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Digeneans Parasitic in Freshwater Fishes (Osteichthyes) of Japan VIII. Allocreadiidae, *Crepidostomum*

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Abstract This paper reviews three species of *Crepidostomum* Braun, 1900 (Trematoda, Digenea, Allocreadioidea, Allocreadiidae) parasitic in freshwater fishes of Japan: *Crepidostomum chaenogobii* Yamaguti and Matumura, 1942, *Crepidostomum farionis* (Müller, 1780), and *Crepidostomum metoecus* (Braun, 1900). Each species is described and figured. *Crepidostomum uchimii* Fujita, 1920 and *Crepidostomum salmonis* Fujita, 1921 are regarded as junior synonyms of *C. farionis* and *C. metoecus*, respectively. Molecular and life-cycle studies of the three species are briefly mentioned. A key to the three species in Japan is presented.
Key words: Digeneans, Allocreadiidae, *Crepidostomum*, freshwater fishes, Japan, review.

Introduction

This is the eighth paper of a series that reviews adult digeneans (Trematoda) parasitic in freshwater fishes (Osteichthyes) of Japan (Shimazu, 2013). This contribution deals with three species of *Crepidostomum* Braun, 1900 in the family Allocreadiidae Looss, 1902 *sensu* Caira and Bogéa (2005) of the superfamily Allocreadioidea Looss, 1902 *sensu* Cribb (2005). In Japan, two genera are known in the family Allocreadiidae: *Crepidostomum* with three pairs of muscular papillae of the oral sucker and *Allocreadium* Looss, 1900 with no muscular papillae (Shimazu, 2016). The Introduction, Materials, and Methods for the review were given in the first paper (Shimazu, 2013).

Abbreviations used in the figures. cp, cirrus pouch; cvd, common vitelline duct; dlmp, dorsolateral muscular papilla; dmmp, dorsomedial muscular papilla; e, esophagus; ed, ejaculatory duct; egg, egg in uterus and metraterm; ep, excretory pore; esp, eyespot pigment; ev, excretory vesicle; ga, genital atrium; gp, genital pore; i, intestine; Lc, Laurer's canal; m, metraterm; Mg, Mehlis' gland; o, ovary; od, oviduct; os, oral sucker; ot, ootype; p, pharynx; pc, prostatic cells; pp, pars prostatica; pr, prepharynx; sd, sperm duct; sr, seminal receptacle; sv, seminal vesicle; t, testis; tnc, transverse nerve commissure; u, uterus; vd, vitelline duct; vf, vitelline follicles; vlmp, ventrolateral muscular papilla; vs, ventral sucker.

Superfamily Allocreadioidea Looss, 1902

Family Allocreadiidae Looss, 1902

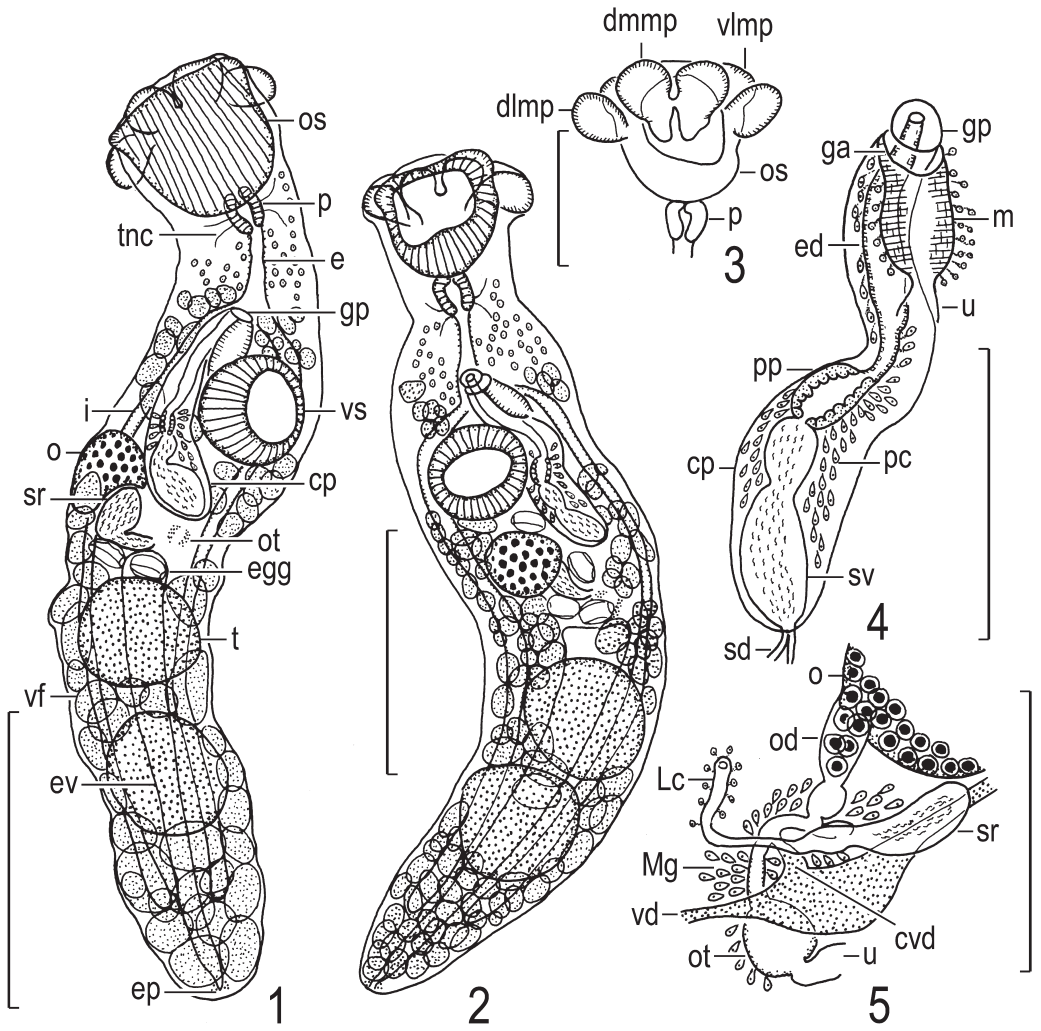
Genus ***Crepidostomum*** Braun, 1900

Crepidostomum chaenogobii Yamaguti and Matumura, 1942

(Figs. 1–5)

Crepidostomum chaenogobii Yamaguti and Matumura, 1942: 117–119, figs. 1–2; Shimazu, 1981: 21–22, figs. 17–20; Shimazu, 1990: 2–3, figs. 1–4.

Hosts in Japan. "*Chaenogobius annularis urotaenia* Hilgendorf" (Gobiidae) (type host) (Yamaguti and Matumura, 1942), *Cottus amblystomopsis* Schmidt, 1904 (Cottidae) (Shimazu, 1990), *Cottus hangiongensis* Mori, 1930 (Shimazu, 1990), *Cottus nozawae* Snyder, 1911 (Shimazu, 1981), and *Gymnogobius opperiens*



Figs. 1–5. *Crepidostomum chaenogobii*, adult specimens. — 1, holotype (MPM Coll. No. 22289) found in intestine of "*Chaenogobius annularis urotaenia* Hilgendorf," entire body, ventral view; 2, specimen (NSMT-Pl 3076) found in intestine of *Cottus hangiongensis*, entire body, ventral view; 3, specimen (NSMT-Pl 1850) found in intestine of *Co. nozawae*, muscular papillae of oral sucker, dorsal view; 4, specimen (NSMT-Pl 3076), terminal genitalia, ventral view; 5, specimen (NSMT-Pl 3078) found in intestine of *Co. hangiongensis*, ovarian complex, dorsal view. Scale bras: 0.5 mm in Figs. 1–2; 0.2 mm in Figs. 3–5.

Stevenson, 2002 (Gobiidae) (Shimazu, 1990; this paper).

Sites of infection. Intestine and pyloric ceca.

Geographical distribution. Hokkaido: Sapporo (type locality) (Yamaguti and Matumura, 1942); Ashibetsu River in Tsurui Village (Shimazu, 1981); Oono River at Chiyoda, Hokuto City (Shimazu, 1990; this paper); and Tobetsu River at Tobetsu, Hokuto City (Shimazu, 1990; this paper).

