DOI: 10.1515/ap-2016-0070

Acta Parasitologica, 2016, 61(3), 529–536; ISSN 1230-2821

DE GRUYTER

Redescription of *Proctophantastes gillissi* (Overstreet et Pritchard, 1977) (Trematoda: Zoogonidae) with discussion on the systematic position of the genus *Proctophantastes* Odhner, 1911

Sergey Sokolov[1], Ilya Gordeev[2] and Daria Lebedeva[3]*

[1]Centre for Parasitology of the A.N. Severtsov Institute of Ecology and Evolution RAS, 33 Leninskij prosp., Moscow, 119071, Russian Federation; [2]Russian Federal Research Institute of Fisheries and Oceanography, V. Krasnoselskaya Str. 17, Moscow 107140, Russian Federation;[3]Institute of Biology of Karelian Research Centre of RAS, Pushkinskaya Str. 11, Petrozavodsk,185910, Russian Federation

Abstract

The redescription of *Proctophantastes gillissi* (Overstreet et Pritchard, 1977) (Trematoda: Zoogonidae) was made on specimens collected from *Muraenolepis marmorata* Günther, 1880 (Gadiformes) caught in the Ross Sea and the Amundsen Sea (Antarctic). The fish is a new host of this parasite. Phylogenetic relations of *P. gillissi* were inferred by Maximum Likelihood and Bayesian inference analysis of partial sequences from 28S rDNA. The findings from analysis of the molecular data are not consistent with the traditional point of view about the position of the genus *Proctophantastes* Odhner, 1911 in the subfamily Lepidophyllinae. The taxonomical position of the genus needs further revision.

Keywords

Zoogonidae, Lepidophyllinae, *Proctophantastes gillissi*, *Muraenolepis marmorata*, 28S rDNA, Antarctic

Introduction

The zoogonid trematode *Proctophantastes gillissi* (Overstreet et Pritchard, 1977) was described from anguilliform fish *Histiobranchus bathybius* (Günther, 1877) (as *Synaphobranchus bathybius* by Overstreet and Pritchard 1977) from the Gulf of Panama at a depth of around 3190 m (Overstreet and Pritchard, 1977). The species was originally placed in the genus *Neosteganoderma* Byrd, 1964. This genus was considered by Yamaguti (1971) as identical with *Proctophantastes* Odhner, 1911, but this point of view was not supported by Bray (1973), Bray and Gibson (1986), Bray (1987) and other authors (Overstreet and Pritchard 1977; Machida *et al.* 2006). Bray and Gibson (1986) found reasonable to move *N. gillissi* to the genus *Proctophantastes*. More recently, Bray (2008) acknowledge that *Proctophantastes* and *Neosteganoderma* were congeneric, retaining the name *Proctophantastes* in accordance with the priority principle.

Trematodes of the genus *Proctophantastes*, which we consider to be conspecific with *P. gillissi*, were found during parasitological examination of deep-water Antarctic fish, and were previously mentioned in the paper of Sokolov and Gordeev (2013). This article provides a description of *P. gillissi* and a phylogenetic analysis of its position in the family, based on partial 28S rDNA nucleotide sequences.

Materials and Methods

Sample collection

Specimens of *P. gillissi* were collected from *Muraenolepis marmorata* Günther, 1880 (Gadiformes) caught in the Ross Sea and in the Amundsen Sea. Twenty six specimens of *M. marmorata* were examined in the Ross Sea and twenty nine in the Amundsen Sea. Fish were caught in December 2012 – February 2013. Total length of fish varied from 30 to 57 cm.

All fish were examined for parasitic infections using standard methods (Bykhovskaya-Pavlovskaya 1985). Worms

*Corresponding author: daryal78@gmail.com

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. Specimens for scanning electron microscopy were dehydrated in a graded ethanol series, then transferred to 100% acetone and dried using critical point drying method. Specimens were sputter-coated of gold and examined using a Tescan Vega TS 5130 MM (CamScan MV 2300) scanning electron microscope.

Voucher specimens were deposited in the Museum of Helminthological Collections of the Centre for Parasitology of the A.N. Severtsov Institute of Ecology and Evolution RAS, Moscow, Russia – MHC IPEE RAS.

Molecular study

For molecular analyses parasites were fixed and stored in 96% ethanol. Total genomic DNA for molecular analysis was isolated from two specimens of *P. gillissi* collected in Ross Sea using the protocol of Miller *et al.* (1988). Specimens for PCR were processed according to the protocols of Olson *et al*. (2003). Amplification of 28S rDNA (D1 – D3 partial) was performed with primers DIG12 (5' – AAG CAT ATC ACT AAG CGG – 3') and 1500R (5' – GCT ATC CTG AGG GAA ACT TCG – 3'). PCR products were purified and sequenced in both directions at ABI 3130 (PE 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').

