zoosystema

2022 • 44 • 15

Redescription and phylogenetic assessment of *Helicometra antarcticae* Holloway & Bier, 1968 (Trematoda, Opecoelidae), with evidence of non-monophyletic status of the genus *Helicometra* Odhner, 1902

Sergey G. SOKOLOV, Sergei V. SHCHENKOV, Fuat K. KHASANOV, Yuliya M. KORNYYCHUK & Ilya I. GORDEEV

art. 44 (15) — Published on 6 September 2022
www.zoosystema.com

PUBLICATIONS SCIENTIFIQUES
MUSÉUM NAL HIST NATURELLE

COUVERTURE / *COVER*:
Helicometra antarcticae Holloway & Bier, 1968 from intestine of the Antarctic toothfish, *Dissostichus mawsoni* Norman, 1937, Ross Sea.

Zoosystema est indexé dans / Zoosystema *is indexed in:*
- Science Citation Index Expanded (SciSearch®)
- ISI Alerting Services®
- Current Contents® / Agriculture, Biology, and Environmental Sciences®
- Scopus®

Zoosystema est distribué en version électronique par / Zoosystema *is distributed electronically by:*
- BioOne® (http://www.bioone.org)

Les articles ainsi que les nouveautés nomenclaturales publiés dans *Zoosystema* sont référencés par /
Articles and nomenclatural novelties published in Zoosystema *are referenced by:*
- ZooBank® (http://zoobank.org)

Zoosystema est une revue en flux continu publiée par les Publications scientifiques du Muséum, Paris / **Zoosystema** *is a fast track journal published by the Museum Science Press, Paris*

Les Publications scientifiques du Muséum publient aussi / *The Museum Science Press also publish:*
Adansonia, ***Geodiversitas***, ***Anthropozoologica***, ***European Journal of Taxonomy***, ***Naturae***, ***Cryptogamie*** **sous-sections** ***Algologie***, ***Bryologie***, ***Mycologie***, ***Comptes Rendus Palevol***.

Diffusion – Publications scientifiques Muséum national d'Histoire naturelle
CP 41 – 57 rue Cuvier F-75231 Paris cedex 05 (France)
Tél.: 33 (0)1 40 79 48 05 / Fax: 33 (0)1 40 79 38 40
diff.pub@mnhn.fr / https://sciencepress.mnhn.fr

ISSN (imprimé / *print*): 1280-9551/ ISSN (électronique / *electronic*): 1638-9387

Redescription and phylogenetic assessment of *Helicometra antarcticae* Holloway & Bier, 1968 (Trematoda, Opecoelidae), with evidence of non-monophyletic status of the genus *Helicometra* Odhner, 1902

Sergey G. SOKOLOV
Centre of Parasitology, A.N. Severtsov Institute of Ecology and Evolution,
Moscow, Leninskiy Av. 33, 119071 (Russia)
sokolovsg@mail.ru

Sergei V. SHCHENKOV
Department of Invertebrate Zoology, St. Petersburg State University,
St. Petersburg, Universitetskaya nab., 7/9, 199034 (Russia)
svshchenkov@yandex.ru

Fuat K. KHASANOV
Centre of Parasitology, A.N. Severtsov Institute of Ecology and Evolution,
Moscow, Leninskiy Av. 33, 119071 (Russia)
fuatka@mail.ru

Yuliya M. KORNYYCHUK
A.O. Kovalevsky Institute of Biology of the Southern Seas,
Sevastopol, Nakhimov Ave., 2, 299011 (Russia)
miju2811@mail.ru

Ilya I. GORDEEV
Department of Pacific Salmon, Russian Federal Research Institute of Fisheries
and Oceanography, Moscow, Okruzhnoy Proyezd 19, 105187 (Russia)
and Department of Invertebrate Zoology, Lomonosov Moscow State University,
Moscow, Leninskiye Gory 1/12, 119234 (Russia)
gordeev_ilya@bk.ru (corresponding author)

Submitted on 6 december 2021 | Accepted on 30 March 2022 | Published on 6 September 2022

urn:lsid:zoobank.org:pub:8A516E81-F1BA-4C79-AF57-0672548CC3FA

Sokolov S. G., Shchenkov S. V., Khasanov F. K., Kornyychuk Y. M. & Gordeev I. I. 2022. — Redescription and phylogenetic assessment of *Helicometra antarcticae* Holloway & Bier, 1968 (Trematoda, Opecoelidae), with evidence of non-monophyletic status of the genus *Helicometra* Odhner, 1902. *Zoosystema* 44 (15): 423-433. https://doi.org/10.5252/zoosystema2022v44a15. http://zoosystema.com/44/15

ABSTRACT

Helicometra antarcticae Holloway & Bier, 1968 is one of the few Antarctic representatives of the species-rich genus *Helicometra* Odhner, 1902. It is traditionally attributed to morphological Group IV of *Helicometra* spp., characterized by a cup-shaped oral sucker with a terminal mouth opening. *Helicometra antarcticae*, similar to other Antarctic representatives of the genus, is quite rare and poorly studied. We redescribe this species based on newly collected material from the Antarctic toothfish, *Dissostichus mawsoni* Norman, 1937 (Nototheniidae Günther, 1861) caught in the Ross Sea (Antarctica) and evaluate its phylogenetic position using a fragment of the nuclear 28S rRNA gene. We provide new morphological details on *H. antarcticae* concerning the arrangement of the ventral part of the fields of vitelline follicles and the morphology of the proximal portion of the oviduct. Additionally, we describe the morphology of *Helicometra* sp. (morphological Group IV) from the Pacific zoarcid fish, *Lycodes* cf. *brunneofasciatus* Suvorov, 1935, caught off Simushir Island (Pacific Ocean) and *Helicometra fasciata sensu lato* (morphological Group I), from the black scorpion fish *Scorpaena porcus* Linnaeus, 1758 from the Black Sea. In our phylogenetic analysis, *H. antarcticae* clustered with a Pacific *Helicometra* sp. This clade has a sister relationship to the well-supported clade containing *Helicometrina nimia* Linton, 1910 and *Helicometra* spp. of Groups I and III respectively, including *H. fasciata sensu lato* from the Black Sea. Thus, our phylogenetic data indicate that *Helicometra* is not a monophyletic genus.

KEY WORDS
Helicometrinae,
Dissostichus,
Helicometrina,
Antarctic,
28S rRNA.

RÉSUMÉ

*Redescription et évaluation phylogénétique d'*Helicometra antarcticae *Holloway & Bier, 1968 (Trematoda, Opecoelidae), et évidence de la non monophylie du genre* Helicometra *Odhner, 1902.*

Helicometra antarcticae Holloway & Bier, 1968 est l'un des rares représentants antarctiques du genre riche en espèces *Helicometra* Odhner, 1902. Il est traditionnellement attribué au groupe morphologique IV d'*Helicometra* spp., caractérisé par une ventouse buccale en forme de coupe avec une ouverture buccale terminale. *Helicometra antarcticae*, comme d'autres représentants antarctiques du genre, est assez rare et peu étudié. Nous redécrivons cette espèce sur la base du matériel nouvellement collecté de la légine antarctique, *Dissostichus mawsoni* Norman, 1937 (Nototheniidae Günther, 1861) capturée dans la mer de Ross (Antarctique) et évaluons sa position phylogénétique à l'aide d'un fragment du gène nucléaire ARNr 28S. Nous précisons les données morhologiques nouvelles sur *H. antarcticae* concernant la disposition de la partie ventrale des champs de follicules vitellins et la morphologie de la partie proximale de l'oviducte. De plus, nous décrivons la morphologie d'*Helicometra* sp. (groupe morphologique IV) du poisson zoarcide *Lycodes* cf. *brunneofasciatus* Suvorov, 1935, pêché au large de l'île de Simushir (océan Pacifique), et de *Helicometra fasciata sensu lato* (groupe morphologique I) de la rascasse noire *Scorpaena porcus* Linnaeus, 1758, originaire de la mer Noire. Dans notre analyse phylogénétique, *H. antarcticae* s'est regroupé avec *Helicometra* sp. originaire du Pacifique. Ce clade est le groupe frère du clade bien soutenu contenant *Helicomerina nimia* Linton, 1910 et *Helicometra* spp. des groupes I et III, y compris *H. fasciata sensu lato* de la mer Noire. Ainsi, nos données phylogénétiques indiquent que *Helicometra* n'est pas un genre monophylétique.