In Russian Far East: Sakhalin Island (Shedko, 2003; Sokolov *et al.*, 2012).

Material examined. (1) 2 specimens (Yamaguti's Collection, MPM Coll. No. 22289, holotype and 1 paratype) of *Crepidostomum chaenogobii*, adult, ex intestine of "*Chaenogobius annularis urotaenia* Hilgendorf" (*Chaenogobius urotaenia* of Shimazu (1990), *Chaenogobius*

urotaenia? of Shimazu (1994)), Sapporo (other data not given) (Yamaguti and Matumura, 1942; Shimazu, 1990, 1994). (2) 8 (NSMT-Pl 3073–3074) of *C. chaenogobii*, immature, adult, ex intestine of *Cottus amblystomopsis*, Oono River near Hakodate, or at Chiyoda, Hokuto City, 20 August 1984 (Shimazu, 1990, 1994). (3) 79 (NSMT-Pl 3076–3085) of *C. chaenogobii*, adult, ex intestine and pyloric ceca of *Co. hangiongensis*, Tobestu River, Kamiiso, or at Tobetsu, Hokuto City, 26 August 1984 (Shimazu, 1990, 1994). (Eleven adult specimens (NSMT-Pl 3075, ex intestine and pyloric ceca of *Co. amblystomopsis*, Tobetsu River, 26 August 1984) of Shimazu (1990) were not reexamined. Probably, they had been lost on loan.) (4) 79 (NSMT-Pl 1846–1852) of *C. chaenogobii*, immature, adult, ex intestine of *Co. nozawae*, Ashibetsu River near Kushiro, or in Tsurui Village, 10 May 1977 (Shimazu, 1981, 1990, 1994). (5) 1 (NSMT-Pl 3072) of *C. chaenogobii*, adult, ex intestine of *Gymnogobius opperiens* (*Chaenogobius urotaenia* (= *Chaenogobius annularis*, the middle-reaches type) of Shimazu (1990)), Tobetsu River, 26 August 1984 (Shimazu, 1990, 1994).

Description. 1) For the original description for *Creptostomum chaenogobii*, see Yamaguti and Matumura (1942). Holotype 1.59 by 0.32 (Fig. 1).

2) Based on specimens (NSMT-Pl 3072–3085), after Shimazu (1990), modified from the present study (Figs. 2–5). Body elongate-ovate, more tapering posteriorly, small, 0.94–1.70 by 0.30–0.52; forebody 0.30–0.52 long, occupying 29–32% of body length. Tegument smooth. Eyespot pigment not seen even in small immature specimens. Small gland cells present in forebody. Oral sucker globular, 0.13–0.20 by 0.14–0.21, ventrally subterminal, with one pair each of ventrolateral, dorsolateral, and dorsomedial muscular papillae; ventrolateral papillae conical, small, 25 by 55 μm in Fig. 3; dorsolateral and ventromedial papillae bluntly rounded, equal in size, large, 79 μm in diameter in Fig. 3. Prepharynx short. Pharynx globular, 0.05–0.07 in diameter; ratio of oral sucker width to pharynx width [not pharynx width to oral sucker width in Shimazu (1981, 1990)] 1 : 0.3–0.5. Esophagus fairly long, 0.08–0.16 long, surrounded by small gland cells, bifurcating anterior to ventral sucker. Intestines (or ceca) terminating blindly at about midlevel of post-testicular region. Ventral sucker subglobular, usually smaller than oral sucker, 0.12–0.17 by 0.14–0.20, situated at about junction of anterior and middle thirds of body; sucker width ratio 1 : 0.8–1.2. Testes two, spherical, large, anterior one always smaller than posterior one, 0.13–0.30 in diameter, median, tandem, in middle third of hindbody, slightly separated by vitelline follicles [not contiguous]. Cirrus pouch (or cirrus-sac) club-shaped, thickened posteriorly, thick-walled, muscular, long, 0.30–0.55 by 0.16–0.19, extending usually to ovarian level but sometimes to anterior testis, including seminal vesicle, prostatic complex, and ejaculatory duct (or cirrus). Seminal vesicle tubular, thick-walled, muscular, short, straight (Figs. 1, 2, and 4) to S-shaped (Shimazu, 1981, fig. 19), occupying posterior third to half of cirrus pouch. Pars prostatica elliptical, 0.05–0.09 by 0.03–0.05; prostatic cells well developed. Ejaculatory duct straight or slightly undulating, thick-walled, 0.16–0.28 by 0.02, surrounded by small gland cells, sometimes slightly everted. Genital atrium small, cup-shaped. Genital pore median, bifurcal or slightly anterior to it. Ovary globular to elliptical, smaller than testes, 0.09–0.17 in diameter, between ventral sucker and anterior testis, dextrally or sinistrally submedian or almost lateral. Ovarian complex postovarian. Seminal receptacle canalicular, club-shaped, 0.04–0.10 by 0.04–0.07. Laurer's canal fairly long. Ootype vesicular, large; Mehlis' gland well developed. Uterus coiled a few times, usually pretesticular, rarely extending slightly into testicular region; metraterm well developed, very thick-walled, much shorter than cirrus pouch, 0.05–0.16 long. Eggs fewer than 20, broad-ovate, operculate, light brown, 60–72 by 40–48 μm, unembryonated; eggshells smooth. Vitellaria follicular; follicles large, slightly entering prebifurcal region, extending to posterior extremity of body, separate anteriorly, confluent

between two testes and in post-testicular region, sometimes interrupted laterally to ventral sucker, ovary, and testes. Excretory vesicle I-shaped, extending anteriorly to seminal receptacle beyond anterior testis; excretory pore posteroterminal or -dorsal.

Remarks. Yamaguti and Matumura (1942) fully described and figured *Crepidostomum chaenogobii* as a new species on the basis of the holotype and paratype. The type host "*Chaenogobius annularis urotaenia* Hilgendorf" is currently assigned to *Gymnogobius*. However, its current scientific name is unknown, because they identified the type host fish from the then classification of *Chaenogobius*. The present specimens agree well with the type specimens in morphology and measurements.

Life cycle. Not known in Japan.

Crepidostomum farionis (Müller, 1780)

(Figs. 6–11)

Fasciola farionis Müller, 1780: 4, pl. 72.
Crepidostomum farionis: Lühe, 1909: 63, fig. 54; Shimazu, 1990, in part: 4, figs. 5–8.
Crepidostomum uchimii Fujita, 1920: 105–107, pl. 2, figs. 1–5.
Crepidostomum uchimii Fujita, 1920, *sp. inq*.: Shimazu, 1990: 10, fig. 21.
For other synonyms, see Hopkins (1934) and Caira (1989).

