Adult Digeneans (Trematoda) Parasitic in *Hypomesus nipponensis* (Osteichthyes, Osmeridae) from Brackish-water Lakes of Japan

Takeshi Shimazu

10486–2 Hotaka-Ariake, Azumino, Nagano 399–8301, Japan E-mail: azygia79@gmail.com

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Abstract Adult digeneans (Trematoda) were found in *Hypomesus nipponensis* McAllister (Osteichthyes, Osmeridae) from a brackish-water lake, Lake Abashiri, in Hokkaido, Japan. Some unidentified digenean specimens that had previously been recorded from *Hypomesus nipponensis* from brackish-water lakes in Japan were also reexamined. The digeneans were classified into three species of marine origin: *Pronoprymna petrowi* (Layman, 1930) Bray and Gibson, 1980 (Microphalloidea, Faustulidae) from Lakes Abashiri and Tofutsu in Hokkaido, Lake Takahoko in Aomori Prefecture, and Lake Koyama in Tottori Prefecture; *Brachyphallus crenatus* (Rudolphi, 1802) Odhner, 1905 (Hemiuroidea, Hemiuridae) from Lakes Abashiri and Tofutsu; and *Lecithaster gibbosus* (Rudolphi, 1802) Lühe, 1901 (Hemiuroidea, Lecithasteridae) from Lakes Abashiri, Tofutsu, and Koyama. They are described and figured. Their geographical distribution and life cycles are briefly discussed.

Key words: Adult digeneans, parasites, Hypomesus nipponensis, brackish-water lakes, Japan.

Introduction

Little is known about adult digeneans (Trematoda) parasitic in Hypomesus nipponensis McAllister (Osteichthyes, Osmeridae) in brackish waters of Japan. Ohtomo (2003) found three species of adult digeneans, Pronoprymna sp., Brachyphallus sp., and Lecithaster sp., in Hypomesus nipponensis from Lake Abashiri in Hokkaido. She neither described nor figured them. Kikuchi (2014) recorded three species of adult digeneans in Hypomesus nipponensis: Digenea sp. 1, Digenea sp. 2, and Digenea sp. 3 from Lake Tofutsu in Hokkaido; and Digenea sp. 1 from Lake Takahoko in Aomori Prefecture and Lake Koyama in Tottori Prefecture. She figured them but did not compare them with Ohtomo's three species in morphology. Their adult specimens have remained unidentified to species level.

In order to obtain these unidentified adult digeneans, I examined *Hypomesus nipponensis* from Lake Abashiri for adult digeneans in 2016

and 2017. In this paper, three species of adult digeneans found in *Hypomesus nipponensis* are identified, described, and figured on the basis of specimens collected by Ohtomo, Kikuchi, and me. Their geographical distribution and life cycles are briefly discussed.

Materials and Methods

Specimens dealt with in this paper were found in *Hypomesus nipponensis* from Lakes Abashiri and Tofutsu (brackish-water lakes) in Abashiri City, Hokkaido, on the coast of the Sea of Okhotsk; and Lake Koyama (or Koyama-ike) (a brackish-water lake) in Tottori City, Tottori Prefecture, on the coast of the Japan Sea.

Some specimens obtained by Ohtomo (2003) and Kikuchi (2014) were made available to me for reexamination by courtesy of Akifumi Ohtaka. Ohtomo's two slides contained only eight specimens of [Trematoda] (most likely referring to "*Pronoprymna* sp.") mounted in Canada balsam. Some of Kikuchi's specimens had been mounted in Canada balsam. Many others were still preserved in 5% formalin. They were stained with Heidenhain's iron hematoxylin and mounted in Canada balsam. Kikuchi's wholemounted specimens also included one each of Digenea sp. 1 and Digenea sp. 2 from Lake Abashiri. Although Kikuchi mentioned nothing about these specimens, she certainly examined some individuals of Hypomesus nipponensis from Lake Abashiri for parasites (Akifumi Ohtaka, personal communication, 12 March 2017). Kikuchi (2014) recorded Digenea sp. 1 from Lake Takahoko (or Takahoko-numa) (a brackish-water lake) in Rokkasho Village, Aomori Prefecture, on the coast of the North Pacific; but her specimens reexamined included no specimen from this lake.