MOTS CLÉS
Helicometrinae,
Dissostichus,
Helicometrina,
Antarctique,
ARNr 28S

INTRODUCTION

The genus *Helicometra* Odhner, 1902 comprises 37 species of opecoelid trematodes (WoRMS 2022) parasitizing marine fish. They are characterized by a single polar filament on the egg, a unique conspicuous helical uterus, two testes and blindly closed intestinal caeca (Cribb 2005; Hassanine 2007; Blend & Dronen 2015). Their life cycles are poorly studied (Blend & Dronen 2015). The morphological type of cercariae are known only for two *Helicometra* spp.: *Helicometra fasciata* (Rudolphi, 1819) Odhner, 1902 and *Helicometra gibsoni* Meenakshi, Madhavi & Swarnkumari, 1993. The former has cercariae of the cotylomicrocercous type (Korniychuk 2008), which is typical of opecoelids, while the latter has extraordinary long-tailed cercariae (Meenakshi *et al.* 1993).

Helicometra antarcticae Holloway & Bier, 1968 was originally described based on specimens from the intestine of the Antarctic toothfish, *Dissostichus mawsoni* Norman, 1937 (Nototheniidae Günther, 1861), and zoarcid eelpout, *Rhigophila dearborni* DeWitt, 1962 (synonym: *Lycodichthys dearborni* [DeWitt, 1962]) (Zoarcidae Swainson, 1839) caught in the Ross Sea, Antarctica (Holloway & Bier 1968). All subsequent reliable records of this species are from *Dissostichus* spp. in Antarctic waters (Holloway & Spence 1980; Brickle *et al.* 2005; Sokolov & Gordeev 2013, 2015; Gordeev & Sokolov 2016). Nototheniids belonging to *Trematomus* spp. have been listed as a host of *H. antarcticae* on the strength of the idea that *H. antarcticae* is conspecific with *Helicometra* sp. of Prudhoe & Bray (1973) from these fish (Zdzitowiecki 1993; Blend & Dronen 2015). However, it also has been suggested that this *Helicometra* sp. is conspecific with *Helicometra rakusai* Zdzitowiecki, 1997 (Zdzitowiecki 1997). The morphology of *H. antarcticae* is described only in the original publication (Holloway & Bier 1968).

Helicometra antarcticae together with some other *Helicometra*-like digeneans was moved to *Neohelicometra* Siddiqi & Cable, 1960 by Sekerak & Arai (1974). This decision was based on their similarities with the type species of this genus, *Neohelicometra scorpaenae* Siddiqi & Cable, 1960, namely, the funnel shape of the oral sucker and the terminal position of the mouth opening. However, both Bray (1979) and Cribb (2005) considered only *N. scorpaenae* within *Neohelicometra* and placed all other species included in this genus by Sekerak & Arai (1974) into *Helicometra*.

Four morphological groups of *Helicometra* spp. have been identified (Hassanine 2007; Blend & Dronen 2015). This taxonomic scheme is based on the ideas of Sekerak & Arai (1974) and Aken'Ova *et al.* (2006). *Helicometra antarcticae* together with *Helicometra dalianensis* (Li, Qiu & Zhang, 1989), *Helicometra insolita* Polyansky, 1955, *Helicometra pisanoae* Zdzitowiecki, 1998, *Helicometra pleurogrammi* (Baeva, 1968), *Helicometra rakusai*, *Helicometra sebastis* (Sekerak & Arai, 1974) belong to Group IV (Hassanine 2007; Blend & Dronen 2015). The morphological features of this group are a funnel-shaped oral sucker and a terminal position of the mouth opening.

A separate subfamily Helicometrinae Bray, Cribb, Littlewood & Waeschenbach, 2016 has been established for *Helicometra* and three genera morphologically close to it (*Helicometrina* Linton, 1910, *Neohelicometra*, and *Proneohelicometra* Hassanine, 2006) by Bray *et al.* (2016). Molecular genetic data indicate the basal position of the Helicometrinae to the rest of the relative opecoelids (Bray *et al.* 2016; Martin *et al.* 2020), but phylogenetic relationships within the subfamily are poorly studied. In particular, phylogenetic data are lacking for most *Helicometra* spp., including all members of Group IV.

The aim of this study was to determine the phylogenetic position of *H. antarcticae* using newly obtained 28S rRNA gene sequences and GenBank data as well as newly obtained sequences on *Helicometra* sp. from the Northwestern Pacific and *H. fasciata sensu lato* from the Black Sea.

MATERIAL AND METHODS

Sample collection and morphological observation

Specimens of *H. antarcticae* were collected from *D. mawsoni* caught in the Ross Sea. In addition, we examined *Helicometra* sp. ex tawnystripe eelpout, *Lycodes* cf. *brunneofasciatus* Suvorov, 1935 (Zoarcidae), from off Simushir Island in the Northwest Pacific, and *H. fasciata senu lato* ex black scorpionfish, *Scorpaena porcus* Linnaeus, 1758 (Scorpaenidae Risso, 1827), caught in Severnaya Bay located in the Black Sea, off the South-West coast of Crimean Peninsula. Specimens of *H. antarcticae* and *H. fasciata sensu lato* collected for the morphological study were fixed with hot 70% alcohol without pressure with a coverslip. Specimens of *Helicometra* sp. were fixed with 70% alcohol at ambient temperature, also without pressing down with glass. Subsequently, whole specimens of all three species were stained with acetocarmine or *alum carmine*, cleared in dimethyl phthalate, and mounted in Canada balsam. The terminal part of the reproductive system and the ovarian complex were extracted from the bodies of the several *H. antarcticae* specimens using needles. These isolated organs were also mounted in Canada balsam with preliminary dehydration and clearing, same as the whole worms. All the measurements in the morphological description of *Helicometra* spp. are given in micrometres; measurements for *H. antarcticae* and *H. fasciata senu lato* are given as range and average (in parentheses), those for *Helicometra* sp. are given only as range due to the deformed nature of the specimens.

DNA extraction, amplification and sequencing, and phylogenetic analysis

Specimens of *Helicometra* spp. collected for molecular analysis were fixed in 96% ethanol and stored at −18°C. Sequences of *H. antarcticae* and *H. fasciata sensu lato* were obtained as follows. Genomic DNA was extracted following the protocol used by Tkach & Pawlowski (1999). Specimens for polymerase chain reaction (PCR) were processed according to the protocols and primers of Olson *et al.* (2003). Amplification of the 28S rRNA gene was performed with the primers dig12 (5' – AAG CAT ATC ACT AAG CGG – 3') and 1500R (5' – GCT ATC CTG AGG GAA ACT TCG – 3'). The thermal cycler parameters were as follows: initial denaturation at 95°C (3 min); 35 cycles of 20 s at 95°C; 20 s at 50.1°C; 120 s at 72°C; and 5 min at 72°C for the final extension. PCR products were purified and sequenced in both directions in the GeneAmp PCR System 9700 (Applied Biosystems) using PCR primers and internal primers 300F (5' – CAA GTA CCG TGA GGG AAA GTT G – 3') and ECD2 (5' – CTT GGT CCG TGT TTC AAG ACG GG – 3') followed by Tkach & Snyder (2007).

To generate the sequence of the 28S rRNA gene of *Helicometra* sp., total DNA was extracted after Sokolov *et al.* (2020). The primers LSU-5 (5'-TAG GTC GAC CCG CTG AAY TTA AGC A-3') and reverse primer 1500R (Tkach *et al.* 2003) were used. The thermal cycler parameters were as follows: initial denaturation at 95°C (3 min); 35 cycles of 20 s at 95°C; 20 s at 56°C; 120 s at 72°C; and 5 min at 72°C for the final extension. DNA fragments localized at the 5' end of the 28S rRNA gene were amplified using the GeneAmp PCR System 9700 Thermal Cycler (Applied Biosystems). PCR were performed in a total volume of 25 μl. Amplicons were sequenced directly using the equipment of the Research Park of St. Petersburg State University (Centre for Molecular and Cell Technologies). The consensus sequence from the forward and the reverse primers was assembled using Chromas Pro 1.7.4. and then manually corrected to a length of 1271 bp.