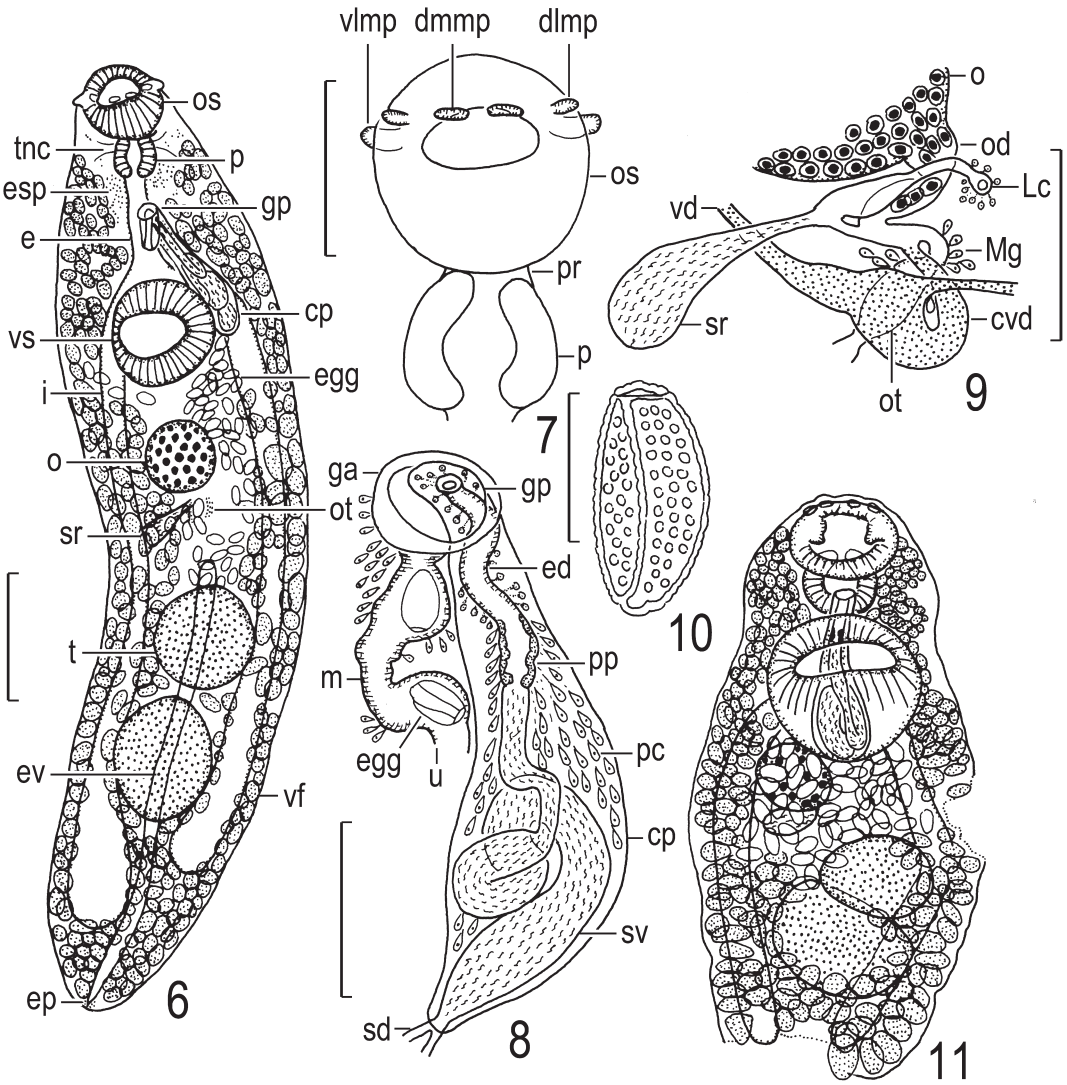
Hosts in Japan. *Oncorhynchus masou masou* (Brevoort, 1856) (Salmonidae) (Fujita, 1920; Shimazu, 1990; this paper), *Oncorhynchus mykiss* (Walbaum, 1792) (Seki, 1975a, b; Shimazu, 1981, 1990; this paper), *Salvelinus fontinalis* (Mitchill, 1814) (Salmonidae) (this paper), *Salvelinus leucomaenis leucomaenis* (Pallas, 1814) (Seki, 1975a, b; this paper), and *Salvelinus malma malma* (Walbaum, 1792) (Shimazu, 1981, 1990; this paper).

Sites of infection. Intestine and pyloric ceca, and also rectum (accidental (?)) and gall bladder (normal (?)).

Geographical distribution. Hokkaido: Lake Panketo at Akan-cho, Kushiro City (Seki, 1975a, b; Shimazu, 1981, 1990, 1994; this paper); Lake Shikaribetsu at Shikaoi Town (Seki, 1975a, b; Shimazu, 1981, 1990, 1994; this paper); Mamachi River at Aoba, Chitose City (this paper); Nishibestu River at Nijibetsu, Shibecha Town (this paper); Nishibetsu River in Shibecha Town (Fujita, 1920; this paper); Nobusha and Shokanbetsu rivers in Mashike Town (Shimazu, 1990, 1994); Onishibetsu River in Sarufutsu Village (Shimazu, 1990, 1994); and Tawaramappu River in Nakashibetsu Town (this paper).

In the Holarctic region (*e.g*., Caira, 1989).

Material examined. (1) 3 specimens (Fujita's Collection, III-10, HUNHM 48659, labeled "*Crepidostomum uchimii* Fujita [Host: *Oncorhynchus masou*] [Intestine] [Nijibestu River] [Hokkaido] [September 1918]," syntypes) of *C. uchimii*, adult, 2 balsam-mounted, 1 in glycerin-alcohol, ex intestine of *O. masou masou* (syn. *O. masou*), Nijibetsu River, Kushiro, or now Nishibestu River in Shibecha Town, eastern Hokkaido, September, 1918 (Fujita, 1920). (2) 11 (NSMT-Pl 3086) of *C. farionis*, adult, ex intestine of *O. masou masou*, Onishibetsu River, 15 July 1984 (Shimazu, 1990). (3) 2 (NSMT-Pl 3087–3088) of *C. farionis*, immature, adult, ex intestine and rectum (accidental (?)) of *O. masou masou*, Shokanbetsu River, 1 August 1984 (Shimazu, 1990). (4) 2 (NSMT-Pl 3089–3090) of *C. farionis*, immature, adult, ex intestine of *O. masou masou*, Nobusha River, 2 August 1984 (Shimazu, 1990). (Seven adult specimens (NSMT-Pl 3091) of Shimazu (1990) were not reexamined. Probably, they had been lost on loan.) (5) 13 (NSMT-Pl 5822–5823), adult, ex intestine of *O. masou masou*, Mamachi River, 18 April 2011, 9 August 2011. (6) 1 (NSMT-Pl 5824), adult, ex gall bladder of *O. masou masou*, Mamachi River, 9 August 2011. (7) 1 (HUNHM 61343), adult, ex intestine of *O. masou masou*, Tawaramappu River, 1 August 2011. (8) 1 (NSMT-Pl 5803), adult, ex intestine of *O. mykiss*, Nishibetsu River at Nijibetsu, 18 April 2011. (9) 3 (NSMT-Pl 5799, HUNHM 61342), immature, adult, ex intestine of *Salvelinus fontinalis* (formalin-fixed and fresh), Nishibetsu River at Nijibetsu, 2



Figs. 6–11. *Crepidostomum farionis*, adult specimens. — 6, specimen (NSMT-Pl 5799) found in intestine of *Salvelinus fontinalis*, entire body, ventral view; 7, specimen (NSMT-Pl 5803) found in intestine of *Oncorhynchus mykiss*, muscular papillae of oral sucker, dorsal view; 8, specimen (NSMT-Pl 5822) found in intestine of *O. masou masou*, terminal genitalia, ventral view; 9, specimen (NSMT-Pl 5799), ovarian complex, dorsal view; 10, egg with warty eggshell; 11, syntype of *C. uchimii* (HUNHM 48659) found in intestine of *O. masou masou*, entire body, ventral view. Scale bars: 0.5 mm in Figs. 6 and 11; 0.2 mm in Figs. 7–9; 0.05 mm in Fig. 10.

October 1986, 18 April 2011. (10) 1 (NSMT-Pl 5798), adult, ex intestine of *S. leucomaenis leucomaenis* (formalin-fixed), Nishibetsu River at Nijibetsu, 2 October 1986. (11) 2 (NSMT-Pl 5806), adult, ex intestine of *S. malma malma*, Tawaramappu River, 1 August 2011.

