

Redescription of trematode *Gonocerca muraenolepisi* Paruchin et Ljadov, 1979 (Hemiuroidea: Derogenidae), a body cavity parasite of Antarctic fishes, with a discussion of its phylogenetic position

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ABSTRACT: The redescription of *Gonocerca muraenolepisi* Paruchin et Ljadov, 1979 was made on the specimens collected from *Muraenolepis marmorata* Günther, 1880 (Gadiformes), caught in the Ross Sea, and on extant paratypes — one of which was designated as neotype — is given in this paper. Phylogenetic relations of *G. muraenolepisi* were inferred by Bayesian analysis of partial sequences from 28S rDNA. Molecular data are not consistent with the traditional point of view about the position of the genus *Gonocerca* Manter, 1925, and subfamily Gonocercinae that are based on this genus in the family Derogenidae. Also, molecular data does not support the presence of the genus *Hemipera* Nicoll 1913, in the subfamily Gonocercinae. The taxonomical position and species lists of representatives of the Gonocercinae need further revision.

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KEY WORDS: trematodes, body cavity, Antarctic, the Ross Sea, the D'Urville Sea, the Amundsen Sea, 28S rDNA, *Muraenolepis*, *Gonocerca muraenolepisi*, Gonocercinae, Derogenidae.

Переписание трематоды *Gonocerca muraenolepisi* Paruchin et Ljadov, 1979 (Hemiuroidea: Derogenidae) — паразита полости тела антарктических рыб, с обсуждением его филогенетического положения

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РЕЗЮМЕ: Переописание *Gonocerca muraenolepisi* Paruchin et Ljadov, 1979 выполнено по оригинальному материалу от рыбы *Muraenolepis marmorata* Günther, 1880 (Gadiformes) из моря Росса, и сохранившимся паратипам, один из которых выделен в качестве неотипа. Филогенетические связи *G. muraenolepisi* были изучены на основе анализа нуклеотидных последовательностей участка 28S рДНК. Молекулярные данные не согласуются с традиционной точкой зрения о членстве рода *Gonocerca* Manter, 1925 и, основанного на нем подсемейства Gonocercinae, в семействе Derogenidae. Также молекулярные данные не поддерживают концепцию вхождения рода *Hemiperu* Nicoll, 1913 в состав подсемейства Gonocercinae. Таксономический статус и состав Gonocercinae требуют уточнения.

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КЛЮЧЕВЫЕ СЛОВА: трематоды, полость тела, Антарктика, море Росса, море Дюрвиля, море Амундсена, 28S рДНК, *Muraenolepis*, *Gonocerca muraenolepisi*, Gonocercinae, Derogenidae.

Introduction

The trematode *Gonocerca muraenolepisi* Paruchin et Ljadov, 1979 is a representative of the southern sub-polar parasitofauna of fishes. The type-host of this species marita is fish *Muraenolepis marmorata* Günther, 1880 (Gadiformes); the type location is the Kerguelen Islands area (Indian Ocean sector of the sub-Antarctic). The first description of *G. muraenolepisi* contains erroneous data about the site of infection of this parasite — intestine and stomach (Parukhin, Lyadov, 1979). According to Lyadov (1980) and Parukhin (1989), this species was actually found in the body cavity. In addition to *M. marmorata*, *Lepidonotothen mizops* (Günther, 1880) and *Channichthys rhinoceratus* Richardson, 1844 are reported hosts of *G. muraenolepisi* (Lyadov, 1980; Parukhin, 1989). There are no data on the distribution of this trematode outside the Kerguelen Islands area.

The parasite was found by us in *M. marmorata* in the Ross Sea, D'Urville Sea and Amundsen Sea. Obtained materials allow us to make sufficient additions to the species' description and to discuss its phylogenetic position.

Material and methods

Sample collection

Eighty-six individuals of *M. marmorata* were collected as by-catch during fishing for the Antarctic toothfish *Dissostichus mawsoni* Norman, 1937 in the Ross Sea from December 2011 to February 2012, and from December 2012 to January 2013; in the D'Urville Sea in February 2011; and in the Amundsen Sea in February 2015. These 86 individuals were examined for parasites. The fishing depth varied from 679 to 1480 m. All individuals were caught using longline ('Mustad' system, auto-line, and trot-line) baited with squid. Fish identification was carried out using Fisher & Hureau (1985). The total length of the examined fishes varied from 27 to 56 cm.

All fishes were examined for parasitic infections using standard methods (Bykhovskaya-Pavlovskaya, 1985). Worms were fixed in 70% ethanol under a cover glass with slight pressure, stained with acetocarmine, and mounted in Canada balsam. Drawings were made using a drawing tube. Voucher specimens studied were specimens that were deposited in the Museum of Helminthological Collections of the Centre for

Parasitology of the A.N. Severtsov Institute of Ecology and Evolution, Moscow, Russia (IPEE RAS); inventory numbers: 1202–1216.