Newly obtained sequences were aligned with those of other helicometrines (Table 1) using custom R script (R core team 2020). The evolutionary models for Maximum likelihood (ML) and Bayesian inference (BI) analysis were chosen with MrModeltest v. 2.4 (Nylander 2004). The model of best fit was GTR + G + I in both cases. Maximum likelihood analysis was performed through the CIPRES portal (Miller *et al.* 2010) with non-parametric bootstrap using 1000 pseudoreplicates. Bayesian analysis was performed using MrBayes 3.2.7 at the CIPRES portal with gamma correction for intersite rate variation (eight categories). Trees were run as two separate chains (default heating parameters) for 15000000 generations. The quality of the chains was estimated using built-in MrBayes tools and additionally with the Tracer 1.6 package (Rambaut *et al.* 2018). Based on the estimates by Tracer, the first 5000 generations were discarded for burn-in. The phylogenetic trees were rooted on the non-opecoelid xiphidiates *Zdzitowieckitrema incognitum* Sokolov, Lebedeva, Gordeev & Khasanov, 2019 and *Zalophotrema hepaticum* Stunkar & Alvey, 1929 based on the findings of Martin *et al.* (2020) and Sokolov *et al.* (2020). Estimates of evolutionary divergence (p-distances) are made with MEGA X software (Kumar *et al.* 2018).

Abbreviations

Institutions

IPEE RAS	Helminthological Museum, Center for Parasitology, A. N. Severtsov Institute of Ecology and Evolution RAS, Moscow;
IBSS RAS	Collection of Marine Parasites, A. O. Kovalevsky Institute of Biology of RAS, Sebastopol;
USNPC	United States National Parasite Collection, Smithsonian National Museum of Natural History, Washington D.C.

Table 1. — List of trematode species involved in molecular analyses in this study. Symbols: *, actual name in Blend & Dronen (2015); **, actual name in Bray *et al.* (2016).

Species	Host species	Geographical region	GenBank accession number	Reference
Helicometra antarcticae Holloway & Bier, 1968	*Dissostichus mawsoni* Norman, 1937 (Actinopterygii: Nototheniidae)	Ross Sea	OK644193	This study
Helicometra equilata (Manter, 1933) Siddiqi & Cable, 1960 (accepted as *Helicometra boseli* Nagaty, 1956)*	*Sargocentron spiniferum* (Forsskål, 1775) (Actinopterygii: Holocentridae)	off New Caledonia, France	KU320600	Bray et *al. 2016*
Helicometra epinepheli Yamaguti, 1934 (accepted as *Helicometra fasciata* (Rudolphi, 1819))**	*Epinephelus fasciatus* (Forsskål, 1775) (Actinopterygii: Serranidae)	off New Caledonia, France	KU320597	Bray *et al.* 2016
Helicometra fasciata (Rudolphi, 1819) Odhner, 1902 *sensu lato*	*Scorpaena porcus* Linnaeus, 1758 (Actinopterygii: Scorpaenidae)	Black Sea, Russia	OK644194	This study
Helicometra manteri Andres, Ray, Pulis, Curran & Overstreet, 2014	*Bellator egretta* (Goode & Bean, 1896) (Actinopterygii: Triglidae)	off West Florida, United States of America	KJ701239	Andres *et al.* 2014
Helicometra sp.	*Lycodes* cf. *brunneofasciatus* (Actinopterygii: Zoarcidae)	off Simushir Island, Russia	OK644195	This study
Helicometrina nimia Linton, 1910	*Syacium papillosum* (Linnaeus, 1758) (Actinopterygii: Cyclopsettidae)	off Yukatan, Mexico	MK908868	Vidal-Martínez *et al.* 2019
Outgroup				
Zdzitowieckitrema incognitum Sokolov, Lebedeva, Gordeev & Khasanov, 2019	*Muraenolepis marmorata* Günther, 1880 (Actinopterygii: Muraenolepididae)	Ross Sea	MF398367	Sokolov *et al.* 2019
Zalophotrema hepaticum Stunkard & Alvey, 1929	*Zalophus californianus* (Lesson, 1828) (Mammalia: Otariidae)	United States of America	AY222255	Olson *et al.* 2003

RESULTS

Family Opecoelidae Ozaki, 1925
Genus *Helicometra* Odhner, 1902

Helicometra antarcticae Holloway & Bier, 1968
(Fig. 1)

Helicometra antarcticae Holloway & Bier, 1968: 31. — Bray 1979: 402.

Neohelicometra antarcticae – Sekerak & Arai 1974: 730.

Type locality. — Ross Sea.

Type material. — **Holotype** • Ross Sea, McMurdo Sound; intestine of the Antactic toothfish *Dissostichus mawsoni*; 11.XI.1964; USNPC1358823.
Paratype • Ross Sea, McMurdo Sound; intestine of zoarcid eelpout *Rhigophila dearborni*; 25.XI.1964; USNPC 1358824.

Material examined. — **Ross Sea** • 6 whole-mounted adult specimens, 2 slides with isolated ovarian complex, 5 slides with isolated terminal genitalia; intestine of *Dissostichus mawsoni*; 75°44'7"S, 172°56'8"W; 12.I.2012; IPEE RAS 14315 (for whole-mounted specimens) • 3 whole-mounted adult specimens; intestine of *Dissostichus mawsoni*; 75°40'3"S, 172°26'1"W; 21.I.2013; IPEE RAS 14316 • 1 whole-mounted adult specimen; intestine of *Dissostichus mawsoni*; 75°28'2"S, 174°37'6"W; 26.I.2013; IPEE RAS 14317 • 1 sequenced adult specimen; intestine of *Dissostichus mawsoni*; 75°25'3"S, 174°32'7"W; 12.I.2012; GenBank: OK644193 (28S rRNA gene).

Description

General morphology and digestive system

Body elongate-oval, length 2.969-5.895 (3.844), maximum width 799-1.527 (1.174) at mid-body. Tegument unarmed. Pre-oral lobe absent. Oral sucker cup-shaped, 357-499 (419) / 271-585 (419), mouth opening terminal. Ventral sucker globular or subglobular, 357-628 (475) / 399-585 (497). Oral sucker to ventral sucker width ratio 1:1.00-1.53 (1:1.22). Forebody 24.5-30.9 (27.7)% of body length. Prepharynx short, distinct. Pharynx well-developed, 113-191 (149) / 106-184 (141). Oesophagus 92-289 (171). Pharyngeal and oesophagus glands distinct. Intestinal bifurcation in middle or posterior third of forebody. Caeca blind; distance from caecal ends to posterior end of body reaching 395-1031 (641).

Male reproductive system

Two testes, variously lobed, separate to slightly overlapped, oblique, post-equatorial; anterior testis sinistro-submedian, 257-514 (390) / 285-499 (384), posterior testis median or dextro-submedian, 299-528 (408) / 314-585 (445). Post-testicular region 23.3-33.3 (27.4)% of body length. Cirrus-sac well developed, 311-735 (589) / 155-261 (201), overlaps usually 20.5-78.8 (44.6)% of ventral sucker, occasionally extends to 142 beyond posterior margin of ventral sucker. Internal seminal vesicle long, tubular, folded. Pars prostatica tubular, surrounded by numerous prostatic gland-cells. Ejaculatory duct and cirrus distinct, surrounded by spongy tissue. Genital atrium distinct. Genital pore usually median, occasionally slightly dextro-submedian, just posterior to intestinal bifurcation, 169-424 (225) from anterior margin of ventral sucker.

Female reproductive system

Ovary variously lobed, median or dextro-submedian, antero-dextral to anterior testis, separate or slightly overlapping, 200-414 (258) / 285-599 (409). Oviduct anterior to ovary,