Description. 1) Based on slightly flattened adult specimens (NSMT-Pl 3086, 3087, 3090–3091, 5803, 5806, 5822–5823; HUNHM 61342–61343) (Figs. 6–10). Body elongate-ovate, widest at level of ventral sucker, fairly small, 1.90–5.36 by 0.57–1.20; forebody 0.52–1.43 long, occupying 24–33% of body length. Eyespot pigment usually dispersed but rarely solid in forebody. Oral sucker small, 0.19–0.32 by 0.21–0.35; ventrolateral papillae ear-shaped, fairly

large, 32–35 by 48–50 μm in Fig. 7; dorsolateral papillae horn-shaped, small, 31–33 by 17–22 μm in Fig. 7; dorsomedial papillae narrow elliptical, small, 13–16 by 40 μm in Fig. 7. Pharynx large, 0.12–0.23 by 0.13–0.23; ratio of oral sucker width to pharynx width 1 : 0.5–0.8. Esophagus bifurcating dorsally to anterior border of ventral sucker or slightly anteriorly to it. Intestines terminating at about midlevel of post-testicular region. Ventral sucker 0.25–0.47 by 0.28–0.46; sucker width ratio 1 : 1.2–1.5. Testes globular, 0.23–0.63 by 0.19–0.44, oblique or tandem, in middle third of hindbody, contiguous or slightly separated by vitelline follicles. Cirrus pouch clavate, thin-walled, long, 0.25–0.90 by 0.09–0.23, lateral to ventral sucker, sometimes extending posteriorly slightly beyond ventral sucker. Seminal vesicle long, thin-walled, thick and convoluted in proximal two-thirds, thin and slender in distal third (Figs. 6 and 8), occupying posterior two-thirds of cirrus pouch. Pars prostatica elliptical to elongate, 0.03–0.12 by 0.03–0.04; prostatic cells well developed. Ejaculatory duct straight or slightly undulating, short, 0.11–0.23 by 0.02, occupying anterior third of cirrus pouch, sometimes slightly everted. Genital atrium large, shallow. Genital pore ventral to pharynx or slightly posterior to it. Ovary almost globular, smaller than testes, 0.21–0.39 by 0.19–0.41, dextrally or sinistrally submedian or sometimes median. Seminal receptacle club-shaped, 0.12–0.32 by 0.06–0.14, between ovary and anterior testis. Laurer's canal short, sometimes making proximal dilatation to store sperm in it. Ootype large; Mehlis' gland well developed. Uterus coiled between anterior testis and ventral sucker, between intestines, slightly overlapping them, rarely extending slightly into testicular region; metraterm much shorter than [not almost as long as in Shimazu (1990)] cirrus pouch. Eggs numerous, broad-ovate, brown, 59–79 by 32–49 μm [70–82 by 42–50 μm in Shimazu (1990)]; eggshells warty (Fig. 10) or smooth. Vitelline follicles distributed from oral sucker to posterior extremity of body, separate anteriorly, confluent in post-testicular region. Excretory vesicle extending anteriorly slightly beyond anterior testis; excretory pore postero-terminal or -dorsal.

2) Based on 3 adult syntypes of *C. uchimii* (HUNHM 48659, 1 lacking posterior part of body) (Fig. 11). Body much contracted, 0.79–(about 1.10) by 0.44–0.54. Eyespot pigment not seen. Oral sucker 0.13–0.15 by 0.17–0.21; ventrolateral papillae bending internally, 20–25 by 28–39 μm; dorsolateral papillae horn-shaped, 24–27 by 9–19 μm; dorsomedial papillae narrow elliptical, 9–14 by 25–37 μm. Pharynx large, 0.09–0.12 by 0.08–0.13; ratio of oral sucker width to pharynx width 1 : 0.5–0.6. Esophagus bifurcating dorsally to ventral sucker. Intestines terminating at about midlevel of post-testicular region. Ventral sucker 0.16–0.26 by 0.20–0.30; sucker width ratio 1 : 1.2–1.4. Testes 0.10–0.17 by 0.12–0.22. Cirrus pouch 0.22–0.34 by 0.07, dorsal to ventral sucker. Seminal vesicle looping in proximal two-thirds, slender in distal third, occupying posterior two-thirds of cirrus pouch. Pars prostatica elliptical, in anterior third of cirrus pouch. Ejaculatory duct short, occupying anterior third of cirrus pouch. Genital pore at posterior half of pharynx. Ovary 0.12 by 0.11, dextrally submedian. Ovarian complex not clearly observed. Uterus extending to dorsal side of anterior testis. Eggs rather numerous, 51–64 by 35–46 μm (collapsed); eggshells warty or smooth. Vitelline follicles distributed between oral sucker and posterior extremity of body. Excretory vesicle not clearly observed.

Remarks. The present specimens, except for Fujita's three specimens, closely resemble *Crepidostomum farionis* as described by Brown (1927), Hopkins (1934), Ślusarski (1958), and Caira (1989). Furthermore, they agreed well in morphology with the following whole-mounted adult specimens of *C. farionis* borrowed from the Institute of Parasitology, Czech Republic: 3 (No. Coll. D-42/3 and D-43/3), ex intestine of *Thymallus thymallus* (Salmonidae), Kamenice River, 13 and 15 November 1978; and 4 (No. Coll. D-43/1), ex intestine of *Salmo trutta fario*, Černovický Brook (Elve River basin), 7 September 1977, 10 October 1977; Osoblaha River

(Oder River basin), 13 May 1961; and Bystřice River (Danube River basin), 6 June 1989, all from former Czechoslovakia. Consequently, I identify the present specimens as *C. farionis*.

Crepidostomum farionis differs from *C. chaenogobii* (see above) mainly in that the oral sucker is smaller, instead of usually larger, than the ventral sucker; the ventrolateral papillae of the oral sucker are ear-shaped instead of conical; the dorsolateral papillae are horn-shaped and small instead of bluntly rounded and large; the dorsomedial papillae are narrow elliptical and small instead of bluntly rounded and large; the ratio of the oral sucker width to the pharynx width is higher, 1 : 0.5–0.8 instead of 1 : 0.3–0.5; the seminal vesicle is long and convoluted instead of short and straight; the genital pore opens ventral to the pharynx or slightly posterior to it instead of at the intestinal bifurcation or slightly anterior to it; and eggshells are sometimes warty instead of smooth.

Fujita (1920) described a new species, *Crepidostomum uchimii*, on the basis of whole-mounted and serially sectioned adult specimens, which had been found in the intestine of *Oncorhynchus masou masou* (syn. *O. masou*) collected in the "Nijibetsu River" [probably the Nishibetsu River of today] in Kushiro [Kushiro no Kuni, now Shibecha Town, eastern Hokkaido]. Fujita's Collection included three adult specimens of *C. uchimii* in a vial (see *Material examined*). Since he did not designate a holotype for *C. uchimii*, I consider them syntypes of *C. uchimii*. I made two of them into stained balsam-mounted preparations, but they were poorly prepared. These two whole-mounts and another specimen in new glycerin-alcohol were used for the present study.

In *C. uchimii* as described by Fujita, (1) the muscular papillae of the oral sucker are diagrammatically figured (fig. 1), lacking morphological details; (2) no eyespot pigment is seen; (3) the ventrolateral papillae of the oral sucker are one-seventh as large as the larger diameter [width] of the oral sucker; (4) the pharynx is small, with the ratio of the oral sucker width to the pharynx width of 1 : 0.4 (my calculation from the description) and 1 : 0.3 (my calculation from fig. 1); but the pharynx is large in a sagittal section (fig. 2); (5) the seminal vesicle is long and convoluted, occupying the posterior half of the cirrus pouch; and the ejaculatory duct is short, occupying the anterior half of the cirrus pouch; (6) the genital pore is located ventral to the pharynx; (7) the egg size is 0.08 by 0.04 mm in the description and 0.08 by 0.04 by 0.03 mm in the English specific diagnosis; and (8) the excretory vesicle extends anteriorly to the anterior border of the anterior testis. In the three syntypes reexamined (Fig. 11), (1) the body was contracted; (2) the ventrolateral papillae bent internally, the dorsolateral papillae were horn-shaped, and the dorsomedial papillae were narrow elliptical; (3) the pharynx was large, with the ratio of oral sucker width to pharynx width of 1 : 0.5–0.6; the convoluted seminal vesicle occupied the posterior two-thirds of the cirrus pouch, and the ejaculatory duct occupied the anterior one-third of the cirrus pouch; (4) the genital pore was located ventral to the pharynx; (5) eggs were 51–64 by 35–46 μm (collapsed), and some eggshells were slightly warty; and (6) the excretory vesicle was not clearly observed.

