

A Revised and Enlarged Version of Shimazu's (1988) Paper Entitled
 "Trematodes of the Genera *Coitocaecum*, *Dimerosaccus* and *Opecoelus*
 (Opecoelidae: Opecoelinae) from Freshwater Fishes of Japan"

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Abstract: This paper is a revised and enlarged version of Shimazu's (1988) paper entitled "Trematodes of the genera *Coitocaecum*, *Dimerosaccus* and *Opecoelus* (Opecoelidae: Opecoelinae) from freshwater fishes of Japan." It describes and illustrates three species in three genera (Digenea: Opecoelidae) from freshwater fishes of Japan: *Coitocaecum plagiorchis* Ozaki, 1926 (Opecoelinae); *Opecoelus ukigori* Shimazu, 1988 (Opecoelinae); and *Dimerosaccus oncorhynchi* (Eguchi, 1931) Shimazu, 1980 (Plagioporinae). Diagnoses of the family, subfamilies, and genera are proposed. Some relevant data obtained since the publication of the previous paper are given.

Key words: *Coitocaecum plagiorchis*, *Dimerosaccus oncorhynchi*, *Opecoelus ukigori*, Digenea, Opecoelidae, freshwater fishes, Japan.

In 1988 I published a paper entitled "Trematodes of the genera *Coitocaecum*, *Dimerosaccus* and *Opecoelus* (Opecoelidae: Opecoelinae) from freshwater fishes of Japan" (Shimazu, 1988b). In this version, the previous paper has been revised and enlarged according to new relevant data obtained since its publication, and some mistakes and errors found in it have been corrected. For the materials and methods, the reader is referred to Shimazu (1988a).

Family Opecoelidae Ozaki 1925

Opecoelidae Ozaki, 1925, p. 53 (type genus, *Opecoelus* Ozaki, 1925).

Coitocaecidae Ozaki, 1929, p. 76 (type genus, *Coitocaecum* Nicoll, 1915).

Podocotylidae Dollfus 1960, pp. 101-102 (type genus, *Podocotyle* Dujardin, 1845).

Diagnosis. Trematoda: Digenea. Body small to medium-sized, elongate or oval, flattened or

cylindrical, aspinose, nonoculate. Oral sucker subterminal. Prepharynx short or practically absent. Pharynx present. Esophagus various in length. Intestinal bifurcation in forebody. Intestines long, terminating blindly, each opening through an anus, united to form a cyclocoel or to open through a common ventral anus, or fusing with excretory vesicle to form a uroproct. Ventral sucker in anterior half of body, sessile or pedunculate, with or without papilliform or tentacular appendages on anterior and posterior lip margins.

Testes usually two, rarely three to ten (usually nine), opposite, oblique, or tandem in hindbody. Cirrus pouch large, enclosing whole male terminal duct (or whole seminal vesicle, prostatic complex, and cirrus); rudimentary, small, enclosing small internal seminal vesicle, prostatic complex, and cirrus, with large external seminal vesicle lying free in parenchyma; or absent. Genital atrium small. Genital pore anterior to ventral sucker, ventral, usually sinistrosbmedian, rarely may be median, occasionally with accessory sucker. Ovary entire to lobed, pretesticular, median or submedian. Ootype-complex preovarian. Laurer's canal preovarian,

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opening dorsally. Seminal receptacle present or absent; uterine seminal vesicle present. Uterus usually preovarian or pretesticular, rarely extending into inter- or post-testicular region; metraterm present. Eggs operculate, occasionally with polar filaments, usually not embryonated or rarely fully embryonated, when laid. Vitellaria follicular, circumcecal, continuous or interrupted, usually reaching posterior end of body and confluent in post-testicular region, various in anterior extent. Excretory vesicle tubular, various in extent, with postero-terminal or almost dorsal excretory pore. Adults parasitic usually in digestive tract, rarely in gall bladder, of teleosts and rarely in digestive tract of amphibians.

Life cycle. Miracidia nonoculate, with one pair of flame cells; epidermal cell formula 6, 7, 4, 2. Cotylomicrocercous cercariae developing in sporocysts in prosobranch snails; flame-cell formula $2 [(2+2) + (2+2)] = 16$. Metacercariae encysting in aquatic arthropods, snails, or leeches, occasionally progenetic.

Discussion. This family diagnosis has been based mainly on Ozaki (1925b, c, 1928), Yamaguti (1971), Gibson and Bray (1982, 1984), Schell (1985), and this study. For the classification of the family, the reader is referred to Yamaguti (1971) and Gibson (1996).

Subfamily Opecoelinae Ozaki, 1925

Opecoelidae Ozaki, 1925, p. 53 (type genus, *Opecoelus* Ozaki, 1925).

Opecoelinae Stunkard, 1931, p. 724 (type genus, *Opecoelus* Ozaki, 1925).

Coitocoecinae Poche, 1926 (imprint 1925), p. 163 (type genus, *Coitocoecum* Nicoll, 1915).

Diagnosis. Opecoelidae. Intestines ending blindly, each opening through an anus, united to form a cyclocoel or to open through a common ventral anus, or fusing with excretory vesicle to form a uroproct. Ventral sucker sometimes with marginal appendages. Testes two. Cirrus pouch rudimentary, small, thick-walled, muscular, surrounding small internal seminal vesicle,

prostatic complex, and cirrus, with large external seminal vesicle lying free in parenchyma; or absent. Genital pore prebifurcal, occasionally with accessory sucker. Seminal receptacle absent; uterine seminal vesicle present. Eggs without polar filaments. Adults parasitic usually in digestive tract, rarely in gall bladder, of marine and freshwater teleosts.

Discussion. This subfamily diagnosis has been based mainly Ozaki (1925b, c, 1928), Yamaguti (1971), Gibson and Bray (1982, 1984), and this study.

Genus *Coitocaecum* Nicoll, 1915

Coitocoecum Nicoll, 1915, pp. 25-26 (type species, *Coitocoecum gymnophallum* Nicoll, 1915).

Coitocaecum: Ozaki, 1929, pp. 76-77.

Ozakia Wiśniewski, 1934, pp. 35, 38, table 1 (type species, *Coitocaecum plagiorchis* Ozaki, 1926).

Pseudocoitocaecum Bilqees, 1972, p. 21 (type species, *Pseudocoitocaecum thrissoclesis* Bilqees, 1972).

Paradactylostomum Zhukov, 1972, p. 347 (type species, *Paradactylostomum indicum* Zhukov, 1972).

