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## CESTODES OF ANTARCTIC AND SUBANTARCTIC FISH: HISTORY AND PROSPECTS OF RESEARCH

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The first information about cestodes of Antarctic and Subantarctic fish appeared at the beginning of the XX century: a cestode *Phyllobothrium dentatum* from an unknown shark was described. Peak of activity of studying Antarctic cestodes fell on 1990–2006. During this period, significant works were published, devoted to description of new species, their life cycles, host specificity of cestodes – fish parasites, and their geographical distribution. A notable contribution to the study of elasmobranch cestodes was made by a group of Polish scientists, headed by Wojciechowska (Rocka). Systematic position of 21 cestode species from 13 genera of 8 families of 6 orders was analyzed. Cestode fauna has been studied in less than 7 % of the total ichthyofauna of this area, while potential definitive and intermediate hosts remain unexplored. The largest number of cestode species (12) was recorded in four ray species of the family Rajidae. Eight cestode species, reaching sexual maturity, have been registered in intestines of teleosts: *Bothriocephalus antarcticus*, *B. kerguelensis*, *Bothriocephalus* sp., *Parabothriocephalus johnstoni*, *P. macruri*, *Clestobothrium crassiceps*, *Neobothriocephalus* sp., and *Eubothrium* sp. Larvae of five cestode species (*Onchobothrium antarcticum*, *Grillotia (Grillotia) erinaceus*, *Lacistorhynchus tenuis*, *Calyptrorhynchium* sp., and *Hepatoxylon trichiuri*), ending their development in elasmobranchs, were found in teleosts. Systematic position of 5 cestode species out of 12, found in rays, is unidentified. Cestode fauna is characterized by a high level of endemism: 67 % of the total cestode fauna is not found to the north of Subantarctic. Coastal areas, mostly covered by research, are those in the Atlantic and Indian sectors of Antarctic. The biodiversity of elasmobranch cestodes, inhabiting Antarctic and Subantarctic, is underestimated, since only one third of species of these fish have been studied so far. Genetic studies of Antarctic cestodes have just begun to develop. Ribosomal sequences from D1–D3 fragments of 28S rDNA are known for 2 species only: *Onchobothrium antarcticum* from the second intermediate (*Notothenia rossii* and *Dissostichus mawsoni*) and definitive hosts (*Bathyraja eatonii*), as well as larvae of *Calyptrorhynchium* sp. from the second intermediate hosts (*D. mawsoni* and *Muraenolepis marmorata*). The main directions of further research on cestode fauna should be developed in combination with morphological, faunistic, genetic, and ecological studies.

**Keywords:** cestodes, fish, fauna, taxonomy, endemism, Antarctic, Subantarctic

Parasitic organisms are representatives of various systematic groups of invertebrates; they form a significant part of the ecosystem's species diversity (Fonseca et al., 2010). Some current calculations show as follows: there are at least 50 % more parasites (75 thousand species have been described) than free-living animals (Poulin & Morand, 2000, 2004). According to preliminary calculations,

with an increase in the intensity of studying parasites, inhabiting vertebrates, their number may reach 300 thousand (de Meeus & Renaud, 2002 ; Dobson et al., 2008). The effect of parasites on their hosts spreads both up and down the food webs, and this affects all the elements of the ecosystem. Like free-living organisms, parasites are affected by biotic and abiotic environmental factors; moreover, they are effective indicators of many aspects of host biology and can act as markers of the state of the free-living biota of the community. So, parasites have to be accounted when studying the state of diversity of any biological community.

Antarctic is a unique and poorly explored region, with a large number of endemics recorded. Peculiarities of Antarctic water (stable low temperature and, as a consequence, good solubility of oxygen in water; narrow shelf; and seasonal fluctuations in illumination) contributed to an emergence of unique adaptations and a high degree of endemism both among representatives of local fauna and among their parasites (Bargelloni et al., 1994 ; Eastman, 1993 ; Klimpel & Pal, 2011 ; Kock, 1992 ; Rocka, 2006). Due to unfavorable climatic conditions during most of the year, Antarctic marine fauna, *inter alia* parasite fauna, has not yet been studied in many aspects.

According to current data, ichthyofauna within the Antarctic Convergence zone is represented by 374 species from 47 families, including 14 elasmobranch species (Chondrichthyes) (Duhamel et al., 2014 ; FishBase..., 2019). More than 115 species out of the entire diversity of Antarctic fish belong to the endemic family Nototheniidae Günther, 1861. In this zone, elasmobranchs are represented by sharks (5 species from 3 families) and rays (10 from 2). Sharks prefer warm water; they are mainly captured in the northern area of the Southern Ocean, in the demersal zone of the islands. So far, only one shark capture is known in the southern Antarctic: in the Ross Sea (Rocka, 2003).

