Bull. Natl. Mus. Nat. Sci., Ser. A, 43(1), pp. 1–28, February 22, 2017

Digeneans Parasitic in Freshwater Fishes (Osteichthyes) of Japan X. Opecoelidae, Plagioporinae

Takeshi Shimazu

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

(Received 24 November 2016; accepted 22 December 2016)

Abstract This paper reviews species of the subfamily Plagioporinae Manter, 1947 in the family Opecoelidae Ozaki, 1925 (Trematoda, Digenea, Allocreadioidea) parasitic in freshwater fishes of Japan: four identified and one unidentified species of *Neoplagioporus* Shimazu, 1990, three identified and one unidentified species of *Urorchis* Ozaki, 1927, and Opecoelidae gen. sp. of Shimazu (1990). Each species is described and figured. A neotype is designated for *Podocotyle ayu* Takahashi, 1928, or now *Neoplagioporus ayu* (Takahashi, 1928). The type host is *Plecoglossus altivelis altivelis* (Temminck and Schlegel, 1846) (Plecoglossidae), which was collected in the Asahi River at Takebe-cho (34°52′N, 133°54′E) (type locality), Kita-ku, Okayama City, Okayama Prefecture, Japan. A neotype is designated for *Urorchis goro* Ozaki, 1927. The type host is *Tridentiger brevispinis* Katsuyama, Arai, and Nakamura, 1972 (Gobiidae), which was collected in the Gantsu River at Yabata (36°0′N, 140°31′E) (type locality), Namegata City, Ibaraki Prefecture, Japan. The life cycle of *U. goro* is briefly mentioned. Morphological differences between *Neoplagioporus* and *Urorchis* are discussed. Keys to genera of the subfamily Plagioporinae in Japan and species of *Neoplagioporus* in Japan are presented.
Key words: Digeneans, Opecoelidae, Plagioporinae, *Neoplagioporus*, *Urorchis*, neotypes, life cycle, freshwater fishes, Japan, review.

Introduction

This is the tenth paper of a series that reviews adult digeneans (Trematoda) parasitic in freshwater fishes (Osteichthyes) of Japan (Shimazu, 2013). Japanese species of the family Opecoelidae Ozaki, 1925 *sensu* Cribb (2005b) in the superfamily Allocreadioidea Looss, 1902 *sensu* Cribb (2005a) are classified into two subfamilies, Opecoelinae Ozaki, 1925 and Plagioporinae Manter, 1947 (Shimazu, 2016). The species of the subfamily Opecoelinae were already reviewed (Shimazu, 2016). This contribution deals with four identified and one unidentified species of *Neoplagioporus* Shimazu, 1990, three identified and one unidentified species of *Urorchis* Ozaki, 1927, and Opecoelidae gen. sp. of Shimazu (1990b) in the subfamily Plagioporinae. In this subfamily, the intestines end blindly; the cirrus pouch encloses the whole bipartite seminal vesicle, prostatic complex, and ejaculatory duct; a canalicular seminal receptacle is present; and a uterine seminal receptacle is absent. Neotypes are designated for *Podocotyle ayu* Takahashi, 1928, or now *Neoplagioporus ayu* (Takahashi, 1928), and *Urorchis goro* Ozaki, 1927. The life cycle of *U. goro* is briefly mentioned. Morphological differences between *Neoplagioporus* and *Urorchis* are discussed. Keys to genera of the subfamily Plagioporinae in Japan and species of *Neoplagioporus* 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; cbp, cercarial body proper; cp,

cirrus pouch; ct, cercarial tail; cvd, common vitelline duct; e, esophagus; ed, ejaculatory duct; egg, egg in uterus and metraterm; ep, excretory pore; ev, excretory vesicle; fc, flame cell; ga, genital atrium; gp, genital pore; gpr, genital primordium; i, intestine; Lc, Laurer's canal; m, metraterm; 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; sr, seminal receptacle; t, testis; tnc, transverse nerve commissure; u, uterus; vd, vitelline duct; vf, vitelline follicles; vs, ventral sucker.

Key to two genera of the subfamily Plagioporinae in this paper

1.1. Intestines ending in testicular region of body or posterior to it; uterus coiled between anterior testis (rarely posterior testis) and ventral sucker, not extending into post-testicular region; uterine eggs not embryonated; vitelline follicles present or absent in post-testicular region ..... *Neoplagioporus* Shimazu, 1990

1.2. Intestines ending in testicular region or anterior to it; uterus coiled in all available space of hindbody, extending into post-testicular region; uterine eggs fully embryonated; vitelline follicles absent in post-testicular region ..... *Urorchis* Ozaki, 1927

Superfamily Allocreadioidea Looss, 1902

Family Opecoelidae Ozaki, 1925

Subfamily Plagioporinae Manter, 1947

Genus ***Neoplagioporus*** Shimazu, 1990

Neoplagioporus zacconis (Yamaguti, 1934)

(Figs. 1–4)

Caudotestis zacconis Yamaguti, 1934: 292–293, fig. 21; Yamaguti, 1938: 20, plate fig. 1; Yamaguti, 1942: 332–333.

Plagioporus (*Caudotestis*) *zacconis*: Yamaguti, 1954 [not 1953]: 76; Manter, 1954: 514; Yamaguti, 1958: 119; Yamaguti, 1971: 185.