The sequences (1251 bp length) were aligned by ClustalW in MEGA 6.0 (Tamura *et al.* 2013). Maximum Likelihood analyses (bootstrap analyses with 500 replicates) of the 28S rDNA dataset were conducted to explore relationships among these taxa. Also the Bayesian inference analysis was run over 1000000 generations using MrBayes version 3.2.2 (Ronquist *et al.* 2012).

Table I. Comparative characteristics of gravid specimens of *Proctophantastes gillissi* from different geographical regions

Characters	Our specimens, n = 27 range (mean)	Holotype (after Overstreet and Pritchard, 1977)
Geographical region	**the Ross Sea and the Amundsen Sea (the Southern Ocean)**	**the Gulf of Panama (the Pacific Ocean)**
Host	*Muraenolepis marmorata* (Gadiformes)	*Histiobranchus bathybius* (Anguilliformes)
Depth	1068–1651 m	about 3190 m
Body: Length, mm	2.0–5.1 (3.3)	3.2
Body: Width, mm	0.9–2.6 (1.6)	1.6
Forebody: % of body length	34.1–50.0 (42.1)	40.0
Oral sucker: Length (L, μm)	339–677 (455)	391
Oral sucker: Width (W, μm)	306–645 (438)	405
Prepharynx: L	40–88 (67)	79
Pharynx: L	122–177 (144)	157
Pharynx: W	88–194 (122)	165
Oesophagus: L	80–280 (184)	304
Ventral sucker: L	339–960 (566)	563
Ventral sucker: W	742–2420 (1378)	1241
Sucker-width ratio:	1:1.9–4.0 (1:3.1)	1:3.1
Left testis: L	272–645 (455)	488
Left testis: W	216–452 (322)	345
Right testis: L	296–516 (476)	534
Right testis: W	176–516 (338)	413
Cirrus sac: L	480–1355 (920)	715
Cirrus sac: W	144–371 (248)	226
Ovary: L	160–468 (293)	362
Ovary: W	192–355 (284)	367
Metraterm: L	400–774 (567)	–
Number of vitelline follicles	12+9; 11+9; 11+8; 10+9; 10+8; 9+9; 9+8	11+9
Size of vitelline follicles: L × W	80–242 (142) × 64–242 (146)	–
Eggs: L	38–46 (40)	35–41 (mean 37)*
Eggs: W	21–22 (21)	21–24 (mean 23)*

*–eggs sizes were measured by Dr. Anna J. Phillips (Smithsonian National Museum of Natural History, Washington, USA)

jModelTestsoftware version 0.1.1 (Posada 2008) was used to estimate the best nucleotide substitution model for the dataset. Both analyses were conducted using the GTR+G model.

The partial 28S rDNA sequences generated in the study were aligned with representatives of members of the family Zoogonidae available in GenBank. *Tanaisia fedchenkoi* Skrjabin, 1924 (family Eucotylidae Cohn, 1904) was used as outgroup taxa for both analyses.

Results

Description

Proctophantastes gillissi (Overstreet et Pritchard, 1977) Bray et Gibson, 1986 (Fig. 1–3; Table I)
Syn.: *Neosteganoderma gillissi* Overstreet et Pritchard, 1977; *Proctophantastes* sp. Sokolov et Gordeev, 2013

Description based on 27 gravid specimens – 8 from the Ross Sea and 19 from the Amundsen Sea; measurements are given in Table. Body fusiform or pyriform. Tegument spinous over entire body-surface. Subtegumentary gland cells numerous and scattered over throughout body. Oral sucker globular or subglobular, subterminal. Large ventral sucker equatorial or slightly post-equatorial, transversely elongate, with horizontal median dorsal cleft and muscular ventral ridge. Ventral ridge of ventral sucker with longitudinal (relative to anterior-posterior axis of body) constrictions in form of deep slits or slight indentations. Prepharynx short, pharynx and oesophagus surrounded by glandular cells. Intestinal bifurcation slightly posterior to mid-forebody. Caeca end blindly at the level of testes in hindbody. Testes in hindbody at the level of posterior edge of ventral sucker, symmetrical, suboval. Cirrus sac claviform, transversal, contains bipartite tubular and coiled seminal vesicle, long pars prostatica and ejaculatory duct with thorn-shaped spines. Proximal end of cirrus sac at the level with anterior edge of ventral sucker, or slightly posterior. Cirrus sac opens into small genital atrium surrounded by lobed periatrial gland. Genital pore submarginal on left side of body, at the level of, or slightly posterior to, intestinal bifurcation. Ovary round or suboval, median or submedian, dorsal to posterior margin of, or slightly posterior to, ventral sucker. Proximal part of oviduct vesicular, terminates with sphincter, middle and distal parts