The extant type material of *G. muraenolepisi* comprises only three paratypes deposited in the Museum of the All-Russian K.I. Skryabin Scientific Research Institute of Helminthology; inventory number: 21508. The slide was registered in the museum by V.N. Lyadov. The species holotype mentioned in the paper of Parukhin & Lyadov (1979) is considered as lost. Parukhin & Lyadov (1979) wrote that the holotype was deposited in the A.O. Kovalevsky Institute of Biology of the Southern Seas (Sevastopol), named now as the A.O. Kovalevsky Institute of Marine Biological Research. However, any specimens of *G. muraenolepisi* are no longer in this institute (Dr Julia M. Korniychuk, personal communication). They were not in the Southern Scientific Research Institute of Marine Fisheries and Oceanography (Kerch), where V.N. Lyadov was employed, either. Based on that, we designated one of the three paratypes in slide #21508 deposited in the All-Russian Scientific Research Institute of Helminthology as a neotype. Data on the neotype: host — *Muraenolepis marmorata* Günther, 1880; site of infection — the body cavity; locality — the Kerguelen Islands area (Indian Ocean sector of sub-Antarctic); collector — V.N. Lyadov. All three type specimens of *G. muraenolepisi* have more or less deformed gonads, the ovary in particular, due to overpressure during fixation.

DNA extraction, amplification and sequencing

Eleven gravid specimens of *Gonocerca muraenolepisi*, with body lengths of 6.7–21 mm that had been taken from *M. marmorata* caught in the Ross Sea and the Amundsen Sea, and were fixed in 96% ethanol and used for molecular analysis. Total genomic DNA was extracted with an invitrogen genomic DNA extraction kit following the manufacturer's protocol. Nuclear 28S rDNA was successfully amplified using a polymerase chain reaction with the following primers: DIGL2 (5' – AAG CAT ATC ACT

AAG CGG – 3') and 1500R (5' – GCT ATC CTG AGG GAA ACT TCG – 3') (Tkach et al., 2003). Negative and positive controls using both primers were included. The PCR products were directly sequenced using an ABI Big Dye Terminator v.3.1 Cycle Sequencing Kit (Applied Biosystems, USA), as recommended by the manufacturer, with the internal sequencing primers 300F, ECD2, 900F and 1200R (Tkach, et al., 2003). The PCR products were analysed using an ABI 3130 genetic analyser at the Institute of Biology and Soil Sciences FEB RAS. The sequences have been submitted to the EMBL database with the following accession numbers: HF543941–HF543948, LN650651, LN865025, and LN865026.

Sequence analysis and reconstruction of phylogeny

The ribosomal DNA sequences were assembled with SeqScape v.2.6 software and aligned using the MEGA 5.0 (Tamura et al., 2011) alignment explorer with default options. The regions that could not be unambiguously aligned were excluded from the analyses. A number of variable and parsimony-informative sites and nucleotide compositions were calculated using MEGA 5.0. Phylogenetic analysis of the nucleotide sequences was performed using Bayesian inference (BI), using MrBayes v.3.1.2 software (Huelsenbeck et al., 2001) with the general time reversible model with gamma distribution, and calculation of proportion of invariable sites (GTR+G+I) (Tavare, 1986). This model showed the best fit to the data using Modeltest v.3.07 software (Posada, Crandall, 1998). A Markov chain algorithm was performed with 10,000,000 generations. Optimisation of the Bayesian inference algorithm was performed by the setting up of priors using Tracer 1.5.0 software (Rambaut, Drummond, 2009). The significance of the phylogenetic relationship was estimated using posterior probabilities.

The phylogenetic position of *G. muraenolepisi* was inferred using nucleotide sequences of 28S rDNA for representatives of the superfamily Hemiuroidea and Azygioidea retrieved

from GenBank: *Accacoelium contortum* (Rudolphi, 1819) [Accacoeliidae]; *Derogenes varicus* (Müller, 1784); *Hemipera manteri* (Crowcroft, 1947) [Derogenidae]; *Didymozon scombri* Taschenberg, 1879 [Didymozoidae]; *Bunocotyle progenetica* Chabaud et Buttner, 1959; *Dinurus longisinus* Looss, 1907; *Lecithocladium excisum* (Rudolphi, 1819); *Merluciotrema praeclarum* (Manter, 1934); *Plerurus digitatus* (Looss, 1899); *Robinia aurata* Pankov, Webster, Blasco-Costa, Gibson, Littlewood et Kostadinova, 2006; *Saturnius* sp. [Hemiuridae]; *Aponurus* sp., *Machidatrema chilostoma* (Machida, 1980) [Lecithasteridae]; *Copiatestes filiferus* (Leuckart in Sars, 1885) [Syncoeliidae]; *Prosogonotrema bilabiatum* Viegas, 1940 [Sclerodistomidae]; and *Otodistomum cestoides* (van Beneden, 1871) [Azygiidae] (Olson *et al.*, 2003; Pankov *et al.*, 2006). *Otodistomum cestoides* was used as an outgroup.

Results

Fam. Derogenidae Nicoll, 1910

Subfam. Gonocercinae Skrjabin
et Guschanskaja, 1955

Gonocerca muraenolepisi
Paruchin et Ljadov, 1979
Figs. 1–4.

Host. *Muraenolepis marmorata* Günther, 1880.

Site of infection. Body cavity.