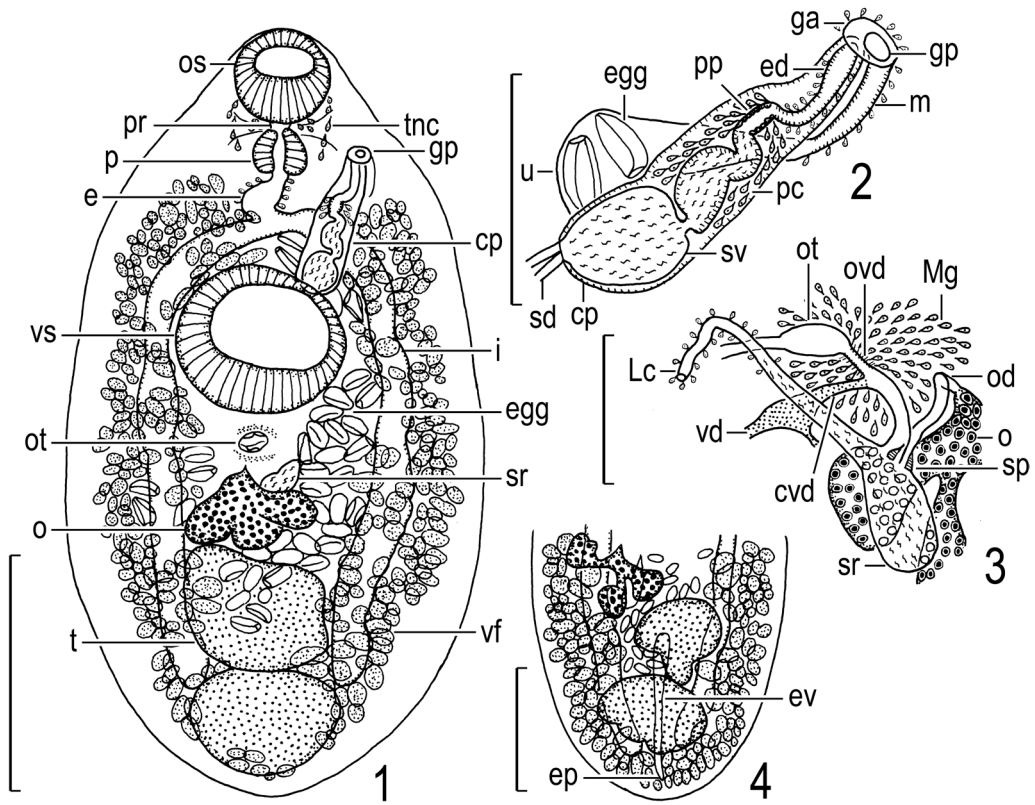
Plagioporus (*Plagioporus*) *zacconis*: Skryabin and Koval, 1958: 533.

Neoplagioporus zacconis: Shimazu, 1990b: 387–388, figs. 1–5; Shimazu and Urabe, 2005: 7–8, figs. 11–14; Shimazu, 2008: 56, fig. 11; Shimazu, Urabe, and Grygier, 2011: 48–50, figs. 62–64.

Hosts in Japan. *Nipponocypris temminckii* (Temminck and Schlegel, 1846) (Cyprinidae) (type host) (Yamaguti, 1934; Shimazu, 1990b, 2008; Nakamura *et al.*, 2000; Shimazu and Urabe, 2005; Urabe and Higa, 2006; this paper), *Liobagrus reinii* Hilgendorf, 1878 (Amblycipitidae) (Shimazu and Urabe, 2005), *Oncorhynchus masou masou* (Brevoort, 1856) (Salmonidae) (Yamaguti, 1942; Shimazu, 1990b), *Opsariichthys uncirostris uncirostris* (Temminck and Schlegel, 1846) (Cyprinidae) (Yoshida and Urabe, 2005; this paper), *Pungtungia herzi* Herzenstein, 1892 (Cyprinidae) (Nakamura *et al.*, 2000), and *Zacco platypus* (Temminck and Schlegel, 1846) (Cyprinidae) (Yamaguti, 1938; Shimazu, 1990b, 2007, 2008; Nakamura *et al.*, 2000; Shimazu and Urabe, 2005; Yoshida and Urabe, 2005; Urabe and Higa, 2006; Shimazu *et al.*, 2011; this paper).

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

Geographical distribution. (1) Ibaraki Prefecture: Lake Kasumigaura at Tsuchiura City (Yamaguti, 1942; Shimazu, 1990b). (2) Saitama Prefecture: Oppe River at Ogose Town; and Iruma River at Hanno City (Shimazu, 1990b). (3) Tokyo: Tama River at Fuchu City (this paper). (4) Nagano Prefecture: Hiroi River at Kotobuki, Iiyama City (Shimazu, 2007); Chikuma River at Ueda City (Shimazu, 1990b); Lake Suwa (Yamaguti, 1938; Shimazu, 1990b); Lake Suwa at Suwa City (Shimazu, 2007); and Tenryu River at Ina City (Shimazu, 2007). (5) Shiga Prefecture: Yasu River at Maeno, Tsuchiyama-cho, Koka



Figs. 1–4. *Neoplagioporus zacconis*, adult specimens found in intestine of *Nipponocypris temminckii*. 1, holotype of *Caudotestis zacconis* (MPM Coll. No. 22221), entire body, ventral view; 2, holotype, terminal genitalia, ventral view; 3, specimen (NSMT-Pl 5270), ovarian complex, dorsal view; 4, specimen (NSMT-Pl 5270), posterior part of body, ventral view. Scale bars: 0.5 mm in Figs. 1 and 4; 0.2 mm in Figs. 2–3.