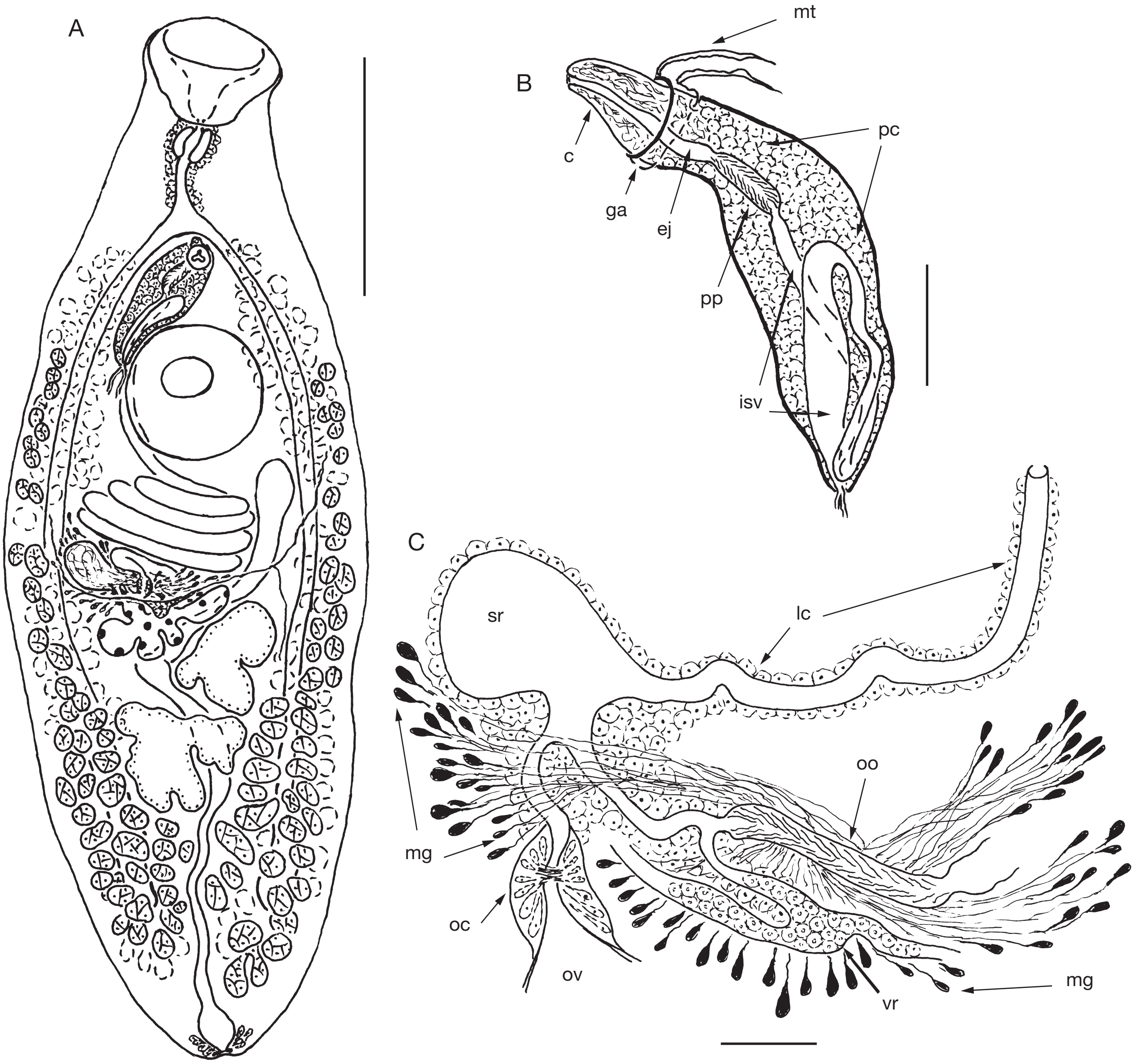

Fig. 1. — *Helicometra antarcticae* Holloway & Bier, 1968 from intestine of the Antarctic toothfish, *Dissostichus mawsoni* Norman, 1937, Ross Sea: **A**, whole mount, ventral view; **B**, terminal genitalia, lateral view; **C**, ovarian complex, ventral view. Abbreviations: **c**, cirrus everted through genital atrium; **ej**, ejaculatory duct; **ga**, genital atrium; **isv**, internal seminal vesicle; **lc**, Laurer's canal; **mg**, Mehlis' gland cells; **mt**, metraterm; **oc**, ovicapt; **oo**, oötype; **ov**, ovary; **pc**, prostatic cells; **pp**, pars prostatica; **sr**, seminal receptacle; **vr**, common vitelline reservoir. Scale bars: A, 1 mm; B, 0.2 mm; C, 0.08 mm.

forming oötype after connecting with canalicular seminal receptacle and common vitelline reservoir duct. Ovicapt distinct. Canalicular seminal receptacle saccular, antero-dextral to ovary. Laurer's canal opening sinistro-submedially approximately at level of anterior margin of seminal receptacle. Mehlis' gland extensive, diffuse. Uterus pre-ovarian, coiled, intercaecal. Metraterm muscular, opening into genital atrium antero-dorsally. Eggs operculate, with long, unipolar filament; length without filament 66.8-85.0 (77.9), width 30.4-42.5 (35.7). Vitellarium follicular; follicles in two lateral fields, extending from intestinal bifurcation level or from genital pore level or, occasionally, from midlevel distance between genital pore and anterior margin of ventral sucker to near posterior end of body; fields overlapping caeca along entire length dorsally and at level of posterior testis and in post-testicular region ventrally, encroaching over ventral surface of caeca at level of proximal uterine coils, ovary and anterior testis, extracaecal on ventral side of body anteriorly to ovary, usually not confluent, occasionally almost confluent in post-testicular region but distinctly separated over excretory vesicle; anterior border of ventral follicles some distance posterior to that of dorsal follicles.

Excretory system

Excretory pore terminal. Excretory vesicle I-shaped, extending approximately to posterior margin of ventral sucker; posterior end surrounded by numerous glands and small subterminal muscular sphincter.

Helicometra sp.
(Fig. 2)

Material examined. — **Northwest Pacific** • 3 strongly deformed adult whole-mounted, 1 sequenced specimens; Simushir Island area; intestine of *Lycodes* cf. *brunneofasciatus*; 47°11'8"N, 152°17'7"E; 21.III.2017; IPEE RAS 14318; GenBank: OK644195 (28SrRNA gene).

Description

General morphology and digestive system

Body elongate-oval, length 2.890-2.940, maximum width 1.042-1.142 in posterior half of body. Tegument unarmed. Pre-oral lobe absent. Oral sucker funnel-shaped, 385-414 / 357-414, mouth opening terminal. Ventral sucker rounded, 442-499 / 457-514. Oral sucker to ventral sucker width ratio 1:1.10-1.44. Forebody strongly contracted, about 30% of body length. Prepharynx short, distinct. Pharynx well-developed, 170-177 / 127-155. Oesophagus 212 in one specimen and strongly contracted in others. Pharyngeal and oesophagus glands distinct. Intestinal bifurcation distinctly anterior to anterior margin of ventral sucker. Caeca blind; distance from caecal ends to posterior end of body reaching 481-537.

Male reproductive system

Two testes, variously lobed, slightly overlapping, almost tandem, post-equatorial; anterior testis slightly sinistro-submedian, 442-742 / 542-628, posterior testis median, 557-571 / 400-571. Post-testicular region 14.8-18.0% of body length. Cirrus-sac well-developed, 607-685 / 183-205, overlapping 77.1-85.7% of ventral sucker. Internal seminal vesicle long, tubular, folded. Pars prostatica tubular, surrounded by numerous prostatic gland-cells. Ejaculatory duct distinct, cirrus not visible. Genital atrium indistinct. Genital pore strongly dextro-submedian, at level of intestinal bifurcation.

Female reproductive system

Ovary variously lobed, dextro-submedian, antero-dextral to and contiguous with anterior testis, 228-214 / 343-542. Ovarian complex not visible. Uterus pre-ovarian, coiled, intercaecal. Metraterm not visible. Eggs operculate, with long, unipolar filament; length without filament 66.7-72.7, width 30.3-36.4. Vitellarium follicular; follicles, in two lateral fields, extending from distinctly anterior to intestinal bifurcation to near posterior end of body; fields overlapping caeca dorsally at level of their distal ends and in pre-ovarian region and ventrally in ovary area and post-ovarian region, extracaecal or encroach caecain post-ovarian regionon dorsal side of body and in pre-ovarian region on ventral side of body, not confluent.

Excretory system

Excretory pore terminal. Excretory vesicle saccular or clavate with lobated anterior end, extending to ovary; posterior end surrounded by numerous glands and small subterminal muscular sphincter.