Locality. The Ross Sea: 71° S, 177° W; 72° S, 176° W; 77° S, 170° E; 76° S, 170° W; 72° S, 175° E; 75° S, 174° E. The D'Urville Sea: 65° S, 139° E; 66° S, 134° E. The Amundsen Sea: 71°–72° S; 118° W.

Prevalence. All of the four examined fishes in the area bounded by the coordinates 76° S, 170° W – 77° S, 170° W; three of the 43 examined fishes in the area bounded by the coordinates 72° S, 175° E–72° S, 176° W; three of the nine examined fishes at coordinates 75° S, 174° E; five of the eight fishes at coordinates

71° S, 177° W; two of the two fishes at coordinates 65° S, 139° E; two of the three fishes at coordinates 66° S, 134° E; 13 of the 25 examined fishes in the area bounded by the coordinates 71°–72° S, 118° W.

Intensity. From one to 18 individuals per host.

Description (by 47 gravid specimens from the Ross Sea and three type specimens; sizes of the three type specimens are given in Table 1). Body fusiform in small specimens and foliate with conical forebody in large specimens (Figs. 1, 3, 4), its size $16.4 \pm 1.0 \times 6.8 \pm 0.5$ mm. Tegument smooth. Oral sucker subterminal, $0.579 \pm 0.021 \times 0.619 \pm 0.027$ mm; preoral lobe present; prepharynx absent; pharynx $0.290 \pm 0.013 \times 0.263 \pm 0.012$ mm; oesophagus short 0.304 ± 0.020 mm. Caeca winding, somewhat inflated, terminate near posterior extremity of body. Ventral sucker larger than oral sucker, pre-equatorial, $1.082 \pm 0.051 \times 1.090 \pm 0.048$ mm; forebody $43.9 \pm 0.5\%$ of body length. Oral/ventral sucker ratio based on mean diameters $1:1.80 \pm 0.03$; ratio based on widths $1:1.76 \pm 0.03$. Testes in posterior part of body, elliptical, spherical or sub-elliptical with irregular protrusions; symmetrical or oblique (Figs. 1, 3, 4). Left testis $2.39 \pm 0.23 \times 1.96 \pm 0.16$ mm, right testis $2.42 \pm 0.22 \times 2.07 \pm 0.19$ mm; post-testicular space $12.4 \pm 0.9\%$ of body length. Seminal vesicle tubular, usually sinuous (Fig. 2 A). Pars prostatica tubular; surrounded by sub-spherical field of dense prostatic cells, $0.307 \pm 0.024 \times 0.266 \pm 0.014$ mm. Short thin-walled ejaculatory duct opens into genital atrium (Fig. 2A). Genital atrium short, its aperture ventromedian, near posterior margin of oral sucker. Ovary between ventral sucker and testes, median, with irregular incisions (Figs. 1, 3, 4), $1.17 \pm 0.09 \times 1.13 \pm 0.09$ mm. Ootype dorsal to ovary. Laurer's canal very long, sinuous, opens dorsally between ovary and testes (their anterior edge or midlevel) (Fig. 1). Middle part of Laurer's canal in most specimens rather dilated and filled with sperm (Fig. 1B). Two vitelline masses at ovarian level, 5–12 lobed, symmetrical or slightly oblique; in contact with testes or clearly separated from them

