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Digeneans Parasitic in Freshwater Fishes (Osteichthyes) of Japan. IX. Opecoelidae, Opecoelinae

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Abstract This paper reviews three species of the subfamily Opecoelinae Ozaki, 1925 in the family Opecoelidae Ozaki, 1925 (Trematoda, Digenea, Allocreadioidea) parasitic in freshwater fishes of Japan: *Coitocaecum plagiorchis* Ozaki, 1926, *Dimerosaccus oncorhynchi* (Eguchi, 1931), and *Opecoelus ukigori* Shimazu, 1988. Each species is described and figured. The life cycle of *C. plagiorchis* is briefly mentioned. A neotype is designated for *Allocreadium oncorhynchi* Eguchi, 1931, or now *D. oncorhynchi*. The type host is *Oncorhynchus masou ishikawae* Jordan and McGregor in Jordan and Hubbs, 1925 (Salmonidae), which was collected in the Nagara River at Arisaka (35°44′N, 136°56′E) (type locality), Hachiman-cho, Gujo City, Gifu Prefecture, Japan. Keys to two subfamiles (Opecoelinae and Plagioporinae Manter, 1947) and three genera (*Coitocaecum* Nicoll, 1915, *Dimerosaccus* Shimazu, 1980, and *Opecoelus* Ozaki, 1925) in the subfamily Opecoelinae in Japan are presented.

Key words: Digeneans, Opecoelidae, Opecoelinae, neotype, freshwater fishes, Japan, review.

Introduction

This is the ninth paper of a series that reviews adult digeneans (Trematoda) parasitic in freshwater fishes (Osteichthyes) of Japan (Shimazu, 2013). This contribution deals with three species in the subfamily Opecoelinae Ozaki, 1925 in the family Opecoelidae Ozaki, 1925 *sensu* Cribb (2005b) in the superfamily Allocreadioidea Looss, 1902 *sensu* Cribb (2005a): *Coitocaecum plagiorchis* Ozaki, 1926, *Dimerosaccus oncorhynchi* (Eguchi, 1931), and *Opecoelus ukigori* Shimazu, 1988. The life cycle of *C. plagiorchis* is briefly mentioned. A neotype is designated for *Allocreadium oncorhynchi* Eguchi, 1931, or now *D. oncorhynchi.* Keys to two subfamilies (Opecoelinae and Plagioporinae Manter, 1947) and three genera (*Coitocaecum* Nicoll, 1915, *Dimerosaccus* Shimazu, 1980, and *Opecoelus* Ozaki, 1925) in the subfamily Opecoelinae in Japan are presented. The Introduction, Materials, and Methods for the review were given in the first paper (Shimazu, 2013).

Abbreviations used in the figures. bp, birth pore; c, cercaria; ca, common anus; cbp, cercarial body proper; cc, cyclocoel; cp, cirrus pouch; ct, cercarial tail; cvd, common vitelline duct; cy, cyst; ds, daughter sporocyst; e, esophagus; ed, ejaculatory duct; egg, egg in uterus and metraterm; ep, excretory pore; ev, excretory vesicle; ga, genital atrium; gp, genital pore; gpr, genital primordium; i, intestine; Lc, Laurer's canal; m, metraterm; ma, marginal appendages; me, metacercaria; Mg, Mehlis' gland; o, ovary; od, oviduct; os, oral sucker; ot, ootype; ovd, ovovitelline duct; p, pharynx; pc, prostatic cells; pgc, penetration gland cells; pp, pars prostatica; pr, prepharynx; s, stylet; sd, sperm duct; sp, sphincter; sv, seminal vesicle; t, testis; tnc, transverse nerve commissure; u, uterus; usr, uterine seminal receptacle; vd, vitelline duct; vf, vitelline follicles; vs, ventral sucker.

Key to subfamilies in the family Opecoelidae in this paper

1.1. Canalicular seminal receptacle absent; uterine seminal receptacle present; cirrus pouch either reduced, enclosing anteriormost part of seminal vesicle, prostatic complex, and ejaculatory duct, or divided into anterior and posterior portions, enclosing whole seminal vesicle, prostatic complex, and ejaculatory duct ..... Opecoelinae Ozaki, 1925
1.2. Canalicular seminal receptacle present; uterine seminal receptacle absent; cirrus pouch entire, enclosing whole seminal vesicle, prostatic complex, and ejaculatory duct ..... Plagioporinae Manter, 1947

Key to genera in the subfamily Opecoelinae in this paper

1.1. Cyclocoel present; cirrus pouch reduced ..... *Coitocaecum* Nicoll, 1915
1.2. Cyclocoel absent; cirrus pouch either reduced or divided into anterior and posterior portions 2
2.1. Cirrus pouch reduced; intestines forming common anus; marginal appendages of ventral sucker present ..... *Opecoelus* Ozaki, 1925
2.2. Cirrus pouch divided; intestines ending blindly; marginal appendages of ventral sucker absent ..... *Dimerosaccus* Shimazu, 1980

Superfamily Allocreadioidea Looss, 1902

Family Opecoelidae Ozaki, 1925

Subfamily Opecoelinae Ozaki, 1925

Genus ***Coitocaecum*** Nicoll, 1915

Coitocaecum plagiorchis Ozaki, 1926

(Figs. 1–7)

(?) [*Cercaria* No. 16]: Nakagawa, 1915: 117, fig. 16.

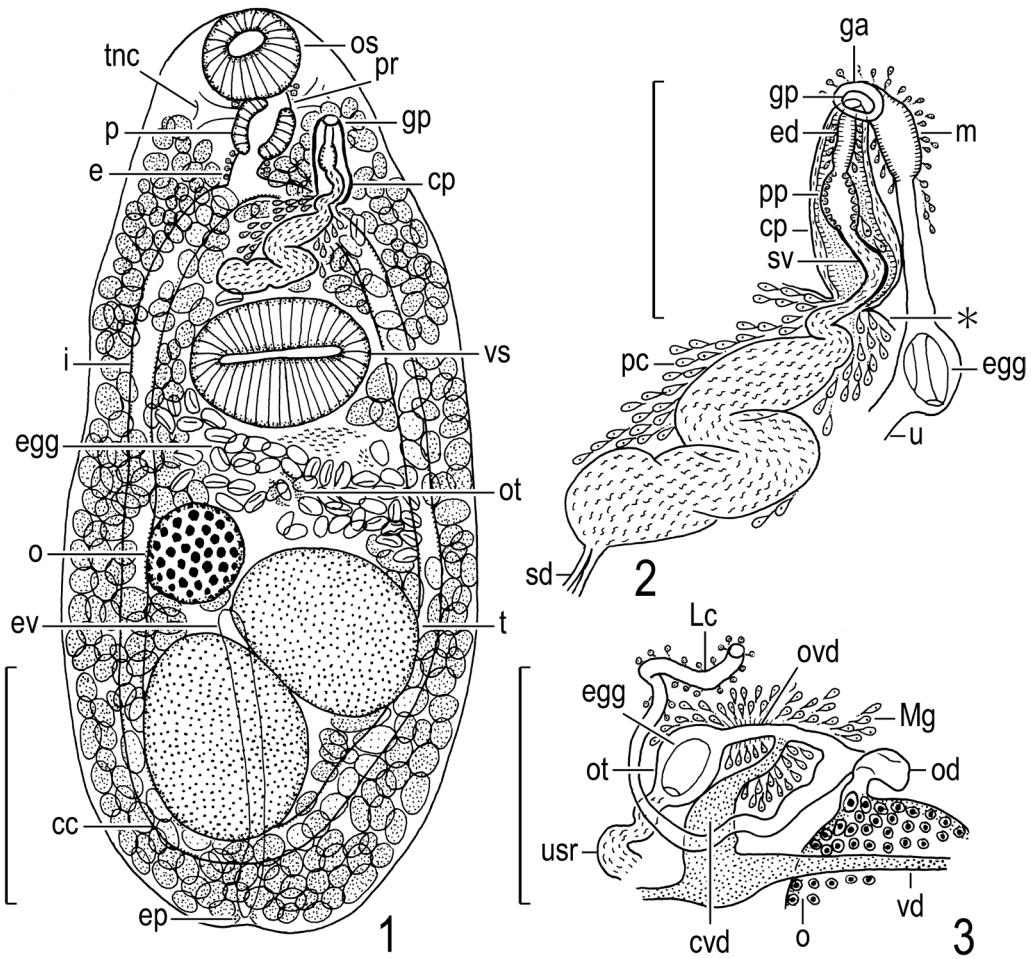
(?) *Cercaria distyloides* Faust, 1924: 295; Ito, 1964: 494, fig. 128; Yoshida and Urabe, 2005: 239–240, figs. 2b–d.

Coitocoecum plagiorchis Ozaki, 1926: 125–128, no figure; Yoshida and Urabe, 2005: 239, fig. 1a–b.