The aim of this work was to evaluate the diversity of cestode fauna of Antarctic and Subantarctic fish, the degree of cestodes studying, the level of endemism of cestode fauna, and the prospects for their further research.

## RESULTS AND DISCUSSION

In this study, we tried to cover as much as possible the most significant works on cestodes of Antarctic and Subantarctic fish, to evaluate the diversity of these helminths in different hosts, and to highlight promising directions of research. For simplicity of perception, we give a combined list of cestodes species in definitive fish hosts (Table 1), except for cestode larvae of various structures, found in teleosts of this area: they are fully presented in the annotated work (Oğuz et al., 2015, see Table 1).

Study areas of fish cestodes are the Atlantic, Indian, and Pacific sectors of Antarctic and Subantarctic (Fig. 1). Systematic position of 21 cestode species from 13 genera of 8 families of 6 orders, as well as their vertebrate hosts, was analyzed according to WoRMS (<http://www.marinespecies.org>) and other sources (Kvach & Kuzmina, 2020 ; Klimpel et al., 2017 ; Kuzmina et al., 2020 ; Muñoz & Cartes, 2020 ; Oğuz et al., 2015).

**History of development of fish cestodes study.** According to Southwell's summary (1925), the first data on cestodes of Antarctic and Subantarctic fish appeared in the early XX century. This applies to the description of *Phyllobothrium dentatum* Linstow, 1907 from an unknown shark, captured off South Georgia coast during the Scottish National Antarctic Expedition (1902–1904). Current systematic position of this species is ambiguous. Southwell (1925), Yamaguti (1959), and Rocka (2003 ; 2006) consider it *species inquirenda*. In Ruhnke's monograph (2017), this species is absent from the list of valid taxa and species of unclear systematic position of the order Phyllobothriidea.

**Table 1.** Fauna of mature cestodes of Antarctic and Subantarctic fish

Cestode species	Species status	Host	Finding areas	Authors
<b>“Tetrphyllidea” Van Beneden, 1850 relics</b>				
<i>Dinobothrium septaria</i> Van Beneden, 1889	valid	<i>Lamna nasus</i> (Bonnater, 1788)	SG, Kerguelen Islands	[45]
<b>Onchoproteocephalidea Caira, Jensen, Waeschenbach, Olson &amp; Littlewood, 2014</b>				
<i>Onchobothrium antarcticum</i> Wojciechowska, 1990	valid	<i>Bathyrāja eatonii</i> (Günther, 1876), <i>B. maccaini</i> S. Springer, 1971	SSI	[61]
			Weddell Sea	[48]
<b>Phyllobothriidea Caira, Jensen, Waeschenbach, Olson &amp; Littlewood, 2014</b>				
<i>Phyllobothrium georgiense*</i> Wojciechowska, 1991	incertae sedis	<i>Amblyrāja georgiana</i> (Norman, 1938)	SG shelf	[55]
<i>Ph. siedleckii</i> Wojciechowska, 1991		<i>B. eatonii</i> , <i>B. maccaini</i>	SSI	[48]
<i>Ph. rakusai</i> Wojciechowska, 1991			Weddell Sea	
<i>Ph. arctowskii</i> Wojciechowska, 1991		<i>B. maccaini</i>	SSI	[55]
<i>Ph. arctowskii</i> Wojciechowska, 1991		<i>Bathyrāja</i> sp. 2	Weddell Sea	[48]
<i>Phyllobothrium</i> sp.	–	<i>B. eatoni</i>	Heard Island plateau	[61]
<i>Guidus antarcticus</i> (Wojciechowska, 1991)	valid	<i>B. eatonii</i> , <i>B. maccaini</i>	SSI	[56]
<i>G. awii</i> (Rocka & Zdzitowiecki, 1998)	valid	<i>B. maccaini</i>	Weddell Sea	[48]
<b>Rhinebothriidea Healy, Caira, Jensen, Webster &amp; Littlewood, 2009</b>				
<i>Notomergarchynchus shetlandicum</i> (Wojciechowska, 1990)	valid	<i>B. eatonii</i> , <i>B. maccaini</i>	Admiralty Bay, Elephant Island	[25]
<i>Pseudanthobothrium minutum</i> Wojciechowska, 1991	valid	<i>B. eatonii</i>	SSI	[56]
<i>Ps. notogeorgianum</i> Wojciechowska, 1990	valid	<i>A. georgiana</i>	SG shelf, Joinville Island, SSI	[54]
<b>Diphylloidea Van Beneden in Carus, 1863</b>				
<i>Echinobothrium acanthocolle</i> Wojciechowska, 1991	valid	<i>A. georgiana</i>	SG shelf	[45 ; 56]
<b>Bothriocephalidea Kuchta, Scholz, Brabec &amp; Bray, 2008</b>				
<i>Bothriocephalus kerguelensis</i> Prudhoe, 1969	valid	<i>Notothenia cyanobranca</i> Richardson, 1844, <i>N. rossi</i> Richardson, 1844	Kerguelen subregion	[43]
<i>B. antarcticus</i> Wojciechowska, Pisano & Zdzitowiecki, 1995	valid	<i>Champscephalus gunnari</i> Lönnberg, 1905, <i>Channichthys rhinocerotus</i> Richardson, 1844	Kerguelen subregion, Heard Island	[61]
<i>Bothriocephalus</i> sp.	–	No data	Kerguelen subregion	[5 ; 35]
			No data	[61]