Diagnosis. Opecoelidae: Opecoelinae. Cyclocoel present. Ventral sucker without marginal appendages. Cirrus pouch rudimentary, small, thick-walled, muscular, enclosing small internal seminal vesicle, prostatic complex, and cirrus; external seminal vesicle large, free in parenchyma. Genital pore prebifurcal, rarely may be postbifurcal. Accessory sucker absent. Vitelline follicles sometimes entering forebody, interrupted or not in distribution. Adults parasitic normally in intestine of marine and freshwater teleosts.

Discussion. Nicoll (1915) established a new genus, *Coitocoecum*, based on a new species, *C. gymnophallum*, from a marine teleost, *Sparus australis* (Sparidae), from Australia. Ozaki (1929) changed the original spelling *Coitocoecum* to *Coitocaecum* without explaining the change (discussed later again). Since then, many subsequent workers have used this subsequent spelling. The subsequent spelling

Coitocaecum is retained in this paper.

Nicoll (1915) stated that in *C. gymnophallum*, no true cirrus pouch is present, and the genital pore is situated near the left side of the middle of the pharynx. Ozaki (1926, 1929) described and figured a well-developed muscular cirrus pouch enclosing a small internal seminal vesicle, prostatic complex, and cirrus; and a large external seminal vesicle lying free in the parenchyma in *C. plagiorchis* Ozaki, 1926 and four other species of the genus. Ozaki said the genital pore as lateral in the generic diagnosis; but the genital pore is distinctly submedian (or sublateral) in front of the left intestine in the five species as in *C. gymnophallum*. Wiśniewski (1934) proposed a new genus, *Ozakia*, to accommodate the five species, separating it from the genus *Coitocaecum* principally by that the cirrus pouch is short and contains the ejaculatory duct and internal seminal vesicle, while an external seminal vesicle is present. However, Crowcroft (1951) and Aken'Ova and Cribb (1996) proved that *C. gymnophallum* also have such a cirrus pouch as seen in *C. plagiorchis*, indicating that the two genera as synonyms. According to Bray (1987, p. 1054, a foot note), the type species of two genera, *Pseudocoitocaecum* Bilgees, 1972 and *Paradactylostomum* Zhukov, 1972, are the same species, which means that the two genera are identical; and further they are synonymous with the genus *Coitocaecum*. It should be mentioned, however, that the submedian genital pore is distinctly postbifurcal in the two genera (Bilgees, 1972; Zhukov, 1972).

This generic diagnosis has been based mainly on Nicoll (1915), Ozaki (1929), Crowcroft (1951), Aken'Ova and Cribb (1996), and this study.

Coitocaecum plagiorchis Ozaki, 1926
(Figs. 1-4)

Coitocaecum plagiorchis Ozaki, 1926, pp. 125-128, no figure.

Coitocaecum plagiorchis: Ozaki, 1929, pp. 77-82, figs. 1-3.

Ozakia plagiorchis: Wiśniewski, 1934, p. 38, table 2.

Material examined. 1) Lot 1. Four (2 immature and 2 gravid) whole-mounts (MPM Coll. No. 22585) of *C. plagiorchis* of Yamaguti (1934) found in intestine of *Mogurnda obscura* [= *Odontobutis obscura obscura*] (Gobiidae) from Lake Ogura, Kyoto (not Shiga) Prefecture, on 15 and 30 May and 4 June 1932.

2) Lot 2. Fifteen (3 immature and 12 gravid) unpublished whole-mounts (MPM Coll. No. 22291) of *C. plagiorchis* in Yamaguti's collection found in intestine of *O. o. obscura* from the Katsura River, Kyoto, on 2 and 5 June and 10 July 1936.

3) Lot 3. Three gravid whole-mounts (MPM Coll. No. 22292) of *C. plagiorchis* of Yamaguti (1942) found in intestine of *M. obscura* [= *O. o. obscura*] (experimental infection).

4) Lot 4. Two gravid whole-mounts (MPM Coll. No. 22587) of *C. plagiorchis* of Yamaguti (1939) found in intestine of *Chaenogobius annularis urotaenia* [= *Ch. urotaenia*] (Gobiidae) from Lake Biwa, Shiga Prefecture, on 3 December 1938.

5) Lot 5. One immature whole-mount (NSMT-P1 3105) of *C. plagiorchis* of Shimazu (1988b) found by Nagasawa in intestine of *Ch. urotaenia* from Lake Biwa at Onoe on 4 February 1980.

6) Lot 6. One immature whole-mount (NSMT-P1 3106) of *C. plagiorchis* of Shimazu (1988b) found in intestine of *Ch. urotaenia* from Lake Biwa at Onoe on 6 June 1980.

7) Lot 7. Two immature whole-mounts (NSMT-P1 3104) of *C. plagiorchis* of Shimazu (1988b) found in intestine of *Ch. isaza* from Lake Biwa at Onoe on 6 June 1980.

8) Lot 8. Three (1 immature and 2 gravid) unidentified and unpublished whole-mounts (MPM Coll. No. 30013) of *C. plagiorchis* of Shimazu (1988b) in Ozaki's collection from "Small Goro" [= *Ch. isaza*?] from Lake Biwa (other data not given).

9) Lot 9. Four (1 immature and 3 gravid) whole-mounts (MPM Coll. No. 22553) of *C. plagiorchis* of Yamaguti (1934) found in intes-

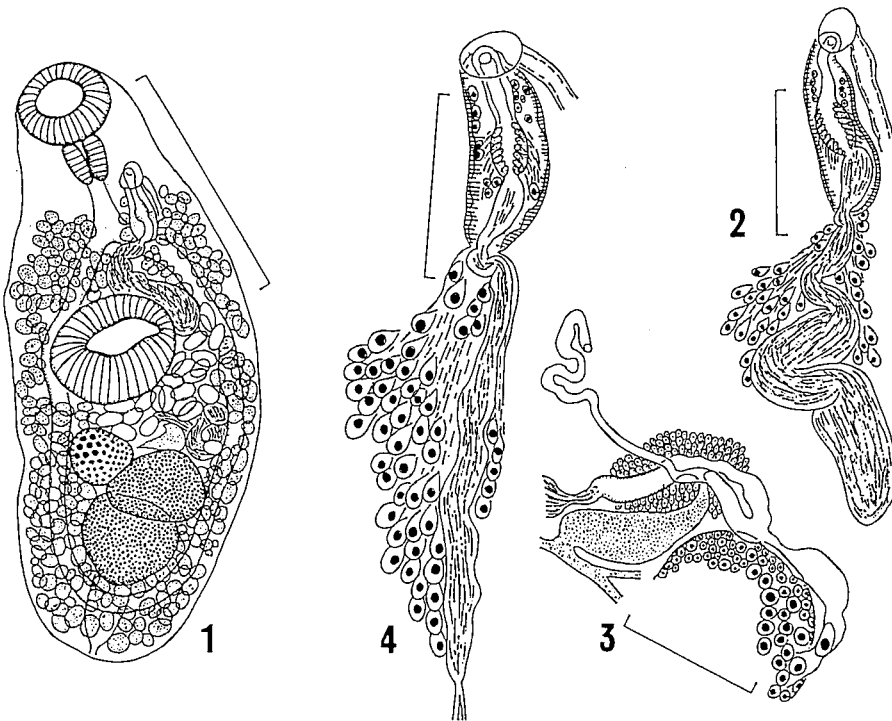


Fig. 1-4. *Coitocaecum plagiorchis* Ozaki, 1926.