A large number of fresh individuals of *Hypomesus nipponensis* collected in Lake Abashiri on 25 January 2016, 28 April 2017, and 4 December 2017 were examined for adult digeneans. Specimens found were either slightly flattened and fixed in AFA or fixed in hot 10% formalin and refixed in AFA. They were then stained with Heidenhain's iron hematoxylin and mounted in Canada balsam.

Measurements (length by width) are given in millimeters unless otherwise stated. Drawings were made with the aid of a camera lucida. The specimens used have been deposited in the Muguro Parasitological Museum (MPM; registration code, MPM Coll. No.), Tokyo; and the National Museum of Nature and Science (NMNS; registration code, NSMT-Pl), Tsukuba.

Abbreviations used in the figures. cp, cirrus pouch; cvd, common vitelline duct; e, esophagus; ed, ejaculatory duct; egg, eggs in uterus and metraterm; ep, excretory pore; eso, ecsoma; ev, excretory vesicle; ga, genital atrium; gev, glandular ejaculatory vesicle; gp, genital pore; hd, hermaphroditic duct; i, intestine; Jo, Juel's organ; Lc, Laurer's canal; m, metraterm; Mg, Mehlis' gland; o, ovary; od, oviduct; os, oral sucker; p, pharynx; pc, prostatic cells; pp, pars prostatica; psp, presomatic pit; sd, sperm duct; so, soma; sr, seminal receptacle; ss, sinus sac; sv, seminal vesicle; t, testis; tnc, transverse nerve commissure; u, uterus; usr, uterine seminal receptacle; v, vitellarium; vd, vitelline duct; vh, ventral hollow; vs, ventral sucker.

Class Trematoda Rudolphi, 1808 Subclass Digenea Carus, 1863 Superfamily Microphalloidea Ward, 1901 Family Faustulidae Poche, 1926 Genus *Pronoprymna* Poche, 1926 *Pronoprymna petrowi* (Layman, 1930) Bray and Gibson, 1980

(Figs. 1-3)

"Monorcheides (?) petrowi" Layman, 1930: 77, 99–100, fig. 35.

- *Orientophorus sayori* Yamaguti, 1942: 367–369, fig. 19; Yamaguti, 1954: 20.
- Orientophorus petrowi: Mamaev, Parukhin, Baeva, and Oshmarin, 1959: 15, fig. 3, table 1.
- Bacciger petrowi: Zhukov, 1959: 199; Zhukov, 1960: 31, fig. 21.

Pentagramma petrowi: Margolis and Ching, 1965: 393– 394, figs. 9–13, table 5.

Faustula sayori: Yamaguti, 1958: 34; Yamaguti, 1971: 74.

Pseudopentagramma petrovi [sic, should be *petrowi*]: Yamaguti, 1971, 74.

Pronoprymna petrowi: Bray and Gibson, 1980: 255.

Host. Hypomesus nipponensis.

Sites of infection. Intestine and pyloric ceca.

Localities. Lake Abashiri (Ohtomo, 2003; this paper); Lake Tofutsu (Kikuchi, 2014; this paper); Lake Takahoko (Kikuchi, 2014); and Lake Koyama (Kikuchi, 2014; this paper).

Material examined. (1) Ohtomo's (2003) 8 specimens (MPM Coll. No. 21351) of [Trematoda] (species name not given, but most likely referring to "*Pronoprymna* sp."), adult, wholemounted, ex intestine, [Lake Abashiri], 12 February 2002. (2) Kikuchi's many specimens of Digenea sp. 1:1 (MPM Coll. No. 21352), adult, whole-mounted, ex intestine, Lake Abashiri, 28 May 2013 (see the Materials and Methods above); many (labeled *Prinoprymna*? [*sic*], Digenea sp. 1 in separate fig. 1) (MPM Coll. 21353a), adult, whole-mounted, site of infection not