Margolis (1982) said that *C. uchimii* might well be a synonym of *C. farionis*, but Shimazu (1990, 1994) preferred to retain *C. uchimii* as a *species inquirenda* until reexamination of Fujita's original material. In the above-mentioned features, *C. uchimii* closely resembles the present specimens of *C. farionis*. In order to obtain some new specimens of *C. uchimii*, I examined formalin-preserved fish (2 individuals of *O. masou masou*, 3 of *O. mykiss*, 5 of *S. leucomaenis leucomaenis*, and 6 of *S. fontinalis*) and fresh fish (13 of *O. masou masou*, 3 of *O. mykiss*, 8 of *S. leucomaenis leucomaenis*, and 15 of *S. fontinalis*) all collected in the Nishibetsu River at Nijibetsu, Shibecha Town, on 2 October 1986 and 18 April 2011, respectively; and fresh fish (32 of *O. masou masou*, 2 of *S. leucomaenis leucomaenis*, and 6 of *S. malma malma* collected in the Tawaramappu River (a tributary of the Shibetsu River, which is the next river on the north of the

Nishibetsu River, both flowing into the Okhotsk Sea) in Nakashibetsu Town on 1 August 2011. Although *C. farionis* was not found in *O. masou masou* from the Nishibetsu River, it was found in *O. mykiss*, *S. leucomaenis leucomaenis*, and *S. fontinalis* from the Nishibetsu River and in *O. masou masou* and *S. malma malma* from the Tawaramappu River (see *Material examined*), which indicates that *C. farionis* is certainly distributed in the Nishibetsu and Tawaramappu rivers in eastern Hokkaido. Furthermore, two contracted adult specimens (NSMT-Pl 5798–5799) of *C. farionis* found in formalin-preserved individuals of *S. leucomaenis leucomaenis* and *S. fontinalis* from the Nishibetsu River were very similar to the contracted syntypes of *C. uchimii* in morphology, having internally bent ventrolateral papillae. In conclusion, I now regard *C. uchimii* as a junior synonym of *C. farionis*.

Seki (1975a, b) reported specimens of *Crepidostomum* from the intestine of salmonids collected in Hokkaido: (1) *C. farionis* (1975a, p. 10, pl. 1, fig. 2) found in *S. leucomaenis leucomaenis* (syn. *S. leucomaenis*) from Lake Panketo and *O. mykiss* (syn. *Salmo gairdneri irideus* (Gibbons, 1855)) from Lake Shikaribetsu; (2) *Crepidostomum metoecus* (Braun, 1900) (1975a, pp. 10–11, pl. 1, fig. 3) found in *S. malma malma* from Lake Shikaribetsu; and (3) *Crepidostomum* sp. (1975a, pp. 11–12, pl. 1, fig. 4) found in *S. malma malma* from Lake Shikaribetsu. Shimazu (1981, 1990) reexamined part of Seki's specimens, which were then deposited in the Department of Parasitology, Faculty of Veterinary Medicine, Hokkaido University, Sapporo. (1) Seki's specimens (No. 374) of *C. farionis* found in *O. mykiss* consisted of specimens of *C. farionis* and those of *C. metoecus*, including the figured one (fig. 2). The uterus occupied all the available space in the hindbody in one of the specimens of *C. farionis*. (2) Seki's specimens (No. 375) of *C. metoecus* found in *S. malma malma* consisted of specimens of *C. metoecus* including the figured one (fig. 3) and those of *C. farionis*. (3) Seki's specimen (No. 376) of *Crepidotomum* sp. (fig. 4) found in *S. malma malma* was identified as *C. farionis*. The uterus descended into the testicular region in this specimen. It is desirable that all of Seki's specimens be reexamined.

Shimazu's (1981, 1990) three specimens (NSMT-Pl 2174) of *C. farionis* found in *S. leucomaenis leucomaenis* from the Ashibetsu River and Shimazu's (1990) specimen (NSMT-Pl 3092) of *C. farionis* found in *Noemacheilus toni* (Homalopteridae) [*sic*] from the Shokanbestu River are identified as *C. metoecus* in the present study (see below).

Life cycle. Not known in Hokkaido.

Crepidostomum metoecus (Braun, 1900)

(Figs. 12–18)

Distomum metoecus Braun, 1900a: 389.

Crepidostomum metoecus: Braun, 1900b: 230–231, fig. 13; Shimazu, 1990: 6–7, figs. 10–19.

Crepidostomum salmonis Fujita, 1921b: 137–140, figs. 1–3.

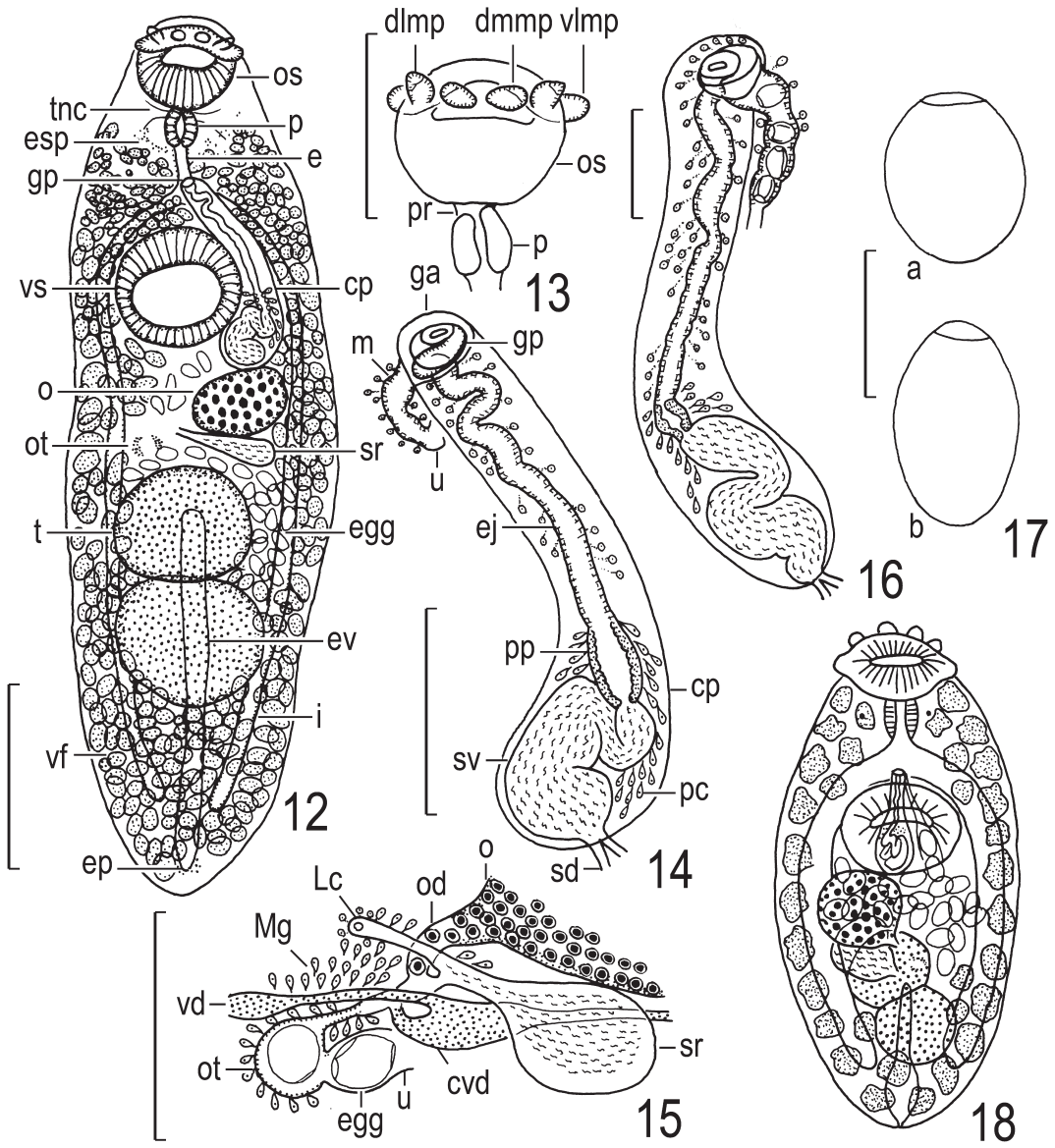
Bunodera luciopercae (not of (Müller, 1776) Stiles and Hassall, 1898): Shimazu, 1981: 19, 21, figs. 11–15.

Crepidostomum farionis (not of (Müller, 1780) Lühe, 1909): Shimazu, 1981: 23–24, figs. 21–24; Shimazu, 1990, in part: 4, fig. 9.

Crepidostomum salmonis Fujita, 1921, *sp. inq*.: Shimazu, 1990: 9, fig. 20.

For other synonyms, see Hopkins (1934) and Caira (1989).