Figs. 1-3. Yamaguti's unpublished gravid specimens (lot 2) from *Odontobutis obscura obscura* from Kyoto. 1: Entire worm, ventral view. 2: Terminal genitalia, ventral view. 3: Ovarian complex, dorsal view.

Fig. 4. Immature specimen (lot 7) from *Chaenogobius isaza* from Lake Biwa, terminal genitalia, showing a thin membrane surrounding distal part of external seminal vesicle and gland cells (prostatic?), ventral view. (Scale bars: 0.5 mm in Fig. 1; 0.1 mm in Figs. 2-4.)

tine of *Bryttosus kawamebari* [= *Coreoperca kawamebari*] (Percichthyidae) from the Asago River, Hyogo Prefecture, on 7 January and 7 April 1932.

10) Lot 10. Two immature whole-mounts (MPM Coll. No. 22586) of *C. plagiorchis* of Yamaguti (1939) found in intestine of *Pelteobagrus nudiceps* (Bagridae) from Lake Biwa on 7 December 1938.

11) Lot 11. One gravid whole-mount (NSMT-P1 3102) of *C. plagiorchis* of Shimazu (1988b) found by Nagasawa in intestine of *P. nudiceps* from Lake Biwa at Onoe on 11 November 1980.

12) Lot 12. Twelve (10 immature and 2 just matured) whole-mounts (NSMT-P1 4614)

found in intestine of *P. nudiceps* from Lake Biwa at Onoe on 4 May 1992.

13) Lot 13. One immature whole-mount (NSMT-P1 3103) of *C. plagiorchis* of Shimazu (1988b) found by Nagasawa in intestine of *Cottus ohmiensis* [= *Co. reinii*] (Cottidae) from Lake Biwa at Onoe on 4 February 1980.

14) Lot 14. Fourteen (12 immature and 2 just matured) whole-mounts (NSMT-P1 4615) found in pyloric ceca of *Co. reinii* from Lake Biwa at Onoe on 4 May 1992.

Description. 1) For the specimens of lots 1 and 9, 4 and 10, and 3, see Yamaguti (1934, 1939, 1942), respectively. Yamaguti (1934) described the excretory vesicle as Y-shaped; but this organ is distinctly I-shaped, as described by

Ozaki (1926, 1929). In one specimen of lot 3, the uterus including many eggs descended along the left side of the testes as far as the posterior border of the posterior testis.

2) Based on the specimens of lots 2, 5-8, and 11-14; 14 gravid whole-mounts measured (Figs. 1-4). Body oblong or lanceolate-oblong, slightly wider in hindbody than in forebody, 0.94-1.60 by 0.44-0.78; forebody 40-50% of total body length. Oral sucker antero-terminal, 0.12-0.20 by 0.13-0.20. Prepharynx very short. Pharynx globular or elliptical, 0.08-0.11 in diameter. Esophagus 0.05-0.12 long, bifurcating midway between pharynx and ventral sucker; cyclocoel ending some distance from posterior end of body. Ventral sucker sessile, 0.20-0.27 by 0.20-0.31; sucker width ratio 1:1.44-1.72.

Testes entire, contiguous, oblique, lying encircled by cyclocoel, 0.12-0.23 by 0.16-0.31. Cirrus pouch rudimentary, club-shaped, thick-walled, muscular, small, 0.12-0.19 by 0.04-0.06, in front of left intestine or slightly overlapping it posteriorly. Internal seminal vesicle small, swelling, containing sperms. Pars prostatica usually ovate, accompanied by prostatic cells. Cirrus short, nonspinous. External seminal vesicle sinuous, rather thick-walled, anterior to ventral sucker or extending to midlevel or rarely to posterior border of ventral sucker, surrounded by dispersed gland cells (prostatic?). Genital atrium small. Genital pore submedian, to left of pharynx. Ovary globular, antero-dextral to lateral to anterior testis, 0.08-0.14 in diameter. Oviduct usually originated from right side of ovary. Ootype located antero-sinistral to ovary; Mehlis' gland compactly massed around ootype. Laurer's canal long, lying usually anterior to ootype, slightly dilated at proximal part (but no sperms seen in this part). Uterus pre-ovarian or -testicular, intercecal; metraterm shorter than cirrus pouch. Eggs rather numerous, 56-68 by 34-38 μm in balsam. Vitelline follicles entering forebody usually to midlevel of esophagus or sometimes to level of pharynx, separated anteriorly, extending close to posterior end of body, confluent in post-testicular region. Excretory vesicle

I-shaped, extending to anterior border of anterior testis.

In the immature specimens of lot 7, a thin membrane enclosed the anterior part of the external seminal vesicle and gland cells (prostatic?); and the membrane was anteriorly connected to the thick-walled cirrus pouch but indiscernible posteriorly (Fig. 4).

Discussion. Ozaki (1926) first described this species as *Coitocoecum plagiorchis* with no figure from adults found in the stomach and intestine of *M. obscura*. Later Ozaki (1929) re-described and figured the species under the name *Coitocaecum plagiorchis*, indicating that the locality was Saijo, Hiroshima Prefecture, Japan; but he did not explain the change of the original spelling *Coitocoecum* by Nicoll (1915) to *Coitocaecum*.

The holotype (No. P. 235) of the species was once deposited in the collection of the Zoological Institute, Science Faculty, Tokyo Imperial University (Ozaki, 1926, 1929); but it is believed that the holotype has already been lost (see Shimazu *et al.*, 1996). However, there have been found 13 slides (MPM Coll. No. 30028) labeled merely "gori" in Japanese by him in Ozaki's collection. The slides include specimens of digeneans, *C. plagiorchis* (6 immature and 15 gravid specimens), *Asymphylogaster macrostoma* Ozaki, 1925 (3 gravid specimens), and *Genarchoopsis goppo* Ozaki, 1925 (1 gravid specimen) (my identification; see also Shimazu, 1992, 1995a, b, 1997). Ozaki (1925a, 1926, 1929) described all of these three species on the basis of the specimens found in *M. obscura* from Saijo, Hiroshima Prefecture (see also Shimazu, 1995b). It seems certain that the above-mentioned specimens are parts of his original ones of the three species (see Shimazu, 1992, 1995a, b). The specimens of *C. plagiorchis* morphologically agree well with Ozaki's (1926, 1929) descriptions for the species and the specimens described in this paper.