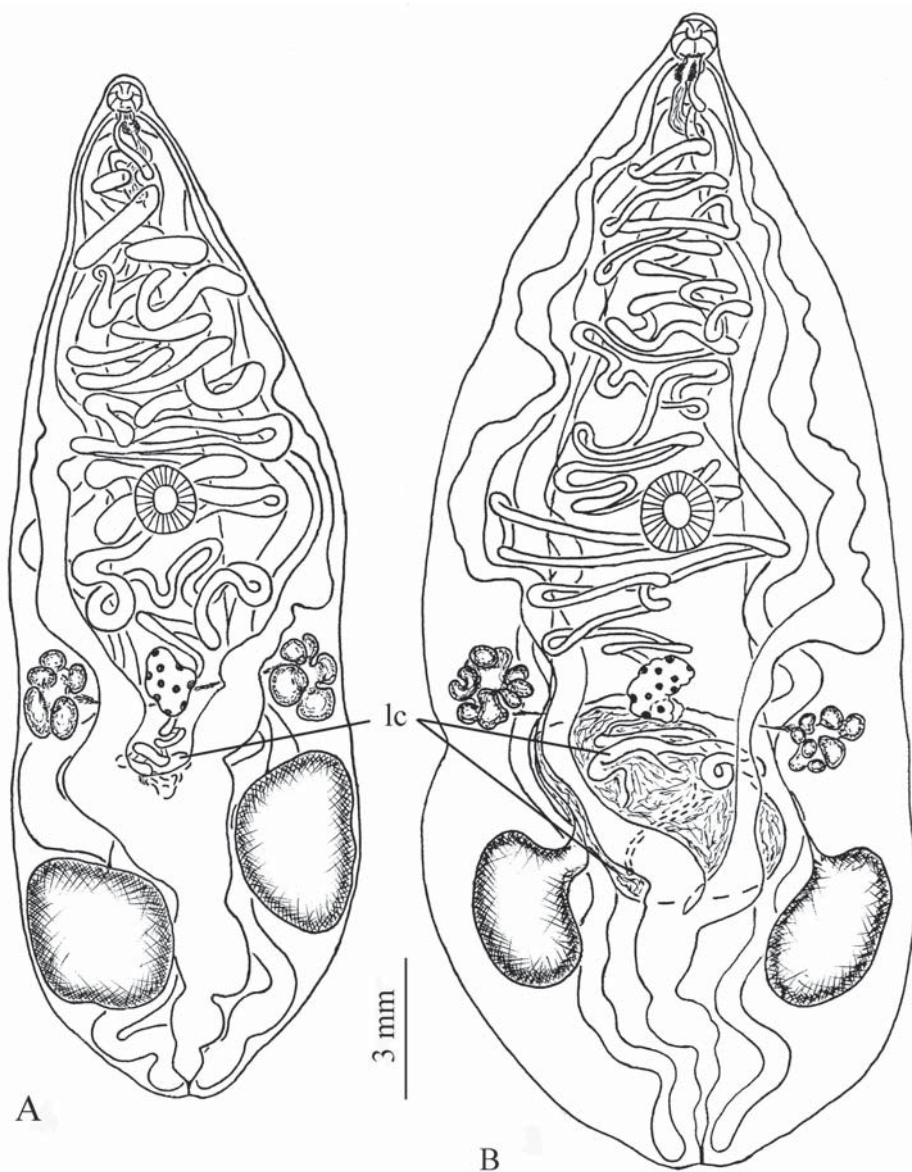


Fig. 1. Large specimens of *Gonocerca muraenolepisi* from body cavity of *Muraenolepis marmorata* caught in the Ross Sea. A — individual with Laurer's canal not filled with sperm; B — individual with Laurer's canal filled with sperm (middle part of the canal is very extended).

Abbreviations: lc — Laurer's canal.

Рис. 1. Крупные особи *Gonocerca muraenolepisi* из полости тела *Muraenolepis marmorata*, пойманных в море Росса. А — экземпляр с Лауреровым каналом без спермы; В — экземпляр, с заполненным спермой Лауреровым каналом (средняя часть канала сильно расширена).

Обозначения: lc — Лауреров канал.

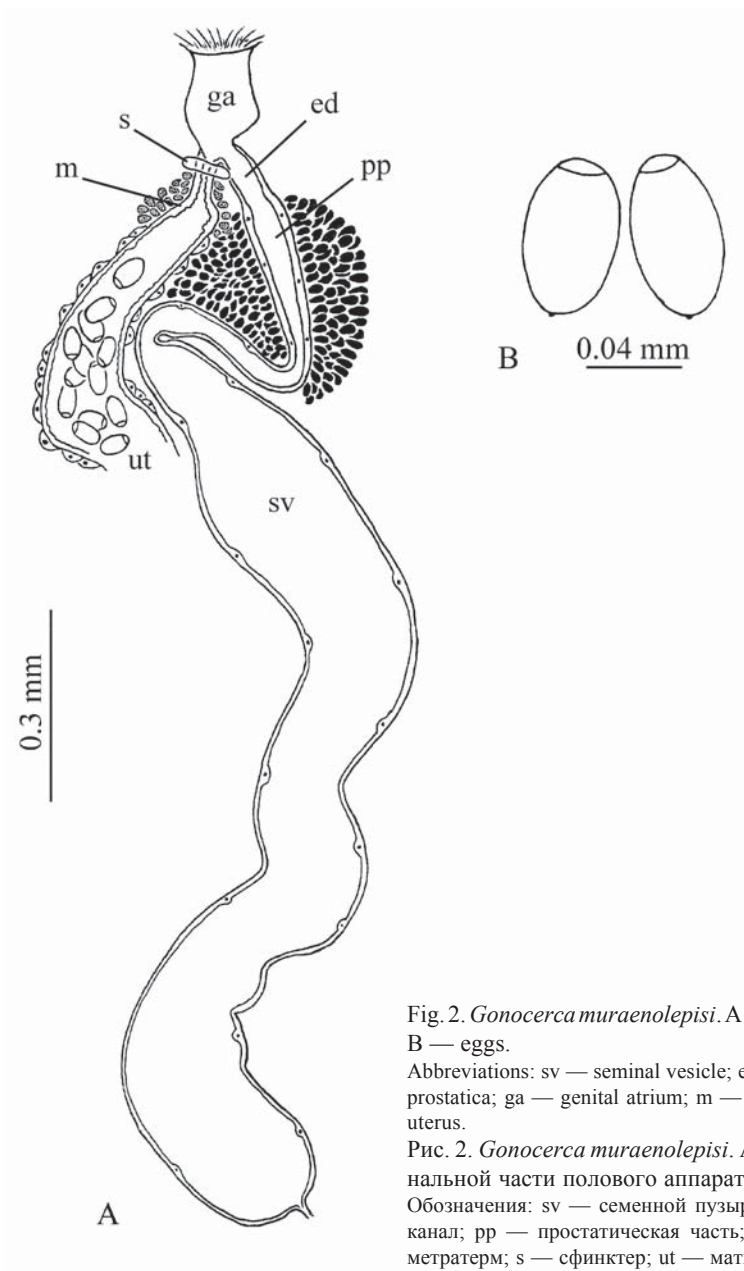


Fig. 2. *Gonocerca muraenolepisi*. A — details of terminal genitalia; B — eggs.