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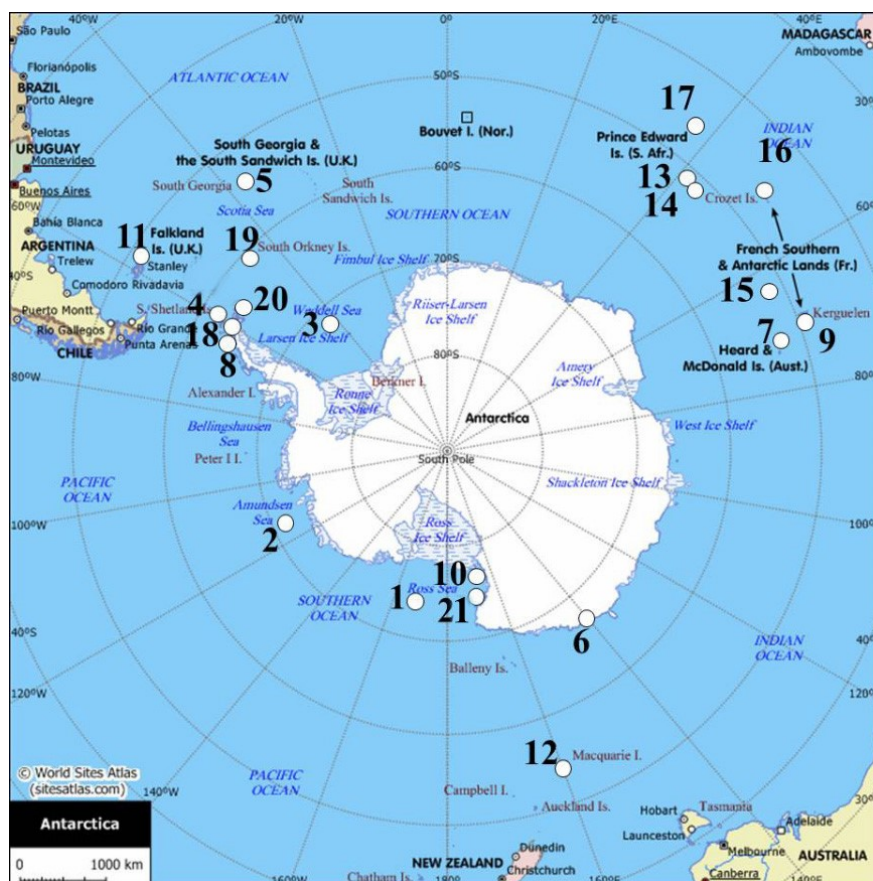
Cestode species	Species status	Host	Finding areas	Authors
<i>Parabothriocephalus macruri</i> Campbell, Correia & Haedrich, 1982	valid	<i>Macrourus berglax</i> Lacépède, 1801	No data	[14]
		<i>Mac. carinatus</i> (Günther, 1878)	Falkland Islands	[1]
<i>Parabothriocephalus johnstoni</i> Prudhoe, 1969	valid	<i>Mac. whitsoni</i> (Regan, 1913), <i>Mac. holotrachys</i> Günther, 1878	Indian sector of the Southern Ocean	[43]
			Weddell Sea	[48]
			Heard Island, Kerguelen Islands	[30]
		<i>Mac. whitsoni</i>	Weddell Sea, SSI	[52]
<i>Clestobothrium crassiceps</i> (Rud., 1819)	valid	<i>Dissostichus eleginoides</i> Smitt, 1898	Falkland Islands	[12]
			SG	[3]
		<i>Merluccius hubbsi</i> Marini, 1933	Patagonian shelf	[44]
<i>Neobothriocephalus</i> sp.	–	No data	Kerguelen subregion	[5]
<i>Eubothrium</i> sp.	–	<i>N. rossii</i>	Crozet Islands, Ob Bank	[9]
			Heard Island, Crozet Islands	[8]
		<i>Lepidonotothen squamifrons</i> (Günther, 1880)	Crozet Islands, Skif, Ob, and Lena banks	[8 ; 9]

**Note:** \* taxonomy of cestodes of the genus *Phyllobothrium* according to (Wojciechowska, 1993c); SG is South Georgia Island; SSI is South Shetland Islands.