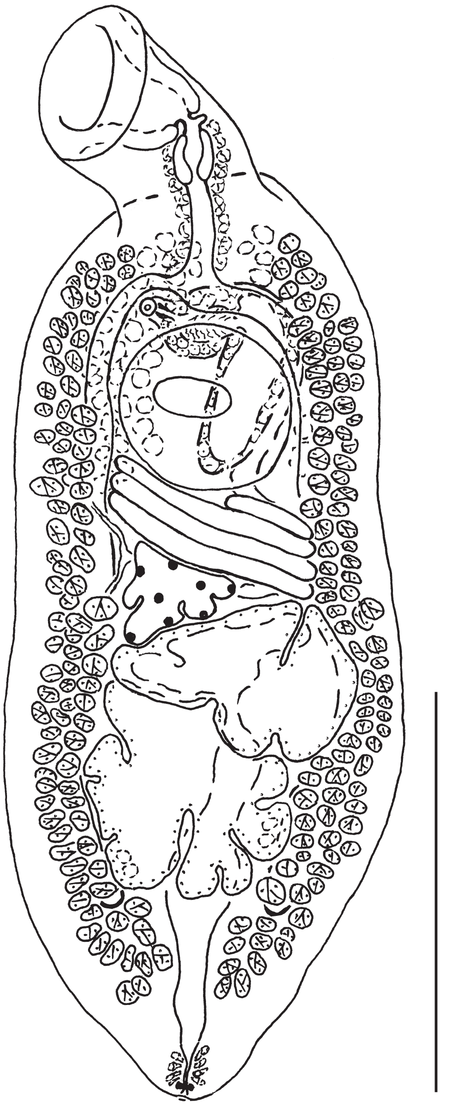

Fig. 2. — *Helicometra* sp. from intestine of tawnystripe eelpout, *Lycodes* cf. *brunneofasciatus* Suvorov, 1935, Northwest Pacific; whole mount, ventral view. Scale bar: 1 mm.

Helicometra fasciata (Rudolphi, 1819)
Odhner, 1902 *sensu lato*
(Fig. 3)

Distoma fasciatum Rudolphi, 1819: 373.

Distoma pulchellum Rudolphi, 1819: 367.

Distoma sinuatum Rudolphi, 1819: 374.

Distomum gobii Stossich, 1883: 116.

Distomum labri Stossich, 1886: 30.

Allocreadium fasciatum – Odhner 1901: 485.

Allocreadium sinuatum – Odhner 1901: 490.

Allocreadium labri – Odhner 1901: 493.

Loborchis mutabilis Stossich, 1902: 579.

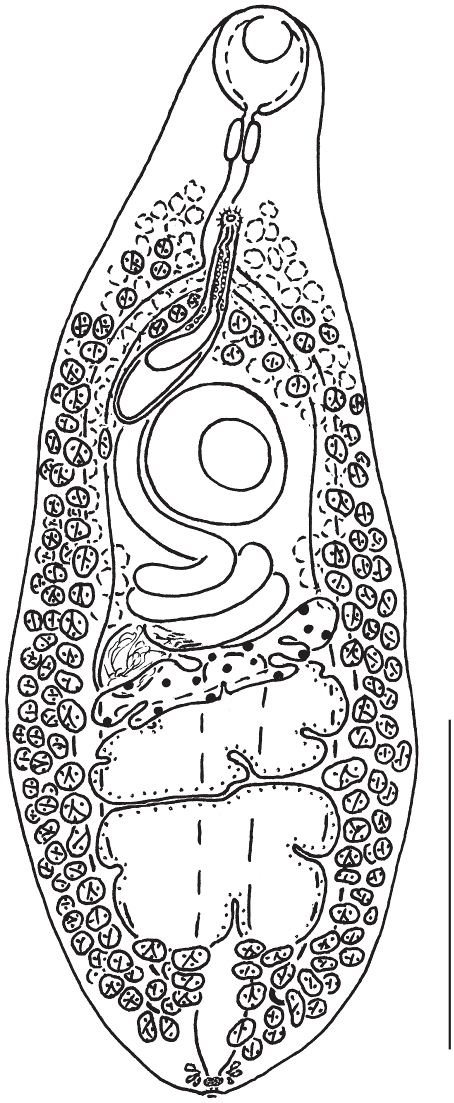

Fig. 3. . — *Helicometra fasciata* (Rudolphi, 1819) Odhner, 1902 *sensu lato* from intestine of black scorpionfish, *Scorpaena porcus* Linnaeus, 1758, Black Sea; whole mount, ventral view. Scale bar: 0.5 mm.

Loborchis fasciatum – Stossich 1902: 582.

Loborchis gobii – Stossich 1902: 582.

Loborchis labri – Stossich 1902: 582.

Helicometra fasciata – Odhner 1902: 162. — Palombi 1929: 262. — Naĭdenova & Dolgikh 1969: 10. — Bray 1979: 401; 1987: 1069. — Hassanine 2007: 20. — Blend & Dronen 2015: 245.

Helicometra pulchella – Odhner 1902: 161. — Nicoll 1910: 336. — Sekerak & Arai 1974: 710.

Helicometra sinuata – Odhner 1902: 162.

Helicometra flava Stossich, 1903: 373.

Helicometra mutabilis – Stossich 1903: 375.

Helicometra gobii – Stossich 1904: 12.

Helicometra hypodytis Yamaguti, 1934: 301.

Helicometra markewitschi Pogorel'tseva, 1954: 133.

Helicometra dochmosorchis Manter & Pritchard, 1960: 653.

Helicometra marmoratae Nagaty & Abdel Aal, 1962: 310.

Helicometra upapalu Yamaguti, 1970: 83.

Helicometra scorpaenae Wang, 1982: 188.

Helicometra neoscorpanae Wang, Wang & Zhang, 1992: 72.

Type locality. — Tyrrhenian Sea.

Type material. — We could find no information about deposition of K. A. Rudolphi's original *H. fasciata* material.

Material examined. — **Black Sea** • 6 adult whole-mounted, 1 sequenced specimens; Severnaya Bay, Crimean Peninsula; intestine of the black scorpionfish, *Scorpaena porcus*; 44°37'32"N, 33°32'7"E; 27.VII.2000; ISSS RAS 1369.Tr.39.v2-15; GenBank: OK644194 (28SrRNA gene).

Description

General morphology and digestive system

Body elongate-oval, length 1.464-2.383 (1840), maximum width 620-726 (675) in posterior half of body. Tegument unarmed. Pre-oral lobe absent. Oral sucker spherical or subspherical, 140-189 (167) / 144-184 (167), mouth opening subterminal. Ventral sucker globular or subglobular, 215-285 (237) / 199-250 (224). Oral sucker to ventral sucker width ratio 1 : 1.21-1.55 (1.35). Forebody 30.5-36.4 (33.9) % of body length. Prepharynx short, distinct. Pharynx well-developed, 47-83 (67) / 43-88 (59). Intestinal bifurcation in second or posterior third of forebody. Caeca blind distance from caecal ends to posterior end of body reaching 95-171 (137).

Male reproductive system

Two testes, variously lobed, contiguous, median, tandem, post-equatorial; anterior testis 172-282 (206) / 283-470 (401), posterior testis 188-394 (268) / 359-447 (381). Post-testicular region 13.3-18.2 (14.9) % of body length. Cirrus-sac well-developed, 319-551 (433) / 65-93 (78), overlapping 2.4-28.7 (22.4)% of ventral sucker. Internal seminal vesicle long, tubular, folded. Pars prostatica tubular, surrounded by numerous prostatic gland-cells. Ejaculatory duct distinct, cirrus not visible. Genital atrium indistinct. Genital pore median, at midlevel of oesophagus.

Female reproductive system

Ovary variously lobed, median or slightly dextro-sumedian, anterior or slightly antero-dextral to and slightly overlapping anterior testis, 89-136 (118) / 290-393 (340). Canalicular seminal receptacle saccular, antero-dextral to ovary. Laurer's canal and oötype together with Mehlis' gland not visible. Uterus preovarian, coiled, intercaecal. Metraterm not visible. Eggs operculate, with long unipolar filament; length without filament 63.0-87.3 (75.1), width 26.1-40.2 (34.2). Vitellarium follicular; follicles in two lateral fields, extending from level anterior quarter or middle of oesophagus to near posterior end of body; fields overlapping caeca dorsally in forebody and uterus area and ventrally in post-testicular region, usually