City (Shimazu *et al.*, 2011). (6) Kyoto Prefecture: Uji River at Uji City (Shimazu and Urabe, 2005); and Uji Power Station pond at Yamada, Uji City (Shimazu *et al.*, 2011). (7) Nara Prefecture: Takami River at Kotsugawa, Higashiyoshino Village (Nakamura *et al.*, 2000; Shimazu and Urabe, 2005). (8) Wakayama Prefecture: Tonda River at Fukusada, Kurisugawa, and Ookawa, all Nakahechi, Tanabe City (Shimazu, 2008). (9) Hyogo Prefecture: Asago River (type locality) (Yamaguti, 1934; Shimazu, 1990b; this paper). (10) Hiroshima Prefecture: Kannose River at Matsugase, Kimita-cho, Miyoshi City (Shimazu, 1990b; this paper); and Nukui River at Hara, Hachihonmatsu-cho, Higashihiroshima City (this paper). (11) Tokushima Prefecture: Kaifu River at Higashikuwabara, Ogawa; Nakano, Aikawa; and Yoshino, all Kaiyo Town (Shimazu, 2008). (12) Kochi Prefecture: Sakura River at Koda, and Matsuda River at Ninomiya, both Sukumo City (Shimazu, 2008). (13) Fukuoka Prefecture: Naka River at Terase Bridge, Narutake, Nakagawa Town (Urabe and Higa, 2006). (14) Oita Prefecture: Chikugo River at Kobuchi Bridge, Miyoshikobuchi-machi (Yoshida and Urabe, 2005; this paper) and Ooyama River at Seiwa Bridge, Ooyama-machi, both Hita City (this paper).

In Korea (*e.g.*, Kim *et al.*, 1998) and China (*e.g.*, Wang *et al.*, 1985).

Material examined. (1) 2 specimens (Yamaguti's Collection, MPM Coll. No. 22221, holotype and 1 paratype of *Caudotestis zacconis*) of *Neoplagioporus zacconis*, adult, ex intestine of *Nipponocypris temminckii* (syn. *Zacco temminckii*), Asago [not Asako] River (exact collect-

ing locality not indicated), 23 March 1932 (Yamaguti, 1934; Shimazu, 1990b). (2) 1 (Yamaguti's Collection, MPM Coll. No. 22222) of *N. zacconis*, adult, ex intestine of *Oncorhynchus masou masou* (syn. *On. masou*) (land-locked form), Lake Kasumigaura, 4 April 1940 (Yamaguti, 1942; Shimazu, 1990b). (3) 9 (NSMT-Pl 5846), adult, ex intestine of *Z. platypus*, Tama River, 3 August 2011. (4) 6 (NSMT-Pl 3624–3626) of *N. zacconis*, immature, adult, ex intestine of *Z. platypus*, Oppe and Iruma rivers, 19 May 1976, 13 October 1976 (Shimazu, 1990b). (5) 3 (Yamaguti's Collection, MPM Coll. No. 22178) of *N. zacconis*, adult, ex intestine of *Z. platypus* (not *Z. temminckii*), Lake Suwa (exact collecting locality not indicated), 17 May 1935 (Yamaguti, 1938; Shimazu, 1990b). (6) 1 (NSMT-Pl 5482) of *N. zacconis*, adult, ex intestine of *Z. platypus*, Lake Suwa at Suwa City, 14 November 1991 (Shimazu, 2007). (7) 5 (NSMT-Pl 3623) of *N. zacconis*, immature, adult, ex intestine of *Z. platypus*, Chikuma River, 1 June 1973 (Shimazu, 1990b). (8) 16 (NSMT-Pl 5483–5487, 5794) of *N. zacconis*, immature, adult, ex intestine of *Z. platypus*, Hiroi River, 24 November 1996, 12 June 1999, 10 July 1999, 26 September 1999, 16 October 1999 (Shimazu, 2007). (9) 2 (NSMT-Pl 5488) of *N. zacconis*, adult, ex intestine of *Z. platypus*, Tenryu River, 9 September 2000 (Shimazu, 2007). (10) 2 (LBM 1-54) of *N. zacconis*, immature, ex intestine of *Z. platypus*, Yasu River, 18 October 1997 (Shimazu *et al.*, 2011). (11) 33 (NSMT-Pl 5268, 5269, [not 5257]) of *N. zacconis*, immature, adult, ex intestine of *Z. platypus*, Uji River, 30 April 1998, 2 May 1998 (Shimazu and Urabe, 2005). (The measurements given are erroneous. Correct measurements will be obtained by multiplying them by 0.8.) (12) 13 (LBM 7-33) of *N. zacconis*, immature, adult, ex rectum (accidental (?)) of *Z. platypus*, Uji Power Station pond, 2 February 2001 (Shimazu *et al.*, 2011). (13) Specimens of *N. zacconis*, Takami River: 22 (NSMT-Pl 5270), adult, ex intestine of *Ni. temminckii*, 26–28 and 30 July 1999; and 15 (NSMT-Pl 5257, 5271), immature, adult, ex intestine of *Liobagrus reinii*, 27, 28, and 30 July 1999 (Shimazu and Urabe, 2005). (The measurements given are erroneous. Correct measurements will be obtained by multiplying them by 0.8.) (14) 3 (NSMT-Pl 3627) of *N. zacconis*, adult, ex intestine of *Z. platypus*, Kannose River at Matsugase, Kimita Village, now Kimita-cho, Miyoshi City, 30 October 1976 (Shimazu, 1990b). (15) 9 (NSMT-Pl 5793), adult, ex intestine of *Ni. temminckii*, Nukui River, 25 July 1991. (16) Specimens of *N. zacconis*: 5 (NSMT-Pl 5547), adult, ex intestine of *Z. platypus*, Tonda River, 3 August 1999; 17 (NSMT-Pl 5548–5550), immature, adult, ex intestine of *Z. platypus*, Kaifu River, 11, 12, 14, and 16 September 1998; 1 (NSMT-Pl 5551), adult, ex intestine of *Z. platypus*, Matsuda River, 6 August 2000; 15 (NSMT-Pl 5552–5554), immature, adult, ex intestine of *Ni. temminckii*, Tonda River, 2–4 August 1999; and 13 (NSMT-Pl 5555), immature, adult, ex intestine of *Ni. temminckii*, Sakura River, 29 July 2000 (Shimazu, 2008). (17) 8 (Urabe's personal collection) of *N. zacconis*, immature, adult, ex intestine of *Z. platypus* and *Opsariichthys uncirostris uncirostris*, Chikugo River, 15 April 2003, 25 August 2003 (Yoshida and Urabe, 2005). (18) 7 (Urabe's unpublished specimens) of *N. zacconis*, adult, ex intestine of *O. uncirostris uncirostris*, Ooyama River, 19 September 2002.