Coitocaecum plagiorchis: Ozaki, 1929: 77–78, 80–82, figs. 1–3; Yamaguti, 1934: 359, fig. 56; Yamaguti, 1939: 218–219; Yamaguti, 1942: 351–352, pl. 24, fig. 1; Shimazu, 1988: 6–7, figs. 1–4; Shimazu, 2000: 18–19, figs. 1–4; Shimazu, 2008: 50–51, fig. 7; Shimazu, Urabe, and Grygier, 2011: 39–41, figs. 47–50.

Ozakia plagiorchis: Wiśniewski, 1934: 36–38, fig. 3c.

Hosts in Japan. *Odontobutis obscura* (Temminck and Schlegel, 1845) (Odontobutidae) (type host) (Ozaki, 1926, 1929; Yamaguti, 1934, 1942; Shimazu, 1988, 2000; Yoshida and Urabe, 2005; Lin *et al.*, 2006; Shimazu *et al.*, 2011; this paper), "Gori" (*Od. obscura*) (Shimazu, 1992, 2000; this paper), *Anguilla japonica* Temminck and Schlegel, 1846 (Anguillidae) (Shimazu *et al.*, 2011), *Coreoperca kawamebari* (Temminck and Schlegel, 1843) (Percichthyidae) (Yamaguti, 1934; Yoshida and Urabe, 2005), *Cottus reinii* Hilgeldorf, 1879 (Cottidae) (Shimazu, 1988, 2000; Shimazu *et al.*, 2011), *Gymnogobius isaza* (Tanaka, 1916) (Gobiidae) (Shimazu, 1988, 2000; Shimazu *et al.*, 2011), *Gymnogobius urotaenia* (Hilgendorf, 1879) (Yamaguti, 1939; Shimazu, 1988, 2000; Shimazu *et al.*, 2011), *Misgurnus anguillicaudatus* (Cantor, 1842) (Cobitidae) (Yamaguti, 1942), *Rhinogobius flumineus* (Mizuno, 1960) (Gobiidae) (Yoshida and Urabe, 2005), "*Rhinogobius* sp." (Yoshida and Urabe, 2005), *Rhinogobius* sp. BW (Shimazu *et al.*, 2011), *Tachysurus aurantiacus* (Temminck and Schelegel, 1846) (Bagridae) (this paper), *Tachysurus nudiceps* (Sauvage, 1883) (Yamaguti, 1939; Shimazu, 1988, 2000; Shimazu *et al.*, 2011; this paper), *Tridentiger brevispinis* Katsuyama, Arai, and Nakamura, 1972 (Gobiidae) (Shimazu, 2008; Shimazu *et al.*, 2011; this paper), "*Gobius similis* Gill" [a species of *Rhinogobius*] (Gobiidae) (Yamaguti, 1942), and "Small GORO" (most likely referring to *G. isaza*)

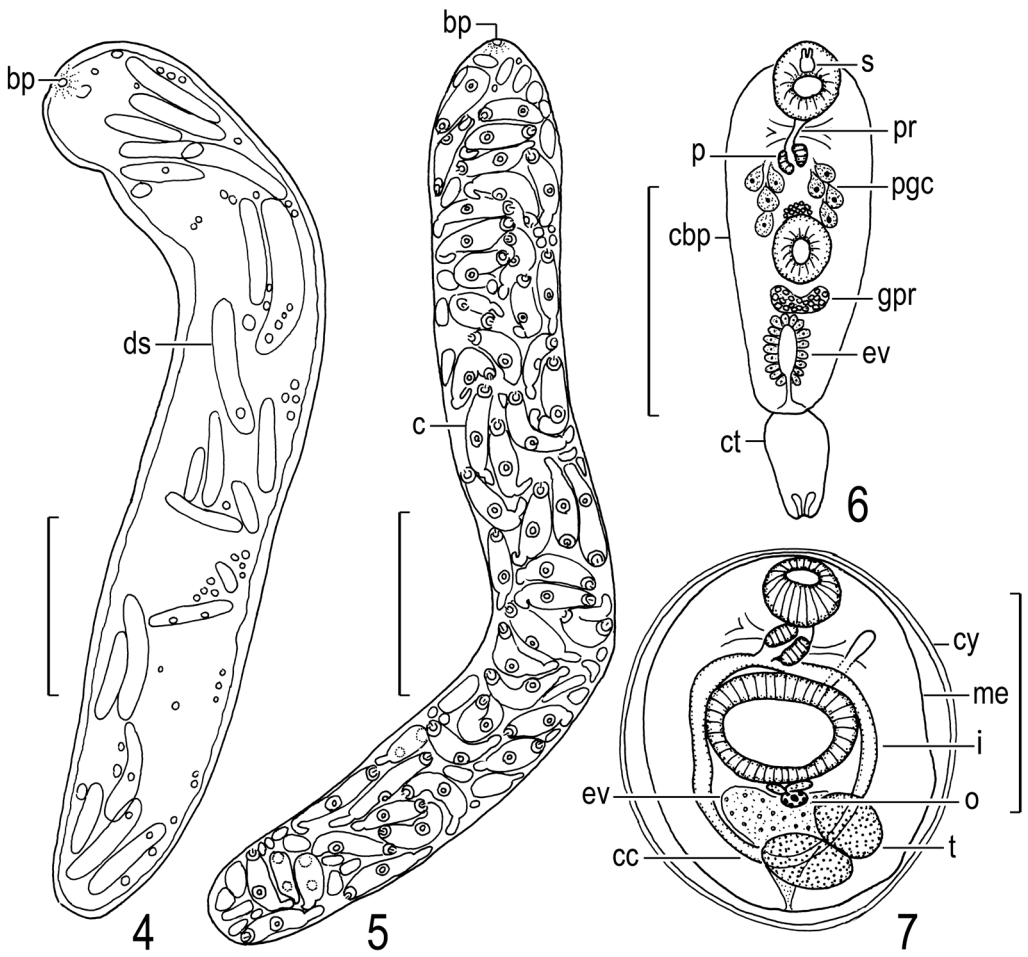


Figs. 1–3. *Coitocaecum plagiorchis*, adult specimen (NSMT-Pl 5527) found in intestine of *Tridentiger brevispinis*. 1, entire body, ventral view; 2, terminal genitalia, remnant (*) of ruptured posterior portion of cirrus pouch, ventral view; 3, ovarian complex, dorsal view. Scale bras: 0.5 mm in Fig. 1; 0.2 mm in Figs. 2–3.

(Shimazu, 1988, 2000; Shimazu *et al.*, 2011).

Sites of infection. Intestine and pyloric ceca, and also stomach and rectum (accidental (?)).

Geographical distribution. (1) Shiga Prefecture: Lake Biwa basin (Lake Biwa; Hachiyado-hama, Hachiyado, Otsu City; irrigation cannal at Hamabun, Imazu-cho, Takashima City; Imazu-cho, Takashima City; Inukami River, Kaideima-cho, Hikone City; Kusano River, Nagahama City; Mano, Otsu City; Mano River, Imakatata, Osu City; Momose, Chinai, Makino-cho, Takashima City; Onoe, Kohoku-cho, Nagahama City; Ukawa River, Takashima City; Uso River, Hinatsu-cho, Hikone City; and Wani, Otsu city) (Yamaguti, 1939; Shimazu, 1988, 2000; Shimazu *et al.*, 2011; this paper). (2) Kyoto Prefecture: Lake Ogura (Yamaguti, 1934; Shimazu, 1988, 2000), Shirakawa (Yamaguti, 1942), and Katsura River (Shimazu, 1988, 2000). (3) Hyogo Prefecture: Asago River (Yamaguti, 1934; Shimazu, 1988, 2000) and Nishinomiya City (Yamaguti, 1942). (4) Hiroshima Prefecture: a brook in the vicinity of Saijo-cho (type locality), Higashihiroshima City (Ozaki, 1926, 1929; this paper); Matsuita River at Umaki, Saijo-cho (this paper); and Karei River at Maruyama, Kurose-cho, Higashihiroshima City (this paper). (5) Tokushima Prefecture: Kaifu River at Yoshino, Kaiyo



Figs. 4–7. *Coitocaecum plagiorchis* (continued), life cycle. 4, mother sporocyst found in *Semisulcospira libertina*, site of infection not given; 5, daughter sporocyst (NSMT-Pl 5439) found in *S. reiniana*, site of infection perhaps rectum; 6, cercaria (NSMT-Pl 5442) found in *S. libertina*, ventral view; 7, encysted metacercaria (NSMT-Pl 5443) found in *Neocaridina denticulata*, 24–25 days after experimental infection, site of infection not given, ventral view. Scale bars: 0.5 mm in Figs. 4–5; 0.2 mm in Fig. 7; 0.1 mm in Fig. 6.

Town (Shimazu, 2008). (6) Fukuoka Prefecture: Futatsu River at Takahatake, Mitsuhashi-machi, Yanagawa City (Yoshida and Urabe, 2005; Lin *et al.*, 2006; this paper). (7) Oita Prefecture: Chikugo River at Kobuchi Bridge, Miyoshikobuchi-machi, Hita City (Yoshida and Urabe, 2005); and Ooyama River at Seiwa Bridge, Ooyama-machi, Hita City (this paper).