Figs. 1–3. Pronoprymna petrowi, adult specimens (NSMT-Pl 6343a) found in intestine and pyloric ceca of Hypomesus nipponicus from Lake Abashiri. 1, relatively young adult specimen, with many malformed eggs in uterus, entire body, ventral view; 2, terminal genitalia, ventral view; 3, ovarian complex, ventral view. Scale bars: 0.3 mm in Fig. 1; 0.1 mm in Figs. 2 and 3.

given [most likely intestine], Lake Tofutsu, 21 April 2013 (Kikuchi, 2014); and many (MPM Coll. No. 21354-a), adult, whole-mounted, site of infection not given [most likely intestine], Lake Koyama, 2 March 2002 (Kikuchi, 2014). (3) Many specimens (MPM Coll. No. 21355-a, NSMT-Pl 6343a, NSMT-Pl 6346b), immature, adult, whole-mounted, ex intestine and pyloric ceca, Lake Abashiri, 25 January 2016. (4) 22 specimens (MPM Coll. No. 21356), adult, whole-mounted, ex intestine, Lake Abashiri, 28 April 2017.

Description. Based on adult specimens from Lake Abashiri (MPM Coll. No. 21355-a, NSMT- Pl 6343a); 10 of them measured (Figs. 1-3). Body fusiform to ovate, small, 1.01-1.54 long, 0.32-0.54 wide at testicular level; forebody 0.30-0.51 long, occupying 28-35% of body length. Tegument unarmed, with fine annular wrinkles. Transverse nerve commissure dorsal to pharynx. Cervical glands well developed. Ventral hollow present, large, 0.23-0.28 by 0.20-0.30, surrounding ventral sucker and genital pore; concentric rings of muscles constituting its internal wall. Oral sucker cup-shaped, 0.11-0.16 by 0.16-0.23, subterminal. Prepharynx very short. Pharynx barrel-shaped, 0.05-0.07 by 0.04-0.05. Esophagus bifurcating anterior to ventral sucker, 0.02–0.05 long. Intestines ending blindly, usually in testicular region. Ventral sucker 0.15-0.21 by 0.14-0.20, sometimes embedded in ventral hollow; sucker width ratio 1: 0.77-0.96. Testes two, globular to broad elliptical, 0.13-0.26 by 0.09-0.16, symmetrical, submedian, at midlevel of body, immediately posterolateral to ventral sucker. Sperm ducts connecting with seminal vesicle in cirrus pouch. Cirrus pouch clavate, thin-walled, 0.20-0.29 by 0.07-0.10, closely enclosing seminal vesicle, prostatic complex, and ejaculatory duct, normally median and dorsal to ventral sucker, often shifted dextrally or sinistrally submedian, extending posteriorly slightly beyond ventral sucker. Seminal vesicle bipartite, thin-walled; anterior portion much smaller, 0.04-0.06 by 0.03-0.05; posterior portion elongate, 0.11-0.21 by 0.06-0.09. Pars prostatica very small; prostatic cells poorly developed. Ejaculatory duct short, changing into long tubular genital atrium (0.05–0.08) after receiving metraterm. Genital pore median, anterior to ventral sucker, in ventral hollow. Ovary deeply 3-lobed, 0.13-0.21 by 0.14–0.20, median, post-testicular, embraced by testes. Ovarian complex ventral to ovary. Oviduct from ovary distinctively thick. Laurer's canal long, almost straight, proximally dilated to form small canalicular seminal receptacle ventral or posterior to ovary; dorsal opening almost median, close to posterior extremity of body. Mehlis' gland emptying into ovovitelline duct. Ootype vesicular. Uterus ventral to gonads,

filling most of hindbody in fully mature adults; metraterm may be short. Eggs numerous, oval, operculate, bright brown, 27–32 by $16-19\,\mu$ m (collapsed). Vitellaria two, entire (not compact clusters of small follicles, enclosed by single membrane), elliptical, 0.13–0.19 by 0.05–0.09, symmetrical, immediately posterolateral to ventral sucker, immediately anterolateral to testes; vitelline ducts running toward median line of body, ventral to testes; common vitelline duct median, running posteriorly between testes. Excretory vesicle almost V-shaped, ventral; arms reaching to esophageal level; excretory pore posteroterminal.

