucioperca</i> (Linnaeus, 1758)	N/A	Visceral cavity
<i>Accidental hosts</i>				

Country, area, year (author)	Nematode species	Host species	Prevalence, %	Site of infection
Turkey, Lake Hazar, 2001–2002 (Saglam & Arıkan, 2006)	<i>Eu. excisus</i>	<i>Rana ridibunda</i> (Pallas, 1771)	14.4	Abdominal cavity, intestine
Iran, Shiraz region, 2020 (León-Régagnon, 2019)	<i>Eustrongylides</i> spp.	<i>Pelophylax ridibundus</i> (Pallas, 1771)	10.6	Mesentery
Asia				
<i>Intermediate hosts</i>				
Japan, Osaka, 2011 (Abe, 2011)	<i>Eu. ignotus</i>	<i>Hypomesus transpacificus nipponensis</i> (McAlister, 1963)	6.3	Abdominal wall
China, Sichuan Province, Hubei Province 2014 (Zhang et al., 2021)	<i>Eustrongylides</i> spp.	<i>Monopterus albus</i> (Zuiew, 1793)	26.7	Mesenteries
India, river Ramganga of Bareilly, Uttar Pradesh, 2019 (Gupta, 2019)	<i>Eu. excisus</i>	<i>Channa punctatus</i> (Bloch, 1793)	24.0	Abdominal cavity, ovaries, muscle tissue
India, Nagawara Lake, Bengaluru, 2020 (Sibina et al., 2020)	<i>Eustrongylides</i> sp.	<i>Glossogobius giuris</i> (Hamilton, 1822)	40.0	Abdominal cavity
East Java, Surabaya, 2020 (Subekti et al., 2020)	<i>Eu. ignotus</i>	<i>Synbranchus bengalensis</i> (McClelland, 1844)	29.3	Stomach and intestine cavity
<i>Definitive hosts</i>				
Japan, Lake Biwa, 2012 (El-Dakhly et al., 2012)	<i>Eu. tubifex</i>	<i>Phalacrocorax carbo</i> (Linnaeus, 1758)	86.7	Stomach
Oceania				
<i>Intermediate hosts</i>				
New Zealand, Lake Ellesmere, Wairarapa streams, 1978 (Hine, 1978)	<i>Eustrongylides</i> spp.	<i>Anguilla australis</i> (Richardson, 1841)	11.7	Abdominal cavity, intestine
Southwestern Australia, salt water rivers, 2006 (Chapman et al., 2006)	<i>Eustrongylides</i> spp.	<i>Galaxias maculatus</i> (Jenyns, 1842)	12.0	Abdominal cavity, intestine
Africa				
<i>Intermediate hosts</i>				
East Africa, Lake Victoria, 1974 (Paperna, 1974)	<i>Eustrongylides</i> spp.	<i>Bagrus docmac</i> (Bosc, 1816)	8.7	Gonads, muscles, abdominal cavity
		<i>Clarias mossambicus</i> (Buechelli, 1822)	19.3	
Ethiopia, Lakes Awassa, Lugo (Hayke), Ziway, 2007 (Gebremedhn & Tsegay, 2017)	<i>Eustrongylides</i> spp.	<i>Oreochromis niloticus</i> (Linnaeus, 1758)	0.9	Abdominal cavity, Mesentery,
		<i>Clarias gariepinus</i> (Buechelli, 1822)	16.5	Muscle tissue
Ethiopia, Southwestern Part of Lake Tana, Central Gondar 2017–2018 (Abiyu et al., 2020)	<i>Eustrongylides</i> spp.	<i>Oreochromis niloticus</i> (Linnaeus, 1758)	1.8	Gastrointestinal tract

Note: * – mean prevalence in the studied species.

South America

In South America the *Eustrongylides* nematodes were reported in Brazil, Argentina and Paraguay. The prevalence of infection of fish as intermediate hosts in Brazil ranged from 3.9% in *Acestrorhynchus lacustris* (Lutken, 1875) to 64.6% in *Pygocentrus nattereri* (Kner, 1858) (De Carvalho et al., 2003; Barros et al., 2010). The *Galaxias maculatus* (Jenyns, 1842) fish population was reported to be infected in the inner waters of Argentina (Brugni & Viozzi, 1999; Guagliardo et al., 2019). Sources define *Acestrorhynchus lacustris* (Lutken, 1875), *Hoplias malabaricus* (Bloch, 1794), *Ictalurus balsanus* (Jordan & Snyder, 1899) and other fishes as the main reservoir hosts for the *Eustrongylides* nematodes (De Carvalho et al., 2003; Barros et al., 2007; Rosas-Valdez et al., 2009). Eustrongylidosis was also found among fish-eating birds as definitive hosts (*Phalacrocorax brasilianus* (Gmelin, 1789), where the prevalence of infection was 2.13% (Monteiro et al., 2011). Eustrongylidosis has been reported in accidental hosts – caimans (*Caiman yacare* (Daudin, 1802)) and amphibians (*Rhinella marina* (Linnaeus, 1758)) (Goldberg et al., 1992; Melo et al., 2015).