Abbreviations: sv — seminal vesicle; ed — ejaculatory duct; pp — pars prostatica; ga — genital atrium; m — metraterm; s — sphincter; ut — uterus.

Рис. 2. *Gonocerca muraenolepisi*. А — детали строения терминальной части полового аппарата; В — яйца.

Обозначения: sv — семенной пузырек; ed — семяизвергательный канал; pp — простатическая часть; ga — половой атриум; m — метратерм; s — сфинктер; ut — матка.

(Fig. 4). Left vitelline mass $1.48 \pm 0.14 \times 1.31 \pm 0.13$ mm, right mass $1.62 \pm 0.22 \times 1.37 \pm 0.16$ mm. Uterus preovarian, transversely coiled, chiefly intracaecal (Fig. 1, 3, 4); metraterm surrounded by gland cells, terminates with

sphincter (Fig. 2A). Eggs numerous, elliptical, $64 \pm 1.1 \times 33 \pm 0.6$ μ m, with operculum and small knob at anopercular pole (Fig. 2B). Excretory vesicle Y-shaped; arms uniting dorsal to pharynx; pore terminal.

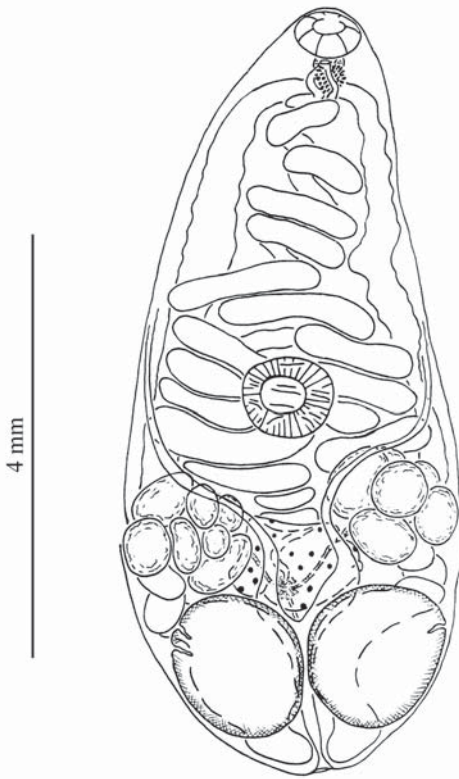


Fig. 3. Neotype of *Gonocerca muraenolepisi*. Slide #21508 from the museum of helminths of the All-Russian Scientific Research Institute of Helminthology, Moscow.

Fig. 3. Неотип *Gonocerca muraenolepisi*. Препарат № 21508 из гельминтологического музея Всероссийского научно-исследовательского института фундаментальной и прикладной паразитологии животных и растений имени К.И. Скрябина.

Phylogenetic analysis

A 28S rDNA fragment of approximately 1300 bp was obtained for *G. muraenolepisi*; the resulting sequences were presented in two variants, which have different lengths. The first one was 1164 bp in length, and was detected for nine specimens from the Ross Sea (#HF543941–HF543948, LN650651). The second one was 1162 bp in length and was detected for two specimens from the Amundsen Sea (#LN865025, LN865026). Overall, 11 variable sites (0.9%)

and two indels were detected between these two sequence variants. We do not make any taxonomical conclusions based on this value of genetic differentiation, because of the lack of molecular data on congeneric species of the subfamily Gonocercinae.

Bayesian inference analysis revealed the separation of the representatives of the superfamily Hemiuroidea into two main clusters (Fig. 5 I, II) and an independent branch (Fig. 5 III) that includes derogenid species *H. manteri*. The first cluster (Fig. 5 I) consists of members of the families Hemiuridae, Lecithasteridae, Accacoeliidae, Syncoeliidae, Derogenidae, Didymozoidae, and Sclerodistomidae. The second cluster (Fig. 5 II) represents species *G. muraenolepisi* (Derogenidae). The species *Derogenes varicus* (type-species of type-genus of Derogenidae) appears closely related to *Didymozoon scombri* (Didymozoidae), but statistical support for this connection is not high. Nevertheless, *D. varicus* and *D. scombri* are included into the large, highly supported cluster (I) that differs considerably from *G. muraenolepisi* and *H. manteri*.

Discussion

Gonocerca muraenolepisi is undoubtedly placed in the genus *Gonocerca* Manter, 1925 because of the post acetabular position of the ovary, the presence of two compact lateral vitelline masses at the ovarian level, the location of the testes posterior to the ovary and vitellarium, the morphology of the eggs, and the morphology of the distal part of the male and female ducts (Gibson, Bray, 1979; Gibson, 1996, 2002). At the same time, the pre-equatorial position of the ventral sucker of most studied specimens of *G. muraenolepisi* is not consistent with the diagnosis of the genus *Gonocerca* provided by Gibson & Bray (1979) and Gibson (1996, 2002). We do not give much importance to this discrepancy. The pre-equatorial position of the ventral sucker is typical for *Gonocerca lobata* Byrd, 1963 and some specimens of *Gonocerca caelorinchi* (Machida et Kuramochi, 1994). Gibson (1976, 2002) recognised these species as

Table 1. Morphological characteristics of small specimens of *Gonosera tugaenolepisi*.
 Таблица 1. Морфологическая характеристика мелких экземпляров *Gonosera tugaenolepisi*.