Remarks. The present specimens including Kikuchi's unpublished specimen (MPM Coll. No. 21352) from Lake Abashiri morphologically agree on the whole with Monorcheides petrowi Layman, 1930 as described by Layman (1930), Orientophorus savori Yamaguti, 1942 as described by Yamaguti (1942), Bacciger petrowi (Lavman, 1930) as described by Zhukov (1960), and Pentagramma petrowi (Layman, 1930) as described by Margolis and Ching (1965). These species are now synonyms of Pronoprymna petrowi (Layman, 1930) Bray and Gibson, 1980 (Microphalloidea, Faustulidae) (Bray and Gibson, 1980; Bray, 2008). Therefore, they are identified as Pronoprymna petrowi. Pronoprymna sp. of Ohtomo (2003) from Lake Abashiri and Digenea sp. 1 of Kikuchi (2014) from Lakes Tofutsu, Takahoko, and Koyama are also regarded as Pronoprymna petrowi.

Layman (1930) originally described a new species, "Monorcheides (?) petrowi," on the basis of two specimens found in the pyloric ceca of Osmerus eperlanus dentex Steindachner (Osmeridae) from Peter the Great Bay on the coast of the Japan Sea, Far Eastern USSR (now Russia). Yamaguti (1942) described a new species, Orientophorus sayori Yamaguti, 1942, on the basis of specimens found in the intestine of a marine migratory fish, Hyporhamphus sayori (Temminck and Schlegel) (Hemirhamphidae), from Tutiura [Tsuchiura] on the coast of Lake Kasumigaura (a brackish-water lake then), Ibaraki Pre-

fecture, Japan, on 3 April 1940. Mamaev *et al.* (1959) and Margolis and Ching (1965) synonymized this species with *Orientophorus petrowi* (Layman, 1930) and *Pentagramma petrowi* (Layman, 1930), respectively. Yamaguti (1942) described that the vitelline follicles were small and formed a compact mass in *Orientophorus sayori*. Yamaguti (1971) stated that this species (or *Faustula sayori*) differed from *Pseudopentagramma petrowi* (syn. *Pentagramma petrowi*) in having distinctly lobed vitellaria. However, the vitellaria were entire, each being enveloped in a single membrane (see below), as in the present specimens. Margolis and Ching (1965) reviewed *Pentagramma petrowi*.

The present specimens had a ventral hollow surrounding the ventral sucker and genital pore (Fig. 1), a 3-lobed ovary (Fig. 1), a long tubular genital atrium (Fig. 2), an almost straight Laurer's canal that opens dorsally near the posterior extremity of the body (Fig. 1), and two elliptical entire vitellaria (Fig. 1). The ventral hollow has not previously been described for Pronoprymna petrowi. Bray (2008, fig. 52.8) found concentric rings of the muscle bundles forming a circle reaching from about the genital pore to the ventral sucker in Faustula basiri Hafeezullah and Siddiqi, 1970 (Faustulidae), which suggests that the ventral hollow is also present in that species. The long tubular genital atrium has not been previously described for Pronoprymna petrowi, either. Bray and Gibson (1980, fig. 15C) described the same structure in Pronoprymna ventricosa (Rudolphi, 1819) Poche, 1926, the type species of the genus Pronoprymna. Margolis and Ching (1965, fig. 11) erroneously described that a long ejaculatory duct in the cirrus pouch opened directly into a wide genital atrium (see Bray and Gibson, 1980), without showing where the uterus or metraterm opened.

Takashi Iwaki (MPM) (personal communication, 5 April 2017) kindly examined the following specimens for me: the holotype and seven paratypes (MPM Coll. No. 22342) of *Orientophorus sayori* Yamaguti, 1942 (see above) and nine specimens (MPM Coll. No. 22758) of *Penta*- gramma petrowi found by Margolis and Ching (1965) in the intestine and pyloric ceca of *Hypomesus pretiosus* (Girard) (Osmeridae) from Point Grey, Vancouver, on the North Pacific coast of British Columbia, Canada, on 16 June 1962, both deposited in Yamaguti's Collection of the MPM. As in the present specimens, they had the ventral hollow, a 3-lobed ovary, an almost straight Laurer's canal, and elliptical entire vitellaria. Yamaguti (1942) and Margolis and Ching (1965) seem to have erroneously described Laurer's canal as turning anteriorly before opening dorsally in their specimens of *Orientophorus sayori* and *Pentagramma petrowi*, respectively.