In China (*e.g.*, Institute of Hydrobiology, Hubei Province (chief ed.), 1973; Wang *et al.*, 1985).

Material examined. (1) 21 specimens (Ozaki's Collection, MPM Coll. No. 30028, labeled "[Gori]," other data not given, probably paratypes) of *Coitocaecum plagiorchis*, immature, adult, ex "Gori" (*Odontobutis obscura*) (Ozaki, 1926, 1929; Shimazu, 1992, 1995b, 2000). (2) 1 (Ozaki's Collection, MPM Coll. No. 30212-b, labeled "SAIJO," other data not given) of *C. plagiorchis*, adult, ex *Od. obscura*, Saijo-cho (Shimazu, 2014). (3) Yamaguti's specimens of *C. plagiorchis*, ex intestine of *Od. obscura* (syn. *Mogurnda obscura*, *Od. obscura obscura*): 4 (MPM Coll. No. 22585), immature, adult, Lake

Ogura, 15 and 30 May 1932, 4 June 1932 (Yamaguti, 1934; Shimazu, 1988, 2000); 15 (MPM Coll. No. 22291), immature, adult, Katsura River (exact collecting locality not indicated), 2 and 5 June 1936, 10 July 1936 (Shimazu, 1988, 2000); and 3 (MPM Coll. No. 22292, experimental infection) (Yamaguti, 1942; Shimazu, 1988, 2000). (4) 7 (Yamaguti's Collection, MPM Coll. No. 22587; NSMT-Pl 3105, 3106; LBM 1-60 to -62) of *C. plagiorchis*, immature, adult, ex intestine and stomach of *Gymnogobius urotaenia* (syn. *Chaenogobius annularis urotaenia*, *Ch. annularis*), Imazu-cho, Lake Biwa (exact collecting locality not indicated), Onoe, 3 December 1938, 4 February 1980, 6 June 1980, 19 May 1998 (Yamaguti, 1939; Shimazu, 1988, 2000; Shimazu *et al.*, 2011). (5) 31 (NSMT-Pl 3104; LBM 1-26 to -29, 3-32, 6-15, -16, -18 to -20, -29) of *C. plagiorchis*, immature, ex intestine and rectum of *G. isaza* (syn. *Chaenogobius isaza* Tanaka, 1916), Hachiyadohama, Imazu-cho, Momose, Onoe, 6 June 1980, 14 and 19 May 1998, 5 May 2000, 1 May 2001 (Shimazu, 1988, 2000; Shimazu *et al.*, 2011). (6) 3 (Ozaki's Collection, MPM Coll. No. 30013, labeled "Small GORO [Lake Biwa]," other data not given) of *C. plagiorchis*, immature, adult, ex "Small GORO" (most likely referring to *G. isaza*), Lake Biwa (exact collecting locality not indicated) (Shimazu, 1988, 2000; Shimazu *et al.*, 2011). (7) 16 (Yamaguti's Collection, MPM Coll. No. 22586; NSMT-Pl 3102, 4614, 5730) of *C. plagiorchis*, immature, adult, ex intestine of *Tachysurus nudiceps* (syn. *Pelteobagrus nudiceps*), Lake Biwa (exact collecting locality not indicated), Onoe, 7 December 1938, 11 November 1980, 4 May 1979, 4 May 1992, (Yamaguti, 1939; Shimazu, 1988, 2000; Shimazu *et al.*, 2011). (8) 76 (NSMT-Pl 3103, 4615; LBM 1-69, 1-71, 8-40 to -49) of *C. plagiorchis*, immature, adult, ex intestine and pyloric ceca and either stomach or intestine of *Cottus reinii* (syn. *Cottus ohmiensis* Watanabe, 1960), Hachiyadohama, Imazu-cho, Momose, Onoe, Ukawa River, Wani, 14 February 1980, 4 May 1992, 14 and 19 May 1998, 25 April 2007, 24 and 27 November 2007 (Shimazu, 1988, 2000; Shimazu *et al.*, 2011). (9) 1 (LBM 1-15) of *C. plagiorchis*, adult, ex "gut" (intestine (?)) of *Od. obscura*, Kusano River, 28 October 1997 (Shimazu *et al.*, 2011). (10) 1 (MPM Coll. No. 21194), immature, ex intestine of *Od. obscura*, Inukami River, 10 May 2009. (11) 1 (LBM 1-6) of *C. plagiorchis*, immature, ex "gut" (intestine (?)) of *Rhinogobius* sp. BW, Imazu-cho, 19 May 1998 (Shimazu *et al.*, 2011). (12) 5 (LBM 1-53, 3-37, 3-38, 1340000027) of *C. plagiorchis*, immature, adult, ex intestine and "gut" (intestine (?)) of *Tridentiger brevispinis*, Hamabun, Imazu-cho, Mano, Mano River, 24 October 1997, 10 June 1999, 5 May 2000, 26 August 2003 (Shimazu *et al.*, 2011). (13) 5 (MPM Coll. No. 21195), adult, ex intestine of *Tr. brevispinis*, Imazu-cho, 20 November 2012. (14) 19 (Urabe's personal collection) of *C. plagiorchis*, immature, ex intestine of *Anguilla japonica*, Uso River, 16 May 2006 (Shimazu *et al.*, 2011). (15) 4 (Yamaguti's Collection, MPM Coll. No. 22553) of *C. plagiorchis*, immature, adult, ex intestine of *Coreoperca kawamebari* (syn. *Bryttosus kawamebari*), Asago River (exact collecting locality not indicated), 7 January 1932, 7 April 1932 (Yamaguti, 1934; Shimazu, 1988, 2000). (16) 11 (NSMT-Pl 5795, 5796), adult, ex intestine of *Od. obscura*, Matsuita and Karei rivers, 18 June 2009. (17) 17 (NSMT-Pl 5527) of *C. plagiorchis*, adult, ex intestine of *Tr. brevispinis*, Kaifu River, 11 September 1998 (Shimazu, 2008). (18) Specimens of *Coitocoecum plagiorchis* [*sic*], Futatsu River: 15 (NSMT-Pl 5437; Urabe's personal collection), immature, adult, ex intestine of *Co. kawamebari*, 24 September 2002, 20 August 2002 (Yoshida and Urabe, 2005); and 18 (Urabe's personal collection), adult, ex stomach and intestine of *Od. obscura*, 22 May 2003, 5 and 21 June 2003. (19) 1 (NSMT-Pl 5441) of *C. plagiorchis*, adult, ex intestine of "*Rhinogobius* sp.," Ooyama River, 19 August 2003 (Yoshida and Urabe, 2005). (20) 4 (Urabe's personal collection) of *C. plagiorchis*, adult, ex intestine of *T. aurantiacus* (syn. *Pseudobagrus aurantiacus*), Chikugo River, 25 August 2003.

Description. Based on adult specimens (NSMT-Pl 5527), after Shimazu (2008), slightly altered from the present study (Figs. 1–3). Body ovate, fairly broad, small, 1.68–2.56 by 0.72–1.14; forebody 0.69–0.99, occupying 35–43% of body length. Tegument smooth. Eyespot pigment absent. Oral sucker globular, 0.17–0.25 by 0.19–0.28, opening ventroterminally. Prepharynx very short; small gland cells seen between oral sucker and prepharynx. Pharynx elliptical, 0.11–0.15 by 0.11–0.19. Esophagus short, surrounded by small gland cells, bifurcating halfway between two suckers. Intestines (or ceca) fusing together to form cyclocoel at near posterior extremity of body; cyclocoel usually post-testicular but rarely intertesticular. Ventral sucker transversely elliptical, 0.26–0.37 by 0.32–0.44, slightly posterior to border between anterior and middle thirds of body; sucker width ratio 1 : 1.6–2.0. Testes two, usually diagonal but nearly tandem, contiguous, in middle third of hindbody; anterior (left) testis 0.23–0.44 by 0.32–0.49, posterior (right) one 0.27–0.45 by 0.35–0.50. Sperm ducts two; common sperm duct absent. Cirrus pouch (or cirrus-sac) reduced, divided into two portions: anterior portion thick-walled, muscular, small, 0.20–0.40 by 0.06–0.09, sinistrally submedian, anterior to left intestine, including short thick-walled anteriormost part of seminal vesicle, pars prostatica, a small number of small gland cells, and short ejaculatory duct surrounded by small gland cells; posterior portion thin-walled, membranous, small, apparently ruptured posteriorly, leaving small remnant (Fig. 2, *); greater posterior part of seminal vesicle external to cirrus pouch, voluminous, sinuous, surrounded by prostatic cells, extending to posterior border of ventral sucker. Genital atrium small. Genital pore sinistrally submedian, at about level of pharynx. Ovary usually globular but rarely triangular, 0.19–0.29 by 0.20–0.37, submedian, anterodextral to anterior testis. Ovarian complex preovarian. Laurer's canal long. Canalicular seminal receptacle absent. Ootype vesicular, large; Mehlis' gland well developed, opening into ovovitelline duct. Uterus coiled usually between ovary, anterior testis, intestines, and ventral sucker, rarely extending to posterior testis; uterine seminal receptacle well developed; metraterm about half as long as anterior portion of cirrus pouch, surrounded by small gland cells. Eggs rather numerous, ovate, operculate, light brown, 54–64 by 35–41 μm, unembryonated. Vitellaria follicular; follicles distributed between usually pharynx or sometimes oral sucker and posterior extremity of body, separate anteriorly, almost confluent between intestinal bifurcation and ventral sucker, confluent in post-testicular region. Excretory vesicle I-shaped, extending anteriorly to anterior testis; excretory pore posterodorsal.