Yamaguti (1934, 1939, 1942) described the specimens of lots 1 and 9, 4 and 10, and 3, respectively. Yamaguti (1942) briefly described the species from *Misgurnus anguil-*

licaudatus (Cobitidae) from Nisinomiya, Hyogo Prefecture; and from *Gobius similis* [*sensu lato*] [= *Rhinogobius* sp.] (Gobiidae) from Sirakawa, Kyoto. His specimens have not yet been located.

In the immature specimens of lot 7, a thin membrane surrounded the distalmost part of the external seminal vesicle and a small number of gland cells (prostatic?) (Fig. 4). Bray (1987) noted the presence of a similar membrane in the adult of *Dactylostomum griffithsi* Bray, 1987 (Opecoelinae). The two genera *Coitocaecum* and *Dactylostomum* Woolcock, 1935 are closely allied. The presence of the membrane suggests that the membrane is the vestige of the posterior membranous portion of the divided cirrus pouch as seen in the genus *Dimerosaccus* Shimazu, 1980 (given later). The cirrus pouch initially formed might be of the same type as that in the adult of the genus *Dimerosaccus*; and the portion later might change in structure with disappearance or degeneration, leaving the anterior small thick-walled portion as seen in adults of genera, *Coitocoecum* and *Opecoelus* Ozaki, 1925 (given later). As to *C. plagiorchis*, the male terminal genitalia in the metacercaria described by Komiya and Tajimi (1943) and Okabe and Shibue (1952) is similar to those in the adult as seen in this paper. The change would take place in earlier stages of development of the metacercaria or cercaria.

The adult of *C. plagiorchis* has been recorded not only from *Odontobutis obscura obscura* but also from *Chaenogobius urotaenia*, *Ch. isaza*, "Small Goro" (= *Ch. isaza*?), *Coreoperca kawamebari*, *Cottus reinii*, *Misgurnus anguillicaudatus*, *Pelteobagrus nudiceps*, and *Rhinogobius* sp. from the Kinki and Chugoku districts, Japan (Ozaki, 1926, 1929; Yamaguti, 1934, 1939, 1942; Shimazu, 1988b; this paper). The species also occurs in China: in *Mastacembelus aculeatus* (Mastacembelidae) in the vicinity of Shanghai (Komiya and Tajimi, 1943) and in *Siniperca chuatsi* (Percichthyidae) in Hubei Province (Institute of Hydrobiology, Hubei Province, 1973).

The metacercaria has been found encysted in shrimps: in *Leander paucidens* [= *Palaemon paucidens*] (Palaemonidae) from [the Katsura River, Kyoto] (Yamaguti, 1942; 1 excysted worm, MPM Coll. No. 22292); in *Caridina denticulata* [= *Neocaridina denticulata*] (Atyidae) near Tosu, Saga Prefecture (Yamaguti and Nisimura, 1944; 7 excysted worms and 10 immature and 1 gravid worms recovered from *M. obscura* fed metacercariae experimentally, MPM Coll. No. 22293); *N. denticulata* from Katayama, Hiroshima Prefecture (Okabe and Shibue, 1952); and *N. denticulata* from Kurume, Fukuoka Prefecture (Shibue, 1953). Yamaguti (1942, lot 3) and Yamaguti and Nisimura (1944) experimentally fed metacercariae to *M. obscura*, from the intestine of which they recovered gravid worms 20 and 40 days later, respectively. In China, Komiya and Tajimi (1943) described the metacercaria from *Macrobrachium nipponense* (Palaemonidae) in the vicinity of Shanghai. The cercaria is not known either in Japan or in China.

Genus *Opecoelus* Ozaki, 1925

Opecoelus Ozaki, 1925, pp. 51-52 (type species, *Opecoelus sphaericus* Ozaki, 1925).

Opecoelus: Ozaki, 1928, pp. 6-7.

Opegaster Ozaki, 1928, p. 17 (type species, *Opegaster ovata* Ozaki, 1928).

Diagnosis. Opecoelidae: Opecoelinae. Intestines fusing with each other to open through a common ventral anus near posterior end of body. Ventral sucker bearing three pairs of marginal appendages. Cirrus pouch rudimentary, small, thick-walled, muscular, enclosing small internal seminal vesicle, prostatic complex, and cirrus. External seminal vesicle large. Accessory sucker absent. Vitelline follicles extending anteriorly to various levels, sometimes entering forebody. Excretory vesicle reaching to ovary. Adults parasitic in intestine of marine and freshwater fishes.

Discussion. Ozaki (1925b) erected this genus

with *Opecoelus sphaericus* as the type species. Later Ozaki (1925c) changed the original spelling *sphaericus* to *sphaericus* without explaining the change. Since then, many subsequent workers have used this subsequent spelling. The subsequent spelling *sphaericus* is retained in this paper. Ozaki (1928) created another new genus, *Opegaster*, with *Opegaster ovata* (originally spelled *ovatus*) as the type species. Many species have since been described in both genera. These two genera are similar. Yamaguti (1951) doubted the validity of the genus *Opegaster*. According to Ozaki (1928), the most striking feature of this species [*Opegaster ovata*] is the distribution of the vitelline follicles, which are not confined to the region posterior to the ventral sucker, as in the *Opecoelus*, but extend into the neck. Cribb (1985) discussed the differences between the two genera in the protrusion of the ventral sucker, the degree of development of the marginal appendages of the ventral sucker, the posterior extent of the seminal vesicle, and the anterior extent of the vitelline follicles; and made the *Opegaster* a synonym of the genus *Opecoelus* in conclusion. I agree with him. Not only in *Opecoelus variabilis* Cribb, 1985 (see Cribb, 1985) but also in *Opecoelus mutu* Yamaguti, 1940 (Yamaguti, 1940, MPM Coll. No. 22135, 17 gravid whole-mounts; see also Yamaguti, 1951) and the digenean to be described below, the vitelline follicles extend anteriorly to various levels from specimen to specimen even in a single species. They are distributed to the postbifurcal or bifurcal or prebifurcal level. It is practically impossible to distinguish the two genera from each other.

This generic diagnosis has been based mainly on Ozaki (1925b, c, 1928) and Cribb (1985).

Opecoelus ukigori Shimazu, 1988
(Figs. 5-10)

Opecoelus ukigori Shimazu, 1988, pp. 13-15, figs. 8-13.