The most significant contribution to the development of studies of elasmobranch cestodes of the area was made by Wojciechowska (1990a ; 1990b ; 1991a ; 1991b ; 1993a ; 1993b ; 1993c) with co-authors (1994 ; 1995). She has described ten new cestode species from four ray species from the family Rajidae Blainville, 1816; currently, six species are considered valid (Table 1). Of her later studies, published under the name of Rocka (2014 ; 2005 ; 2007 ; 2003 ; 2006 ; 2017 ; 1998), the work (2006) is of particular interest. It is devoted to study of life cycles, specificity, and geographic distribution of helminths of Antarctic fish.

The first works on cestodes of Antarctic and Subantarctic teleosts were published in the late 1960s. Prudhoe (1969) has described *Parabothriocephalus johnstoni* Prudhoe, 1969 from macrourids and *Bothriocephalus kerguelensis* Prudhoe, 1969 from notothenium fish in Kerguelen Island area. Later, Reimer and Jessen (1974) found *Clestobothrium crassiceps* (Rud., 1819) in *Merluccius hubbsi* Marini, 1933 on the Patagonian shelf. The description of another species – *Parabothriocephalus macruri* Campbell, Correia & Haedrich, 1982 from *Macrourus berglax* Lacépède, 1801 – marked the 1980s (Campbell et al., 1982). This discovery was re-confirmed by Gaevskaya and Rodyuk in another host species: *Macrourus carinatus* Günther, 1878 (Gaevskaya & Rodyuk, 1988).

In the same period, in a series of works by Parukhin (1981 ; 1982) and Lyadov (1981 ; 1985), mature cestodes, not identified to species level, were found in Kerguelen Island area: *Bothriocephalus* sp., *Neobothriocephalus* sp., and *Eubothrium* sp. The last species of Antarctic cestodes



**Fig. 1.** Sampling localities of cestodes of Antarctic and Subantarctic fish: the Atlantic (3–5, 8, 11, and 18–20), Indian (6, 7, 9, and 13–17), and Pacific (1, 2, 10, 12, and 21) sectors. 1 – Ross Sea; 2 – Amundsen Sea; 3 – Weddell Sea; 4 – South Shetland Islands (Deception Island, King George Island, Admiralty Bay, and Elephant Island); 5 – South Georgia (Cumberland Bay); 6 – Adélie Land; 7 – Heard Island; 8 – Archipelago Melchior; 9 – Kerguelen Island; 10 – McMurdo Sound; 11 – Falkland Islands; 12 – Macquarie Island; 13 – Ob Bank (guyot); 14 – Lena Bank; 15 – Skif Bank; 16 – Crozet Islands; 17 – Prince Edward Islands; 18 – Bransfield Strait; 19 – South Orkney Islands (Signy Island); 20 – Joinville Island; 21 – Terra Nova Bay

described – *Bothricephalus antarcticus* Wojciechowska, Pisano & Zdzitowiecki, 1995 – was registered by Wojciechowska and co-authors (1995) from *Champscephalus gunnari* Lönnberg, 1905 and *Channichthys rhinoceratus* Richardson, 1844, captured in Heard Island area (the Indian sector of Antarctic).

Since 1965, a large number of articles have been published on the finding of various cestode larvae in teleosts of this area. In the general number of publications, the works of Polish scientists stand out, in particular a series of articles by Wojciechowska with co-authors (1993a ; 1993b ; 1993c ; 1994), in which variations in the forms of cestode larvae from the orders Tetraphyllidea Carus, 1863 and Tetrabothriidea Baer, 1954 were studied. The authors tried to systematize the variety of forms of cestode larvae of these orders, since in most cases, morphology of larval stages differs significantly from morphology of mature cestodes. To date, three more orders have been isolated from Tetraphyllidea (Caira et al., 2014): Onchoproteocephalidea, Phyllobothriidea, and Rhinebothriidea. Therefore, Wojciechowska and co-authors (1993a ; 1993b ; 1993c ; 1994) analyzed the diversity of morphology of cestode larvae of five orders. The works of Zdzitowiecki with co-authors (2001 ; 2004 ; 1999 ; 1997 ; 1998) and Laskowski with co-authors (2005 ; 2007) are devoted to the study of helminth fauna of certain fish species, in which cestode larvae are registered, being identified only to order level, as well as to the study of indicators of their abundance. Of domestic studies, the publications

of Parukhin and Lyadov (1981 ; 1986 ; 1981 ; 1982 ; 1985), as well as those of Gaevskaya with co-authors (1988 ; 1987 ; 1990), have to be highlighted. These works are dedicated to the study of fish helminths, *inter alia* matures and cestode larvae, in the Kerguelen subregion, Falklands-Patagonian region, South Georgia Island, and Ob and Lena banks.