Remarks. The original spelling of the generic name given by Nicoll (1915) for this genus is *Coitocoecum*. Ozaki (1926) also used it when he described his two new species *Coitocoecum plagiorchis* and *Coitocoecum orthorchis*. However, Ozaki (1929) changed it to *Coitocaecum* with no explanation when he described these two species and his three other new species in the genus. Shimazu (2008) was of the opinion that this subsequent spelling *Coitocaecum* should be adopted.

Ozaki (1926, 1929) described *C. plagiorchis* on the basis of adult specimens found in the stomach and intestine of *Odontobutis obscura* (syn. *Mogurnda obscura*) (Japanese name: Donko, but Goppo of Ozaki (1925)) from a brook (Ozaki, 1925, 1929) in the vicinity of Saijo, now Saijo-cho, Higashihiroshima City, Hiroshima Prefecture. Ozaki (1926, 1929) designated the holotype (No. P. 235) for *C. plagiorchis*, but the holotype was lost (Shimazu, 2013).

Ozaki's Collection includes a set of 13 old slides (MPM Coll. No. 30028), which are labeled merely "Gori" directly on some of the slide glasses. They contain specimens of *Genarchopsis goppo* Ozaki, 1925, *Asymphylodora macrostoma* Ozaki, 1925 (now *Asymphylodora innominata* (Faust, 1924)), *C. plagiorchis*, *Nippotaenia mogurndae* Yamaguti and Miyata, 1940 (Cestoda), and *Bothriocephalus* sp. (Cestoda) (Shimazu, 1992, 1995a, b, 2000, 2015, 2016; this paper). Ozaki (1925, 1926) described these three digeneans as new species from *Od. obscura* of

the brook, but he mentioned nothing about the two cestode species. In addition, Ozaki's Collection includes another set of 14 old slides labeled "*Phyllodistomum mog*. SAIJO," which contain specimens of *Phyllodistomum mogurndae* Yamaguti, 1934 (MPM Coll. No. 30212-a) and *C. plagiorchis* (MPM Coll. No. 30212-b) (Shimazu, 2014; this paper).

I also found some specimens of *G. goppo*, *A. innominata*, *C. plagiorchis*, *P. mogurndae*, and *Ni. mogurndae* (probably specific to *Od. obscura*) in *Od. obscura* from Higashihiroshima City: *G. goppo* from the Nukui River at Hachihonmatsu-cho and Matsuita River at Saijo-cho, and Karei, Irasuke, Takeyasu, and Kurose rivers at Kurose-cho (Shimazu, 1995a, 2015); *A. innominata* from the Matsuita and Irasuke rivers (Shimazu, 1992, 2016a); *C. plagiorchis* from the Matsuita and Karei rivers (this paper); *P. mogurndae* from the Nukui River (Shimazu, 2014); and *Ni. mogurndae* from the Nukui River (Shimazu, 1992, 1997; MPM Coll. No. 21210, 28 December 1991). The Nukui, Matsuita, Irasuke, and Takeyasu rivers belong to the Kurose River system in Higashihiroshima City. Although the holotype of *C. plagiorchis* was lost, the labels of Ozaki's existent specimens are incomplete, and the fish name Gori did not appear as the Japanese name of *Od. obscura* in any of his papers, I now conclude that the scientific name of the fish Gori is *Od. obscura* (see also Shimazu, 1992, 1995a, 2000, 2015, 2016). The 21 specimens (MPM Coll. No. 30028) in Ozaki's Collection are probably paratypes of *C. plagiorchis*. The name of the brook is still unknown.

As seen in *Geographical distribution*, *C. plagiorchis* has been recorded from Kinki Region (Shiga, Kyoto, and Hyogo Prefectures), Chugoku Region (Hiroshima Prefecture), Shikoku Region (Tokushima Prefecture), and Kyushu Region (Fukuoka and Oita Prefectures).

Life cycle. Yoshida and Urabe (2005) studied the life cycle of *Coitocoecum plagiorchis* [*sic*] in the Futatsu and Chikugo rivers (see *Geographical distribution*). Mother sporocysts (site of infection not given, unpublished, Urabe's personal collection, Fig. 4) and daughter sporocysts (perhaps in the rectum, NSMT-Pl 5438–5439, Urabe's personal collection, Fig. 5) were found in pleurocerid snails, *Semisulcospira libertina* (Gould, 1859) (Japanese name: Kawanina), *Semisulcospira reiniana* (Brot, 1874) (Japanese name: Chirimen-kawanina), and their hybrids (natural first intermediate hosts). Cotylomicrocercous cercariae (NSMT-Pl 5442, Fig. 6) were produced in the daughter sporocysts. Metacercariae (NSMT-Pl 5444) were found encysted in an atyid shrimp, *Neocaridina denticulata* de Haan, 1844 (Atyidae) (Japanese name: Minami-numa-ebi) (a natural second intermediate host). Metacercariae (NSMT-Pl 5443, Fig. 7) were also recovered from *Ne. denticulata*, to which cercariae had been experimentally exposed. The site of infection of the metacercaria was not indicated. Natural final hosts were *Co. kawamebari*, *Od. obscura*, *R. flumineus*, and "*Rhinogobius* sp."

Yoshida and Urabe (2005) identified their cercaria as *Cercaria distyloides* Faust, 1924. This cercaria was originally described as [*Cercaria* No. 16] on the basis of cercariae in rediae [*sic*, should be sporocysts] in the liver [*sic*] of a freshwater snail (Japanese name: "Kawanina B") [*Semisulcospira* sp. (?)] from Nanga-sho, Shinchiku-cho, Taiwan (Nakagawa, 1915; Faust, 1924). Their identification is somewhat questionable (Shimazu, 2008; Shimazu *et al.*, 2011). The stylet is 2-pointed in their cercaria (Fig. 6) instead of 1-pointed in *Ce. distyloides* (Nakagawa, 1915, fig. 16). The intestines are not yet developed in both cercariae (Fig. 6; Nakagawa, 1915, fig. 16). They become fully differentiated and then united to form a cyclocoel in the metacercarial stage within 15 days after infection (Yoshida and Urabe, 2005). Further, it is unknown whether *C. plagiorchis* actually occurs in Taiwan. It is desired that *Ce. distyloides* and the cercaria of *C. plagiorchis* be further comparatively studied, because *C. plagiorchis* was described after *Ce. distyloides*, which may thus be the senior synonym.

Komiya (1965), Shimazu (1988, 1999, 2000, 2003), Yoshida and Urabe (2005), and Shimazu

et al. (2011) gathered previous records of metacercariae of *C. plagiorchis* from Japan and China. Yamaguti (1942) fed metacercariae found in a palaemonid shrimp, *Palaemon paucidens* de Haan, 1844 (syn. *Leander paucidens*) (Japanese name: Suji-ebi), to *Od. obscura*, and subsequently recovered adults (MPM Coll. No. 22292) from the intestine of the fish 20 days later (see also Shimazu, 2000). Metacercariae encyst in the body muscles of the shrimps.

As mentioned above, immature and adult worms have been recorded from fishes of many species in seven families. It is not necessarily certain that these fishes acquire infection with *C. plagiorchis* by eating shrimps (second intermediate hosts). At least *Tachysurus aurantiacus* and *T. nudiceps* may acquire infection by eating infected fish as well as by eating shrimps. Yamaguti (1942) briefly described specimens found in *Misgurnus anguillicaudatus* from Nisinomiya [Nishinomiya] and "*Gobius similis* Gill" [a species of *Rhinogobius*] from Sirakawa [Shirakawa], Kyoto. None of them is deposited in Yamaguti's Collection today. Since *M. anguillicaudatus* is unlikely to eat shrimps, this record from *M. anguillicaudatus* is questionable.

Genus ***Dimerosaccus*** Shimazu, 1980

Dimerosaccus oncorhynchi (Eguchi, 1931)

(Figs. 8–11)

Allocreadium oncorhynchi Eguchi, 1931: 21–22, no figure; Eguchi, 1932: 24–28, figs. 1–6.

Plagioporus oncorhynchi: Peters, 1957: 140.