Material examined. 1) Lot 1. Three gravid

whole-mounts (3 paratypes, NSMT-PI 2933 and 3107) of *O. ukigori* of Shimazu (1988b) found in intestine of *Chaenogobius* sp. (for the middle-reaches type of *Chaenogobius annularis*) (Gobiidae) from the Oono River in Oono, southern Hokkaido, on 20 and 23 August 1984.

2) Lot 2. Eighteen gravid whole-mounts (holotype, NSMT-PI 3114; 17 paratypes, 3108-3113 and 3115-3117) of *O. ukigori* of Shimazu (1988b) found in intestine and rectum (accidental?) of *Chaenogobius* sp. (type host) and *Ch. urotaenia* (for the freshwater type of *Ch. annularis*) from the Tobetsu River (type locality) in Kamiiso, southern Hokkaido, on 26 August 1984.

Description. Eighteen better-prepared specimens measured (measurements of holotype in parentheses) (Figs. 5-10). Body elongate, aspinose, 1.40-2.90 by 0.36-0.70 (1.77 by 0.43); forebody 0.44-0.70 (0.53) long, 27-35 (30) % of total body length. Several pairs of gland cells present in esophageal region. Oral sucker round, subterminal, 0.11-0.17 by 0.13-0.20 (0.12 by 0.14). Prepharynx very short. Pharynx elliptical, 0.06-0.08 by 0.07-0.09 (0.08 in diameter). Esophagus short, 0.05-0.16 (0.10) long, bifurcating fairly anterior to ventral sucker; intestines united to open through a single ventral anus near posterior end of body. Ventral sucker globular, slightly protruded, located at about junction of anterior and middle one-thirds of body, 0.17-0.27 by 0.19-0.31 (0.21 by 0.23), with 3 pairs of finger-shaped marginal appendages; sucker width ratio 1:1.33-1.73 (1:1.72).

Testes subspherical, entire or sometimes slightly indented irregularly, tandem, in middle one-third of hindbody, 0.10-0.27 by 0.20-0.43 (0.16-0.23 by 0.21-0.25). Cirrus pouch rudimentary, thick-walled, muscular, small, 0.06-0.10 by 0.03-0.04 (0.11-0.04), not extending posteriorly beyond left intestine; internal seminal vesicle short, tubular; pars prostatica small, surrounded by a small number of prostatic cells; cirrus short. External seminal vesicle elongated-claviform, large, 0.24-0.43 (0.31) long, extending to posterior bor-

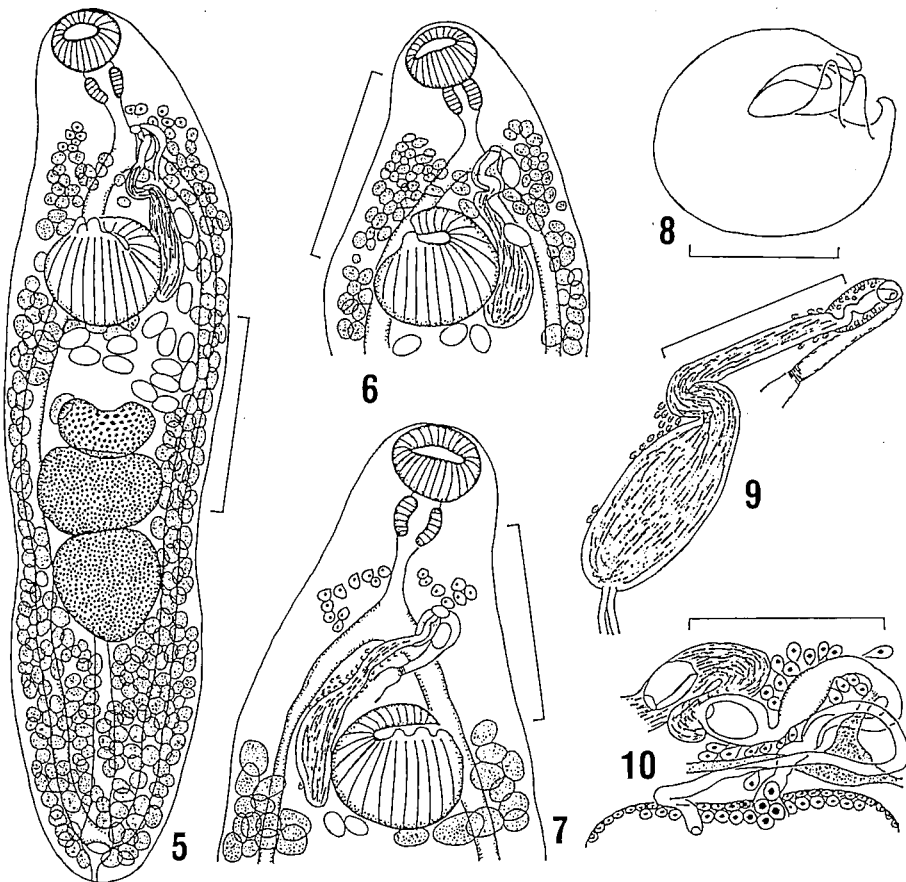


Fig. 5-10. *Opcoelus ukigori* Shimazu, 1988, gravid specimens (lot 2) from *Chaenogobius urotaenia* (formerly the freshwater type of *Ch. annularis*) and *Chaenogobius* sp. (formerly the middle-reaches type of *Ch. annularis*) from the Tobetsu River, Kamiiso, southern Hokkaido. 5: Entire worm, holotype, ventral view. 6-7: Anterior part of body, paratypes, showing anterior extent of vitellaria, ventral view. 8: Ventral sucker, paratype, ventral view. 9: Terminal genitalia, paratype, ventral view. 10: Ovarian complex, paratype, dorsal view.

(Scale bars: 0.4 mm in Figs. 5-7; 0.2 mm in Figs. 8-10.)

der of ventral sucker, surrounded partly by gland cells (prostatic?). Genital atrium small. Genital pore sinistro-submedian, a little prebifurcal. Ovary transversely reniform, median or submedian, just pretesticular, 0.08-0.16 by 0.16-0.35 (0.18 by 0.19). Ootype-complex preovarian. Laurer's canal running transversely between ootype and ovary. Seminal receptacle not seen; uterine seminal receptacle present. Uterus preovarian, with a few inter-

cecal folds; metraterm short, with a sphincter. Eggs not numerous, 58-64 by 36-40 (62-64 by 38-40) μm in balsam. Vitelline follicles rather small, ending anteriorly at from level of anterior border of ventral sucker to midlevel of esophagus (at bifurcal level in holotype), confluent post-testicularly, rarely with a few follicles located dorsal and anterior to ventral sucker; vitelline reservoir anterior or anterodextral to ovary. Excretory vesicle reaching to

ovary; excretory pore dorso- or postero-terminal.