Hosts in Japan. *Barbatula toni* (Dybowski, 1869) (Nemacheilidae) (Shimazu, 1990; this paper), *Cottus nozawae* (Cottidae) (Shimazu, 1981), *Gasterosteus aculeatus* Linnaeus, 1758 (Gasterosteidae) (Shimazu, 1990; this paper), *Gymnogobius castaneus* (O'Shaughnessy, 1875) (Gobiidae) (Shimazu, 1990; this paper), *Gymnogobius urotaenia* (Hilgendorf, 1879) (Shimazu, 1990; this paper), *Oncorchynchus keta* (Walbaum, 1792) (Salmonidae) (Fujita, 1916, 1921b; Shimazu, 1990), *Oncorchynchus masou masou* (Kurata, 1992; this paper), *Oncorchynchus mykiss* (Shimazu, 1981, 1990; Kurata, 1992; this paper), *Parahucho perryi* (Brevoort, 1856) (Salmonidae) (Shimazu, 1981; this paper), *Pungitius pungitius* (Linnaeus, 1758) (Gasterosteidae) (this paper), *Pungitius tymensis* (Nikolskii, 1889)



Figs. 12–18. *Crepidostomum metoecus*, adult specimens. — 12, specimen (NSMT-Pl 5801) found in intestine of *Salvelinus fontinalis*; entire body; 13, specimen (NSMT-Pl 5801), muscular papillae of oral sucker, dorsal view; 14, specimen (NSMT-Pl 5801), terminal genitalia, ventral view; 15, specimen (NSMT-Pl 5826) found in intestine of *Salmo trutta*, ovarian complex, dorsal view; 16, specimen (NSMT-Pl 3092) found in intestine of *Barbatula toni*, terminal genitalia, ventral view; 17, abnormal egg of specimen (NSMT-Pl 3092) (a), normal egg of specimen (NSMT-Pl 5801) (b); 18, specimen of *C. salmonis* found in alimentary canal of *Oncorhynchus keta* (fry), entire body, ventral view, scale unknown, redrawn from Fujita (1921b). Scale bars: 0.5 mm in Fig. 12; 0.2 mm in Figs. 13–16; 0.05 mm in Fig. 17.

(Shimazu, 1990; this paper), *Salmo trutta* Linnaeus, 1758 (Salmonidae) (this paper), *Salvelinus fontinalis* (Salmonidae) (this paper), *Salvelinus leucomaenis leucomaenis* (Shimazu, 1981, 1990; Kurata, 1992; this paper), and *Salvelinus malma malma* (Seki, 1975a, b; Shimazu, 1990; Kurata, 1992; this paper).

Sites of infection. Intestine and pyloric ceca,

and also rectum (accidental (?)).

Geographical distribution. Hokkaido: Brooks near Sapporo (Fujita, 1921b; Shimazu, 1990, 1994); Ashibetsu and Settsuri rivers in Tsurui Village (Shimazu, 1981, 1990, 1994); Izari River at Eniwa City (this paper); Kushiro River (locality not specified) (Kurata, 1992; Shimazu, 1994); Lake Panketo at Akan-cho, Kushiro City (Shimazu, 1981, 1990; this paper); Lake Shikaribetsu at Shikaoi Town (Seki, 1975a, b; Shimazu, 1990, 1994); Lakes Shirarutoro and Toro at Toro, Shibecha Town (Shimazu, 1990, 1994); Mamachi River at Aoba, Chitose City (this paper); Nishibestu River at Nijibetsu, Shibecha Town (Kurata, 1992; Shimazu, 1994; this paper); Shin River in Hamanaka Town (Shimazu, 1990, 1994); Shokanbetsu River in Mashike Town (Shimazu, 1990, 1994; this paper); Sorachi River (locality not specified) (Kurata, 1992; Shimazu, 1994); and Tawaramappu River in Nakashibetsu Town (this paper).

In the Holarctic region (*e.g*., Caira, 1989).

Material examined. (1) 1 specimen (NSMT-Pl 3092) of *C. farionis*, adult, ex intestine of *Barbatula toni* (syn. *Noemacheilus toni*), Shokanbetsu River, 31 July 1984 (Shimazu, 1990, 1994). (2) 4 (NSMT-Pl 5831), adult, ex intestine of *B. toni*, Izari River, 1 June 2011. (3) 34 (NSMT-Pl 5828–5830), immature, adult, ex intestine of *B. toni*, Mamachi River, 18 April 2011, 20 May 2011, 9 August 2011. (4) 36 (NSMT-Pl 1846–1849, *B. luciopercae* of Shimazu (1981)) of *C. metoecus*, immature, adult, ex intestine of *Cottus nozawae*, Ashibetsu River, 10 [not 19] May 1977 (Shimazu, 1981, 1990, 1994). (5) 1 (NSMT-Pl 3071) of *C. metoecus*, adult, ex intestine of *Gasterosteus aculeatus* (syn. *Ga. aculeatus aculeatus*), Lake Shirarutoro, 19 September 1981 (Shimazu, 1990, 1994). (6) 11 (NSMT-Pl 3068) of *C. metoecus*, immature, adult, ex *Gymnogobius castaneus* (now not *Chaenogobius laevis* (Steindachner, 1879)), Shin River, 28 May 1981 (Shimazu, 1990, 1994). (7) 31 (NSMT-Pl 3066–3067) of *C. metoecus*, immature, adult, ex intestine of *G. urotaenia* (*Chaenogobius urotaenia* (the freshwater type) of Shimazu (1990), *Chaenogobius* sp. 1 of Prince Akihito), Shin River, 28 May 1981, 11 June 1981 (Shimazu, 1990, 1994). (8) 57 (NSMT-Pl 3057–3065) of *C. metoecus*, adult, ex intestine and rectum (accidental (?)) of *G. urotaenia*, Lake Toro, 28 June 1984 (Shimazu, 1990, 1994). (Thirty-one adult specimens (NSMT-Pl 3056) of Shimazu (1990) were not reexamined. Probably, they had been lost on loan.) (9) 6 (NSMT-Pl 3070) of *C. metoecus*, adult, ex intestine of *Oncorchynchus keta* (smolt), Shin River, 11 June 1981 (Shimazu, 1990, 1994). (10) 13 (NSMT-Pl 5822–5823), adult, ex intestine of *O. masou masou*, Mamachi River, 18 April 2011, 9 August 2011. (11) 1 (NSMT-Pl 5800), adult, ex intestine of *O. masou masou*, Nishibetsu River at Nijibetsu, 18 April 2011. (12) 8 (NSMT-Pl 5804), immature, adult, ex intestine of *O. masou masou*, Tawaramappu River, 1 August 2011. (13) 13 (NSMT-Pl 5826), adult, ex intestine of *Salmo trutta*, Mamachi River, 18 April 2011. (14) 77 (NSMT-Pl 5799, 5801, HUNHM 61342), immature, adult, ex intestine of *Salvelinus fontinalis* (formalin-preserved and fresh), Nishibetsu River at Nijibetsu, 2 October 1986, 18 April 2011. (15) 3 (NSMT-Pl 2174) of *C. farionis*, adult, ex pyloric ceca of *S. leucomaenis leucomaenis* (syn. *S. leucomaenis*), Ashibetsu River, 10 May 1977 (Shimazu, 1981, 1990, 1994). (16) 34 (NSMT-Pl 2175, *Bunodera luciopercae* of Shimazu (1981)) of *C. metoecus*, immature, adult, ex intestine and pyloric ceca, *S. leucomaenis leucomaenis* (syn. *S. leucomaenis*), Ashibetsu River, 10 May 1977 (Shimazu, 1981, 1990, 1994). (17) About 60 (NSMT-Pl 3069) of *C. metoecus*, immature, adult, ex intestine of *S. leucomaenis leucomaenis*, Lake Toro, 15 May 1981 (Shimazu, 1990, 1994). (18) 1 (NSMT-Pl 5825), adult, ex intestine of *S. leucomaenis leucomaenis*, Mamachi River, 18 April 2011. (19) 5 (NSMT-Pl 5798, 5802), immature, adult, ex intestine of *S. leucomaenis leucomaenis* (formalin-preserved and fresh), Nishibetsu River at Nijibetsu, 2 October 1986, 18 April 2011. (20) 1 (NSMT-Pl 5805), adult, ex intestine of *S. leucomaenis leucomaenis*, Tawaramappu River, 1 August 2011. (21) 11