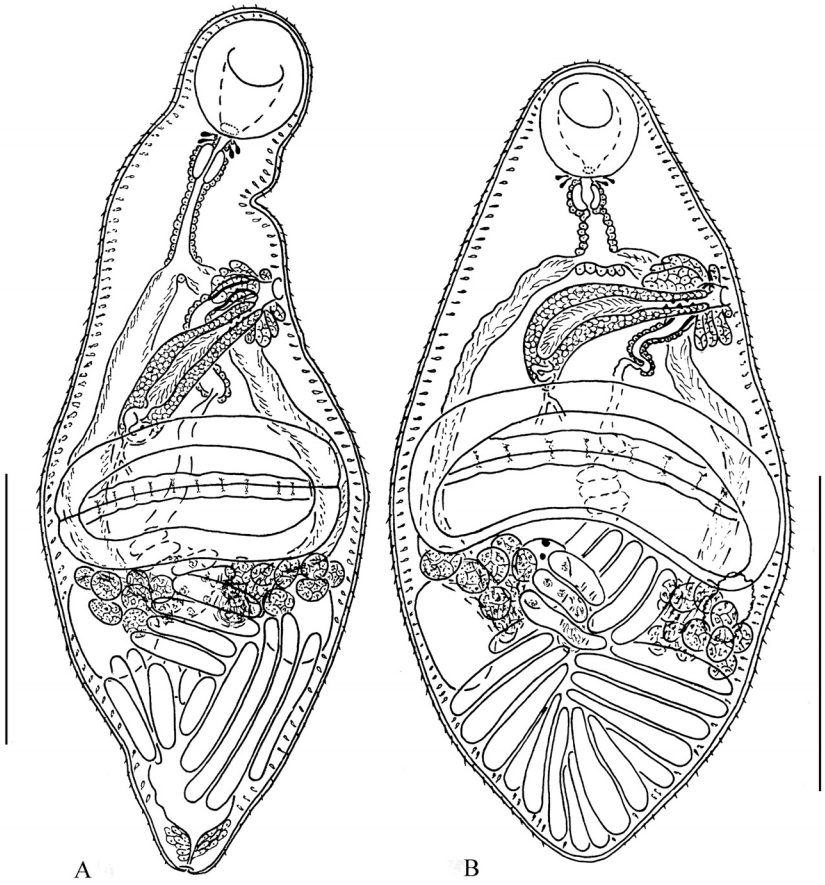

Fig. 1. *Proctophantastes gillissi*, whole view. A – specimens from the Ross Sea, with body length 3.1 mm; B– specimens from the Amundsen Sea, with body length 5.1 mm (left testis is rudimentary). Scale bars: A – 1 mm; B – 2 mm

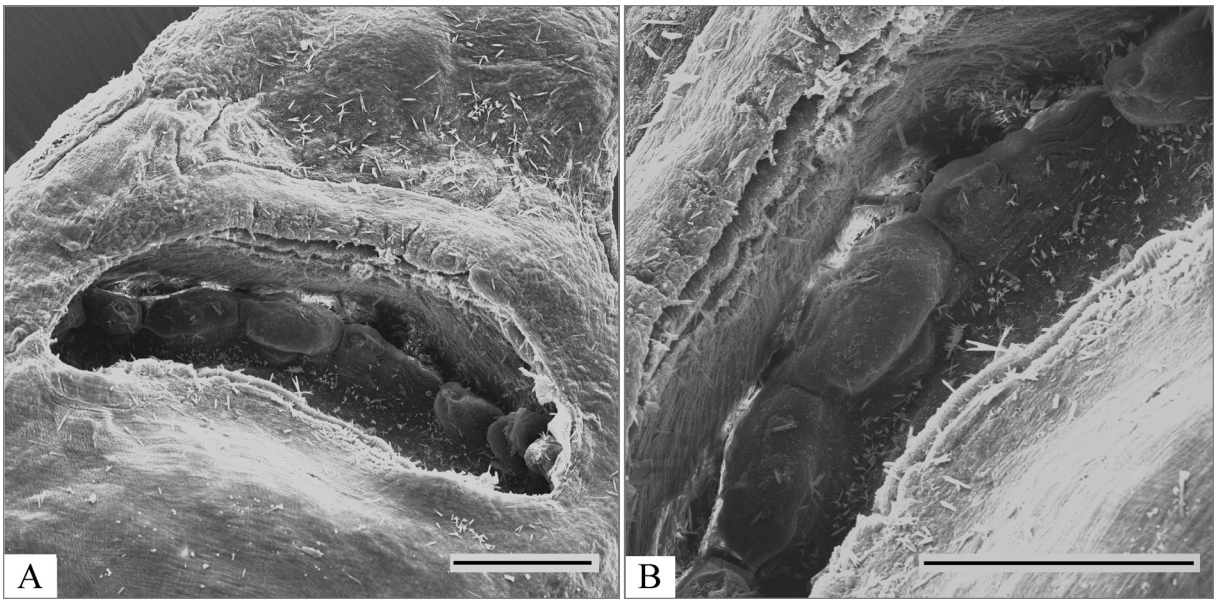

Fig. 2. *Proctophantastes gillissi*, scanning electron micrographs of ventral sucker. A – general view; B–fragment of horizontal ventral ridge. Scale bars: A, B – 0.2 mm