Description. Based on 77 adult specimens (MPM Coll. No. 22221, NSMT-Pl 3623–3627, 5268–5271) (Figs. 1–4). Body broad-ovate, small, 1.42–3.33 by 0.67–1.56 (holotype, 1.61 by 0.88, Figs. 1–2); forebody 0.63–1.46 long, occupying 35–47% of body length. Oral sucker 0.18–0.28 by 0.17–0.30. Prepharynx very short. Pharynx 0.10–0.17 by 0.09–0.17. Esophagus bifurcating about halfway between pharynx and ventral sucker. Intestines ending blindly at about midlevel of testicular region or posterior border of posterior testis. Ventral sucker 0.29–0.58 by 0.31–0.53; sucker width ratio 1 : 1.4–2.1. Testes entire or slightly indented irregularly, 0.09–0.62 by 0.10–0.75, median, tandem or slightly oblique, contiguous, in posterior half of hindbody, close to posterior extremity of body. Cirrus

pouch entire, clavate, thick-walled, overlapping ventral sucker posteriorly, 0.28–0.80 by 0.08–0.18. Seminal vesicle straight or sinuous, distinctly bipartite, occupying posterior half of cirrus pouch; anterior portion clavate, thick-walled; posterior portion globular, thin-walled. Pars prostatica small; prostatic cells well developed. Ejaculatory duct short, sometimes slightly everted. Genital atrium small. Genital pore sinistrally submedian, at pharyngeal level. Ovary deeply 3-lobed, 0.16–0.34 by 0.16–0.69, immediately pretesticular and median, or dextrally submedian and anterolateral to anterior testis; lobes rarely further lobulated; oviduct long, connecting to side of seminal receptacle on its way to ovovitelline duct, with sphincter at pore going into seminal receptacle, with no sphincter at pore going out of seminal receptacle, two pores opening side by side (Fig. 3). Seminal receptacle canalicular, clavate, 0.10–0.43 by 0.05–0.16, almost median, dorsal to ovary, tapering anteriorly to change into short Laurer's canal. Ootype vesicular, large; Mehlis' gland well developed, emptying into ovovitelline duct. Uterus coiled several times between anterior testis and ventral sucker, slightly overlapping intestines, extending posteriorly to middle of anterior testis (Fig. 4) or rarely of posterior testis (see Shimazu, 1990b, fig. 5); metraterm about half as long as cirrus pouch. Eggs fairly numerous, light brown, 63–80 by 38–44 μm (collapsed). Vitelline follicles distributed from pharynx to posterior extremity of body, usually absent from lateral and posterior peripheral fields of body (Fig. 1) but rarely present in these fields (Fig. 4), separate anteriorly, confluent posteriorly. Excretory vesicle reaching to middle of anterior testis; excretory pore posterodorsal.

Remarks. Yamaguti (1934) described *Caudotestis zacconis* as a new species on the basis of four adult specimens. Yamaguti's Collection includes only two (MPM Coll. No. 22221) of them at present (Shimazu, 1990b; this paper). Shimazu (1990b) established a new genus, *Neoplagioporus*, with *C. zacconis*, or now *N. zacconis* (Yamaguti, 1934), as the type species.

The ovary in this species is usually deeply 3-lobed, and the lobes were rarely further lobulated (Yamaguti, 1934, 1938, 1942; Shimazu, 1990b; Shimazu and Urabe, 2005; Shimazu, 2008; this paper). However, Kim *et al.* (1998) described it as usually deeply 2-lobed but rarely deeply 3-lobed in adult specimens found in *Z. platypus* from Korea. It is immediately pretesticular and median, or dextrally submedian and anterolateral to the anterior testis, or rarely almost opposite (or dextral to) the anterior testis (Yamaguti, 1938; Shimazu, 2008, fig. 11; this paper). The adult specimen (LBM 7-33) found in *Z. platypus* from Uji Power Station pond had a 3-lobed ovary located sinistral to the anterior testis (Shimazu *et al.*, 2011, fig. 65).