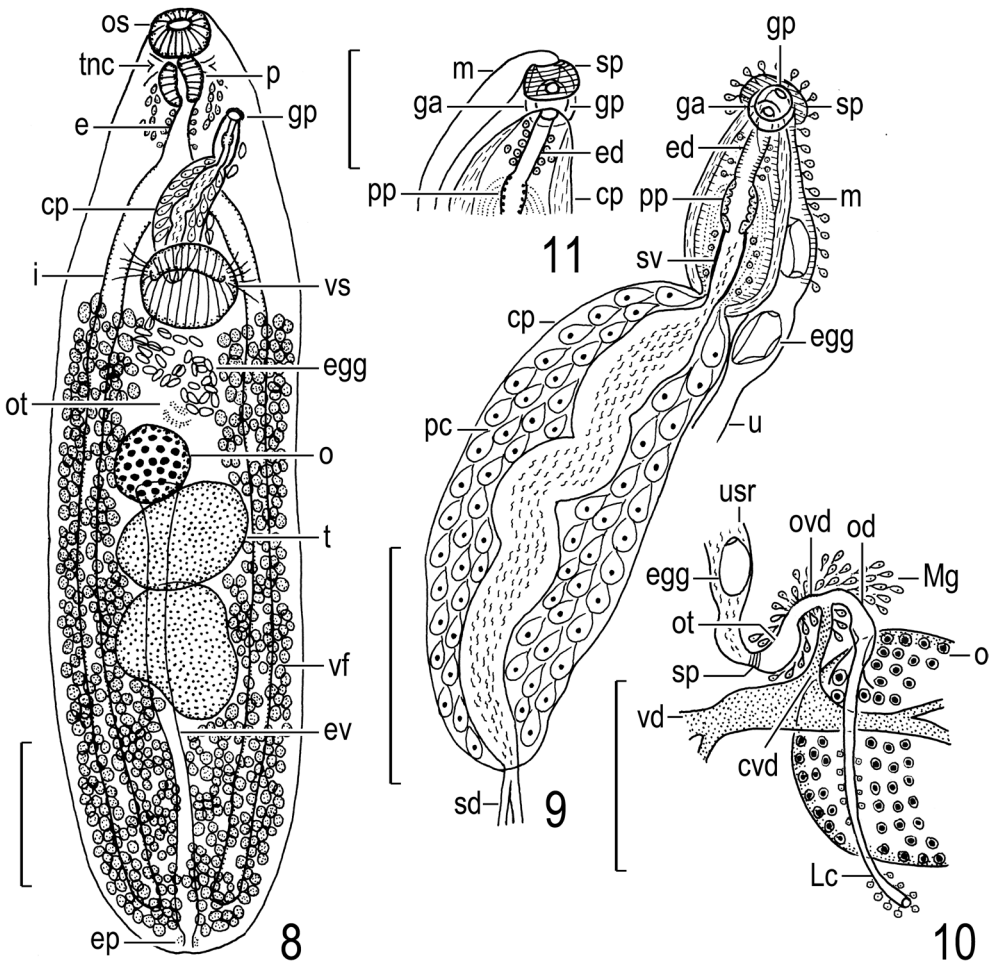
Dimerosaccus oncorhynchi: Shimazu, 1980: 164, 166, table 1, figs. 1–7; Shimazu, 1988: 10–11, figs. 5–7; Shimazu and Awakura, 1993: 1, 3, figs. 1–4; Shimazu, 2000: 25–26, figs. 11–13; Shimazu and Urabe, 2005: 4–5, fig. 4–7; Shimazu, 2007: 22; Shimazu, 2008: 52–54, fig. 8; Shedko, Sokolov, and Atopkin, 2015: 177–181, tables 3–4, figs. 1–3.

Plagioporus honshuensis Moravec and Nagasawa, 1998: 283–284, fig. 1A–D.

Hosts in Japan. *Oncorhynchus masou ishikawae* Jordan and McGregor in Jordan and Hubbs, 1925 (Salmonidae) (type host) (Eguchi, 1931, 1932; Shimazu, 1980, 1988, 2000, 2008; this paper), *Cottus nozawae* Snyder, 1911 (Cottidae) (Shimazu, 1988, 1994, 2000), *Cottus pollux* Günther, 1873 (Shimazu, 2000), *Liobagrus reinii* Hilgendorf, 1878 (Amblycipitidae) (Moravec and Nagasawa, 1998; Shimazu and Urabe, 2005), *Odontobutis obscura* (Odontobutidae) (this paper), *Oncorhynchus masou masou* (Brevoort, 1856) (Shimazu, 1980, 1988, 1994, 2000; Shimazu and Awakura, 1993; this paper), *Rhinogobius brunneus* (Temminck and Schlegel, 1845) (Gobiidae) (Shimazu, 2008; this paper), *Rhinogobius flumineus* (Nakamura *et al.*, 2000; Shimazu and Urabe, 2005; Shimazu, 2008), *Rhinogobius fluviatilis* Tanaka, 1925 (Shimazu, 2008; this paper), *Rhinogobius nagoyae* Jordan and Seale, 1906 (Shimazu, 2008), "*Rhinogobius* sp." (this paper), *Rhinogobius* spp. CO and OR (Shimazu, 2008; this paper), *Salvelinus leucomaenis leucomaenis* (Pallas, 1814) (Salmonidae) (Shimazu, 1988, 1994, 2000), *Salvelinus leucomaenis pluvius* (Hilgendorf, 1876) (Shimazu, 1980, 1988, 2000, 2007; this paper), and *Tridentiger brevispinis* (Gobiidae) (Shimazu, 2008).

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

Geographical distribution. (1) Hokkaido: Shokanbetsu River at Mashike Town (Shimazu, 1988, 1994, 2000). (2) Aomori Prefecture: Anmon River at Nishimeya Village (this paper). (3) Iwate Prefecture: Horei River at Sanriku-cho, Oofunato City (Shimazu, 1980, 1988, 2000; this paper). (4) Yamagata Prefecture: Shirabuzawa at Iritazawa, Yonezawa City (this paper). (5) Toyama Prefecture: Sho River at Ohta [Tochinami City (?)] (Moravec and Nagasawa, 1998). (6) Nagano Prefecture: Samu River at Fujisawa, Iiyama City (Shimazu, 1980, 1988, 2000, 2007); Ide River at Araya, Iiyama City (Shimazu, 2000, 2007); Hime and Matsu rivers and Nakakurozawa (a small mountain river) at Hakuba Village (Shimazu, 1988, 2000, 2007). (7) Gifu Prefecture: Nagara River (Eguchi, 1931, 1932); Nagara River at Hachiman-cho, Gujo City (Shimazu, 1980, 1988, 2000; this paper); and Nagara River at Arisaka (type locality), Hachiman-cho (this paper). (8) Nara Prefecture: Takami River at



Figs. 8–10. *Dimerosaccus oncorhynchi*, neotype, adult specimen (NSMT-Pl 5850) found in intestine of *Oncorhynchus masou ishikawae*. 8, entire body, ventral view; 9, terminal genitalia, ventral view; 10, ovarian complex, dorsal view. Scale bars: 0.5 mm in Fig. 8; 0.2 mm in Figs. 9–10.

Fig. 11. *D. oncorhynchi*, adult specimen, showing sphincter of metraterm, redrawn from Shimazu and Urabe (2005). Scale bar: 0.1 mm.

Kotsugawa, Higashiyoshino Village (Nakamura *et al.*, 2000; Shimazu and Urabe, 2005). (9) Wakayama Prefecture: Tonda River at Fukusada, Kurisugawa, and Ookawa, Nakahechi, Tanabe City (Shimazu, 2008). (10) Tokushima Prefecture: Kainose River at Kainose, Ogawa; Sasamudani River at Sasamudani, Aikawa; Kaifu River at Higashikuwabara, Ogawa; and Yoshino, all Kaiyo Town (Shimazu, 2008). (11) Kochi Prefecture: Sakura River at Koda, Susaki City; Oshioka River at Oshioka, Susaki City; and Matsuda River at Idei and Chuo, Sukumo City (Shimazu, 2008). (12) Oita Prefecture: Chikugo River at Kobuchi Bridge, Miyoshikobuchi-machi, Hita City (Yoshida and Urabe, 2005; this paper); and Akaishi River at Nishiooyama, Ooyama-machi, Hita City (this paper).

In Russia: Primorsky Territory (Shedko *et al.*, 2015).