Pronoprymna petrowi is a marine species and has been recorded from the intestine and pyloric ceca of various species of marine and migratory fishes in northern North Pacific and adjacent seas (*e.g.*, Zhukov, 1960; Margolis and Ching, 1965; Boyce, 1969; Machida and Araki, 1994; Gibson, 1996; this paper). Bray and Gibson (1980) questioned the validity of records of this species from the Black Sea and Indian waters. The life cycle is not known.

Ohtomo (2003) carried out an extensive study of non-migrating and seaward-migrating populations of *Hypomesus nipponensis* in Lake Abashiri, using its parasites as biological tags, and concluded that "*Pronoprymna* sp.," or now *Pronoprymna petrowi*, was a good indicator of seaward-migrating populations in this lake.

Superfamily Hemiuroidea Looss, 1899 Family Hemiuridae Looss, 1899 Genus *Brachyphallus* Odhner, 1905 *Brachyphallus crenatus* (Rudolphi, 1802) Odhner, 1905

(Figs. 4-6)

Fasciola crenata Rudolphi, 1802: 76–77, pl. 2, fig. 5a, b.

Brachyphallus crenatus: Odhner, 1905: 354–355, pl. 4, figs. 3–5.

Brachyphallus amuriensis Babaskin, 1928: 214–217, 1 table, figs. 1–3.

(See Odhner (1905) and Gibson and Bray (1986), for other synonyms.)



Figs. 4–6. Brachyphallus crenatus, adult specimen (MPM Coll. No. 21411) found in stomach of Hypomesus nipponensis from Lake Abashiri. 4, entire body, ventral view; 5, terminal genitalia, ventral view; 6, ovarian complex, dorsal view. Scale bars: 0.3 mm in Fig. 4; 0.1 mm in Figs. 5 and 6.

Host. Hypomesus nipponensis.

Sites of infection. Stomach and intestine.

Localities. Lake Abashiri (Ohtomo, 2003; this paper) and Lake Tofutsu (Kikuchi, 2014; this

paper)

Material examined. (1) 1 specimen (NSMT-Pl 6344) of Digenea sp. 2 (Digenea sp. 2 in separate fig. 1) of Kikuchi (2014), adult, whole-mounted,

ex intestine (Ahifumi Ohtaka, personal communication, 12 March 2017), Lake Abashiri, 28 May 2013 (see the Materials and Methods above). (2) 2 (MPM Coll. No. 21353-b) among many specimens of Digenea sp. 1 of Kikuchi (2014), immature, whole-mounted, site of infection not given, Lake Tofutsu, 21 April 2013. (3) 1 (NSMT-Pl 6346c), immature, whole-mounted, ex intestine, Lake Abashiri, 25 January 2016. (4) 3 (MPM Coll. No. 21411), immature, adult, whole-mounted, ex stomach, Lake Abashiri, 4 December 2017.

Description. Based on 1 immature and 3 adult specimens (Figs. 4-6). Body fusiform to ovate, small; soma 1.15-1.60 by 0.27-0.36; ecsoma 0.24-0.89 long; forebody 0.20-0.43 long, occupying 20-25% of length of soma. Tegument with annular plications. Presomatic pit present, anterior to ventral sucker. Transverse nerve commissure dorsal to pharynx (not illustrated). Oral sucker subterminal, 0.11-0.16 by 0.15-0.16. Prepharynx absent. Pharynx barrel-shaped, 0.07-0.08 by 0.07-0.08. Esophagus small. Drüsenmagen globular. Intestines extending to near posterior extremity of ecsoma. Ventral sucker 0.05-0.16 by 0.16-0.18; sucker width ratio 1: 1.1-1.2. Testes two, globular, large, 0.10-0.25 by 0.07-0.23, diagonal, contiguous, immediately posterior to ventral sucker. Sperm ducts leading to seminal vesicle. Seminal vesicle free in parenchyma, thin-walled, bipartite, 0.05-0.09 by 0.03-0.08, anterolateral to ventral sucker; posterior portion much larger. Pars prostatica tubular, surrounded by prostatic cells, leading to ejaculatory vesicle in sinus sac. Sinus sac small, 0.03-0.08 by 0.02-0.03, including globular glandular ejaculatory vesicle, anterior part of metraterm, and hermaphroditic duct. Genital atrium absent. Genital pore almost median, ventral to pharynx or immediately posterior to it. Ovary globular, 0.07-0.14 by 0.07-0.18, median, far posterior to testes. Ovarian complex not observed clearly. Juel's organ anterior to Mehlis' gland, both dorsal to vitellaria. Mehlis' gland may be free in parenchyma. Uterus strongly coiled in hindbody of soma; metraterm connecting with ejaculatory duct to form hermaphroditic duct in sinus sac.