The work of Laskowski and Rocka (2014) on the molecular identification of plerocercoids from *Notothenia rossii* Richardson, 1844 is of significant interest. The authors have shown the co-specificity of plerocercoids and matures of *Onchobothrium antarticum* Wojciechowska, 1990 from stingray *Bathyraja eatonii* (Günther, 1876), caught in the Atlantic sector of Antarctic. The publications of Gordeev and Sokolov (2016 ; 2017) contain data on the helminth fauna of teleosts *Dissostichus mawsoni* Norman, 1937 and *Muraenolepis marmorata* Günther, 1880 from the Pacific sector of Antarctic. The authors confirmed, *inter alia* by molecular genetics methods, that the plerocercoids found belong to the species *Onch. antarticum*. These data expanded information on species composition of the second intermediate hosts of *Onch. antarticum* cestodes in Antarctic. Moreover, this is of particular interest in terms of the first finding of *Calyptrorobothrium* sp. cestode larvae in *D. mawsoni* and *M. marmorata*, confirmed by molecular genetic data. At the same time, mature *Calyptrorobothrium* Monticelli, 1893 have not yet been found in Antarctic and Subantarctic elasmobranchs. It should be emphasized that *Calyptrorobothrium* spp. are cosmopolitans, parasites of rays Torpedinidae Henle, 1834, found in temperate and tropical seas.

In recent years, generalizing publications appear, devoted not only to helminth fauna of certain teleost species, but also to their role in the transmission of helminth larvae of different taxa to definitive hosts (fish, birds, and mammals), community structure, and pathogenic effect of helminths on their hosts. Thus, Brickle and co-authors (2005 ; 2006) have studied changes in fauna and structure of parasite communities of the Patagonian toothfish *Dissostichus eleginoides* Smitt, 1898, depending on body length, sex, season, and depth of the host habitat; the researchers have used the example of various helminths, *inter alia* trypanorhynch larvae (*Grillotia (Grillotia) erinaceus* (Van Beneden, 1858) Guiart, 1927 and *Hepatoxylon trichiuri* (Holten, 1802) Bosc, 1811), diphyllorobothriids, and tetraphyllids.

The study of parasite communities of *Notothenia coriiceps* J. Richardson, 1844, depending on its size, was continued by Kuzmina and co-authors (2020). In addition to the previously identified helminths, the researchers have found in this host cestode larvae of the orders Diphyllorobothriidea Kuchta, Scholz, Brabec & Bray, 2008 (*Diphyllorobothrium* sp.) and Tetraphyllidea (three morphotypes: with monolocular, bilocular, and trilocular bothridia). Out of the identified cestode larvae, the dominating ones in terms of abundance were *Diphyllorobothrium* sp., whose definitive hosts are marine mammals. It was found that the intensity of infestation with *Diphyllorobothrium* sp. and tetraphyllide larvae increases with fish age.

Palm with co-authors (1998 ; 2007) have studied possible life cycles of some helminths in Antarctic. It was revealed that larvae of mammalian parasites, for example cestode larvae of the order Diphyllorobothriidea, use teleosts as paratenic hosts, especially those from the families Nototheniidae and Channichthyidae T. N. Gill, 1861. The authors claim that some teleost helminths, *e. g.* cestode larvae of the order Tetraphyllidea, have concurrently adopted different benthic host systems in order to reach their definitive hosts: elasmobranchs. Walter and co-authors (2002) analyzed species composition of parasites in three macrourus species from two Antarctic areas and identified factors, contributing to the similarity of parasite faunas: macrourus nutrition, migration, and close phylogenetic relationships. Santoro with co-authors (2013) studied pathological changes in five teleost species as a result of parasitizing of Diphyllorobothriidea and Tetraphyllidea larvae (with monolocular and bilocular bothridia).

Muñoz and Cartes (2020) have analyzed the diversity and abundance of endoparasites of Antarctic and Subantarctic fish. It was revealed that a number of parasite species in Antarctic fish is larger. The authors suggested as follows: high abundance of parasites in Antarctic fish is caused by sympatric speciation in certain parasitic lines or by exploitation of new resources, contributing to the appearance of more parasite species than in Subantarctic environments.

Based on the foregoing, we summarize that the Atlantic and Indian sectors of Antarctic are more fully covered by research than the Pacific one. The largest number of mature cestodes of teleosts was recorded in the Indian sector (Table 1). All this indicates the fragmental character of the ongoing studies of Antarctic cestodes and the need for more thorough and systematic work to obtain a complete faunistic picture.

**Biodiversity of cestodes of Antarctic and Subantarctic fish.** Parasites of Antarctic and Subantarctic are represented by various taxa among invertebrates and vertebrates. Most of marine vertebrates' fauna in this area is represented by fish: 374 species have been recorded (Duhamel et al., 2014; Eastman, 1993). Currently, 135 species of Antarctic fish have 189 species of parasitic organisms from 11 taxonomic groups: Coccidia – 6 species; Microsporidia – 2; Myxosporea – 13; Monogenea – 23; Trematoda – 65; Cestoda – 21; Nematoda – 14; Acanthocephala – 19; Hirudinea – 16; Copepoda – 7; and Isopoda – 3 species. Thus, a little more than a third of the total ichthyofauna of this area was examined for the presence of parasites. The ratio of cestodes, recorded in Antarctic and Subantarctic fish, is 11 % of the parasite species, known for this area. This indicates lack of knowledge of these helminths' fauna.