(NSMT-Pl 5806), immature, adult, ex intestine of *S. malma malma*, Tawaramappu River, 1 August 2011. (22) 28 (NSMT-Pl 2176, *Bunodera luciopercae* (?) of Shimazu (1981)) of *C. metoecus*, immature, adult, ex intestine of *Parahucho perryi* (syn. *Hucho perryi*) (formalin-preserved), Settsuri River, 10 April 1976 (Shimazu, 1981, 1990, 1994). (23) Kurata's (1992) specimens of *C. metoecus*, adult: 1 (NSMT-Pl 3986), ex intestine of *S. malma malma*, Sorachi River (locality not specified), 6 September 1992; 2 (NSMT-Pl 3987–3988), ex intestine of *S. leucomaenis leucomaenis*, Nishibetsu River at Nijibetsu, 24 July 1992; and 1 (NSMT-Pl 3989), ex intestine of *O. masou masou* (syn. *O. masou*), Nishibetsu River at Nijibetsu, 24 July 1992 (Shimazu, 1994). (24) 3 (NSMT-Pl 5827), adult, ex intestine of *Pungitius pungitius*, Mamachi River, 18 April 2011. (25) 3 (Ozaki's Collection, MPM Coll. No. 30010, labeled "*Crepidostomum uchimii*") of *C. metoecus*, immature, adult, ex *Pungitius tymensis* (syn. *P. pungitius tymensis*), Hokkaido (other data not given) (Shimazu, 1990, 1994).

Description. 1) Based on specimens (NSMT-Pl 5798–5802, 5804–5806, 5822–5823, 5825–5827), relatively large ones of them measured (Figs. 12–15). Body elongate-ovate, more tapering posteriorly, small, 1.62–3.33 by 0.52–0.92; forebody 0.55–1.03 long, occupying 28–34% of body length. Eyespot pigment solid or dispersed in forebody. Oral sucker small, 0.18–0.28 by 0.20–0.31; ventrolateral papillae ear-shaped, fairly large, 38–55 by 40–48 μm in Fig. 13; dorsolateral papillae horn-shaped, fairly large, 37–48 by 30–32 μm in Fig. 13; dorsomedial papillae broad elliptical, fairly large, 24 by 40–43 μm in Fig. 13. Pharynx small, 0.08–0.13 by 0.06–0.12; ratio of oral sucker width to pharynx width 1 : 0.3–0.4. Esophagus bifurcating anterior to ventral sucker. Intestines terminating at about middle of post-testicular region. Ventral sucker 0.25–0.43 by 0.28–0.43, located at about junction of anterior and second thirds of body; sucker width ratio 1 : 1.3–1.4. Testes round or slightly indented irregularly, large, 0.22–0.47 by 0.32–0.54, tandem, in middle third of hindbody, contiguous. Cirrus pouch clavate, fairly thick-walled, muscular, 0.35–0.63 by 0.09–0.16, extending posteriorly beyond ventral sucker sometimes to ovary. Seminal vesicle short, thickened posteriorly, fairly thick-walled, muscular, sinuous in about posterior third of cirrus pouch (Figs. 12 and 14). Pars prostatica elliptical, small; prostatic cells well developed. Ejaculatory duct long, undulating in anterior two-thirds to one-half of cirrus pouch, sometimes everted. Genital atrium large. Genital pore at intestinal bifurcation or slightly anterior to it. Ovary triangular, elliptical, or globular, rather small, 0.20–0.28 by 0.20–0.32, dextrally or sinistrally submedian. Seminal receptacle club-shaped, 0.19–0.32 by 0.08–0.13. Laurer's canal short, sometimes dilated proximally to store sperm in it. Ootype large; Mehlis' gland well developed. Uterus coiled between anterior testis and ventral sucker, often entering testicular or rarely post-testicular space, between intestines, slightly overlapping intestines; metraterm well developed, much shorter than cirrus pouch. Eggs numerous, broad-ovate, thin-shelled, light brown, 56–68 by 40–48 μm; eggshells smooth. Vitelline follicles distributed from pharyngeal level to posterior extremity of body, close but separate anteriorly, confluent post-testicularly. Excretory vesicle ending at middle of anterior testis; excretory pore postero-dorsal or -terminal.

Remarks. The present specimens closely resemble *Crepidostomum metoecus* as described by Hopkins (1934), Ślusarski (1958), and Caira (1989). Furthermore, they were consistent in morphology with the following whole-mounted adult specimens of *C. metoecus* borrowed from the Institute of Parasitology, Czech Republic: 1 (No. Coll. D-42/1, 1247-36), ex pyloric cecum of *Salmo trutta fario*, Petrovický Brook, former Czechoslovakia, 30 March 1961; 6 (No. Coll. D-42/1, 1714a, b), ex intestine of *S. trutta fario*, Černovický Brook, former Czechoslovakia, 13 April 1978; and 1 (Coll. No. D-42/1), ex intestine of *S. trutta fario*, Velke Březno, Homolský Brook, Czech Republic, 12 April 2000. Consequently.

I identified them as *C. metoecus*.

Crepidostomum metoecus differs from *C. chaenogobii* (see above) mainly in that the oral sucker is smaller, instead of usually larger, than the ventral sucker; the ventrolateral papillae of the oral sucker are ear-shaped instead of conical; the dorsolateral papillae are horn-shaped and small instead of bluntly rounded and large; the dorsomedial papillae are broad elliptical and small instead of bluntly rounded and large; the vitelline follicles are separate, instead of confluent, between the two testes; and the excretory vesicle extends anteriorly to the middle of the anterior testis instead of to the seminal receptacle beyond the anterior testis. Further, *C. metoecus* is also different from *C. farionis* (see above) mainly in that the dorsomedial papillae of the oral sucker are broad elliptical instead of narrow elliptical; the ratio of the oral sucker width to the pharynx width is lower, 1 : 0.3–0.4 instead of 1 : 0.5–0.8; the seminal vesicle is short and sinuous in the posterior third of the cirrus pouch instead of long and convoluted in the posterior two-thirds; the ejaculatory duct is long in the anterior two-thirds of the cirrus pouch instead of short in the anterior third; the genital pore opens at the intestinal bifurcation or slightly anterior to it instead of ventral to the pharynx or slightly posterior to it; eggshells are smooth instead of sometimes warty; and the excretory vesicle extends anteriorly to the middle of the anterior testis instead of slightly beyond the anterior testis.

Fujita (1916) found a digenean (*Crepidostomum* sp.), a nematode (*Cucullanus* sp.), and an acanthocephalan (*Acanthocephalus* sp.) in the alimentary canal of fry of *Oncorhynchus keta* collected in a brook about 300 m west of the campus of the Agricultural College, Tohoku Imperial University (currently the Faculty of Agriculture, Hokkaido University), Sapporo, in 1913–1915. These three parasites were described as new species: the acanthocephalan as *Acanthocephalus oncorhynchi* Fujita, 1921 from the "Hassabu River near Sapporo" (Fujita, 1921a), the digenean as *Crepidostomum salmonis* Fujita, 1921 from "brooks near Sapporo" (Fujita, 1921b), and the nematode as *Cystidicola oncorhynchi* Fujita, 1921 from "brooks in Sapporo" (Fujita, 1921c). Therefore, the name of the brook is uncertain.