The seminal receptacle in *Neoplagioporus* and *Urorchis* is canalicular and clavate, tapering anteriorly to change into Laurer's canal at its anterior end (Takahashi, 1928, 1929; Yamaguti, 1934, 1942; Shimazu, 1990a, b, 2016; Shimazu and Urabe, 2005; Shimazu *et al.*, 2011; this paper, Figs. 3 and 14). The oviduct connects to the side of the seminal receptacle on its way to the ovovitelline duct, with a sphincter at the pore going into the seminal receptacle, but with no sphincter at the pore going out of the seminal receptacle. The two pores open side by side.

As seen above, *N. zacconis* has been recorded from cyprinids (four species), an amblycipitid, and a salmonid in rivers and lakes (including a pond) in Kanto Region (Ibaraki and Saitama Prefectures and Tokyo), Chubu Region (Nagano Prefecture), Kinki Region (Shiga, Kyoto, Nara, Wakayama, and Hyogo Prefectures), Chugoku Region (Hiroshima Prefecture), Shikoku Region (Tokushima and Kochi Prefectures), and Kyushu Region (Fukuoka and Oita Prefectures).

Life cycle. Not known.

Neoplagioporus ayu (Takahashi, 1928)

(Fig. 5)

Podocotyle ayu Takahashi, 1928: 51–55, figs. 1–3; Takahashi, 1929: 1927–1928, pl. 2, fig. 8; Yamaguti, 1934: 295, fig. 22.

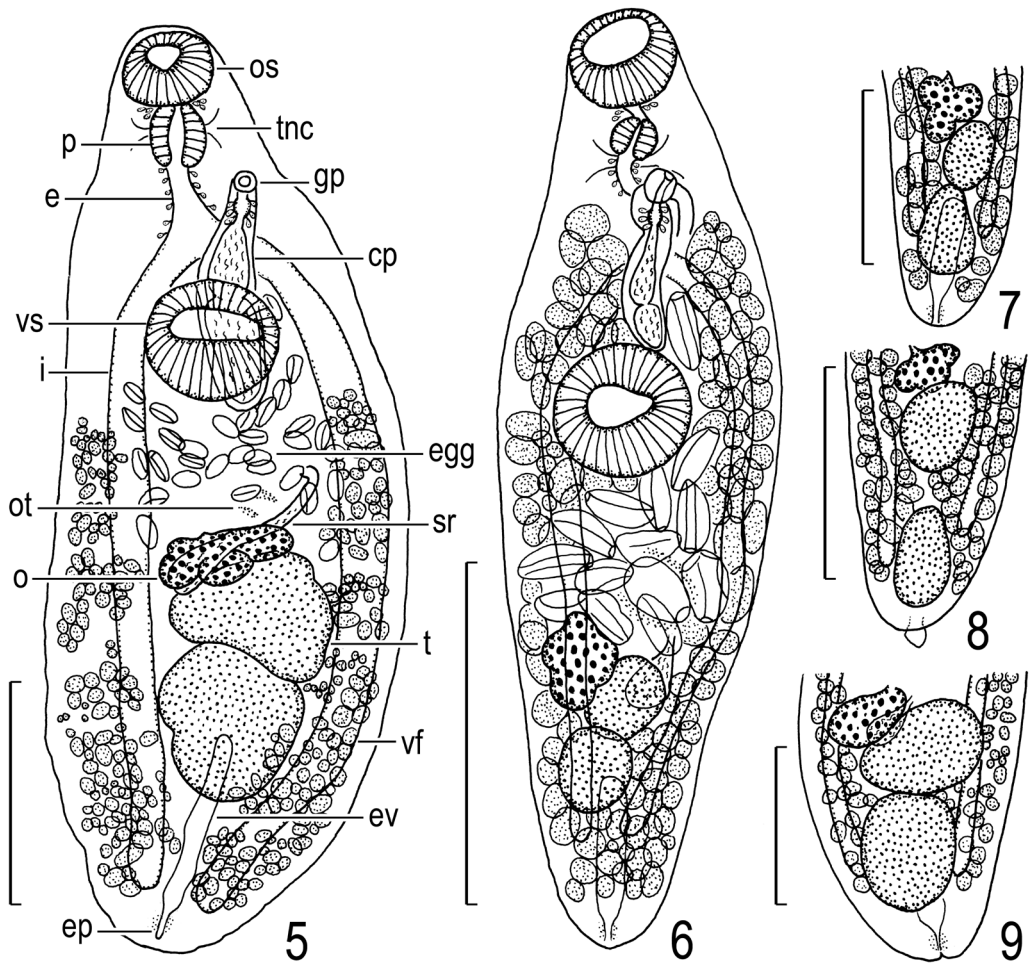


Fig. 5. *Neoplagioporus ayu*, neotype (NSMT-Pl 5889), adult specimen found in intestine of *Plecoglossus altivelis altivelis*, entire body, ventral view. Scale bar: 0.5 mm.