– tubular. Distal part of oviduct expands slightly to form ootype. Mehlis' gland distinct. Common vitelline duct enters oviduct just before ootype– Mehlis' gland complex. Seminal receptacle canalicular, sinistral to ovary. Laurer's canal long, surrounded by glandular cells. Hindbody filled with numerous uterine loops. Metraterm dorsal to cirrus sac. Proximal and middle parts of metraterm with thin wall and surrounded by glandular cells. Distal part of metraterm with very thick muscular wall. Eggs operculated, with additional slight thickening at anopercular end. Vitelliarium follicular, in two symmetrical lateral clusters, at level with testes. Excretory vesicle entire or only anterior part of vesicle obscured by eggs. Posterior part of excretory vesicle surrounded by a wide ring of glandular cells; excretory pore terminal.

Taxonomic summary

Hosts: deep-water arrowtooth eel *Histiobranchus bathybius* (Günther, 1877) (Anguilliformes: Synaphobranchidae) – type host (as *Synaphobranchus bathybius* by Overstreet and Pritchard, 1977), marbled moray cod *Muraenolepis marmorata* Günther, 1880 (Gadiformes: Muraenolepididae) – new host (Sokolov and Gordeev, 2013; this paper).

Localities: the Pacific Ocean between 6°42′N, 78°56′W and 6°44′N, 78°54.5′W at approximately 3173 to 3208 m – type locality (Overstreet and Pritchard, 1977), and the Ross Sea (71°S, 177°W, depth – 1068 m; 72°S, 177°E, depth – 1651 m) and the Amundsen Sea (69°S,126°W, depth –1428 m) – new data (Sokolov and Gordeev, 2013; this paper).

Site of infection: intestine.

Type specimens: holotype (#74493) in Smithsonian National Museum of Natural History, Washington.

Prevalence/intensity: the Ross Sea (71°S, 177°W) – 12.5%/3–8 (n = 24), the Ross Sea (72°S, 177°E) – in 2 specimens/2–5 (n = 2), the Amundsen Sea – 10.3% / 1–11 (n = 29).

Molecular sequence data: 28S rDNA, 2 replicates deposited to GenBank, KU163452 and KU163453.

Specimens deposited 27 whole specimens on 9 slides deposited in MHC IPEE RAS, Moscow; inventory numbers – 14244–14252.

Phylogenetic analysis

Phylograms from both Maximum Likelyhood and Bayesian inference methods placed *P. gillissi* in one clade with *Deretrema nahaense* Yamaguti, 1942, within the Faustulidae + Zoogonidae clade (Fig. 4). As shown previously by Olson *et al*. (2003), Bray *et al*. (2005) and Cutmore *et al*. (2014) representatives of families Faustulidae and Zoogonidae form a one clade, in which faustulids are closely related with members of subfamily Zoogoninae – *Zoogonoides viviparus* (Olsson, 1868) and *Diphterostomum* sp.

Species *D. nahaense* and *P. gillissi* (Lepidophyllinae) together formed a well-supported clade with members of the family Faustulidae and subfamily Zoogoninae. In its turn, this major clade is sister to that comprising *L. steenstrupi* – a type species for type genus of Lepidophyllinae and *Plectognathotrema kamegaii* Cutmore, Miller, Bray et Cribb, 2014 belongs to the subfamily Cephaloporinae Yamaguti, 1934. The presented data indicates paraphyly of the subfamily Lepidophyllinae.