Characters	Specimens from original material, N = 17; range (mean)	Parukhin, Lyadov (1979); range	Neotype (two paratypes)
Body size, mm	4.8–14.8 (9.4) × 1.7–6.4 (3.6)	4.3–12.0 × 2.0–6.0	7.3 × 3.2 (7.5 × 4.7; 5.0 × 2.4)
Body width as % of body length	31.3–46.4 (37.9)	51.2*	44.0 (62.6; 48.5)
Forebody as % of body length	32.0–46.1 (41.0)	39.3*	45.6 (41.9; 37.9)
Posttesticular space as % of body length	8.5–20.6 (12.7)	7.5*	–
Oral sucker size, mm	0.37–0.74 (0.45) × 0.37–0.67 (0.46)	0.34–0.65 × 0.40–0.82	0.42 × 0.64 (– × ? 0.73; – × 0.47)
Pharynx size, mm	0.18–0.26 (0.22) × 0.17–0.26 (0.19)	0.20–0.25 × 0.18–0.25	0.22 × 0.31 (0.23 × 0.30; 0.21 × 0.23)
Oesophagus length, mm	0.24–0.32 (–)	–	–
Ventral sucker size, mm	0.54–1.47 (0.74) × 0.54–1.47 (0.77)	0.57–1.10 × 0.57–1.14	0.76 × 0.89 (0.85 × 0.91; 0.68 × 0.71)
Oral sucker/ventral sucker width ratio	1:1.43–2.43 (1.69)	1:1.33*	1:1.40 (1:1.25; 1:1.49)
Oral sucker/ventral sucker ratio based on mean diameter	1:1.45–2.43 (1.63)	1:1.46*	1:1.56 (–)
Left testis size, mm	0.53–2.04 (1.04) × 0.45–1.44 (0.85)	0.84–1.57 × 0.61–1.62	1.41 × 1.21 (2.15 × 1.31; 1.07 × 0.84)
Right testis size, mm	0.45–1.80 (0.99) × 0.38–1.75 (0.87)	1.10–1.20 × 0.71–1.65	1.42 × 1.26 (1.64 × 1.61; 1.04 × –)
Field of prostatic cells diameter, mm	0.11–0.26 (0.17)	–	0.30 (0.24; 0.20)
Ovary size, mm	0.27–1.31 (0.62) × 0.29–1.08 (0.56)	0.65–0.80 × 0.48–0.65	0.96 × 1.34 (0.91 × 1.46; –)
Left vitelline mass size, mm	0.50–1.40 (0.73) × 0.34–1.32 (0.65)	0.94–0.97 × 0.51–0.62	1.14 × 1.26 (1.44 × 1.33; –)
Right vitelline mass, mm	0.38–1.34 (0.70) × 0.34–1.23 (0.66)	0.94–0.97 × 0.51–0.62	1.25 × 1.22 (1.51 × 1.38; 1.21 × 0.62)
Number of lobes on vitelline masses	5–8 (6)	5–6	6, 10 (8, 5; 6)

Note. * calculated basing on data from description or drawn of the holotype (Parukhin, Lyadov, 1979).