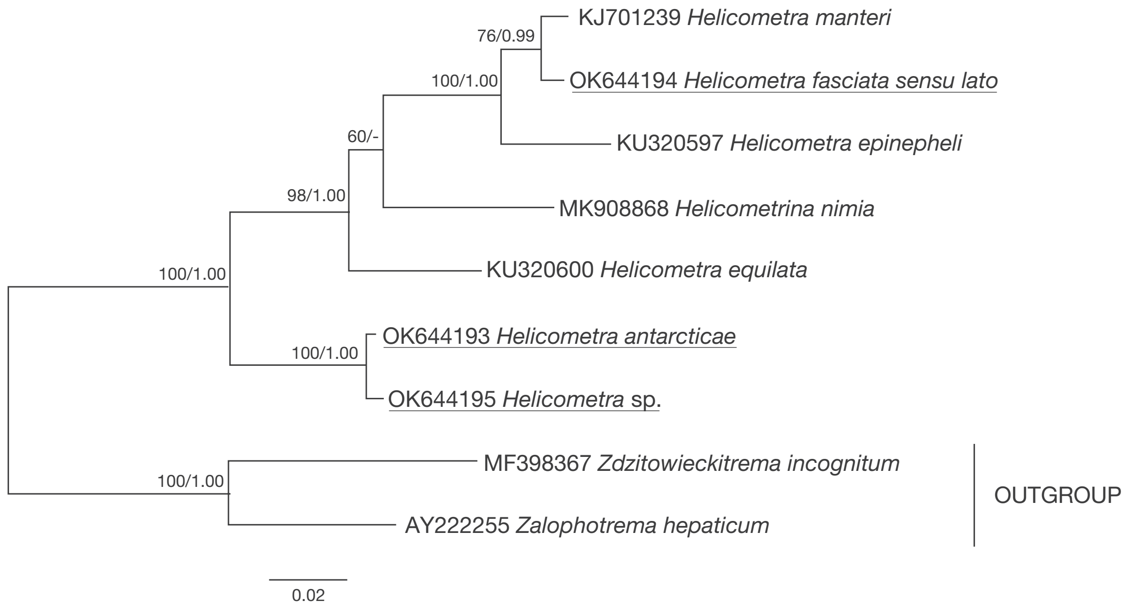

Fig. 4. — Phylogenetic relationships of helicometrine species based on dataset of 28S rRNA gene sequences. The bootstrap (≥ 50) and posterior probability (≥ 0.90) values are given near the nodes for ML and BI analyses, respectively. Newly obtained sequences are underlined.

encroaching caeca along rest of their length ventrally and dorsally, not confluent in post-testicular region, usually confluent on dorsal side of forebody; anterior border of ventral follicles some distance posterior to that of dorsal follicles.

Excretory system
Excretory pore terminal. Excretory vesicle clavate, extending to ovary, posterior end surrounded by numerous glands and small subterminal muscular sphincter.

Phylogenetic data
BI and ML analyses supported the sister position of *H. antarcticae* to *Helicometra* sp. described in this study (Fig. 4). The divergence between these species was low (p-distance = 0.7%). The *H. antarcticae* + *Helicometra* sp. clade had a sister relationship with the well-supported clade containing *Helicometrina nimia* Linton, 1910 and other *Helicometra* spp. *Helicometrina nimia* was sister taxon to the well-supported terminal *Helicometra epinepheli* Yamaguti, 1934 + (*H. fasciata sensu lato* + *Helicometra manteri* Andres, Ray, Pulis, Curran & Overstreet, 2014) subclade, though this sister relationship was poorly supported in both analyses. *Helicometra equilata* (Manter, 1933) Siddiqi & Cable, 1960 occupied a basal position to *H. nimia* and members of the terminal subclade mentioned above.

DISCUSSION

Helicometra antarcticae and *Helicometra* sp. examined in our study clearly belong to morphological Group IV of *Helicometra* spp. based on the presence of the cup-shaped oral sucker with a terminal mouth opening (compare with Blend & Dronen 2015). Our specimens of *H. antarcticae* corresponded to the original description of this species in numerous key characteristics, namely, the body size and shape, the shape and arrangement of the gonads, the arrangement of the fields of vitelline follicles, relative arrangement of the ventral sucker and the cirrus-sac, the sucker width ratio, and the size of the eggs (compare with Holloway & Bier 1968). Our specimens have a slightly different position of the genital pore than described by Holloway & Bier (1968): just post-bifurcal *vs* bifurcal. However, this morphological difference is unlikely to be important since some representatives of *Helicometra* are known to be variable in positon of the genital pore along the longitudinal body axis (Baeva 1968; Machida 1984). We clarified several morphological details of this species, namely, the arrangement of the ventral part of the fields of vitelline follicles and the morphology of the proximal portion of the oviduct (a distinct ovicapt is present).

Only two nominal species of the morphological Group IV of *Helicometra* spp. are known in the Northwestern Pacific: *H. insolita* and *H. pleurogrammi* (Zhukov 1960; Baeva 1968; Machida 1984). *Helicometra* sp. described in this paper is strikingly different from these species by the arrangement of the fields of vitelline follicles: not confluent in the post-testicular region vs confluent, and passing anteriorly from anterior to intestinal bifurcation level vs only to midlevel of ventral sucker (Polyansky 1955; Baeva 1968; Bray 1979; Machida 1984). In addition, *Helicometra* sp. also differs from *H. pleurogrammi* in the sucker ratio (1:1.10-1.44 vs 1:0.75-0.80) (Machida 1984). *Helicometra* sp. is very similar to *H. antarcticae* by the location of the cirrus-sac (not extending posteriorly to the ventral sucker), the arrangement of fields of vitelline follicles (extending anteriorly to the ventral sucker) and the sucker ratio (> 1.0). However, *Helicometra* sp. differs from *H. antarcticae* by the position of the ventral and dorsal vitelline follicles anterior to the intestinal bifurcation, strongly dextro-submedian position of the genital pore (Figs 1; 2), fish host and geographical distribution. We assume that *Helicometra* sp. is a new species, but do not describe it formally in this study because we only have deformed specimens at our disposal.

Helicometra fasciata complex (that is *Helicometra fasciata sensu lato*) from the Black Sea fishes shows great morphological diversity, which until recently has been considered as a manifestation of intraspecific variability (Korniychuk 1999, 2000, 2009). However, new data indicate that *H. fasciata* complex in this water body is represented by two species, differing in the cox 1 gene (Katokhin & Kornyychuk 2020). One of them parasitizes the East Atlantic peacock wrasse, *Symphodus tinca* (Linnaeus, 1758) (Labridae Cuvier, 1816), while another is a parasite of several other Black Sea fish hosts, including *Sc. porcus* (Katokhin & Kornyychuk 2020). Specimens of *H. fasciata* complex from Black Sea *Sym. tinca* are characterized by relatively short fields of the vitelline follicles, which extend anteriorly only to the level of the ventral sucker. However, for specimens of this species complex from *Sc. porcus* and a number of other Black Sea fishes, an extensive distribution of the follicles both in the hindbody and in the forebody is typical (Korniychuk 1999, 2000, 2009). Our specimens of *H. fasciata* complex from *Sc. porcus* are similar in morphology to those previously recorded from the same host in the Black Sea (Korniychuk 1999, 2000, 2009). The original description of *H. fasciata* is based on worms from *Sym. tinca* (type host), the corkwing wrasse, *Symphodus melops* (Linnaeus, 1758), and the painted comber, *Serranus scriba* (Linnaeus, 1758) off Napoli (the Tyrrhenian Sea) (Rudolphi 1819). According to Stossich (1904), the vitellarium extending anteriorly to the level of anterior ventral sucker is typical for *H. fasciata sensu stricto*. We conjecture that specimens of *H. fasciata* complex from *Sym. tinca* in the Black Sea are actually *H. fasciata sensu stricto*. The issue of conspecificity of *Helicometra* trematodes from *Sc. porcus* with other nominal species of *H. fasciata* complex described in the Black Sea – Mediterranean Region – *Helicometra gobii* (Stossich, 1883), *Helicometra flava* Stossich, 1903, *Helicometra labri* (Stossich, 1886), *Helicometra markewitschi* Pogorel'tseva, 1954, *Helicometra mutabilis* (Stossich, 1902), *Helicometra pulchella* (Rudolphi, 1819) and *Helicometra sinuata* (Rudolphi, 1819) – requires an additional study.

Our phylogenetic data are consistent with the monophyly of *Helicometra* spp. with a funnel- or a cup-shaped oral sucker and a terminal mouth opening (*i.e.* Group IV) and the sister relationship of this group with the well-supported clade uniting *H. nimia*, *H. equilata*, *H. fasciata sensu lato* (from the Black Sea), *H. epinepheli*, and *H. manteri*. *Helicometra equilata* belongs to morphological Group III (Blend & Dronen 2015), while *H. fasciata sensu lato*, *H. epinepheli* and *H. manteri* belong to morphological Group I (Andres *et al.* 2014; Blend & Dronen 2015). Notably, the *Helicometra* spp. listed above form a paraphyletic assemblage, in which members of Group III have no direct phylogenetic connection with members of Group I.