The anterior extent of the vitelline follicles varied widely. Out of the 21 specimens studied, in 10, the vitelline follicles extended into the forebody, but not reaching the pharyngeal level; in 7, to the bifurcal level; and in 3, only just to the level of the anterior margin of the ventral sucker (Figs. 5-7).

Prevalence. In June to August, 1984, this trematode was found in *Ch. urotaenia* and *Chaenogobius* sp. only from the Oono and Tobetsu rivers in southern Hokkaido: in 5 (60-67 mm in standard body length) of 59 fish (*Chaenogobius* sp., 50-85 mm) from the Oono River; and in 3 (80-87 mm) of 6 fish (*Ch. urotaenia*, 70-100 mm) and 7 (70-85 mm) of 14 fish (*Chaenogobius* sp., 70-85 mm) from the Tobetsu River. The trematode was not found in 20 fish (*Ch. urotaenia*, 90-130 mm) from Lake Toro near Kushiro, eastern Hokkaido; in 3 fish (*Chaenogobius* sp., 45-80 mm) from the Shokanbetsu River in Mashike, central Hokkaido; in 20 fish (*Chaenogobius* sp., 70-75 mm) from the Shubunbetsu River in Mashike; or in 3 fish (*Chaenogobius* sp., 85-95 mm) from the Chitose River in Ebetsu, central Hokkaido.

Discussion. This species is most closely similar in morphology to *O. mutu* Yamaguti, 1940 and *O. variabilis* Cribb, 1985. The species differs from *O. mutu* as described by Yamaguti (1940, 1951; the type series, MPM Coll. No. 22135) from a marine teleost, *Scombrops boops* (Scombroidae), from Hamazima, Mie Prefecture, central Japan, mainly in that the external seminal vesicle is shorter, extending only to the posterior edge of the ventral sucker instead of about halfway between the ventral sucker and the ovary. The species also is different from *O. variabilis* as described by Cribb (1985) from freshwater fishes of several species of the Brisbane River system, Australia, mainly in a larger body, a shorter external seminal vesicle, longer finger-shaped appendages of the ventral sucker, and smaller eggs (58-64 by 36-40 μ m instead of 67-77 by 43-48 μ m).

The vitelline follicles were various in ante-

rior extent in the species, as in *O. variabilis*. With increasing the body size, they do not extend as far anteriorly in the latter species (see Cribb, 1985). This tendency was not clear in the present species.

The present trematode was obtained from the fish caught in the strictly freshwater region of the Oono and Tobetsu rivers. All the hitherto described species of the genus *Opecoelus* (including *Opegaster*), except at least two, are parasitic in marine fishes. *Opecoelus variabilis* completes a freshwater life cycle in Australia (Cribb, 1985). Manter (1963) reported a trematode under the name *Opecoelus mutu* from freshwater fishes in Fiji, but its life cycle is unknown. There is the possibility that the present trematode also is a true freshwater species. According to Ishino (personal communication), (1) although both types of the host fishes are amphidromous, once they have ascended from salt to fresh water, they usually never return to salt water again; and (2) it is considered that the infected fish (60-87 mm) caught in the two rivers during the months of July and August, 1984, were 2+ or 3+ years old, which means that they migrated from salt to fresh water during the months of July and August, 1981 or 1982, or that they had spent as long as two or three years in fresh water. Most presumably, they acquired infection with the trematode during the freshwater life after the upstream migration.

The species lives in *Chaenogobius urotaenia* (formerly the freshwater type of *Ch. annularis*) and *Chaenogobius* sp. (formerly the middle-reaches type of *Ch. annularis*) in southern Hokkaido. The elucidation of the life cycle is indeed needed.

Subfamily Plagioporinae Manter, 1947

Plagioporinae Manter, 1947, p. 286 (type genus, *Plagioporus* Stafford, 1904).

Diagnosis. Opecoelidae. Intestines usually ending blindly, rarely each opening through anus, united to form a cyclocoel or to open

through a common ventral anus. Ventral sucker sessile or pedunculate, without appendages. Testes usually two, rarely three to ten. Cirrus pouch enclosing whole male terminal duct, entire or divided into anterior small thick-walled and posterior large thin-walled portions. Genital pore prebifurcal, usually submedian, rarely median. Accessory sucker absent. Ovary entire to lobed. Seminal receptacle well-developed or vestigial; uterine seminal vesicle usually absent, rarely present. Eggs filamented or not. Vitelline follicles various in anterior extent. Adults parasitic usually in intestine of marine and freshwater teleosts and rarely in small intestine of amphibians.

Discussion. This subfamily diagnosis has been based chiefly on Manter (1947), Shimazu (1990), Gibson (1996), and this study.

Genus *Dimerosaccus* Shimazu, 1980

Dimerosaccus Shimazu, 1980, pp.163-164 (type species, *Allocreadium oncorhynchi* Eguchi, 1931).

Diagnosis. Opacoelidae: Plagioporinae. Intestines ending blindly. Cirrus pouch divided into two portions. Eggs not filamented. Vitelline follicles occasionally entering forebody. Excretory vesicle reaching ovary. Adults parasitic in intestine of freshwater fishes, rarely in small intestine of salamanders.

Discussion. Eguchi (1931) briefly described a new species, *Allocreadium oncorhynchi* (Allocreadiidae), with no figure. Later Eguchi (1932) gave a full description with figures for the species. Peters (1957) reexamined one of Eguchi's specimens and tentatively transferred the species to the genus *Plagioporus* Stafford, 1904 (Opacoelidae), but with some hesitancy because its cirrus pouch differs considerably from that of other species of the genus. Yamaguti (1958, 1971), who also reexamined the syntype of the species, retained the species within the genus *Allocreadium*, stating that it should be referred to an opacoelid genus. Shimazu (1980) proposed a new genus, *Dimerosaccus*, based on the species in the subfamily

Opacoelinae on account of the characteristic male terminal genitalia (see also Shimazu, 1988b). Shimazu and Awakura (1993) removed the genus to the subfamily Plagioporinae because in *D. oncorhynchi*, the cirrus pouch enclosed the whole male terminal genitalia, though divided; and the proximal part of Laurer's canal had a small dilatation, a possible vestigial seminal receptacle (or a canalicular seminal vesicle), with a small number of sperms in it. The genus is readily separated from the genus *Plagioporus* by that the cirrus pouch is divided (Eguchi, 1931, 1932; Shimazu, 1980, 1988b; this paper) instead of entire (Stafford, 1904; Miller, 1940; Shimazu, 1990; Gibson, 1996).