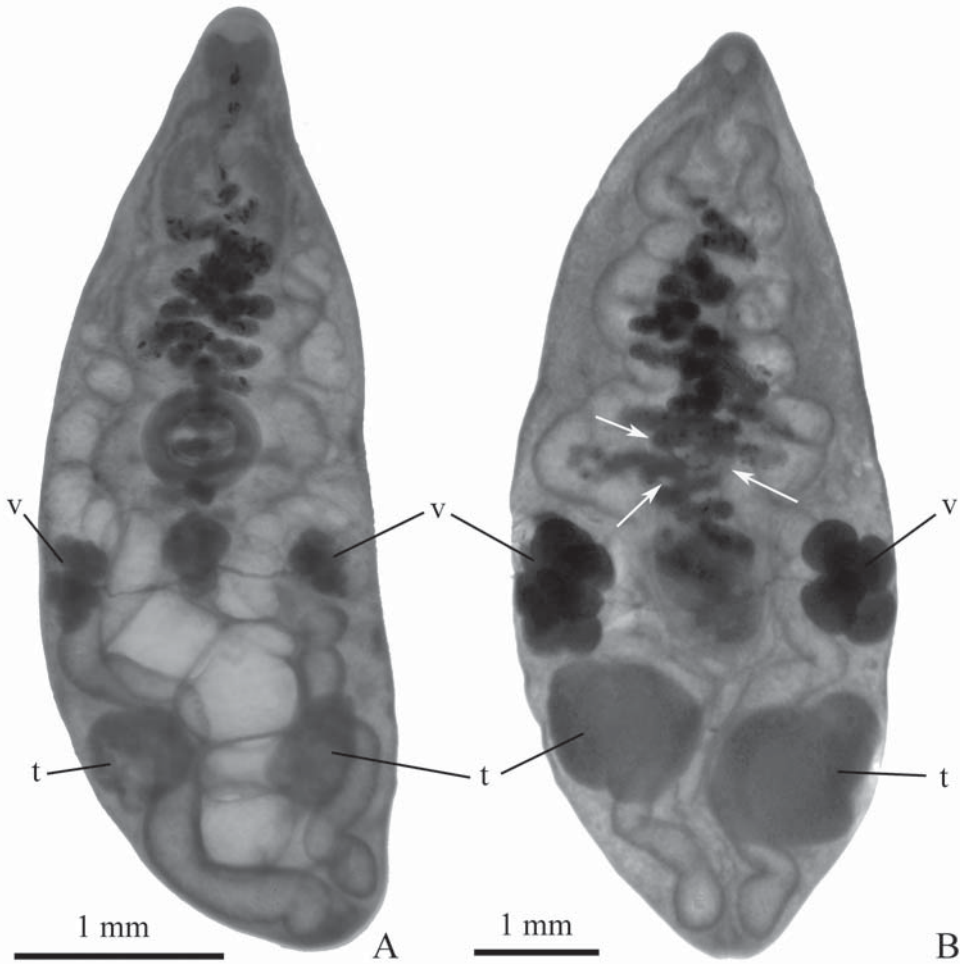


Fig. 4. Small specimens of *Gonocerca muraenolepisi* from body cavity of *Muraenolepis marmorata* caught in the Ross Sea. A, B — Examples of different remoteness of the testes from the vitelline masses.

Abbreviations: t — testes; v — vitelline masses; arrows — ventral sucker.

Рис. 4. Мелкие экземпляры *Gonocerca muraenolepisi* из полости тела *Muraenolepis marmorata*, пойманных в море Росса. А, В — примеры разной удаленности семенников от желточных телец.

Обозначения: t — семенники; v — желточные тельца; стрелки — брюшная присоска.

unambiguous members of the genus *Gonocerca*.

The studied sample of trematodes contained small (< 15 mm) and large (\geq 15 mm) specimens (Table 1, 2; Fig. 1, 3, 4). All specimens were mature with eggs in uterus. Analysis of 28S rDNA sequences indicates that large (sample #HF543948, body length: 17 mm) and small (#HF543941–HF543947, LN650651, body

length: 6.7–14 mm) specimens are conspecific. Possibly, trematodes of deep-water fishes, parasitizing in the body cavity, can live for several years, and studied specimens of different sizes have different ages. The small specimens of *G. muraenolepisi* morphologically coincide with the type-specimens of this species (Table 1).

The large specimens of *G. muraenolepisi* are similar to *G. caelorinchi*, found in the body

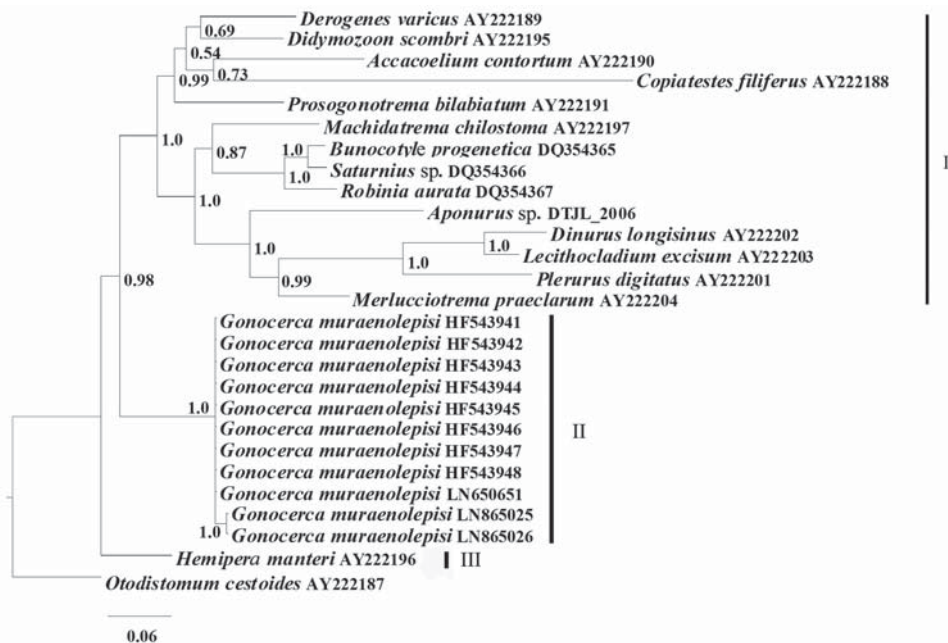


Fig. 5. Phylogenetic tree of the superfamily Hemiuroidea, reconstructed using Bayesian algorithm using 28S rDNA partial sequences. Posterior probability values are given at nodes.

Рис. 5. Филогенетическое древо надсемейства Hemiuroidea, реконструированное с помощью алгоритма Байеса по данным частичного секвенирования последовательностей 28S рДНК. Значения постериорных вероятностей указаны в узлах.

cavity of macrourid fish from the North Pacific (Table 2) Nevertheless, the mean value of the body width and forebody length (in both cases as a percentage of body length), the width of the pharynx, and the length and width of both suckers and diameter of the field of prostatic cells in *G. muraenolepisi* are lower than or equal to the minimum values for these characters in *G. caelorinchi* (Table 2). Clarification of the taxonomic relationships between these two species requires molecular data on *G. caelorinchi*.