According to the recent report on Antarctic cestodes (Rocka, 2017), 12 species from 5 orders were found in spiral intestines of 5 elasmobranch species (Table 1). The highest species richness was recorded for the orders Phyllobothriidea (*Phyllobothrium* Van Beneden, 1850 – 4 species; *Guidus* Ivanov, 2006 – 2) and Rhinebothriidea (*Pseudanthobothrium* Baer, 1956 – 2; *Notomegarhynchus* Ivanov & Campbell, 2002 – 1). The smallest number of cestode species (one species each) was registered for the orders Onchoproteocephalidea (*Onchobothrium* de Blainville, 1828) and Diphyllidea (*Echinobothrium* Van Beneden, 1849). Out of 12 cestode species, only 7 have a recognized taxonomy (Table 1); the status of the rest is *incertae sedis* (Ruhnke et al., 2017).

Eight cestode species from five genera of the order Bothriocephalidea (Table 1) reach maturity in intestines of Antarctic and Subantarctic teleosts (Parukhin & Lyadov, 1981, 1982; Rocka, 2017). Three cestode species, identified in teleosts, were representatives of the genus *Bothriocephalus* Rudolphi, 1808; two cestode species were of the genus *Parabothriocephalus* Yamaguti, 1934; one species each were identified from the genera *Clestobothrium* Lühe, 1899, *Neobothriocephalus* Mateo & Bullock, 1966, and *Eubothrium* Nybelin, 1922. The findings of mature cestodes of the genus *Eubothrium* (Table 1) in intestines of Antarctic notothenium fish (Parukhin & Lyadov, 1981, 1982) are unique: these cestodes were not repeatedly recorded in fish of this family (Kuchta & Scholz, 2017). To date, only six species of the genus *Eubothrium* have a recognized taxonomy; they are found in Salmonidae G. Cuvier, 1816, Gadidae Rafinesque, 1810, Acipenseridae Bonaparte, 1831, Clupeidae Cuvier, 1817, Zoarcidae Swainson, 1839, Osmeridae Jordan, 1923, Cyprinidae Rafinesque, 1815 (*Phoxinus* L., 1758), and Trichodontidae Bleeker, 1859 (Kuchta & Scholz, 2017). In addition to mature cestodes, larvae of unclear species identity and of various morphology were found in intestines of teleosts (Oğuz et al., 2015). Only five species of cestode larvae, whose definitive hosts are elasmobranchs, were identified: *Onchobothrium antarticum*, *Calyptrbothrium* sp., *Grillotia* (*Grillotia*) *erinaceus*,

*Lacistorhynchus tenuis* (Van Beneden, 1858) Pintner, 1913, and *Hepatoxylon trichiuri* (Gaevsкая & Rodyuk, 1988 ; Gaevsкая et al., 1990 ; Brickle et al., 2005 ; Brickle, 2006 ; Gordeev & Sokolov, 2016, 2017).

In addition to fauna, life cycles, and ecology of cestodes of Antarctic and Subantarctic hydrobionts, authors began studying phylogeny of these helminths. The research of genetic diversity of Antarctic cestodes just started developing. To date, data on ribosomal sequences from D1–D3 fragments of 28S rDNA are known for 2 species only: *Onchobothrium antarcticum* from the second intermediate (*Notothenia rossii* and *Dissostichus mawsoni*) and definitive hosts (*Bathyrāja eatonii*) and larvae of *Calyptrorhynchium* sp. from the second intermediate hosts (*D. mawsoni* and *Muraenolepis marmorata*) (Gordeev & Sokolov, 2016, 2017 ; Laskowski & Rocka, 2014).

The biodiversity of cestodes of Antarctic and Subantarctic elasmobranchs has been studied fragmentarily. Within the Antarctic Convergence zone, there are 15 elasmobranch species (5 shark and 10 ray ones) (Duhamel et al., 2014 ; FishBase..., 2019), and only for 5 species (4 ray and 1 shark one) there are data about their infestation with cestodes. Systematic position of 5 cestode species out of 12, found in rays, is unidentified. Taxonomic identification of these helminths is often difficult due to their poor morphological preservation and unsuitability for genetic research.