Figs. 6–9. *Neoplagioporus elongatus*, adult specimens. 6, syntype (MPM Coll. No. 30024) of *Lebouria elongata* found in "*Sarcocheilichthys variegatus* (Temminck et Schlegel)," entire body, ventral view, *elongatus* type of *N. elongatus*; 7, syntype of *L. elongata*, posterior part of body, ventral view, *elongatus* type; 8, holotype of *Caudotestis orientalis* (MPM Coll. No. 22219) found in intestine of "*Sarcocheilichthys variegatus* (Temm. et Schl.)," posterior part of body, ventral view, *orientalis* type; 9, holotype (MPM Coll. No. 22220) of *C. gnathopogonis* found in intestine of *Gnathopogon elongatus elongatus*, posterior part of body, ventral view, *orientalis* type. Figs. 7 and 9 and Fig. 8 redrawn from Shimazu *et al.* (2011) and Shimazu (1990b), respectively. Scale bars: 0.5 mm in Figs. 6 and 8; 0.3 mm in Figs. 7 and 9.

Neoplagioporus ayu: Shimazu, 1990b: 390–391, figs. 6–9; Shimazu, 2008: 54–55, fig. 10.

Host in Japan. Plecoglossus altivelis altivelis (Temminck and Schlegel, 1846) (Plocoglossidae) (type host) (Takahashi, 1928, 1929; Yamaguti, 1934; Shimazu, 1990b, 2008; Yanagi *et al.*, 2010).

Sites of infection. Intestine and pyloric ceca.

Geographical distribution. (1) Kyoto Prefecture: Hozu River; and Yura River at Komori, Ooe-cho, Fukuchiyama City (Yamaguti, 1934; Shimazu, 1990b; this paper). (2) Wakayama Prefecture: Tonda River at Fukusada and Ookawa, Nakahechi, Tanabe City (Shimazu, 2008). (3) Okayama Prefecture: Asahi River (Takahashi, 1928) and Asahi River at Takebe-cho (type local-

ity), Kita-ku, Okayama City (this paper); and in the vicinity of Okayama City (Takahashi, 1929). (4) Kochi Prefecture: Matsuda River at Nakatsuno and Ninomiya, Sukumo City (Shimazu, 2008). (5) Oita Prefecture: Chikugo River at Kobuchi Bridge, Miyoshikobuchi-machi, Hita City (Yoshida and Urabe, 2005; this paper) and at Hita City (Yanagi *et al.*, 2010).

Material examined. (1) 5 specimens (Yamaguti's Collection, MPM Coll. No. 22579, *Podocotyle ayu*) of *Neoplagioporus ayu*, adult, ex intestine of *Plecoglossus altivelis altivelis* (syn. *Pl. altivelis*), Hozu River (exact collecting locality not indicated), 15 July 1929, 16 July 1932 (Yamaguti, 1934; Shimazu, 1990b). (2) 3 (Yamaguti's Collection, MPM Coll. No. 22624, *Po. ayu*) of *N. ayu*, adult, ex intestine of *Pl. altivelis altivelis*, Yura River at Komori, now in Ooe-cho, Fukuchiyama City, 20 November 1929 (Yamaguti, 1934; Shimazu, 1990b). (3) 45 (NSMT-Pl 5889, slightly flattened, 21 September 2012; 5890, heat-killed, 21 September 2013), adult, ex intestine of *Pl. altivelis altivelis*, Asahi River at Takebe-cho. (4) 2 (NSMT-Pl 5543, 5544) of *N. ayu*, adult, ex intestine of *Pl. altivelis altivelis*, Tonda River, 2 and 3 August 1999 (Shimazu, 2008). (5) 6 (NSMT-Pl 5545, 5546) of *N. ayu*, adult, ex intestine and pyloric ceca of *Pl. altivelis altivelis*, Matsuda River, 6 and 7 August 2000 (Shimazu, 2008). (6) 55 (Urabe's personal collection) of *N. ayu*, immature, adult, ex intestine of *Pl. altivelis altivelis*, Chikugo River at Kobuchi Bridge, 22 September 2003 (Yoshida and Urabe, 2005).

Description. 1) Based on 30 slightly flattened adult specimens (NSMT-Pl 5889) (Fig. 5). Body elongate-ovate, small, 1.40–2.06 by 0.60–0.81; forebody 0.48–0.68 long, occupying 28–34% of body length. Oral sucker 0.14–0.17 by 0.16–0.20. Prepharynx very short. Pharynx large, 0.11–0.15 by 0.11–0.13. Esophagus bifurcating between pharynx and ventral sucker. Intestines extending to near posterior extremity of body. Ventral sucker 0.21–0.27 by 0.25–0.30; sucker width ratio 1 : 1.4–1.6. Testes globular or slightly indented irregularly, 0.12–0.25 by 0.32–0.35, tandem, contiguous, in middle third of hindbody. Cirrus pouch clavate, 0.32–0.53 by 0.11–0.15, extending posteriorly slightly beyond ventral sucker. Seminal vesicle occupying posterior two-thirds of cirrus pouch. Pars prostatica small; prostatic cells well developed. Ejaculatory duct short. Genital atrium shallow. Genital pore at midlevel of esophagus. Ovary 3-lobed, 0.08–0.19 by 0.21–0.30. Seminal receptacle 0.28–0.33 by 0.08–0.12. Laurer's canal fairly long. Uterus coiled between ovary and ventral sucker, overlapping intestines; metraterm about half as long as cirrus pouch. Eggs numerous, light brown, 67–78 by 39–48 μm (collapsed). Vitelline follicles distributed usually from ventral sucker to near posterior extremity of body, sometimes from intestinal bifurcation on one side or both sides of body. Excretory vesicle extending to middle or posterior border of posterior testis; excretory pore posterodorsal.