With regard to the divided cirrus pouch, a similar cirrus pouch is present in *Margolisia vidalensis* Bray, 1987, *Plagioporus* (*Plagioporus*) *schizothoraci* Zhang, 1992, *P. (P.) alloveris* Zhang, 1992, and *Hysterozonoides disaccus* Zhang, 1992 (Bray, 1987; Zhang, 1992). The genus *Margolisia* from a marine fish has the intestines united to open through a common ventral anus. Provided that the anatomical structure of the reproductive system is taxonomically more valuable than that of the digestive system in this case, it seems to me that the genus *Margolisia* is a member of the subfamily Plagioporinae rather than the subfamily Opacoelinae, in which Bray (1987) placed it, though. *P. (P.) schizothoraci* and *P. (P.) alloveris* both from freshwater fishes do not belong at least to the genus *Plagioporus* owing to the divided cirrus pouch. They somewhat resemble *D. oncorhynchi* (described below). However, the former has a 4-lobed ovary; and the latter, an ovary with many prominences. Zhang (1992) assigned the genus *Hysterozonoides* from a freshwater fish to the family Lepocreadiidae Odhner, 1905 (for the family diagnosis, see Gibson, 1996). However, the genus should be transferred to the family Opacoelidae because the tegument is smooth, because the ootype-complex is preovarian, and because the seminal receptacle is absent. It differs from the genus *Dimerosaccus* in having

the intestines and vitelline follicles both extending posteriorly only to the midlevel of the hindbody and the diagonal testes near the posterior end of the body.

Dimerosaccus oncorhynchi (Eguchi, 1931)

Shimazu, 1980

(Figs. 11-13)

Allocreadium oncorhynchi Eguchi, 1931, pp. 21-22, no figure.

Allocreadium oncorhynchi: Eguchi, 1932, pp. 24-28, figs. 1-6.

Plagioporus oncorhynchi: Peters, 1957, p. 140.

Dimerosaccus oncorhynchi: Shimazu, 1980, pp. 164-166, figs. 1-7.

Plagioporus honshuensis Moravec and Nagasawa, 1998, pp. 283-284, fig. 1. *N. Syn.*

Material examined. 1) Lot 1. Ten gravid whole-mounts (NSMT-P1 2169-2172) of *D. oncorhynchi* of Shimazu (1980) found in intestine of *Oncorhynchus rhodurus* f. *macrostomus* [= *O. masou ishikawae*] (Salmonidae) from the Nagara River at Gujohachiman, Gifu Prefecture, on 12 September 1975, 20 January 1977, and 31 March 1979.

2) Lot 2. Fifty-four (18 immature and 36 gravid) whole-mounts (NSMT-P1 1945-1950 and 2168) of *D. oncorhynchi* of Shimazu (1980) found in pyloric ceca and intestine of *Salvelinus leucomaenis pluvius* (Salmonidae) from the Samu River (a tributary of the Chikuma River) at Fujisawa, Iiyama, Nagano Prefecture, on 16, 17, and 24 September 1978 and 18 March 1979.

3) Lot 3. One gravid whole-mount (NSMT-P1 2173) of *D. oncorhynchi* of Shimazu (1980) found in intestine of *S. l. pluvius* from the Hime River in Hakuba, Nagano Prefecture, on 13 July 1979.

4) Lot 4. Twelve (4 immature and 8 gravid) whole-mounts (MPM Coll. No. 19260) of *D. oncorhynchi* of Shimazu (1980) found in intestine of *O. masou* f. *ishikawai* [= *O. masou masou*] from the Horei River in Sanriku, Iwate Prefecture, on 19 March 1978.

5) Lot 5. Two gravid whole-mounts (NSMT-P1 3094 and 3095) of *D. oncorhynchi* of Shimazu (1988b) found in intestine of *O. m. masou* from the Shokanbetsu River in Mashike, Hokkaido, on 1 and 2 August 1984.

6) Lot 6. Two gravid whole-mounts (NSMT-P1 3096 and 3097) of *D. oncorhynchi* of Shimazu (1988b) found in intestine of *S. leucomaenis* [= *S. l. leucomaenis*] from the Shokanbetsu River in Mashike on 26 July 1984 and 2 August 1984.

7) Lot 7. Two gravid whole-mounts (NSMT-P1 3098 and 3099) of *D. oncorhynchi* of Shimazu (1988b) found in rectum (accidental?) of *Cottus nozawae* (not *Cottus pollux*) (Cottidae) from the Shokanbetsu River in Mashike on 1 August 1984.

8) Lot 8. Twenty-three (13 immature and 10 gravid) whole-mounts (NSMT-P1 4609 and 4610) found in intestine of *S. l. pluvius* from the Matsu River in Hakuba on 25 and 26 September 1993 and 4 April 1994.

9) Lot 9. Fifty-seven (39 immature and 18 gravid) whole-mounts (NSMT-P1 4611 and 4612) found in pyloric ceca and intestine of *S. l. pluvius* from Nakakurozawa (a small stream) in Hakuba on 5 and 13 September 1994, 25 November 1994, and 24 May 1995.

Description. 1) Shimazu (1980) described the specimens of lots 1, 2, and 4. Reexamination of them has indicated that the metraterm is shorter than the anterior portion of the cirrus pouch and possesses, around the orifice, a sphincter with a crescent-shaped thickening between the cirrus and the metraterm; and that, in one specimen of lot 4, the vitellaria reach the bifurcal level. The specimen of lot 3 was similar to them in morphology and measurements. Shimazu (1980) described and figured anomalous specimens bearing probably incompletely divided testes in the specimens of lot 4.

2) Based on the specimens of lots 5-7 (Figs. 11-13). Body lanceolate-oblong, sometimes with truncate posterior end, 1.36-2.30 by 0.50-0.78; forebody 34-44% of total body length. Oral sucker 0.16-0.20 by 0.16-0.21. Prepharynx very short. Pharynx 0.11-0.16 by 0.11-

0.15. Esophagus 0.12–0.20 long. Intestinal ceca extending to near posterior end of body. Ventral sucker sessile, postbifurcal, 0.24–0.29 by 0.26–0.32; sucker width ratio 1:1.39–1.71.