Our data do not support the monophyly of *Helicometra* and indicate that previous taxonomic hypotheses concerning this genus should be reconsidered. Two hypotheses now appear possible. The first suggests that species with a funnel-shaped or a cup-shaped oral sucker and a terminal mouth opening (Group IV) should be placed into *Allostenopera* Baeva, 1968, while those with a short forebody and a long cirrus-sac (Group III) should be placed into *Stenopera* Manter, 1933. The second hypothesis suggests that all *Helicometra*-like trematodes with the blind-ending intestine should be united into a single genus, *Helicometra sensu lato*, and implies that *Helicometrina* is a junior synonym of *Helicometra* as suggested by Hafeezullah (1971). At present these two hypotheses are equally plausible. More molecular genetic data on *Helicometra*-like trematodes are necessary for their verification.

Acknowledgements
The authors are grateful to the crew of the fishing vessels *Yantar-35* (ORION Ltd., Khabarovsk) and *Antoliy Torchinov* (Primorskaya Ribolobnaya Companiya Ltd., Yuzhno-Sakhalinsk) for help in collecting the hosts. This work is a part of the state-supported studies in the A. N. Severtsov Institute of Ecology and Evolution of Russian Academy of Sciences (project no. FFER-2021-0005) and the A. O. Kovalevsky Institute of Biology of the Southern Seas of Russian Academy of Sciences (project no. 121030100028-0)

REFERENCES

Aken'Ova T. O. L., Cribb T. H. & Bray R. A. 2006. — *Helicometra* Odhner, 1902 (Digenea: Opecoelidae) in Australian waters: problems of species identification and a description of *H. sprenti* n. sp. *Systematic Parasitology* 63: 17-27. https://doi.org/10.1007/s11230-005-5500-0

Andres M. J., Ray C. L., Pulis E. E., Curran S. S. & Overstreet R. M. 2014. — Molecular characterization of two opecoelid trematodes from fishes in the Gulf of Mexico, with a description of a new species of *Helicometra*. *Acta Parasitologica* 59 (3): 405-412. https://doi.org/10.2478/s11686-014-0258-7

Baeva O. M. 1968. — Helminth fauna of *Pleurogrammus azonus* Jordan et Metz in the Sea of Japan, *in* Skrjabin K. I. & Mamaev Y. L. (eds), *Helminths of animals of Pacific Ocean*. Nauka, Moscow: 80-88 (In Russian).

Blend C. K. & Dronen N. O. 2015. — A review of the genus *Helicometra* Odhner, 1902 (Digenea: Opecoelidae: Plagioporinae) with a key to species including *Helicometra overstreeti* n. sp. from the cusk-eel *Luciobrotula corethromycter* Cohen, 1964 (Ophidiiformes: Ophidiidae) from the Gulf of Mexico. *Marine Biodiversity* 45: 183-270. https://doi.org/10.1007/s12526-014-0250-3

Bray R. A. 1979. — Digenea in marine fishes from the eastern seaboard of Canada. *Journal of Natural History* 13: 399-431. https://doi.org/10.1080/00222937900770331

Bray R. A. 1987. — Some helminth parasites of marine fishes of South Africa: Family Opecoelidae (Digenea). *Journal of Natural History* 21 (4): 1049-1075. https://doi.org/10.1080/00222938700770651

Bray R. A., Cribb T. H., Littlewood D. T. J. & Waeschenbach A. 2016. — The molecular phylogeny of the digenean family Opecoelidae Ozaki, 1925 and the value of morphological characters, with the erection of a new subfamily. *Folia Parasitologica* 63: 013. https://doi.org/10.14411/fp.2016.013

Brickle P., MacKenzie K. & Pike A. 2005. — Parasites of the Patagonian toothfish, *Dissostichus eleginoides* Smitt 1898, in different parts of the Subantarctic. *Polar Biology* 28: 663-671. https://doi.org/10.1007/s00300-005-0737-2

Cribb T. H. 2005. — Family Opecoelidae Ozaki, 1925, *in* Jones A., Bray R. A. & Gibson D. I. (eds), *Keys to the Trematoda, vol. 2*. CABI and Natural History Museum, Wallingford: 443-531.

Gordeev I. I. & Sokolov S. G. 2016. — Parasites of the Antarctic toothfish (*Dissostichus mawsoni* Norman, 1937) (Perciformes, Nototheniidae) in the Pacific sector of the Antarctic. *Polar Research* 35: 29364. https://doi.org/10.3402/polar.v35.29364

Hafeezullah M. 1971. — A review on the validity of *Helicometrina* Linton, 1910 and *Stenopera* Manter, 1933 (Trematoda). *Acta Parasitologica Polonica* 19: 133-139.

Hassanine R. M. E. 2007. — Trematodes from Red Sea fishes: on the validity of *Helicometra marmoratae* Nagaty et Abdel-Aal, 1962 and the description of *H. aegyptense* sp. nov. (Opecoelidae Ozaki, 1925). *Acta Parasitologica* 52 (1): 18-23. https://doi.org/10.2478/s11686-007-0004-5

Holloway H. L. & Bier J. W. 1968. — *Helicometra antarcticae* sp. nov. from Antarctic coastal fishes. *Proceedings of the Helminthological Society of Washington* 35: 30-34.

Holloway H. L. & Spence A. 1980. — Ecology of animal parasites in McMurdo Sound, Antarctica. *Comparative Physiology and Ecology* 5: 262-284.

Nagaty H. F. & Abdel Aal T. M. 1962. — Trematodes of fishes of the Red Sea. Part 17. On three allocreadiid sp. and one schistorchiid sp. *Journal of the Egyptian Veterinary Medical Association* 22: 307-314.

Naĭdenova N. N. & Dolgikh A. V. 1969. — On a revision of some species of *Helicometra* Odhner, 1902 (Trematoda: Opecoelidae). *Nauchnye doklady vysshei shkoly. Biologicheskie nauki* 7: 7-12 (in Russian).

Nicoll W. 1910. — On the entozoa of fishes from the Firth of Clyde. *Parasitology* 3 (3): 322-359. https://doi.org/10.1017/S0031182000002183

Katokhin A. V. & Kornyychuk Yu. M. 2020. — Genotyping of Black Sea trematodes of the family Opecoelidae by mitochondrial markers. *Marine Biological Journal* 5 (4): 15-27 (In Russian). https://doi.org/10.21072/mbj.2020.05.4.02

Korniychuk Yu. M. 1999. — Phenotypic hostal differentiation of *Helicometra fasciata* (Rud., 1891) maritae. *Ekologiya Morya* 49: 44-48 (In Russian). https://doi.org/10.21072/ecol-morya-1999-49-44-48

Korniychuk Yu. M. 2000. — Morphological variability of genus *Helicometra* (Trematoda: Opecoelidae) maritae from the Black Sea. *Ekologiya Morya* 51: 40-44 (In Russian). https://doi.org/10.21072/ecol-morya-2000-57-40-44

Korniychuk Yu. M. 2008. — Parthenogenetic generations of *Helicometra fasciata* Rud., 1819 (Trematoda: Opecoelidae) in the Black Sea molluscs *Gibbula adriatica*. *Parazitologiya* 42: 41-52 (In Russian).

Korniychuk Yu. M. 2009. — Additional description of hermaphroditic generation of trematodes Black Sea fishes, *Helicometra fasciata* (Trematoda, Opecoelidae). *Vestnik Zoologii* 23: 63-68 (In Russian).

Kumar S., Stecher G., Li M., Knyaz C. & Tamura K. 2018. — MEGA X: Molecular evolutionary genetics analysis across computing platforms. *Molecular Biology and Evolution* 35 (6): 1547-1549. https://doi.org/10.1093/molbev/msy096

Machida M. 1984. — Trematodes of marine fishes from depth of 200-400 m off Yamagata, the Japan Sea. *Memoirs of the National Science Museum, Tokyo* 17: 101-110.

Manter H. W. & Pritchard M. H. 1960. — Some digenetic trematodes of eels of Hawaii. *Journal of Parasitology* 46 (5): 651-658. https://doi.org/10.2307/3274956

Martin S. B., Downie A. J. & Cribb T. H. 2020. — A new subfamily for a clade of opecoelids (Trematoda: Digenea) exploiting marine fishes as second-intermediate hosts, with the first report of opecoelid metacercariae from an elasmobranch. *Zoological Journal of the Linnean Society* 188 (2): 455-472. https://doi.org/10.1093/zoolinnean/zlz084

Meenakshi M., Madhavi R. & Swarnakumari V. G. M. 1993. — The life-cycle of *Helicometra gibsoni* n. sp. (Digenea: Opecoelidae). *Systematic Parasitology* 25: 63-72. https://doi.org/10.1007/BF00017001

Miller M. A., Pfeiffer W. & Schwartz T. 2010. — Creating the CIPRES Science Gateway for inference of large phylogenetic trees, *in Proceedings of the Gateway Computing Environments Workshop*. New Orleans: 1-8.