To date, five nominal species of the genus *Gonocerca*: *G. haedrichi* Campbell et Munroe, 1977, *G. lobata*, *G. muraenolepisi*, *G. phycidis* Manter, 1925, *G. trematomi* Byrd, 1963 have been recorded from the Southern Ocean (Byrd, 1963; Gibson, 1976; Parukhin, 1989; Zdzitowiecki, 1991; Walter et al., 2002; the present study). However, some authors believe that *G. trematomi* and probably *G. lobata* should be synonymised with *G. phycidis* (Prudhoe, Bray, 1973; Gibson, 1976; Zdzitowiecki, 1979; Zdzitowiecki et al., 1999).

Within Hemiuroidea, the genera *Gonocerca* and *Hemipera* Nicoll, 1913 are grouped into the subfamily Gonocercinae, within the family Derogenidae, by the location of the testes which are posterior to the ovary and vitellarium (Skryabin, Gushanskaya, 1955; Yamaguti, 1971; Gibson, Bray, 1979; Gibson, 1996, 2002). The first studies on the taxonomical status of the Gonocercinae by molecular data were performed by Olson et al. (2003) and Pankov et al. (2006), using complete 18S rDNA and partial 28S rDNA sequences of different species of Hemiuroidea, including two derogenid species: *H. manteri* (Gonocercinae) and *D. varicus* (Derogeninae). Phylogenetic tree topologies, reconstructed by these authors, showed that genetic differentiation between these two species corresponded with the familial genetic divergence level of Hemiuroidea. Olson et al. (2003) and Pankov et al. (2006) suggested that the family Derogenidae is polyphyletic, and noted that the subfamily Gonocercinae can possibly be recognised as a distinct family. Our data also showed that trem-

Table 2. Comparative data on *Gonocerca caelorinchi* and large specimens of *Gonocerca muraenolepisi*.
 Таблица 2. Сравнительные данные по *Gonocerca caelorinchi* и крупным особям *Gonocerca muraenolepisi*.

Characters	<i>Gonocerca muraenolepisi</i> , N = 17; range (mean)	<i>Gonocerca caelorinchi</i> After: Machida, Kuramochi (1994), Machida, Kamegai (1997), N = 12; range
Body size, mm	15.0–28.4 (20.9) × 5.3–10.6 (7.6)	15.4–32.2 × 5.0–12.7
Body width as % of body length	27.8–44.1% (36.5%)	52.5%*
Forebody as % of body length	29.9–44.6 (39.1)	46.0–56.0
Posttesticular space as % of body length	2.9–19.7 (11.7)	11.0–17.0
Oral sucker size, mm	0.51–0.91 (0.66) × 0.50–0.99 (0.73)	0.85–1.30 × 0.90–1.40
Pharynx size, mm	0.26–0.47 (0.34) × 0.23–0.38 (0.31)	0.28–0.51 × 0.37–0.57
Oesophagus length, mm	0.18–0.43 (0.32)	to 0.40
Ventral sucker size, mm	0.88–1.75 (1.29) × 0.95–1.64 (1.29)	1.45–2.00 × 1.45–2.15
Oral sucker/ ventral sucker width ratio	1:1.46–2.22 (1.78)	1:1.40–1.80**
Oral sucker/ ventral sucker ratio based on mean diameter	1:1.63–2.24 (1.87)	
Left testis size, mm	1.27–3.78 (2.76) × 1.52–2.61 (2.27)	0.70–2.55 × 1.05–2.95
Right testis size, mm	1.67–3.70 (2.81) × 1.23–3.19 (2.40)	1.25–2.85 × 0.85–3.50
Field of prostatic cells diameter, mm	0.24–0.42 (0.31)	0.31–0.56
Ovary size, mm	0.75–1.57 (1.31) × 0.85–1.50 (1.28)	0.60–1.30 × 0.75–1.65
Left vitelline mass size, mm	0.92–2.68 (1.69) × 1.00–2.47 (1.49)	0.92–2.10 × 1.20–2.10
Right vitelline mass, mm	0.84–4.22 (1.89) × 0.96–2.88 (1.58)	1.05–1.85 × 1.25–2.25
Number of lobes on vitelline masses	5–12 (8)	3–8
Eggs size, μm	57–72 (63) × 31–39 (34)	47–68 × 28–39

Note. * calculated by the figure of Machida, Kuramochi (1994); ** options of oral/ventral suckers ratio (width or mean diameter) were not specified.

atodes of the family Derogenidae do not form a single phylogenetic cluster, indicating polyphyly of this taxon. Nevertheless, we consider the discussion of the Gonocercinae's taxonomical status premature. Genetic study of the type-species of the genus *Gonocerca* — *G. phycidis* is needed for an adequate decision on this question. Moreover, we cannot integrate *G. murraenolepisi* and *H. manteri* into the one subfamily based on the molecularly-based analysis of phylogenetic relationships (Fig. 5). Therefore, genus *Hemipera* belonging to the subfamily Gonocercinae needs confirmation.

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