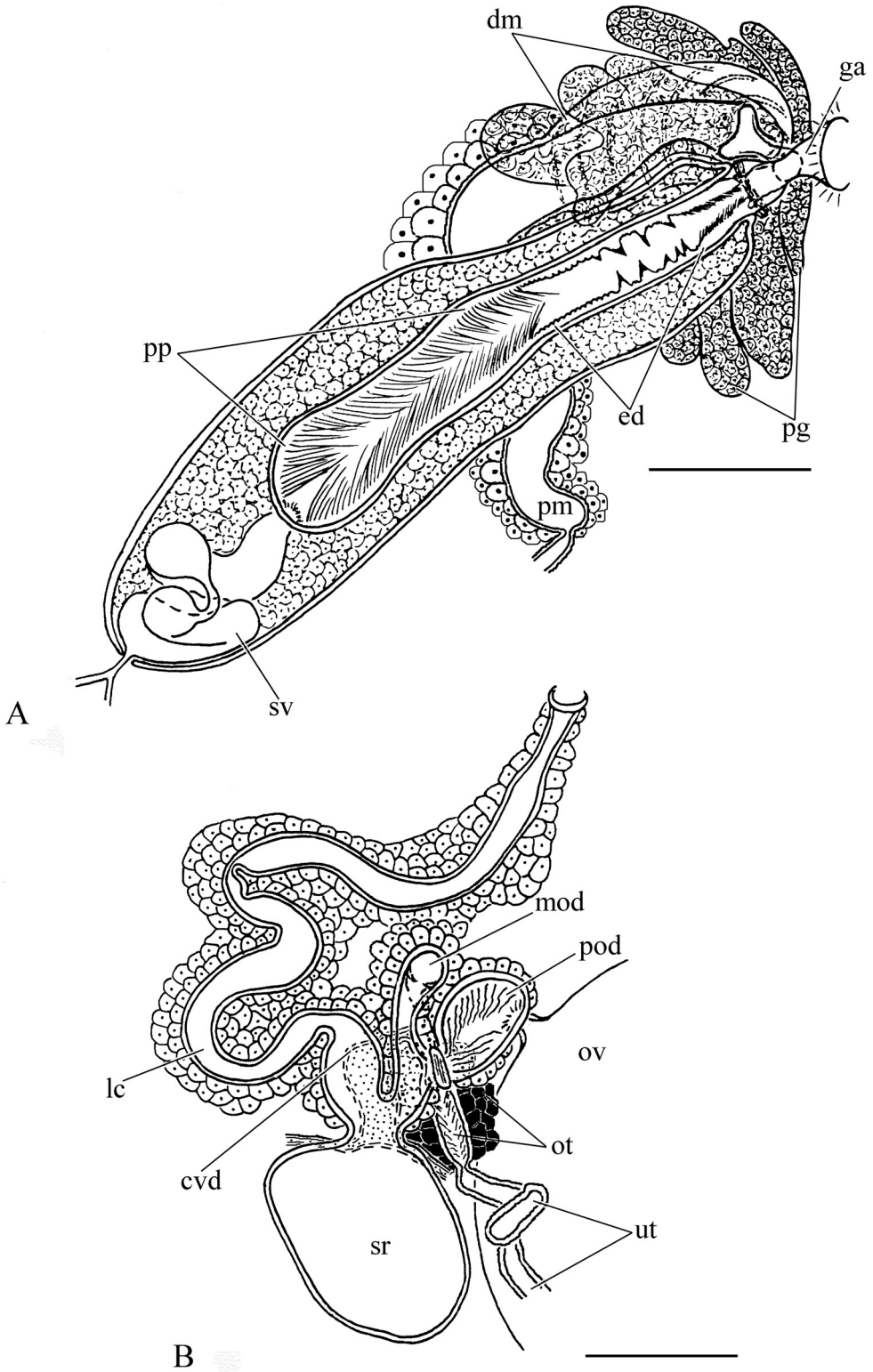

Fig. 3. *Proctophantastes gillissi*, detailed morphology of reproductive system. A – terminal genitalia; B – ovarian complex; cvd – common vitelline duct; dm – distal part of metraterm; ed – ejaculatory duct; ga – genital atrium; lc – Laurer's canal; mod – middle part of oviduct; ot – ootype with Mehlis' gland; ov – ovary; pg – periatrial gland; pm – proximal part of metraterm; pod – proximal part of oviduct; pp – pars prostatica; sr – seminal receptacle; sv – seminal vesicle; ut – uterus. Scale bars: A – 0.15mm; B – 0.05 mm