Eggs numerous, oval, operculate, brown, 22–28 by 11–14 μ m (collapsed), embryonated. Vitellaria two, globular to 4-lobed, 0.09–0.21 by 0.07–0.14, median, almost contiguous, immediately posterior to ovary. Excretory vesicle dorsal, Y-shaped, bifurcating just posteriorly to ventral sucker (not illustrated), villous in posterior part; arms united dorsal to pharynx or oral sucker; excretory pore posteroterminal.

Remarks. The present specimens are identified as Brachyphallus crenatus (Rudolphi, 1802) Odhner, 1905 (Hemiuroidea, Hemiuridae) (Gibson, 2002a, b), because they are similar on the whole to this species as described by Odhner (1905), Ślusarski (1958), Zhukov (1960), and Gibson and Bray (1986). They also resembled the following specimens of Brachyphallus crenatus in morphology: (1) four adult specimens (MPM Coll. No. 23087) found in the stomach of Oncorhvnchus kisutch (Walbaum) (syn. Oncorhynchus milktschitsch (Walbaum)) (Salmonidae) of unknown provenance on 31 August 1930 (Yamaguti, 1934) and (2) many adult specimens found in formalin-preserved stomachs of juveniles of Oncorhynchus masou (Brevoort) caught in the coastal waters of the North Pacific near Cape Erimo, Hokkaido, on 10 June 1994 (Asami et al., 2016; some of them, MPM Coll. No. 21420).

Brachyphallus sp. of Ohtomo (2003) from Lake Abashiri is regarded as *Brachyphallus crenatus* from the present study, though none of her specimens was reexamined in the present study. Digenea sp. 2 of Kikuchi (2014) from Lakes Abashiri and Tofutsu (Digenea sp. 2 in separate fig. 1) is evidently identical with *Brachyphallus crenatus*. The site of infection of her fully mature adult specimen (NSMT-Pl 6344) may actually have been the stomach, not the intestine.

Brachyphallus amuriensis Babaskin, 1928 was originally described by Babaskin (1928) on the basis of adult specimens found in the stomach and sometimes the esophagus of Oncorhynchus keta (Walbaum) (Salmonidae) from the Amur River, Russian Far East. Zhukov (1960) synonymized this species with Brachyphallus crenatus. *Brachyphallus crenatus* is also a marine species and has been recorded mainly from the stomach of various species of marine and migratory fishes in the North Pacific and North Atlantic and adjacent seas (*e.g.*, Odhner, 1905; Babaskin, 1928; Yamaguti, 1934; Ślusarski, 1958; Mamaev *et al.*, 1959; Strelkov, 1960; Zhukov, 1960; Køie, 1983; Awakura and Nomura, 1983; Gibson and Bray, 1986; Machida and Araki, 1992, 1994; Gibson, 1996; Asami *et al.*, 2016). The species may not have a circumpolar distribution (Gibson and Bray, 1986; Gibson, 1996).