Crepidostomum salmonis was described by Fujita (1921b) on the basis of four whole-mounted and sectioned adult specimens, but none of them are deposited in Fujita's Collection today (see also Shimazu, 1990). According to his description and figures of *C. salmonis* (this paper, Fig. 18), (1) the oral sucker has six muscular papillae, though they are diagrammatically drawn and lack morphological details; (2) an eyespot is present on either side of the pharynx; (3) the ventral sucker is larger than the oral sucker, with the width ratio of 1 : 1.4 (my calculation); (4) the pharynx is small, with the ratio of the oral sucker width to the pharynx width of 1 : 0.3 (my calculation); (5) the testes are slightly larger than the ventral sucker and ovary [but smaller in fig. 1]; (6) the cirrus pouch extends posteriorly to the posterior border of the ventral sucker; (7) the seminal vesicle is long and convoluted in the posterior half of the cirrus pouch; (8) the ejaculatory duct is long in the anterior half of the cirrus pouch; (9) the genital pore opens at the intestinal bifurcation (fig. 1); (10) the uterus extends posteriorly to the posterior border of the anterior testis; (11) eggs are elliptical and 0.08 by 0.07 mm; and (12) the excretory vesicle reaches to the middle of the anterior testis. Margolis (1982) said that *C. salmonis* might well be a synonym of *C. metoecus*. Shimazu (1990) preferred to retain *C. salmonis* as a *species inquirenda* until reexamination of Fujita's original specimens. Since they were lost, it is now impossible to reexamine them. *Crepidostomum salmonis* is very similar to the present specimens of *C. metoecus* especially in the size of the pharynx, size of the seminal vesicle, size of the ejaculatory duct, position of the genital pore, and anterior extent of the excretory vesicle. The egg size (0.08 by 0.07 mm) given is probably erroneous. Although I found no specimen of *Crepidostomum* in 18 smolts of *O. keta* and 5 individuals of *O. masou masou* collected in the Kotonihassamu River on

7 April 2011 (my unpublished data), the present specimens of *C. metoecus* were obtained from a variety of freshwater fishes in a wide range in Hokkaido and include those (NSMT-Pl 3070) found in smolts of *O. keta* from the Shin River in Hamanaka Town. Consequently, I now consider *C. salmonis* a junior synonym of *C. metoecus*.

Shimazu (1990, fig. 9) identified an adult specimen (NSMT-Pl 3092) found in *Barbatula toni* (syn. *Noemacheilus toni*) from the Shokanbetsu River as *C. farionis*. Further, he regarded it as *Crepidostomum nemachilus* Krotov, 1959, which was originally described from *Nemachilus barbatulus toni* on Sakhalin Island, Russian Far East (Krotov, 1959). However, my present reexamination of the specimen shows that the pharynx was small, 0.14 [not 0.16] mm in diameter, with the ratio of the oral sucker width to the pharynx width of 1 : 0.4; the seminal vesicle was short [not long] and S-shaped in the posterior third [not two-thirds] of the cirrus pouch; and the ejaculatory duct was long [not short] in the anterior two-thirds [not third] of the cirrus pouch (Fig. 16); and eggs were broad-elliptical, 52–57 by 46–48 μm (Fig. 17a). The specimen is consistent with the present specimens of *C. metoecus* including new ones found in *B. toni* (see *Material examined*) in every essential feature, except for that the eggs were broad-elliptical, 52–57 by 46–48 μm (Fig. 17a) instead of elliptical to ovate, 59–70 by 40–48 μm (Fig. 17b). Evidently, Shimazu (1990) misidentified the specimen as *C. farionis* owing to his misinterpretation of the seminal vesicle and ejaculatory duct, or the position of the pars prostatica, in it. It has smaller abnormal eggs unlike the other specimens found in *B. toni* as mentioned above.

Seki (1975a, b) reported *C. metoecus* and *C. farionis* from salmonids caught in Hokkaido, as mentioned in *Remarks* in *C. farionis*. Kurata (1992) also found *C. metoecus* in *O. masou masou*, *O. mykiss*, and *S. leucomaenis leucomaenis* from the Nishibetsu River at Nijibetsu; *S. leucomaenis leucomaenis* from the Kushiro River (locality not specified); and *S. malma malma* from the Sorachi River (locality not specified) (see also *Material examined*).

Life cycle. Not known in Japan.

Discussion on *Crepidostomum*

The present study shows that, in Japan, the following three species of *Crepidostomum* are distributed in Hokkaido only: *C. chaenogobii*, *C. farionis*, and *C. metoecus*. *Crepidostomum chaenogobii* occurs in Hokkaido and Sakhalin Island, Russian Far East. *Crepidostomum farionis* and *C. metoecus* occur widely in the Holarctic region including Hokkaido. These three species are easily distinguished from one another in morphology (see above and below). Atopkin and Shedko (2010, 2014) demonstrated that the group (*C. farionis*) and the group (*C. metoecus* + *C. nemachilus*) in the Russian Far East also differed from each other in partial 28S ribosomal DNA sequences. However, they neither sequenced any specimens of *C. chaenogobii* from Sakhalin Island nor used any molecular data on *C. farionis* and *C. metoecus* from Europe or North America.

The life cycle has not yet been studied for any of the three species in Japan. In *C. farionis* and *C. metoecus*, first intermediate hosts are small bivalves of *Sphaerium* and *Pisidium* (Sphaeriidae), in which ophthalmoxiphidiocercariae are produced in daughter rediae; second intermediate hosts are aquatic arthropods (amphipods and ephemerids), in which metacercariae encyst; and final hosts are freshwater fishes, in the intestine of which adults live (*e.g.*, Brown, 1927; Crawford, 1943; Stenko, 1982; Moravec, 1982; Margolis and Moravec, 1982; Caira, 1989; Sokolov and Gordeev, 2014). Transmission from small fish to large fish-eating fish also occurs (Moravec, 1982). Awachie (1968) recorded cercariae of *C. metoecus* from the pulmonate snail *Lymnaea peregra*, but this species identification of the cercaria is doubtful (Moravec, 1982). On Sakhalin Island, *C. chaenogobii* uses a bivalve, possibly *Henslowiana* sp. (Euglesidae), as a first intermediate host; *Gammarus koreanus* (Amphipoda) as a second intermediate host; and *Pungitius pungitius tymensis* as a final host (Shedko, 2003).

Perhaps, neither the cercaria nor the metacercaria nor the adult has yet been described.

Crepidostomum metoecus was first described by Braun (1900a) as a new species, *Distomum metoecus*, on the basis of adult specimens found in bats of two species (type hosts) (see Hopkins, 1934; Caira, 1989). Soon after that Braun (1900b) created a new genus, *Crepidostomum*, with *D. metoecus*, or now *C. metoecus* (Braun, 1900), as the type species. Subsequent records of *C. metoecus* have been appeared from fishes only but not from bats. Most probably, fishes are the "natural hosts" of *C. metoecus* and bats are only "occasional" or "accidental" hosts (Hopkins, 1934). The bats may merely have eaten second intermediate hosts that harbored oviferous progenetic metacercariae (Hopkins, 1934). However, no progenetic metacercariae of *C. metoecus* have been reported. Adults of the present three species of *Crepidostomum* are found usually in the intestine and pyloric ceca of fishes but sometimes in the rectum and gall bladder (Faust, 1918; Brown, 1927; Hopkins, 1934; this paper). Since worms grow into fully gravid adults in the gall bladder, the gall bladder may also be a normal site of infection. Gibson and Valtonen (1988) referred to previous records of worms from the gall bladder. According to them, most of the ovigerous adults of their new species *Credidostomum wikgreni* occurred in the gall bladder of *Coregonus acronius* (Salmonidae) from Lake Yli-Kitka in northeastern Finland.

Key to the three species of *Crepidostomum* in Japan

1.1. Oral sucker usually larger than ventral sucker; ventrolateral papillae of oral sucker conical, small; dorsolateral and ventromedial papillae bluntly rounded, large ..... *C. chaenogobii*

1.2. Oral sucker smaller than ventral sucker; ventrolateral papillae ear-shaped, fairly large; dorsolateral papillae horn-shaped fairly large or small 2

2.1. Dorsomedial papillae narrow elliptical; pharynx large, with ratio of oral sucker width to pharynx width of 1 : 0.5–0.8; seminal vesicle long, convoluted, in posterior two-thirds to half of cirrus pouch; ejaculatory duct short, in anterior third to half of cirrus pouch; genital pore ventral to pharynx or slightly posterior to it; excretory vesicle extending slightly beyond anterior testis ..... *C. farionis*

2.2. Dorsomedial papillae broad elliptical, large; pharynx small, with ratio of 1 : 0.3–0.4; seminal vesicle short, sinuous, in posterior third to half of cirrus pouch; ejaculatory duct long, in anterior two-thirds to half of cirrus pouch; genital pore at intestinal bifurcation or slightly anterior to it; excretory vesicle extending to middle of anterior testis ..... *C. metoecus*

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