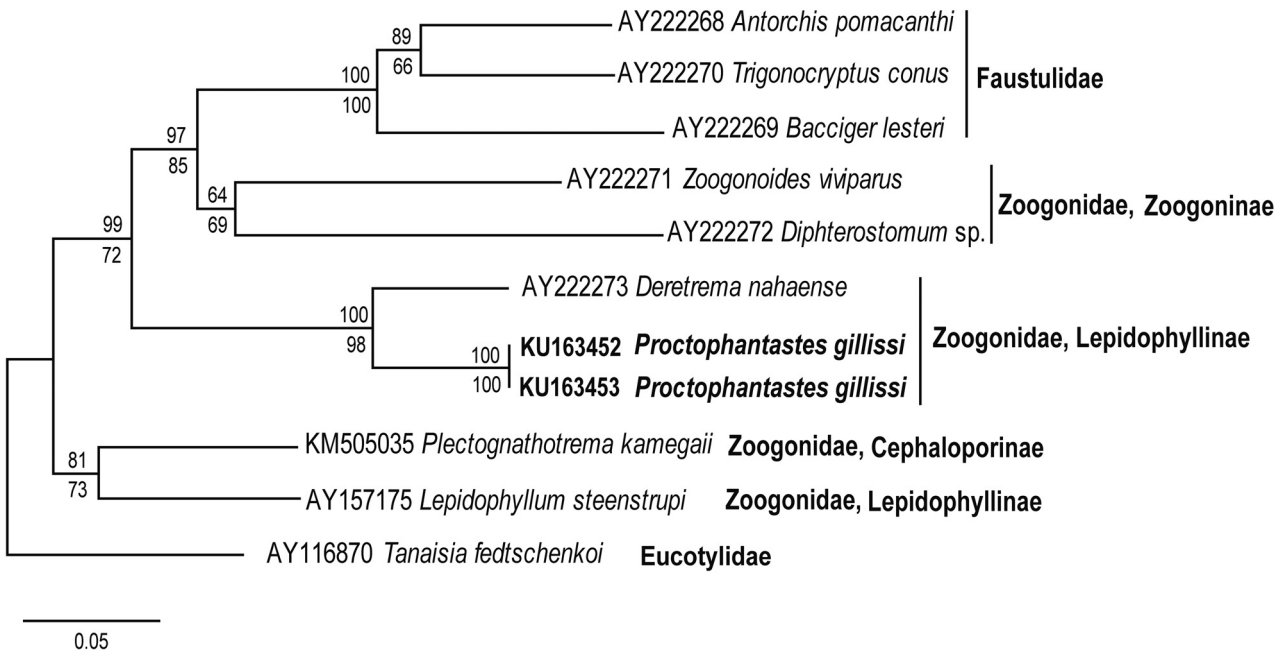

Fig. 4. Relationships between *Proctophantastes gillissi* and related taxon based on Bayesian inference and Maximum Likelihood analyses of the 28S rDNA dataset. *Tanaisia fedchenkoi* is designated as outgroup taxa. Posterior probabilities are shown above the nodes and bootstrap support values below the nodes. A subfamilial affiliation of the zoogonid species is given in accordance with Bray (2008) and Cutmore *et al*. (2014)

Discussion

We infer that the described specimens belong to genus *Proctophantastes* due to of the presence of two postacetabular clusters of vitelline follicles, the postacetabular position of testes, the position of the posterior end of the intestinal caeca at the level of testes and the presence an equatorial dorsal cleft and ventral ridge at the ventral sucker, as well as the shape of eggs (Bray and Justine 2008; Bray 2008). This genus currently consist of six species: *P. abyssorum* Odhner, 1911, *P. brayi* Mouahid, Faliex, Allienne et Cribb, 2008, *P. gillissi*, *P. glandulosum* (Byrd, 1964), *P. infundibulum* Kamegai, 1973 and *P. nettastomatis* Machida, Kamegai et Kuramochi, 2006 (Bray and Gibson 1986; Bray 1987; Mouahid *et al.* 2008, 2012).

We exclude that the studied specimens are *P. abyssorum*, *P. brayi*, *P. glandulosum*, *P. infundibulum* and *P. nettastomatis.* Our specimens differed from *P. abyssorum* in having a longer body, the gland cells surrounding oesophagus, pharynx and prepharynx, spined ejaculatory duct, as well as in the degree of development of the periatrial gland (Odhner 1911; Bray 1973; Bray and Gibson 1986). Compared with *P. brayi*, our specimens differ in the morphology of the anterior portion of the oral sucker, degree of development of the periatrial gland, the lack of vesicle-like processes on the metraterm, and the presence of Laurer's canal and spines on the ejaculatory duct (Mouahid *et al.* 2008). Specimens investigated differed from *P. infundibulum* in having a shorter body, a globular or subglobular oral sucker, gland cells surrounding oesophagus, pharynx and prepharynx, as well as in the shape and length of oesophagus, equatorial or slightly post-equatorial position of ventral sucker, position of cirrus sac, testes and vittellarium relative to ventral sucker, and the absence of atrial recesses (Kamegai 1973). Our specimens differed from *P. glandulosum* in having the gland cells surrounding oesophagus, pharynx and prepharynx, and having no atrial recesses (Byrd 1964; Yamaguti 1970; Bray 1973; Bray and Gibson 1986; Machida *et al.* 2006). These specimens differ from *P. nettastomatis* in a possession of a large cirrus sac, large periatrial gland, as well as the presence of gland cells around oesophagus, pharynx and prepharynx, and spines on the ejaculatory duct (Machida *et al.* 2006; Mouahid *et al*. 2012).