Gibson and Bray (1986) gathered much information on the life cycle of Brachyphallus crenatus. According to Køie (1992), cystophorous cercariae of this species were found in a marine snail, Retusa obtusa (Montagu) (Retusidae) (a natural first intermediate host), in the North Atlantic off Denmark; and they developed into infective metacercariae in a copepod, Acartia tonsa (Dana) (an experimental second intermediate host). Køie (1992) revealed that the annular plications of the tegument were scalelike in metacercariae and adults. Further, metacercariae have been recorded in Acartia sp. in the Baltic and in transport intermediate hosts, Sagitta elegans (Chaetognatha) in the White Sea and Pleurobrachia pileus (Ctenophora) from the northern Øresund (Gibson and Bray, 1986). In the Sea of Okhotsk (the North Pacific), Sokolov et al. (2016) first discovered metacercariae in copepods, Pseudocalanus newmani and Acartia longiremis, from waters of the Prostor Gulf of Iturup Island, Russian Far East (or Etorofu-to, Hokkaido). The first intermediate host is not known in the North Pacific.

> Family Lecithasteridae Odhner, 1905 Genus *Lecithaster* Lühe, 1901 *Lecithaster gibbosus* (Rudolphi, 1802) Lühe, 1901

(Figs. 7-9)

Fasciola gibbosa Rudolphi, 1802: 81, pl. 2, fig. 7. *Lecithaster gibbosus*: Lühe, 1901: 480.

Lecithaster salmonis Yamaguti, 1934: 486–488, fig. 123. (See Odhner (1905), Zhukov (1960), and Gibson (1996),

for other synonyms.)

Host. Hypomesus nipponensis. Site of infection. Intestine.

Localities. Lake Abashiri (Ohtomo, 2003; this paper), Lake Tofutsu (Kikuchi, 2014; this paper), and Lake Koyama (this paper).

Material examined. (1) 2 specimens (NSMT-Pl 6345) of Digenea sp. 3 (Digenea sp. 3 in separate fig. 1) of Kikuchi (2014), adult, wholemounted, site of infection not given [most likely intestine], Lake Tofutsu, 21 April 2013. (2) 14 (MPM Coll. No. 21353-c) of Digenea sp. 3 of Kikuchi (2014), immature, adult, wholemounted, site of infection not given [most likely intestine], Lake Tofutsu, 21 April 2013. (3) About 30 (MPM Coll. No. 21354-b) of Digenea sp. 1 of Kikuchi (2014), adult, whole-mounted, site of infection not given [most likely intestine], Lake Koyama, 2 March 2002. (4) About 30 (MPM Coll. No. 21355-b, NSMT-Pl 6343b), immature, adult, whole-mounted, ex intestine, Lake Abashiri, 25 January 2016. (5) Many (NSMT-Pl 6346a), immature, adult, wholemounted, ex intestine, Lake Abashiri, 25 January 2016. (6) 1 (MPM Coll. No. 21357), adult, whole-mounted, ex intestine, Lake Abashiri, 28 January 2017. (7) 8 (MPM Coll. No. 21412), immature, adult, whole-mounted, ex intestine, Lake Abashiri, 4 December 2017.

Description. Based on adult specimens; 4 (MPM Coll. No. 21355-b, NSMT-Pl 6343b) from Lake Abashiri measured (Figs. 7-9). Body ovate, rounded anteriorly, tapering posteriorly, very small to small, 0.87-1.21 by 0.27-0.39; forebody 0.30-0.44 long, occupying 32-48% of body length. Preoral lip developed. Tegument unarmed, with fine annular wrinkles. Transverse nerve commissure dorsal to pharynx. Oral sucker subterminal, 0.09–0.11 by 0.10–0.11. Prepharynx absent. Pharynx 0.05-0.08 by 0.06-0.07. Esophagus short. Drüsenmagen globular. Intestines thick, ending blindly at ovarian level. Ventral sucker 0.17-0.23 by 0.18-0.20; sucker width ratio 1: 1.6 -1.9. Testes two, globular, 0.12-0.20



Figs. 7–9. Lecithaster gibbosus, adult specimens found in intestine of Hypomesus nipponensis from Lake Abashiri. 7, specimen (MPM Coll. No. 21355-b), entire body, ventral view; 8, specimen (NSMT-Pl 6346a), anterior part of terminal genitalia, glandular vesicle (*) (?) of hermaphroditic duct, ventral view; 9, specimen (NSMT-Pl 6343b), ovarian complex, lateral view. Scale bars: 0.3 mm in Fig. 7; 0.1 mm in Figs. 8 and 9.