Europe

In Europe the *Eustrongylides* nematodes have been reported in the UK, Norway, Italy, Romania, Bulgaria, Lithuania, Poland, Serbia, Moldova, Ukraine, and Russia. The prevalence of infection of fish as intermediate hosts ranged from 0.13% in *Atherina boyeri* (Risso, 1810) (Moshu, 2014) to 100% in the population of *Perca fluviatilis* (Linnaeus, 1758), *Silurus glanis* (Linnaeus, 1758) and *Esox lucius* (Linnaeus, 1758) (Branziari et al., 2016). The highest prevalence of eustrongylidosis was found in Eastern Europe: Moldova (up to 100%), Ukraine (12–100%), and Russia (33.1–62.2%). Most commonly the *Eustrongylides* nematodes were found in fishes of Acipenseridae, Cyprinidae, Salmonidae, Gobiidae, Percidae families (Chemova, 1975; Kennedy & Lie, 1976; Mikailov et al., 1992; Sloboda et al., 2010; Goga & Codreanu-Balcescu, 2013; Moshu, 2014). The reports also mentioned the invasion of definitive hosts, such as waterfowl (*Phalacrocorax carbo sinensis* (Linnaeus, 1758) with the pre-

valence of infection 7.14% (Švažas et al., 2011) and wild ducks (Anseriformes: Anatidae) – 3.71% (Kavetska et al., 2012). Accidental hosts for *Eustrongylides* nematodes were reptiles (*Natrix tessellata* (Laurenti, 1768)) and mammals (*Phoca caspica* (Gmelin, 1788)) (Shchupakov, 1936; Kurochkin, 1958; Sloboda et al., 2010).

The Middle East

In the Middle East, eustrongylidosis was mostly reported in Turkey and Iran. The prevalence of infection among fish as intermediate hosts ranged from 3.5% in *Rutilus rutilus* (Linnaeus, 1758) to 100% in *Sander lucioperca* (Linnaeus, 1758) (Selver et al., 2009; Metin et al., 2014). The *Eustrongylides* nematodes were found among other fish such as *Abramis brama* (Linnaeus, 1758), *Perca fluviatilis* (Linnaeus, 1758) and *Esox lucius* (Linnaeus, 1758) (Karatoy & Soylu, 2006; Selver et al., 2010; Soylu, 2013; Fallah et al., 2015). Amphibians *Rana ridibunda* (Linnaeus, 1758) and *Pelophylax ridibundus* (Pallas, 1771) were reported as accidental hosts (Saglam & Arıkan, 2006; León-Régagnon, 2019). Despite the high prevalence of eustrongylidosis in the Middle East, there was no mention of cases of a human infection in the literature. There was no information on infection of fish-eating birds as definitive hosts either.

Asia

In Asia the *Eustrongylides* nematodes were found in Japan, China, India, and Java. The prevalence of infection among fish as intermediate hosts ranged from 6.3% in *Hypomesus transpacificus nipponensis* (McAlister, 1963) to 29.3% in *Synbranchus bengalensis* (McClelland, 1844) (Abe, 2011; Subekti et al., 2020). Japan is characterized by the highest prevalence of eustrongylidosis in fish. Eustrongylidosis has been reported in the inner waters of some of Chinese provinces (Yangtze River, Danjiangkou Reservoir, Hubei; Minjiang River, Fujian; Poyang Lake, Jiangxi; Chaohu Lake, Yangtze River, Anhui; Pearl River, Guangdong; Taihu Lake, Jiangsu) among the local fishes *Monopterus albus* (Zuiew, 1793), *Odontobutis obscurus* (Temminck & Schlegel, 1845), *Silurus asotus* (Linnaeus, 1758), *Pelteobagrus fulvidraco* (Richardson, 1846), *Siniperca*

chuatsi (Basilewsky, 1855), *Culter mongolicus* (Basilewsky, 1855), *Channa argus* (Cantor, 1842), *Hemibarbus maculatus* (Bleeker, 1871), *Elopichthys bambusa* (Richardson, 1845) (Xiong et al., 2012). *Eustrongylides* nematodes were also found in waters of some Japanese prefectures in the Kurose River, Higashi-Hiroshima, Hiroshima Prefecture, Kamo River, Lake Shinji, Matsue, Shimane Prefecture among the populations of *Amur catfish* (Linnaeus, 1758), *Silurus asotus* (Linnaeus, 1758), *Channa argus* (Cantor, 1842) (Moravec & Nagasawa, 2018). The infection of the definitive hosts, such as *Phalacrocorax carbo* (Linnaeus, 1758), was much less common (El-Dakhly et al., 2012). There is no data about other species (including humans) being infected in Asia.

Oceania

In Oceania the *Eustrongylides* nematodes were reported in New Zealand and Australia. The prevalence of infection among fish as intermediate hosts ranged from 11.7% in *Anguilla australis* (Richardson, 1841) (Hine, 1978) to 12.0% in *Galaxias maculatus* (Jenyns, 1842). Cases of eustrongylidosis in accidental and definitive hosts were not reported.