The trematodes in our studies were however similar to *P. gillissi* (Table I). The following characteristics identify them as: size of the body and of most organs, presence of gland cells coating oesophagus, pharynx and prepharynx, and spines on the ejaculatory duct, degree of development of the periatrial gland, as well as the morphology of the ventral ridge of ventral sucker. To re-examine the holotype of *P. gillissi*, we asked Dr. Anna J. Phillips (Smithsonian National Museum of Natural History) to take photographs of the holotype at different magnifications. This way we were able to find that the ventral ridge of the holotype of *P. gillissi* also has indistinct longitudinal constrictions. We therefore concluded that the trematodes studied belong to *P. gillissi*.

We understand that a genus can only be placed systematically based on the position of their type species, thus we now suggest only the systematic position of the genus *Proctophantastes*. The consolidation of *P. gillissi* and *D. nahaense*

and position of the species relative to other zoogonids shown on the phylogram (Fig. 4) lead to at least two conclusions. First, the genera *Proctophantastes* and *Deretrema* may belong to the one subfamily of the family Zoogonidae. Second, this subfamily is independent in relation to the three subfamilies (Cephaloporinae Yamaguti, 1934, Lepidophyllinae Stossich, 1903, and Zoogoninae Odhner, 1902) currently recognized as accepted (Bray 2008; Cutmore *et al.* 2014). Our results contradict the point of view expressed by Bray (1987, 2008), Bray and Gibson (1986) about the genus *Proctophantastes* belonging to the subfamily Lepidophyllinae Stossich, 1903. In the same time, they conform to Price (1934) and Brooks` (1990) findings about phylogenetic proximity of genera *Proctophantastes* and *Deretrema* based on morphological data. At present it is hard to say which of the subjective synonyms of Lepidophyllinae (see Bray 1987, 2008) could be used as name of the subfamily that includes the genera.

Marbled moray cod is a new host and the Ross Sea and the Amundsen Sea are new localities for *P. gillissi*. Previously this parasite was recorded only from deep-water arrowtooth eel *H. bathybius* caught in another location half of the Earth away from Antarctic (Table I). The deep-water arrowtooth eel and the marbled moray cod belong to different orders (Table I). The deep-water arrowtooth eel is apparently a benthopelagical fish that feed mainly on fishes and little bit on crustaceans (Karmovskaya and Merrett 1998). Therefore, we cannot exclude that this fish species is not an original definitive host, but a postcyclic host for *P. gillissi*. The marbled moray cod has mainly invertebrates among its food items (Permitin and Tarverdijeva 1972; Chechun 1984; Kompowski 1993), so this fish species most likely is the original definitive host for *P. gillissi*. But do not forget that only one specimen of *P. gillissi* was recorded in deep-water arrowtooth eel (Overstreet and Pritchard 1977). Thus, we consider thorough discussion of the host specificity of this parasite as premature. We believe that discovered wide geographical distribution of *P. gillissi* can be explained by similarity of deep waters environmental conditions in the Ocean, like stable temperature, salinity and other condition (Talley 2007).

Acknowledgments. The authors wish to thank Research Zoologist Anna J. Phillips, PhD (Smithsonian Institution, Washington, USA) for essential help with examination of the *Proctophantastes gillissi* holotype stored in the National Museum of Natural History. The work was supported by RFBR grant # 15-29-02528 and state order 0221–2014–0004.

References

Bray R.A. 1973. Some digenetic trematodes in fishes from the Bay of Biscay and nearby waters. *Bulletin of British Museum of National History (Zoology)*, 26, 151–183

Bray R.A. 1987. A revision of the family Zoogonidae Odhner, 1902 (Plathyhelminthes: Digenea): subfamily Lepidophyllinae and comments on some aspects of biology. *Systematic Parasitology*, 9, 83–123

Bray R.A. 2008. Family Zoogonidae. In: (Eds. R. A. Bray, D. I. Gibson and A. Jones) Keys to the Trematoda. Vol 3. CABI Publishing and Natural History Museum, Wallingford, 609–629

Bray R.A., Gibson D.I. 1986. The Zoogonidae (Digenea) of fishes from the northeast Atlantic. *Bulletin of British Museum of National History Zoology*, 51, 127–206

Bray R.A., Webster B.L., Bartoli P., Littlewood D.T.J. 2005. Relationships within the Acanthocolpidae Lühe, 1906 and their place among the Digenea. *Acta Parasitologica*, 50, 4, 281–291

Brooks D.R. 1990. Phylogenetic systematic evaluation of a classification of the Zoogonidae Odhner, 1902 (Cercomeria: Trematoda: Plagiorchiiformes). *Systematic Parasitology*, 16, 127–137

Bykhovskaya-Pavlovskaya I.E. 1985. Parasites of fishes. Nauka, Leningrad, pp. 121 (in Russian)

Byrd M.A. 1964. *Neosteganoderma glandulosa* gen. n., sp. n. (Trematoda: Steganodermatidae) from an Atlantic fish. *Proceedings of the Helminthological Society of Washington*, 31, 105–108