**Endemism of cestode fauna of Antarctic and Subantarctic fish.** Endemism of parasites of Antarctic and Subantarctic invertebrates and vertebrates is studied insufficiently. According to Rocka (2006), all cestodes, found in elasmobranchs, are endemic to this area, except for *Dinobothrium septaria*, registered also in the great white shark *Carcharodon carcharias* (L., 1758) in the northwestern Atlantic, Woods Hole, Massachusetts (Dailey & Vogelbein, 1990). It should be mentioned that *Ph. georgiense* was previously considered an Antarctic endemic. Meanwhile, it was recently found in the ray *Bathyrāja sexocuada* Mysawa, Orlov, Orlova, Gordeev, Ishihara, 2020 in Simushir Island water in the northwestern Pacific (Gordeev & Polyakova, 2020), which allows us to consider its distribution bipolar. Consequently, 11 cestode species are endemic to elasmobranchs (Table 1).

In teleosts, endemics are represented by mature cestodes: Antarctic species *Parabothriocephalus johnstoni* and Subantarctic ones *Bothriocephalus kerguelensis* (Prudhoe, 1969) and *B. antarcticus* (Wojciechowska et al., 1995). Moreover, in teleosts of this area, bipolar species *Parabothriocephalus macruri* and cosmopolitan *Clestophrium crassiceps* can be found (Wojciechowska et al., 1995).

The analyzed data indicate a high endemism of cestode fauna of Antarctic and Subantarctic fish (67 % of all cestode fauna): out of 21 cestode species, 14 are not found to the north of this area.

**Study of larval stages of cestode development in Antarctic and Subantarctic fish.** Cestode larvae of different structure are often found in Antarctic teleosts (Rocka, 2003, 2006, 2017). It is difficult to identify systematic position of these larvae, parasitizing at proceroid and plerocercoid stages of crustaceans and teleosts, since their scolices differ significantly in structure from those of matures. To date, many various forms of cestode larvae have been identified on the basis of different scolex structure (cercooid I, II, III, IV, V, VI; cercooid VIII (without bothria); monolocular, bilocular and others) (Wojciechowska, 1993a, b, c ; Wojciechowska et al., 1994). A complete list of all morphological variations of cestode larvae with an indication of the hosts, in which they were found, is given in the annotated list of parasites of Antarctic hydrobionts, compiled by Oğuz with co-authors (2015, see Table 1). It should be mentioned that such classification by different researchers of cestode larvae without establishing their taxonomic affiliation, in particular on the basis of molecular genetic data, leads to considerable confusion.



Researchers attempted to systematize and identify various cestode larvae in teleosts of the area. The most recognized works are those of Rocka (2003 ; 2006), in which five larvae morphotypes were distinguished: cercoids with bothridia, subdivided into one, two, and three loculi; cercoids with undivided bothridia with hook-like projections; and cercoids with subcylindrical bothridia. Rocka suggested as follows: cercoids with undivided bothridia are representatives of the genus *Anthocephalum* Linton, 1890, and cercoids with bilocular bothridia are cestode larvae from the genera *Pseudanthobothrium* Baer, 1956, *Notomegarhynchus* Ivanov & Campbell, 2002, and *Anthobothrium* Van Beneden, 1850. It should be noted that mature cestodes of the genera *Anthocephalum* and *Anthobothrium* have not yet been found in Antarctic and Subantarctic rays; therefore, it is impossible to confirm this assumption.

By molecular genetic methods (Laskowski & Rocka, 2014), it was proved that cercoids with trilocular bothridia, parasitizing teleosts, belong to the species *Onchobothrium antarcticum* (Oncobothriidae) from spiral intestine of rays. Also, Rocka suggested that cercoids with undivided bothridia with hook-like projections are of the species *Dinobothrium septaria*: a parasite of the pelagic shark *Lamna nasus* (Bonnaterre, 1788). Finally, cercoids with subcylindrical bothridia are probably representatives of the genus *Guidus* Ivanov, 2006 (syn. *Marsupiobothrium* Yamaguti, 1952). This assumption is confirmed by the presence of two cestode species of this genus in Antarctic rays (Table 1). Other common larval form of cestodes, found in teleosts, is larvae of Diphyllobothriidae, whose definitive hosts are seals and birds (Rocka, 2006, see Table V). Plerocercoids without bothridia, registered in intestines of teleosts in South Georgia Island water, are similar to plerocercoids of the family Tetrabothriidae: common parasites of Antarctic birds and mammals (Rocka, 2006). Rocka suggested that the presence of different cestode larvae in teleosts, being endemic to Antarctic, indicates that full life cycles of most cestodes are realized in this area (Rocka, 2006).