Material examined. (1) 2 specimens (NSMT-Pl 3094, 3095) of *Dimerosaccus oncorhynchi*, adult, ex intestine of *Oncorhynchus masou masou* (syn. *On. masou*) (now not *On. masou* f. *ishikawai*), Shokanbetsu River, 1 and 2 August

1984 (Shimazu, 1988, 1994, 2000). (2) 2 (NSMT-Pl 3096, 3097) of *D. oncorhynchi*, adult, ex intestine of *Salvelinus leucomaenis leucomaenis* (syn. *S. leucomaenis*), Shokanbetsu River, 26 July 1984, 2 August 1984 (Shimazu, 1988, 1994, 2000). (3) 2 (NSMT-Pl 3098, 3099) of *D. oncorhynchi*, adult, ex rectum (accidental (?)) of *Cottus nozawae* (not *Cottus pollux*), Shokanbetsu River, 1 August 1984 (Shimazu, 1988, 1994, 2000). (4) 1 (MPM Coll. No. 21196, collected by A. Ohtaka), adult, ex intestine of *S. leucomaenis pluvius*, Anmon River, 18 July 1997. (5) 12 (MPM Coll. No. 19260) of *D. oncorhynchi*, immature, adult, ex intestine of *On. masou masou* (syn. *On. masou*) (now not *On. masou* f. *ishikawai*), Horei River at Sanriku Town, now Sanriku-cho, Oofunato City, 19 March 1978 (Shimazu, 1980, 1988, 2000). (6) 3 (MPM Coll. No. 21197), adult, Shirabuzawa (a mountain river), 16 December 2015. (7) 54 (NSMT-Pl 1945–1950, 2168) of *D. oncorhynchi*, immature, adult, ex intestine and pyloric ceca of *S. leucomaenis pluvius* (syn. *S. pluvius*), Samu River, 16, 17, and 24 September 1978, 18 March 1979 (Shimazu, 1980, 1988, 2000). (8) Many (NSMT-Pl 5463, 5464) of *D. oncorhynchi*, immature, adult, ex intestine of *S. leucomaenis pluvius*, Ide River, 26 May 1995, 1 October 1995 (Shimazu, 2007). (9) 1 (NSMT-Pl 2173) of *D. oncorhynchi*, adult, ex intestine of *S. leucomaenis pluvius*, Hime River, 13 July 1979 (Shimazu, 1988, 2000). (10) 80 (NSMT-Pl 4609–4612) of *D. oncorhynchi*, immature, adult, ex intestine and pyloric ceca of *S. leucomaenis pluvius*, Matsu River and Nakakurozawa, 25 and 26 September 1993, 4 April 1994, 5 and 13 September 1994, 25 November 1994, 24 May 1995 (Shimazu, 2000). (11) 3 (NSMT-Pl 5026–5028, 3 paratypes of *Plagioporus honshuensis*) of *D. oncorhynchi*, adult, ex intestine of *Liobagrus reinii*, Sho River at Ohta [Tochinami City (?)], 18 July 1995 (Moravec and Nagasawa, 1998; Shimazu, 2000). (12) 10 (NSMT-Pl 2169–2172) of *D. oncorhynchi*, adult, ex intestine of *On. masou ishikawae* (syn. *On. rhodurus* f. *macrostomus* (Günther, 1877), *Oncorhynchus rhodurus* Jordan and McGregor in Jordan and Hubbs, 1925), Nagara River at Gujo-gun [Gujohachiman, now Hachiman-cho, Gujo City], 12 September 1975, 20 January 1977, 31 March 1979 (Shimazu, 1980, 1988, 2000). (13) 18 (NSMT-Pl 5849, 5850, hot formalin-fixed), Nagara River at Arisaka, 6 July 2011, 11 March 2012. (14) Specimens of *D. oncorhynchi*, immature, adult, Takami River: 22 (NSMT-Pl 5257, 5258), ex intestine of *L. reinii*, 28 and 30 July 1999, 12 August 2000; and 11 (NSMT-Pl 5259, 5260), ex intestine of *Rhinogobius flumineus*, 26–28 July 1999, 12, 14, and 15 August 2000 (Shimazu and Urabe, 2005). (The measurements given are erroneous. Correct measurements will be obtained by multiplying them by 0.8.) (15) 61 (NSMT-Pl 5528, 5529) of *D. oncorhynchi*, adult, ex intestine of *On. masou ishikawae*, Kainose and Sasamudani rivers, 12 September 1998 (Shimazu, 2008). (16) 14 (NSMT-Pl 5530, 5531) of *D. oncorhynchi*, immature, adult, ex intestine of *R. flumineus*, Kaifu River at Higashikuwabara, Sakura River at Konda, 16 September 1998, 29 July 2000 (Shimazu, 2008). (17) Specimens of *D. oncorhynchi*: 15 (NSMT-Pl 5532–5534), immature, adult, ex intestine of *Rhinogobius nagoyae*, Tonda River at Kurisugawa, Oshioka River at Oshioka, Matsuda River at Idei, 3 and 4 August 1999, 20 July 2000, 5 August 2000; 3 (NSMT-Pl 5535–5537), immature, adult, ex intestine of *Rhinogobius* sp. CO, Tonda River at Fukusada and Ookawa, Matsuda River at Chuo, 2 August 1999, 5 August 2000; 4 (NSMT-Pl 5538), immature, adult, ex intestine of *Rh. brunneus* (syn. *Rhinogobius* sp. DA), Kaifu River at Higashikuwabara, 16 September 1998; 2 (NSMT-Pl 5539) of *D. oncorhynchi*, adult, ex intestine of *Rh. fluviatilis* (syn. *Rhinogobius* sp. LD), Kaifu River at Higashikuwabara, 16 September 1998; 9 (NSMT-Pl 5540, 5541), immature, ex intestine of *Rhinogobius* sp. OR, Kaifu River at Higashikuwabara and Yoshino, 16 and 11 September 1998; and 1 (NSMT-Pl 5542), adult, ex intestine of *Tridentiger brevispinis*, Tonda River at Ookawa, 3 August 1999 (Shimazu, 2008). (18) 2 (Urabe's personal collection) of *D. oncorhynchi*, adult, ex

intestine of *On. masou masou*, Chikugo River, 19 June 2003 (Yoshida and Urabe, 2005). (19) 1 (Urabe's unpublished specimen), adult, ex intestine of *Odontobutis obscura*, Akaishi River, 18 August 2003. (20) 1 (Urabe's unpublished specimen), adult, ex intestine of "*Rhinogobius* sp.," Akaishi River, 30 September 2004.

Description. Based on hot formalin-fixed specimens (NSMT-Pl 5849–5850), ten measured (Figs. 8–10). Similar to *Coitocaecum* in every essential feature, except for intestines ending blindly and cirrus pouch being divided into small anterior and large posterior portions and including whole seminal vesicle. Body elongate-ovate, fairly small, 2.70–3.49 by 0.65–0.95; forebody 0.79–0.95 long, occupying 27–30% of body length. Oral sucker 0.13–0.19 by 0.19–0.22. Prepharynx very short. Pharynx large, 0.13–0.16 by 0.13–0.15. Esophagus bifurcating between pharynx and ventral sucker. Intestines ending blindly near posterior extremity of body. Ventral sucker usually embedded slightly in body wall or rarely protruded, 0.28–0.32 by 0.30–0.36; sucker width ratio 1: 1.5–1.8. Testes usually transversely elliptical, rarely globular, or rarely slightly indented, 0.23–0.47 by 0.30–0.42, tandem, contiguous, in middle third of hindbody. Cirrus pouch distinctly divided into two portions: anterior portion thick-walled, muscular, small, 0.13–0.20 by 0.07–0.09, enclosing short thick-walled anteriormost part of seminal vesicle, a small number of small gland cells around seminal vesicle, pars prostatica, and short ejaculatory duct; posterior portion thin-walled, membranous, large, 0.28–0.44 by 0.13–0.19, enclosing greater posterior part of sinuous tubular seminal vesicle and a large number of prostatic cells, extending posteriorly usually to middle of ventral sucker or sometimes anterior to ventral sucker. Genital atrium small. Genital pore at level of pharynx or slightly posterior to it. Ovary usually transversely reniform, rarely globular, or rarely slightly indented, 0.19–0.22 by 0.22–0.31, submedian or median, immediately anterior to anterior testis. Laurer's canal long, sometimes proximally dilated slightly to contain a small number of sperm. Sphincter present between ootype and uterus. Uterus coiled a few times between ovary, ventral sucker, and intestines; uterine seminal receptacle present; metraterm slightly smaller than anterior portion of cirrus pouch, with crescent dorsal sphincter around dorsal its opening (see also Fig. 11). Eggs fairly numerous, 55–63 by 32–37 μm. Vitelline follicles distributed usually between ventral sucker and posterior extremity of body, but rarely entering forebody to midlevel of esophagus, rarely almost confluent there, usually separate anteriorly, confluent posteriorly. Excretory vesicle extending anteriorly to ovary; excretory pore posteroterminal.

Remarks. Eguchi (1931) briefly described a new species, *Allocreadium oncorhynchi*, on the basis of adult specimens found in the intestine of *Oncorhynchus masou ishikawae* (syn. *On. macrostomus*) from the Nagara River (exact collecting locality not indicated). Later, Eguchi (1932) fully redescribed this species.

Peters (1957) reexamined a syntype of the species and tentatively transferred the species to *Plagioporus* Stafford, 1904 (Opecoelidae, Plagiopolinae) as *Plagioporus oncorhynchi* (Eguchi, 1931). Shimazu (1980) erected a new genus, *Dimerosaccus* (Opecoelidae, Opecoelinae), with *A. oncorhynchi*, or now *D. oncorhynchi* (Eguchi, 1931), as the type species. Moravec and Nagasawa (1998) described a new species, *Plagioporus honshuensis* (Plagioporinae), on the basis of adult specimens found in the intestine of *Liobagrus reinii* from the Sho River in Toyama Prefecture. Reexamining the three paratypes of this species, Shimazu (2000) synonymized the species with *D. oncorhynchi*.