Chechun I.S. 1984. Feeding and food interrelation-ships of some sub-Antarctic fishes of the Indian Ocean. *Trudi Zoologicheskogo instituta AN SSSR*, 127, 38–68. (In Russian)

Cutmore S.C., Miller T.L., Bray R.A., Cribb T.H. 2014. A new species of *Plectognathotrema* Layman, 1930 (Trematoda: Zoogonidae) from an Australian monacanthid, with a molecular assessment of the phylogenetic position of the genus. *Systematic Parasitology*, 89, 237–246. DOI 10.1007/s11230-014-9523-2

Kamegai S. 1973. Zoogonid trematodes from marine fishes near the Tsushima Islands in the Sea of Japan. *Research Bulletin Meguro Parasitology Museum*, 7, 19–23

Karmovskaya E.S., Merrett N.R. 1998. Taxonomy of the deep-sea eel genus, *Histiobranchus* (Synaphobranchidae, Anguilliformes), with notes on the ecology of *H. bathybius* in the eastern North Atlantic. *Journal of Fish Biology*. 53, 5, 1015–1037

Kompowski A. 1993. Food and feeding behaviour of eel-cod *Muraenolepis* sp., (Pisces, Gadiformes, Muraenolepididae) from the region of South Georgia. *Acta Ichthyologica et Piscatoria*, 23, 1, 59–68

Machida M., Kamegai S., Kuramochi T. 2006. Zoogonidae (Trematoda, Digenea) from fishes of Japanese waters. *Bulletin of the National Science Museum*. Ser A, 32, 3, 95–104

Miller S.A., Dykes D.D., Polesky H.F. 1988. A simple salting out procedure for extracting DNA from human nucleated cells. *Nuclear Acids Research*, 16, 3, 1215

Mouahid G., FaliexE., Allienne J.-F., Cribb T.H. 2008. *Proctophantastes brayi*, n. sp. (Digenea: Zoogonidae) parasite of the deep-sea fish *Polymixia* Lowe, 1838 from Vanuatu. *Parasitology International*, 57, 25–31. DOI:10.1016/j.parint.2007.07.002

Mouahid G., Faliex E., Allienne J.-F., Cribb T.H., Bray R.A. 2012. *Proctophantastes nettastomatis* (Digenea: Zoogonidae) from Vanuatu deep-sea fish: new morphological features, allometric growth, and phenotypic plasticity aspects. *Parasitology Research*, 110, 1631–1638. DOI 10.1007/s00436-011-2674-z

Odhner T. 1911. Zum natürlichen system der digenen Trematoden II. *Zoologischer Anzeiger*, 37, 237–253

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

Overstreet R.M., Pritchard M.H. 1977. Two new zoogonid Digenea from deep-sea fishes in the gulf of Panama. *Journal of Parasitology*, 63, 840–844

Permitin Yu.E., Tarverdijeva M.I. 1972. Feeding of some species of Antarctic fishes in the South Georgia Island area. *Voprosy ichtiologii*, 12, 1, 120–132. (In Russian)

Posada D. 2008. jModelTest: Phylogenetic model averaging. *Molecular Biology and Evolution*, 25, 7, 1253 – 1256

Price E.W. 1934. New digenetic trematodes from marine fishes. *Smithsonian Miscellaneous Collections*, 91, 7, 1–8

Ronquist F., Teslenko M., van der Mark P., Ayres D. L., Darling A., Höhna S., Larget B., Liu L., Suchard M. A., Huelsenbeck J. P. 2012. MrBayes 3.2: Efficient Bayesian Phylogenetic Inference and Model Choice Across a Large Model Space. *Systematic Biology*, 61, 3, 539–542

Sokolov S.G., Gordeev I.I. 2013. New data on trematodes (Plathelminthes, Trematoda) of fishes in the Ross Sea (Antarctic). *Invertebrate Zoology*, 10, 2, 255–267

Talley L.D. 2007. Pacific Ocean. In: (Eds. Sparrow M., Chapman P. and J. Gould) Hydrographic Atlas of the World Ocean Circulation Experiment. Vol. 2. International WOCE Project Office, Southampton, U.K., ISBN 0–904175–54–5

Tamura K., Stecher G., Peterson D., Filipski A., Kumar S. 2013. MEGA6: Molecular Evolutionary Genetics Analysis version 6.0. *Molecular Biology and Evolution*, 30, 2725–2729

Yamaguti S. 1970. Digenetic trematodes of Hawaiian fishes. Keigaku Publishing Company, Tokyo, pp. 436

Yamaguti S. 1971. Synopsis of digenetic trematodes of vertebrates. Vol. 1. Keigaku Publishing Company, Tokyo, pp. 1074

Received: December 14**,** 2015
Revised: February 15, 2016
Accepted for publication: March 10, 2016