Africa

On the African continent eustrongylidosis was reported in Lake Victoria in Eastern Africa and the inner waters of Ethiopia. The prevalence of eustrongylidosis ranged from 0.9% in *Oreochromis niloticus* (Linnaeus, 1758) (Gebremedhn & Tsegay, 2017) to 19.3% in *Clarias mossambicus* (Scopoli, 1777) (Papema, 1974). Cases of eustrongylidosis in accidental and definitive hosts were not reported except for two cases of humans being infected in Sudan (Eberhard & Ruiz-Tiben, 2014).

Summary of evidence on the prevalence of *Eustrongylides* spp.

Summarizing the distribution of eustrongylidosis in the world, there are clear differences in the prevalence of infection between different hosts. In North America, the main intermediate hosts for the *Eustrongylides* nematodes are fish-eating birds, rarely – fishes. In Europe, Asia, the Far East, Oceania and Africa fishes are the predominantly infected species. The main spreaders of the infection, fish-eating birds, are rarely reported to be infected.

There were several reports of human infection from the USA and Sudan. Other species are rarely infected and act as accidental hosts. These species include turtles, snakes, amphibians, and marine mammals. These facts suggest the bias in the diagnosis of eustrongylidosis, which does not show the objective picture of distribution of the *Eustrongylides* nematode in the world among different species.

Among intermediate hosts, the highest prevalence of infection was found in *Perca fluviatilis* (Linnaeus, 1758), *Sander lucioperca* (Linnaeus, 1758), *Silurus glanis* (Linnaeus, 1758), *Esox lucius* (Linnaeus, 1758). Most commonly, fish-eating birds of the Ciconiidae family are infected, the highest prevalence of infection among definitive hosts was found in the birds of the Ciconiformes and Phalacrocoracidae families, which serve as definitive hosts for *Eustrongylides* nematodes. The highest prevalence among definitive hosts was found in *Phalacrocorax carbo* (Linnaeus, 1758) (86.7%) in Japan.

Overall, continents with a warm climate, such as South America and Asia, have more species of fishes, reptiles, and fish-eating birds that serve as a potential hosts for the *Eustrongylides* nematodes (Svirezhev, 1987).

The dominating species of the *Eustrongylides* nematodes differed between countries and regions. *Eu. ignotus* and *Eu. tubifex* were predominantly found in the North America region, while *Eu. excisus* was found predominantly in Europe and the Middle East.

Conclusion

In the present review, the authors highlighted the distribution of eustrongylidosis in different countries and regions, and in different species. The *Eustrongylides* spp. nematodes, Jägerskiöld, 1909 were first described and substantiated as species of the *Eustrongylides* genus by Jäger-

skiöld in 1909, as they were taken from waterfowl from East Africa during the autopsy.

This parasitic species is very widespread across the world. In North America it is mostly reported among fishes and birds, sometimes – humans. In South America the disease was also reported in reptiles and amphibians. In Europe, Africa and Asia, Oceania, and the Middle East, the disease is mostly reported in fishes, rarely in birds. *Eu. ignotus* and *Eu. tubifex* are the main parasitic species reported in North America, while for Europe, Asia, Africa, and the Middle East the most prevalent species was *Eu. excisus*.

Eustrongylides spp. nematodes in their life cycle require both intermediate and definitive hosts to live in the water or close to the water. We suggest that this is a result of adaptation of the parasite to the habitat of fish-eating birds, the definitive hosts for the *Eustrongylides* spp. nematodes. These hosts play a crucial role in the spreading of the nematodes during seasonal migration, which could explain the emergence of the eustrongylidosis infections in the regions that never had it before. In our review we found that most often the euryhaline fish species are infected with *Eustrongylides* spp. nematodes.

Based on the number of publications on the prevalence of eustrongylidosis in different regions we suggest that there is an increased interest in this nematode infection and, possibly, an increased prevalence of eustrongylidosis throughout the world. Studies on the prevalence of eustrongylidosis in Asia and the Middle East have been published in the last 20 years. We also suggest that such trend cannot be explained by the lack of diagnostic possibilities alone. *Eustrongylides* spp. nematodes have a distinctive morphology that makes microscopic identification very straightforward. Most likely, the wider distribution of *Eustrongylides* spp. nematodes in recent years is due to the ecological plasticity of the parasite and adaptation to the new habitats and new hosts for its life cycle.

Most often *Eustrongylides* spp. nematodes were found in fish and other intermediate hosts, whereas infection of fish-eating birds (definitive hosts) was reported less often. One possible explanation for that is that infection of the birds has mostly scientific interest among researchers while infection of fish has an impact on fisheries and the industry; hence, closer attention to the intermediate hosts (fish). We did not find the literature that investigated the prevalence of eustrongylidosis in the definitive hosts in Africa or Oceania.

Based on the available literature we concluded that *Eustrongylides* spp. nematodes are adapted the best to the continental climate as the prevalence of the infection in countries with continental climate was much higher than in countries with a tropical and subtropical climate. Considering the increasing distribution of the *Eustrongylides* spp. nematodes and reported cases of infection in humans we believe that closer attention to these nematodes is required to prevent the outbreaks of the infection in humans and other mammals.

The authors declare the absence of any conflict of interest.

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