Shimazu (1980, 1988) originally suggested that *Dimerosaccus* belonged to the subfamily Opecoelinae, because it appeared to be morphologically related to *Opecoelus* Ozaki, 1925, *Opecoelina* Manter, 1934, *Opegaster* Ozaki, 1928, and *Ozakia* Wiśniewski, 1933 of the subfamily. Shimazu and Awakura (1993) and Shimazu (2000) placed the genus in the subfamily Plagioporinae, because the cirrus pouch enclosed the whole seminal vesicle, though divided; and

Laurer's canal was proximally dilated to include a small number of sperm in it as a possible vestigial canalicular seminal receptacle. Cribb (2005b) retained the genus in the subfamily Opecoelinae, stating that the absence of a canalicular seminal receptacle confirmed the genus as an opecoeline rather than a plagioporine. Shedko *et al.* (2015) and Bray *et al.* (2016) demonstrated that the genus should be assigned to the subfamily Opecoelinae in their molecular studies.

In *D. oncorhynchi*, a canalicular seminal receptacle is absent, but Laurer's canal has a dilatation at its proximal part (Shimazu, 1980; Shimazu and Awakura, 1993; Shimazu, 2000; Shimazu and Urabe, 2005; Shedko *et al.*, 2015; this paper). The dilatation is empty or contains a small number of sperm and ova. Eguchi (1931, 1932) seems to have described this dilatation as a pear-shaped seminal receptacle. Further, the following morphological variations have been reported in *D. oncorhynchi*. (1) The ventral sucker is usually slightly embedded in the body wall or rarely protruded rather than stalked. (2) There are normally two testes but abnormally a single testis, which is apparently incompletely divided into two testes (Shimazu, 1980, fig. 7). (3) The anterior limit of distribution of the vitelline follicles is various from the ventral sucker to the midlevel of the esophagus (Shimazu, 1980, 1988, 2000, 2007, 2008; Shimazu and Awakura, 1993; Shimazu and Urabe, 2005).

Eguchi (1931, 1932) obtained his specimens of *A. oncorhynchi* from *On. macrostomus* collected in the Nagara River. He neither indicated the exact collecting locality of the host fish nor designated the holotype for *A. oncorhynchi*. Later, Peters (1957) and Yamaguti (1958, a footnote) reexamined the same syntype of *A. oncorhynchi* (L. E. Peters, personal communication, July, 1978), However, this syntype is not deposited either in the US National Parasite Collection, Agricultural Research Service, USDA, Beltsville, MD 20705, USA (now Department of Invertebrate Zoology, Smithsonian's National Museum of Natural History, Washington, DC 20560, USA) or in the Meguro Parasitological Museum, Tokyo. Further, I was unsuccessful in tracing any other original specimens of Eguchi in Japan. Therefore, it is believed that all of his original specimens of *A. oncorhynchi* were lost (see also Shimazu, 1980). Fortunately, the present 18 new adult specimens (NSMT-Pl 5849–5850) found in *On. masou ishikawae* from the Nagara River were fixed in hot formalin and made into better whole-mounts in Canada balsam. I here designate one of them as a neotype for the species, as follows.

Designation of a neotype of Allocreadium oncorhynchi *Eguchi*, *1931*, *or now* Dimerosaccus oncorhynchi *(Eguchi*, *1931)*. Neotype: a whole-mounted adult specimen (NSMT-Pl 5850), heat-killed, 3.25 mm long by 0.87 mm wide, Figs. 8–10, 11 March 2012.

Type host. *Oncorhynchus masou ishikawae* Jordan and McGregor in Jordan and Hubbs, 1925 (Salmonidae).

Site of infection. Intestine.

Type locality. Nagara River at Arisaka (35°44′N, 136°56′E), Hachiman-cho, Gujo City, Gifu Prefecture.

As seen in *Geographical distribution*, *D. oncorhnchi* has been recorded from mountain rivers, in which the temperature of the water is relatively low: Hokkaido, Tohoku Region (Aomori, Iwate, and Yamagata Preferctures), Chubu Region (Toyama, Nagano, and Gifu Prefectures), Kinki Region (Nara and Wakayama Prefectures), Shikoku Region (Tokushima and Kochi Prefectures), and Kyushu Region (Oita Prefecture). A large number of individuals of freshwater fishes collected in Hokkaido have so far been examined for digeneans, but *D. oncorhynchi* has been found only in *On. masou masou* from the Shokanbetsu River at Mashike Town in western part of Hokkaido (see also other monographs of this series).

A few specimens of *D. oncorhynchi* were found in the intestine of *Cottus pollux* from the Ide River at Araya, Iiyama City, on 24 September 1995; but they were lost (Shimazu, 2000). Shedko *et al.* (2015) recorded *D. oncorhynchi* from *On. masou*, *Salvelinus curilus*, and *Brachymystax*

tumensis (Salmonidae) in Primorsky Territory, Russia.

Life cycle. Not known.

Awakura (1989) and Shimazu and Awakura (1993) reported adult specimens of *D. oncorhynchi* (NSMT-Pl 3985) from *On. masou masou* caught at sea. Some adults of *D. oncorhynchi* of river origin are evidently capable of surviving in the host fish in the sea for at least five to nine months after the host's seaward migration from its nursery river (Shimazu and Awakura, 1993).

I attemped to elucidate the life cycle of *D. oncorhynchi* in Nakakurozawa, where *Salvelinus leucomaenis pluvius* was infected with *D. oncorhynchi* (see *Material examined*), in Hakuba Village without success. An adult specimen (NSMT-Pl 4613) was found in the small intestine of a larva of the salamander *Onychodactylus japonicus* (Houttuyn, 1782) (Amphibia, Urodela, Hynobiidae) from this river on 25 November 1994 (Shimazu, 2000).

As mentioned above, adults of *D. oncorhynchi* have been recorded from freshwater fishes of many species in five families and a larval salamander. An aquatic insect may serve as a second intermediate host. It may be that salmonids aquire infection with *D. oncorhynchi* not only by eating larvae and adults of the aquatic insect but also by eating infected small fish. It is interesting that *D. oncorhynchi* has never been found in cyprinids.

Genus ***Opecoelus*** Ozaki, 1925

Opecoelus ukigori Shimazu, 1988

(Figs. 12–14)

Opecoelus ukigori Shimazu, 1988: 13–15, figs. 8–13; Shimazu, 2000: 21–23, figs. 5–10.

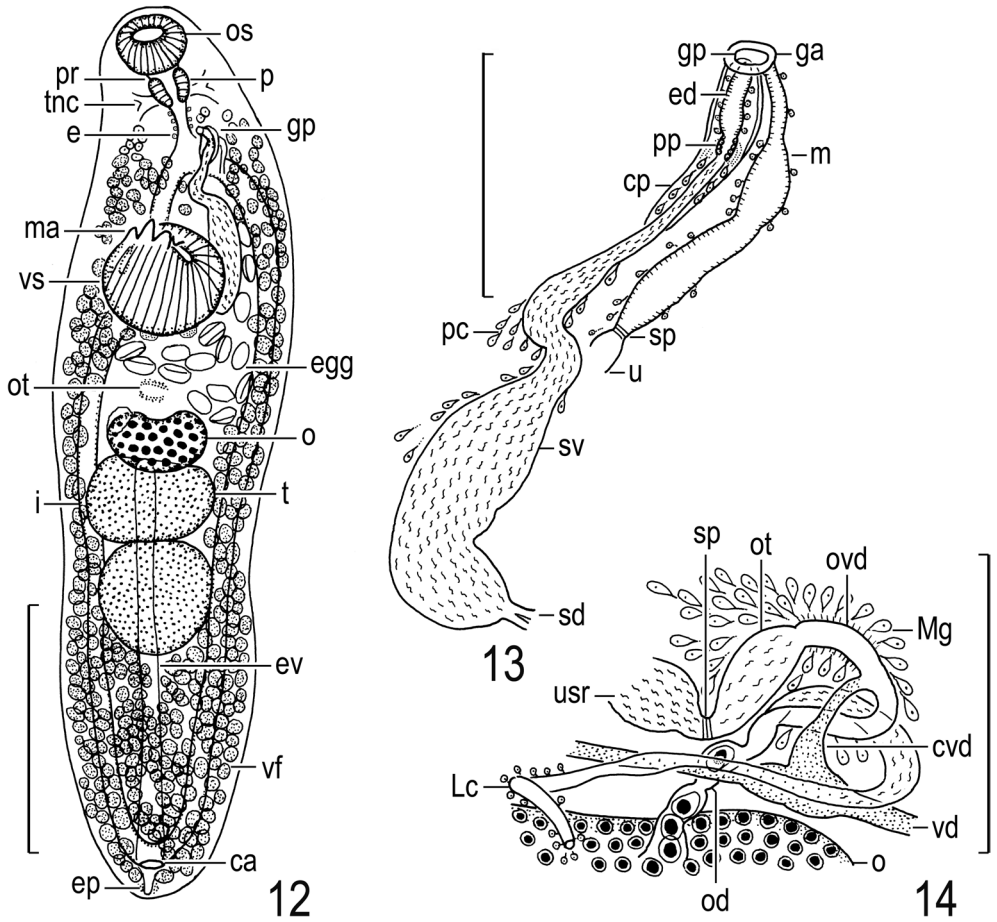
Hosts in Japan. *Gymnogobius opperiens* Stevenson, 2002 (Gobiidae) (type host) and *Gymnogobius urotaenia* (Shimazu, 1988, 1994, 2000; this paper).