Testes entire or slightly indented, in middle one-third of hindbody, 0.11–0.27 by 0.20–0.35. Anterior portion of cirrus pouch thick-walled, muscular, small, 0.08–0.13 by 0.05–0.06, enclosing very short distal part of seminal vesicle, small pars prostatica, a small number of prostatic cells, and short cirrus; posterior portion thin-walled, membranous, large, 0.16–0.30 long, not extending posteriorly beyond midlevel of ventral sucker, enclosing undulating tubular proximal part of seminal vesicle and a large number of gland cells (prostatic?). Genital atrium small. Genital pore sinistro-submedian at pharyngeal level. Ovary transversely reniform, triangular, or weakly trilobed, 0.09–0.16 by 0.16–0.24. Ootype-complex anterior or anterolateral to ovary. Laurer's canal having a small dilatation to contain a small number of sperms and ova at proximal part, opening dorsally to ovary. Uterus preovarian, intercecal; metraterm well-developed, shorter than anterior portion of cirrus pouch; sphincter bearing a crescent thickening. Eggs about 20, 58–64 by 34–38 μm in balsam. Vitellaria extending anteriorly to midlevel of esophagus. Excretory vesicle reaching ovary.

There was not seen a clear-cut boundary between the two portions of the cirrus pouch in some specimens (Fig. 12). The cirrus pouch was constricted and at this constriction it was divided into the two portions. The anatomical structure of the cirrus pouch appeared to transform gradually from the muscular to the membranous wall.

3) The specimens of lots 8 and 9 were morphologically similar to those of lots 1–4.

Discussion. Eguchi (1931, 1932) described this species as *A. oncorhynchi* from the digestive tract (mostly the intestine) of *Oncorhynchus macrostomus* [= *O. masou ishikawae*] from the Nagara River (the exact locality not specified). Probably, all of Eguchi's original specimens have already been lost (Shimazu,

1980). Shimazu (1980) described the specimens of lots 1–4, and Shimazu (1988b) reexamined them and described the specimens of lots 5–7. Shimazu and Awakura (1993) reported adults of the species from *O. m. masou* caught at sea. Moravec and Nagasawa (1998) proposed a new species, *Plagioporus honshuenensis*, on the basis of the specimens found in the intestine of *Liobagrus reini* (Amblycipitidae) from the Sho River at Ohta, Toyama Prefecture, Japan. My reexamination of three paratypes of this species (NSMT-P1 5026–5028) has shown that the species is conspecific with *D. oncorhynchi*. Many worms of the species were found in the intestine of *Co. pollux* and *S. l. pluvis* from the Ide River at Araya, Iiyama, on 24 September and 1 October 1995, respectively; but these specimens have already been lost (my unpublished data).

The specimens from Honshu (lots 1–4, 8, and 9; Shimazu, 1980, figs. 1 and 3; and those of Moravec and Nagasawa, 1998) and those from Hokkaido (lost 5–7) agree well with each other but differ in anterior extent of the vitelline follicles. In the former (Honshu form), the vitelline follicles end posterior to the bifurcal level; but in the latter (Hokkaido form), anterior to it (see also Shimazu, 1988b; Shimazu and Awakura, 1993; Shimazu, 1994). It is not certain as yet whether this difference is sufficiently significant to distinguish species.

The adult stage of the species has so far been recorded from *Cottus nozawae*, *Co. pollux*, *Liobagrus reini*, *Oncorhynchus masou ishikawae*, *O. m. masou*, *Salvelinus leucomaenis leucomaenis*, and *S. l. pluvis* from the Hokkaido, Tohoku, and Chubu districts, Japan (Eguchi, 1931, 1932; Shimazu, 1980, 1988b; this paper). In addition, one gravid worm (NSMT-P1 4613) of the Honshu form was found in the small intestine of the salamander *Onychodactylus japonicus* (Amphibia: Caudata: Hynobiidae) from Nakakurozawa in Hakuba on 25 November 1994 (my unpublished data). The life cycle remains unknown.

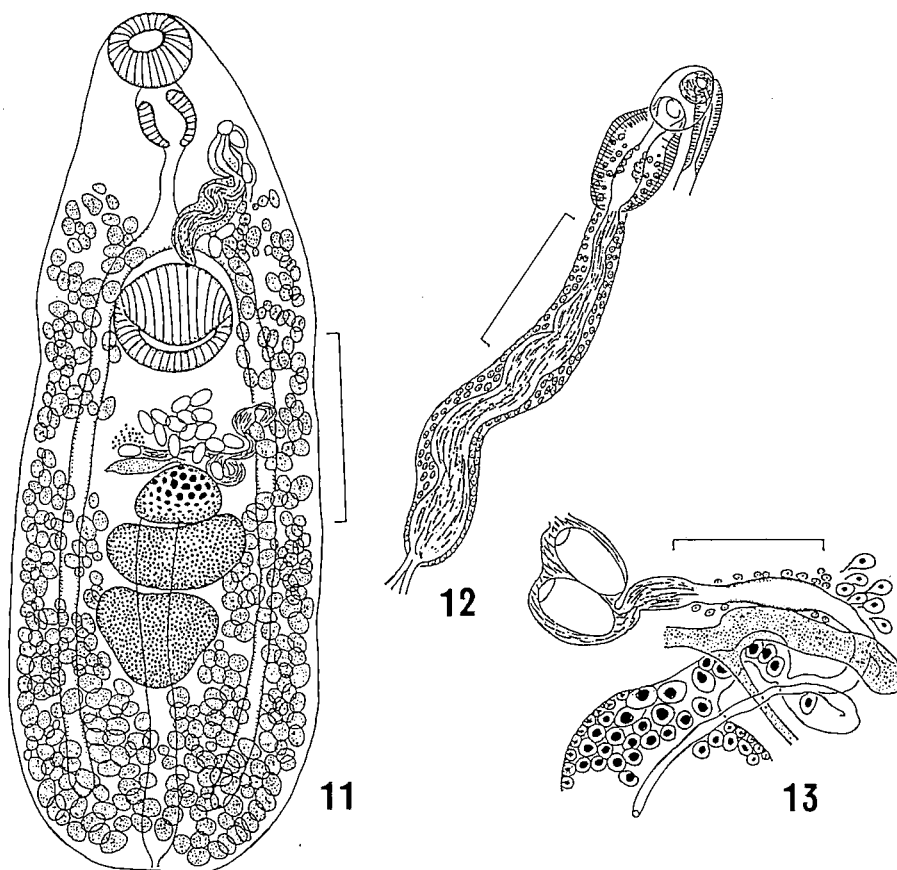


Fig. 11-13. *Dimerosaccus oncorhynchi* (Eguchi, 1931) Shimazu, 1980, gravid specimens (lot 5) from *Oncorhynchus masou masou* from the Shokanbetsu River, Mashike, Hokkaido. 11: Entire worm, ventral view. 12: Terminal genitalia, ventral view. 13: Ovarian complex, dorsal view. (Scale bars: 0.5 mm in Fig. 11; 0.1 mm in Figs. 12-13.)

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