**Conclusion.** Faunistic and taxonomic studies of Antarctic cestodes are still sporadic, despite diversity of these helminths in Antarctic and Subantarctic water. In 25 Antarctic and Subantarctic fish species, 21 cestode species are found at different stages of their development. Cestode fauna has been studied in less than 7 % of fish of this area, while potential definitive and intermediate hosts remain unexplored. Of Antarctic and Subantarctic fish, the highest cestode species richness (12 species) was registered in 4 ray species of the family Rajidae. In teleosts, 8 species of mature cestodes and 5 species of cestode larvae were found. The most intensive studies of fish cestodes were carried out in the Atlantic and Indian sectors of Antarctic. The Pacific sector, due to the low degree of study of fish cestode fauna, is the most promising one. Biodiversity of elasmobranch cestodes is underestimated. Out of 15 ray and shark species, cestodes has been studied in 5 species only, *i. e.* one third of the total elasmobranch fauna has been examined for the presence of cestodes. Systematic position of 5 cestode species out of 12, found in rays, is unidentified. Cestode fauna is characterized by a high level of endemism: 67 % of their species are not registered to the north of Subantarctic. Despite the facts that faunistic and ecological studies of cestodes of Antarctic and Subantarctic fish have been carried out for more than 100 years and a significant amount of knowledge has been accumulated, so far little has been done to genetically confirm the systematic affiliation of previously discovered species. Genetic researches on cestodes has just begun to develop. Ribosomal sequences are known only for 2 out of 21 cestode species, *i. e.* molecular genetic data are available for less than 10 % of the total cestode fauna of Antarctic and Subantarctic. The main directions of further research on cestode fauna should be developed in combination with morphological, faunistic, genetic, and ecological studies. Ecological and genetic directions are especially promising, since there are no data on host – parasitic relationships of cestodes with definitive hosts: elasmobranchs.

There is no information on the effect of physiological characteristics of definitive hosts (sex, size/age, age-related changes in nutrition, and degree of maturity) on cestode number and its seasonal dynamics, on their inter- and intraspecific relationships, *etc.* Moreover, molecular data on the latent biodiversity of parasites, in particular cestodes, can be useful for studying speciation and geographic distribution of cryptic parasite species.

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## ЦЕСТОДЫ РЫБ АНТАРКТИКИ И СУБАНТАРКТИКИ: ИСТОРИЯ И ПЕРСПЕКТИВЫ ИССЛЕДОВАНИЯ

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Первые сведения о цестодах рыб Антарктики и Субантарктики появились в начале XX века: от неизвестной акулы была описана цестода *Phyllobothrium dentatum*. Пик активности изучения антарктических цестод пришёлся на 1990–2006 гг. В этот период опубликованы значимые работы, посвящённые описанию новых видов, изучению их жизненных циклов, гостальности цестод — паразитов рыб, их географическому распространению. Существенный вклад в изучение цестод хрящевых рыб внесла группа польских учёных во главе с А. Войцеховской (Рока). Проанализировано систематическое положение 21 вида цестод из 13 родов 8 семейств 6 отрядов. Фауна цестод изучена менее чем у 7 % от ихтиофауны данного региона, в то время как потенциальные окончательные и промежуточные хозяева остаются неисследованными. Наибольшее количество видов цестод (12) зарегистрировано у четырёх видов скатов семейства Rajidae. В кишечнике костистых рыб обнаружено восемь видов цестод, достигающих половой зрелости: *Bothriocephalus antarcticus*, *B. kerguelensis*, *Bothriocephalus* sp., *Parabothriocephalus johnstoni*, *P. macruri*, *Clestobothrium crassiceps*, *Neobothriocephalus* sp. и *Eubothrium* sp. В костистых рыбах зарегистрированы личинки пяти видов цестод (*Onchobothrium antarcticum*, *Grillotia (Grillotia) erinaceus*, *Lacistorhynchus tenuis*, *Calyptrorbothrium* sp. и *Hepatoxylon trichiuri*), заканчивающих своё развитие в хрящевых рыбах. Из 12 видов цестод, обнаруженных у скатов, для пяти не установлено систематическое положение. Фауна цестод характеризуется высоким уровнем эндемизма: 67 % от всей фауны не встречается севернее Субантарктики. В наибольшей степени исследованиями охвачены прибрежные области в Атлантическом и Индийском секторах Антарктики. Разнообразие цестод хрящевых рыб, обитающих в Антарктике и Субантарктике, недооценено: к настоящему времени изучена всего треть видов этих рыб. Генетические исследования антарктических цестод только начали развиваться. Известны рибосомальные последовательности из области D1–D3 рДНК 28S лишь для двух видов — *Onchobothrium antarcticum* от вторых промежуточных (*Notothenia rossii* и *Dissostichus mawsoni*) и окончательного хозяев (*Bathyraja eatonii*), а также личинок цестоды *Calyptrorbothrium* sp. от вторых промежуточных хозяев (*D. mawsoni* и *Muraenolepis marmorata*). В дальнейшем основные направления изучения фауны цестод следует развивать в сочетании с морфологическими, фаунистическими, генетическими и экологическими исследованиями.

**Ключевые слова:** цестоды, рыбы, фауна, систематика, эндемизм, Антарктика, Субантарктика