Nylander J. A. A. 2004. — *MrModeltest v2. Program distributed by the author*. Evolutionary Biology Centre, Uppsala University, Uppsala.

Odhner T. 1901. — Revision einiger Arten der Distomengattung *Allocreadium* Lss. *Zoologische Jahrbücher. Abteilung für Systematik, Geographie und Biologie der Tiere* 14: 483-520 (In German).

Odhner T. 1902. — Mitteilungen zur Kenntnis der Distomen. II. *Centralblatt für Bakteriologie, Parasitenkunde und Infektionskrankheiten* 31: 152-162 (In German).

Olson P. D., Cribb T. H., Tkach V. V., Bray R. A. & Littlewood D. T. J. 2003. — Phylogeny and classification of the Digenea (Platyhelminthes: Trematoda). *International Journal for Parasitology* 33: 733-755. https://doi.org/10.1016/S0020-7519(03)00049-3

Palombi A. 1929. — Ricerche sul ciclo evolutivo di *Helicometra fasciata* (Rud.). Revisione delle specie del genere Helicometra Odhner. *Pubblicazioni della Stazione Zoologica di Napoli* 9: 237-292 (In Italian).

Pogorel'tseva T. P. 1954. — New species of digenetic trematodes from fishes in the Black Sea. *Naukovi Zapiski Kievskogo Derjavnogo Pedagogicheskogo Institutu* 25: 133-137 (In Ukrainian).

Polyansky Yu. I. 1955. — Materials on the parasitology of fish of the northern seas of SSSR. Parasites of fish of the Barents Sea. *Trudy Zoologicheskogo Instituta AN SSSR* 19: 5-170 (In Russian).

Prudhoe S. & Bray R. A. 1973. — Digenetic trematodes from fishes. *BANZ Antarctic Research Expedition Reports, Series B* 8: 199-225.

R Core Team 2020. — *R: A language and environment for statistical computing. R Foundation for Statistical Computing*. Accessed at: http://www.r-project.org/index.html on 2020-08-17

Rambaut A., Drummond A. J., Xie D., Baele G. & Suchard M. A. 2018. — Posterior summarisation in Bayesian phylogenetics using Tracer 1.7. *Systematic Biology* 67 (5): 901-904. https://doi.org/10.1093/sysbio/syy032

Rudolphi K. A. 1819. — *Entozoorum synopsis cui accedunt mantissa duplex et indices locupletissimi*. Sumtibus A. Rücker, Berolini. https://doi.org/10.5962/bhl.title.9157

Sekerak A. D. & Arai H. P. 1974. — A revision of *Helicometra* Odhner, 1902 and related genera (Trematoda: Opecoelidae), including a description of *Neohelicometra sebastis* n. sp. *Canadian Journal of Zoology* 52: 707-738. https://doi.org/10.1139/z74-095

Sokolov S. G. & Gordeev I. I. 2013. —New data on trematodes (Plathelminthes, Trematoda) of fishes in the Ross Sea (Antarctic). *Invertebrate Zoology* 10: 255-267. https://doi.org/10.15298/invertzool.10.2.04

Sokolov S. G. & Gordeev I. I. 2015. — New data on trematodes of Antarctic fishes. *Parazitologiya* 49: 93-97 (In Russian).

Sokolov S. G., Lebedeva D. I., Gordeev I. I. & Khasanov F. K. 2019. — *Zdzitowieckitrema incognitum* gen. et sp. nov. (Trematoda, Xiphidiata) from the Antarctic fish *Muraenolepis marmorata* Günther, 1880 (Gadiformes: Muraenolepidae): ordinary morphology but unclear family affiliation. *Marine Biodiversity* 49: 451-462. https://doi.org/10.1007/s12526-017-0830-0

Sokolov S. G., Lebedeva D. I., Shchenkov S. V. & Gordeev I. I. 2020. — *Caudotestis dobrovolski* n. sp. (Trematoda, Xiphidiata) in North Pacific scorpaeniform fish: A crisis of concept of the opecoelid subfamily Stenakrinae Yamaguti, 1970. *Journal of Zoo-*

logical Systematics and Evolutionary Research 58 (4): 1111-1122. https://doi.org/10.1111/jzs.12359

STOSSICH M. 1883. — Brani di elmintologia tergestina. Serie prima. *Bollettino della Società adriatica di scienze naturali in Trieste* 8: 111-121 (In Italian).

STOSSICH M. 1886. — *I distomi dei pesci marini e d'acqua dolce*. Tipografia del Lloyd Austro-Ungarico, Trieste.

STOSSICH M. 1902. — Sopra una nuova specie delle Allocreadiinae Osservazioni. *Archives de Parasitologie* 5: 578-582 (In Italian).

STOSSICH M. 1903. — Una nuova specie de *Helicometra* Odhner. *Archives de Parasitologie* 7: 373-376 (In Italian).

STOSSICH M. 1904. — Alcuni distomi della collezione elmintologica del museo zoologico di Napoli. *Annuario del Museo Zoologico della R. Università di Napoli, Nuova Serie* 1: 1-14 (In Italian).

TKACH V. & PAWLOWSKI J. 1999. — A new method of DNA extraction from the ethanol-fixed parasitic worms. *Acta Parasitologica* 44: 147-148.

TKACH V. V., LITTLEWOOD D. T. J., OLSON P. D., KINSELLA J. M. & SWIDERSKI Z. 2003. — Molecular phylogenetic analysis of the Microphalloidea Ward, 1901 (Trematoda: Digenea). *Systematic Parasitology* 56: 1-15. https://doi.org/10.1023/A:1025546001611

TKACH V. V. & SNYDER S. D. 2007. — *Aptorchis megacetabulus* n. sp. (Platyhelminthes: Digenea) from the northern long-necked turtle, *Chelodina rugosa* (Pleurodira: Chelidae), in Australia. *Journal of Parasitology* 93: 404-408. https://doi.org/10.1645/GE-998R.1

VIDAL-MARTÍNEZ V. M., VELÁZQUEZ-ABUNADER I., CENTENO-CHALÉ O. A., MAY-TEC A. L., SOLER-JIMÉNEZ L. C., PECH D., MARIÑO-TAPIA I., ENRIQUEZ C., ZAPATA-PÉREZ O., HERRERA-SILVEIRA J., HERNÁNDEZ-MENA D. I., HERZKA S. Z., ORDOÑEZ-LÓPEZ U., AGUIRRE-MACEDO M. L. 2019. — Metazoan parasite infracommunities of the dusky flounder (*Syacium papillosum*) as bioindicators of environmental conditions in the continental shelf of the Yucatan Peninsula, Mexico. *Parasites & Vectors* 12: 277. https://doi.org/10.1186/s13071-019-3524-6

WANG P. Q. 1982. — Some digenetic trematodes of marine fishes from Fujian Province, China. *Oceanologia et Limnologia Sinica* 13: 179-194 (In Chinese).

WANG Y. Y., WANG P. Q. & ZHANG W. H. 1992. — Opecoelid trematodes of marine fishes from Fujian Province. *Wuyi Science Journal* 9: 67-89 (In Chinese).

WORMS. 2022. — *Helicometra* Odhner, 1902. Accessed at: http://www.marinespecies.org/aphia.php?p=taxdetails&id=108528 on 2022-02-28

YAMAGUTI S. 1934. — Studies on the helminth fauna of Japan. Part 2. Trematodes of fishes, I. *Japanese Journal of Zoology* 5: 249-541.

YAMAGUTI S. 1970. — *Digenetic trematodes of Hawaiian fishes*. Keigaku Publishing, Tokyo, 436 p.

ZDZITOWIECKI K. 1993. — A re-examination of some Antarctic and subantarctic fish digeneans from the collection of the British Museum (Natural History). *Acta Parasitologica* 38: 157-160.

ZDZITOWIECKI K. 1997. — Digenea of fishes of the Weddell Sea. IV. Three opecoelid species of the genera *Neolebouria*, *Helicometra* and *Stenakron*. *Acta Parasitologica* 42: 138-143.

ZHUKOV E. V. 1960. — Endoparasitic worms of the fishes in the Sea of Japan and South Kuril shallow-waters. *Trudy Zoologicheskogo Instituta AN SSSR*, Leningrad 28: 3-146 (In Russian).

Submitted on 6 december 2021;
accepted on 30 March 2022;
published on 6 September 2022.