Remarks. Takahashi (1928) described *Podocotyle ayu* as a new species on the basis of adult specimens found in *Plecoglossus altivelis altivelis* from the Asahi River (exact collecting locality not indicated). He did not designate the holotype for this species. Shimazu (1990b) transferred the species from *Podocotyle* Dujardin, 1845 to *Neoplagioporus* as a new combination, *N. ayu* (Takahashi, 1928).

Takahashi (1928, fig. 2) and Shimazu (1990b, fig. 9) described Mehlis' gland as surrounding the ootype. However, Mehlis' gland actually empties into the ovovitelline duct (Takahashi, 1929; Yamaguti, 1934; this paper). Yamaguti (1934, fig. 22) described Laurer's canal as narrow with no cellular coat in its distal portion and ending blindly. However, this description is erronous: Laurer's canal is normal, opening dorsally; and what he called its distal portion is a bundle of sperm that had come out of the aperture of Laurer's canal (Shimazu, 1990b). The vitelline follicles are anteriorly distributed usually to the ventral sucker on both sides of the body but sometimes to the bifurcal level on one or both sides (Takahashi, 1928; Shimazu, 1990b, 2008; this paper). The excretory vesicle reaches usually

to the middle of the posterior testis [not to the ovary as described by Shimazu (2008)] but sometimes only to the posterior border of the posterior testis (Takahashi, 1928; Shimazu, 1990b; Shimazu, 2008, fig. 10).

As mention above, *N. ayu* has been recorded from *Pl. altivelis altivelis* in rivers in Kinki Region (Kyoto and Wakayama Prefectures), Chugoku Region (Okayama Prefecture), Shikoku region (Kochi Prefecture), and Kyushu Region (Oita Prefecture).

None of Takahashi's (1928, 1929) specimens of *Podocotyle ayu* are deposited in the collection of the Faculty of Medicine (formerly Okayama Igaku Senmon Gakko), Okayama University, Okayama (Toshiki Aji, personal communication, 14 November 2012), which suggests that all of them were lost. Therefore, I here designate a neotype for *Po. ayu*, as follows.

Designation of a neotype of Podocotyle ayu *Takahashi*, *1928*, *or now* Neoplagioporus ayu (*Takahashi*, *1928*). Neotype: a whole-mounted adult specimen (NSMT-Pl 5889), slightly flattened, 2.03 mm long by 0.79 mm wide, Fig. 5, 21 September 2012.

Type host. *Plecoglossus altivelis altivelis* (Temminck and Schlegel, 1846) (Plecoglossidae).

Site of infection. Intestine.

Type locality. Asahi River at Takebe-cho (34°52′N, 133°54′E), Kita-ku, Okayama City, Okayama Prefecture, Japan.

It is noteworthy that Takahashi (1929, fig. 9) described the ovarian complex of "a new species of *Podocotyle*" found in the intestine of *Pseudorasbora parva* (Temminck and Schlegel, 1846) (Cyprinidae) collected in the vicinity of Okayama City. Although he intended to describe this new species, he did not. It differs from *Po. ayu*, or now *N. ayu* (see above), in that the ovary is elliptical and the oviduct connects to the posterior end of the seminal receptacle. Takahashi's (1929) species may have been either *Neoplagioporus elongatus* (Goto and Ozaki, 1930) or *Urorchis acheilognathi* Yamaguti, 1934 (see below).

Life cycle. Not known.

The only final host *Pl. altivelis altivelis* is amphidromous. It has been uncertain whether *N. ayu* is a freshwater species or a marine (or brackish-water) species. Yanagi *et al.* (2010) proved that *N. ayu* was a freshwater species. After fry of *Pl. altivelis altivelis* raised artificially in hatcheries were released in the upper reaches of the Chikugo River at Hita City, they became infected with *N. ayu* there.

Neoplagioporus elongatus
(Goto and Ozaki, 1930)

(Figs. 6–9)

Lebouria elongata Goto and Ozaki, 1930: 75, fig. 2.
Plagioporus elongata [*sic*, should be *elongatus*]: Price, 1934: 6.
Caudotestis orientalis Yamaguti, 1934: 288–289, fig. 19.
Caudotestis gnathopogonis Yamaguti, 1934: 290–292, fig. 20.
Plagioporus (*Caudotestis*) *elongatus*: Yamaguti, 1954 [not 1953]: 76; Manter, 1954: 512; Yamaguti, 1958: 118; Yamaguti, 1971: 185.
Plagioporus (*Caudotestis*) *gnathopogonis*: Yamaguti, 1954 [not 1953]: 76; Manter, 1954: 512; Yamaguti, 1958: 118; Yamaguti, 1971: 185.
Plagioporus (*Plagioporus*) *elongatus*: Skryabin and Koval, 1958: 459, fig. 148.
Plagioporus (*Plagioporus*) *orientalis*: Skryabin and Koval, 1958: 494, 497–498, figs. 163 and 163a.
Plagioporus orientalis: Koval, 1959: 129.
Neolebouria elongatus [*sic*, should be *elongata*]: Gibson, 1976: 252.
Neoplagioporus elongatus: Shimazu, 1990b: 393–394, figs. 10–17; Shimazu and Urabe, 2005: 6–7, figs. 8–10; Shimazu, Urabe, and Grygier, 2011: 43, 45, 47, figs. 51–61.