Sites of infection. Intestine, and also rectum (accidental (?)).

Geographical distribution. Hokkaido: Tobestu River (type locality) at Tobetsu, Hokuto City; and Oono River at Chiyoda, Hokuto City (Shimazu, 1988, 1994, 2000; this paper).

Material examined. (1) 15 specimens (NSMT-Pl 3114, holotype; 3111–3113, 3115–3117, 14 paratypes) of *Opecoelus ukigori*, adult, ex intestine and rectum of *Gymnogobius opperiens* (syn. *Chaenogobius annularis* (the middle-reaches type), [not *Ch. urotaenia*]), Tobestu River at Tobetsu, Kamiiso Town, now in Hokuto City, 26 August 1984 (Shimazu, 1988, 1994, 2000). (2) 3 (NSMT-Pl 3108–3110, 3 paratypes) of *O. ukigori*, adult, ex intestine of *G. urotaenia* (syn. *Ch. annularis* (the freshwater type), *Chaenogobius* sp. 1 of Prince Akihito), Tobetsu River at Tobetsu, 26 August 1984 (Shimazu, 1988, 1994, 2000). (3) 3 (NSMT-Pl 2933, 3107, 3 paratypes) of *O. ukigori*, adult, ex intestine of *G. opperiens*, Oono River at Chiyoda, Oono Town, now in Hokuto City, 20 and 23 August 1984 (Shimazu, 1988, 1994, 2000).

Description. After Shimazu (1988, 2000), altered from the present study (Figs. 12–14). Similar to *Coitocaecum* (see above) in every essential feature, except for intestines forming common anus and ventral sucker having three pairs of marginal appendages. Body elongate-ovate, small, 1.40–2.90 by 0.36–0.70 (holotype 1.77 by 0.43); forebody 0.44–0.70 long, occupying 27–35% of body length. Gland cells present in forebody. Oral sucker 0.11–0.17 by 0.13–0.20. Pharynx 0.06–0.08 by 0.07–0.09. Esophagus bifurcating between oral and ventral suckers. Intestines united to open through ventral common anus near posterior extremity of body. Ventral sucker 0.17–0.27 by 0.19–0.31, with three pairs of finger-shaped marginal appendages; sucker width ratio 1 : 1.3–1.7. Testes entire or sometimes slightly indented irregularly, 0.10–0.27 by 0.20–0.43, tandem, in middle third of hindbody. Cirrus pouch reduced, small, thick-walled in anterior half, thin-walled in posterior half, 0.06–0.10 by 0.03–0.04, including short anteriormost part of seminal vesicle, pars prostatica, a few prostatic cells, and short ejaculatory; greater posterior part of seminal vesicle external



Figs. 12–14. *Opecoelus ukigori*, adult specimens found in intestine of *Gymnogobius opperiens*. 12, holotype (NSMT-Pl 3114), entire body, ventral view; 13, paratype (NSMT-Pl 3116), terminal genitalia, ventral view; 14, paratype (NSMT-Pl 3116), ovarian complex, dorsal view. Scale bars: 0.5 mm in Fig. 12; 0.2 mm in Figs. 13–14.

to cirrus pouch along with prostatic cells, large, sinuous, extending to posterior border of ventral sucker. Genital atrium small. Genital pore sinistrally submedian, a little prebifurcal. Ovary transversely reniform, 0.08–0.16 by 0.16–0.35, median or submedian. Laurer's canal long, including sperm. Ootype with sphincter at distal end. Uterus coiled a few times between ovary, ventral sucker, and intestines; uterine seminal receptacle well developed; metraterm about half as long as cirrus pouch, with sphincter at posterior end. Eggs fairly numerous, yellow, 58–64 by 36–40 μm. Vitelline follicles reaching anteriorly to level of posterior border of ventral sucker to midlevel of esophagus, separate there, confluent in post-testicular region. Excretory vesicle reaching to ovary; excretory pore dorso- or posteroterminal.

Remarks. Most of the known species of *Opecoelus* are parasitic in marine fishes. *Opecoelus variabilis* Cribb, 1985 is a real freshwater species in Australia (Cribb, 1985). Considering that both *G. opperiens* and *G. urotaenia* had acquired infection with *O. ukigori* during their freshwater life in the Tobetsu and Oono rivers, Shimazu (1988, 1994, 2000) treated *O. ukigori* as a freshwater species.

Life cycle. Not known.

Discussion on the male terminal genitalia in the subfamily Opecoelinae

With regard to the male terminal genitalia in the subfamily Opecoelinae, Cribb (2005b) defined as "Cirrus-sac [cirrus pouch] frequently completely absent, often reduced and encloses only terminal portion of male genitalia so that seminal vesicle is external, rarely membranous and encloses seminal vesicle."

In *Dimerosaccus*, the cirrus pouch is entire but distinctly divided into two portions: the anterior portion is thick-walled, muscular, and small, enclosing a short thick-walled anteriormost part of the seminal vesicle, the pars prostatica, a small number of small gland cells, and the ejaculatory duct; and the posterior portion is thin-walled, membranous, and large, enclosing the greater posterior part of the seminal vesicle and a large number of the prostatic cells (Shimazu and Awakura, 1993, fig. 3; Shimazu, 2000, fig. 12; Shimazu and Urabe, 2005, fig. 6; Shimazu, 2008, figs. 8–9; this paper, Fig. 9). Regarding only the anterior portion as the cirrus pouch, Shimazu (1980, fig. 4; 1988, fig. 6) and Shedko *et al.* (2015, fig. 3C) described the cirrus pouch as enclosing the pars prostatica, prostatic cells, and the ejaculatory duct (or cirrus) and the membranous sac (or pouch) as enclosing the external seminal vesicle and large gland cells. These descriptions indicate neither what the large gland cells are nor where they discharge.

In *Coitocaecum*, the cirrus pouch is reduced and also bipartite. The anterior portion is the same as that of *Dimerosaccus*. It appears that the posterior portion is ruptured posteriorly, leaving a small remnant, so that the greater posterior part of the seminal vesicle becomes external to the cirrus pouch, along with a large number of the prostatic cells (this paper, Fig. 2, *; see also Shimazu, 1988, fig. 4; 2000, fig. 4; Shimazu *et al.*, 2011, fig. 49). In *Opecoelus*, the cirrus pouch is also reduced, thick-walled in the anterior half, and thin-walled in the posterior half, enclosing a short anteriormost part of the seminal vesicle, the pars prostatica, a few prostatic cells, and the ejaculatory; and the greater posterior part of the seminal vesicle is external, along with the remaining prostatic cells.

It seems to me that the structure of the cirrus pouch is fundamentally the same in the three genera. The membranous posterior portion may have been merely ruptured posteriorly, leaving its small remnant (this paper, Fig. 2, *), in the early stages of the formation in *Coitocaecum*. The greater posterior part of the seminal vesicle may have protruded out of the membranous portion, breaking through its posterior end, in *Opecoelus*. I here interpret the short male duct in the anterior portion of *Dimerosaccus* and *Coitocaecum* and in the cirrus pouch of *Opecoelus* as the anteriormost (or distalmost) part of the seminal vesicle, though it is slightly thicker-walled than the greater posterior part of the seminal vesicle and surrounded by a small number of gland cells smaller than the prostatic cells (see also Shedko *et al.*, 2015, fig. 3C); and the large gland cells in the membranous posterior portion in *Dimerosaccus* and around the greater posterior part of the seminal vesicle in *Coitocaecum* and *Opecoelus* as the prostatic cells, each discharging into the pars prostatica with a long cellular duct as usual. The problem remains what the small gland cells surrounding the anteriormost part of the seminal vesicle are. Possibly, they are also part of the small gland cells that discharge into the ejaculatory duct. It is desired that the structure and formation of the male terminal genitalia in the subfamily be further critically studied.

Incidentally, a divided cirrus pouch that is very similar to that of *Dimerosaccus* is also known in three freshwater species from China: *Plagioporus* (*Plagioporus*) *schizothoraci* Zhang, 1992 (Opecoelidae), *Plagioporus* (*Plagioporus*) *allovaris* Zhang, 1992, and *Hysterogonoides disaccus* Zhang, 1992 (Lepocreadiidae) [*sic*] (Zhang, 1992). The former two closely resemble *Dimerosaccus* (Opecoelinae), but not *Plagioporus* Stafford, 1904 (Plagioporinae), owing to the absence of a canalicular seminal receptacle. The last is also likely to belong to the subfamily Opecoelinae, because it is a freshwater species, the

tegument is smooth, and a canalicular seminal receptacle is absent, though Zhang (1992) and Bray (2005) assigned it to the family Lepocreadiidae Odhner, 1905.

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