by 0.09–0.14, almost symmetrical, submedian, posterior to ventral sucker. Seminal vesicle free in parenchyma, thin-walled, elliptical, 0.14–0.18 by 0.07–0.10, normally median, posterodorsal to ventral sucker, pretesticular. Pars prostatica thick, long, tubular; its internal lining may be cellular; prostatic cells large. Ejaculatory duct short, con-

necting with metraterm at base of sinus sac to form hermaphroditic duct. Sinus sac thickwalled, elliptical, small, 0.05–0.09 by 0.03–0.07, ventral to esophagus and pharynx. Hermaphroditic duct in sinus sac may be slightly dilated in proximal part and surrounded by small cells to form glandular vesicle (* in Fig. 8). Genital atrium absent. Genital pore ventral to pharynx. Ovary 4-lobed, 0.12-0.20 by 0.11-0.17, median, post-testicular. Ovarian complex preovarian. Laurer's canal absent. Seminal receptacle blind, elliptical, 0.07-0.19 by 0.04-0.12, dorsal to ovary and testes. Uterus dorsal, coiling in hindbody, extending into postvitelline region and forebody in fully matured worms. Eggs numerous, oval, operculate, yellow, 21-27 by 13-14 um, embryonated. Vitellarium single, 7-lobed, 0.11-0.25 by 0.11-0.15, median, postovarian, near posterior extremity of body; lobes massive, slightly longer than wide. Excretory vesicle dorsal, Y-shaped, bifurcating at testicular level (not illustrated), villous in posterior part posterior to vitellarium; arms may be separate anteriorly; excretory pore posteroterminal.

Remarks. The present specimens are identified as *Lecithaster gibbosus* (Rudolphi, 1802) Lühe, 1901 (Hemiuroidea, Lecithasteridae) (Gibson, 2002c), because they are similar on the whole to this species as described by Odhner (1905), Zhukov (1960), and Gibson (1996). *Lecithaster salmonis* Yamaguti, 1934 was described by Yamaguti (1934) as a new species from the intestine of *Salmo keta* Walbaum (now in *Oncorhynchus*) from an unknown locality. Zhukov (1960) considered this species to be a junior synonym of *Lecithaster gibbosus*.

It appeared that the hermaphroditic duct formed a glandular vesicle (* in Fig. 8) at the proximal part in the sinus sac in the present specimens. Further studies of this structure are needed, because the structure like this is not known in the family Lecithasteridae (*e.g.*, Gibson, 2002c)

Digenea sp. 3 of Kikuchi (2014) from Lake Tofutsu (Digenea sp. 3 in separate fig. 1) is evidently identical with *Lecithaster gibbosus*. Many unpublished specimens of *Lecithaster gibbosus* were also found among her many specimens of Digenea sp. 1 from Lake Koyama in the present study. *Lecithaster* sp. of Ohtomo (2003) from Lake Abashiri is considered to be *Lecithaster gibbosus* from the present study, though none of her specimens was reexamined in the present study.

Lecithaster gibbosus is also a marine species and has been recorded from the intestine of various species of marine and migratory fishes in the North Pacific, Arctic, North Atlantic, and adjacent seas (*e.g.*, Layman, 1930; Yamaguti, 1934; Strelkov, 1960; Zhukov, 1960; Boyce, 1969; Margolis and Boyce, 1969; Awakura and Nomura, 1983; Køie, 1983, 1989; Machida and Araki, 1992, 1994; Gibson, 1996).

The life cycle of Lecithaster gibbosus is not understood well. Cystophorous cercariae referred to this species were recorded from marine snails, species of Thais (now Nucella) and Nucella (Nucellidae), in the North Pacific off British Columbia, Canada, and off Washington, USA (Boyce, 1969; Ching, 1991) and Odostomia eulimoides (Pyramidellidae) in the North Atlantic off Denmark (Køie, 1983, 1989). Since these host snails are quite different in species, there is some question whether cercariae specimens of Lecithaster from the two oceans are really the same species (Køie, 1983; Gibson, 1996). The cercariae developed into infective metacercariae in copepods (Boyce, 1969; Margolis and Boyce, 1969; Køie, 1989).

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