Hosts in Japan. "*Sarcocheilichthys variegatus* (Temminck et Schlegel)" (Cyprinidae) (type host) (Goto and Ozaki, 1930; Shimazu, 1990b; Shimazu *et al.*, 2011), "*Sarcocheilichthys variegatus* (Temm. et Schl.)" (Yamaguti, 1934), "*S. variegatus*" (Shimazu, 1990b; Shimazu *et al.*, 2011), *Biwia zezera* (Ishikawa, 1895) (Cyprinidae) (Shimazu *et al.*, 2011), *Carassius auratus* subsp. 1 (Japanese name: Naga-buna) (Shimazu, 2007; this paper), *Coreoperca kawamebari* (Temminck and Schlegel, 1843) (Percichthyidae) (Urabe and Higa, 2006; this paper), *Gnatho-*

pogon elongatus elongatus (Temminck and Schlegel, 1846) (Cyprinidae) (Yamaguti, 1934; Shimazu, 1990b, 2007; Shimazu *et al.*, 2011), *Gymnogobius isaza* (Tanaka, 1916) (Gobiidae) (Shimazu *et al.*, 2011), *Gymnogobius urotaenia* (Hilgendorf, 1879) (Shimazu, 2007; Shimazu and Urabe, 2005), *Hemibarbus barbus* (Temminck and Schlegel, 1846) (Cyprinidae) (Shimazu, 1990b, 2007; Shimazu and Urabe, 2005; Shimazu *et al.*, 2011), *Hemibarbus labeo* (Pallas, 1776) (Shimazu *et al.*, 2011), *Odontobutis obscura* (Temminck and Schlegel, 1845) (Odontobutidae) (Shimazu, 1990b), *Pseudogobio esocinus esocinus* (Temminck and Schlegel, 1846) (Cyprinidae) (Yamaguti, 1934; Shimazu, 1990b, 2007; Urabe and Higa, 2006; Shimazu *et al.*, 2011; this paper), *Pseudorasbora parva* (Cyprinidae) (Shimazu, 2007), *Pungtungia herzi* (Cyprinidae) (Yoshida and Urabe, 2005; Urabe and Higa, 2006; Shimazu *et al.*, 2011; this paper), *Rhinogobius flumineus* (Mizuno, 1960) (Gobiidae) (Shimazu *et al.*, 2011), "*Rhinogobius* sp." (this paper), *Rhinogobius* sp. BW (Shimazu *et al.*, 2011), *Rhinogobius* sp. OR (Shimazu and Urabe, 2005), *Sarcocheilichthys variegatus microoculus* Mori, 1927 (Cyprinidae) (Shimazu, 1990b, 2007; Shimazu *et al.*, 2011; this paper), *Sarcocheilichthys variegatus variegatus* (Temminck and Schlegel, 1846) (Shimazu and Urabe, 2005), *Squalidus chankaensis biwae* (Jordan and Snyder, 1900) (Cyprinidae) (Shimazu and Urabe, 2005; Shimazu *et al.*, 2011), *Squalidus japonicus japonicus* Sauvage, 1883 (Shimazu *et al.*, 2011), *Tribolodon hakonensis* (Günther, 1877) (Cyprinidae) (Shimazu, 1990b; Shimazu *et al.*, 2011), and *Tridentiger brevispinis* Katsuyama, Arai, and Nakamura, 1972 (Gobiidae) (Shimazu and Urabe, 2005; Shimazu *et al.*, 2011).

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

Geographical distribution. (1) Nagano Prefecture: Lake Suwa (Shimazu, 1990b) and Lake Suwa at Suwa City (Shimazu, 2007). (2) Shiga Prefecture: Lake Biwa (type locality) (Goto and Ozaki, 1930; Yamaguti, 1934; Shimazu, 1990b; Shimazu *et al.*, 2011) and Lake Biwa basin (Daido river-2 at Kinose, Shigaraki-cho, Koka City; Hachiyadohama, Hachiyado, Otsu City; Harie River at Harie, Shin'asahi-cho, Takashima City; Imazu-cho, Takashima City; Mano, Otsu City; Momose, Chinai, Makino-cho, Takashima City; Moriyama City; Omatsu, Minamikomatsu, Otsu City; Onoe, Kohoku-cho, Nagahama City; Seta River-1 at Sekinotsu, Otsu City; and Yasu river at Maeno, Tsuchiyama-cho, Koka City) (Shimazu, 1990b; Shimazu *et al.*, 2011; this paper). (3) Kyoto Prefecture: Lake Ogura (Yamaguti, 1934; Shimazu, 1990b); Kowata Pond in Uji City (Shimazu, 1992; this paper); and Uji River at Uji City (Shimazu and Urabe, 2005). (4) Osaka Prefecture (?): Yodo River (Yamaguti, 1934; Shimazu, 1990b). (5) Hiroshima Prefecture: Seki and Kozu rivers at Shiraki-cho, Asakita-ku, Hiroshima City (this paper). (6) Fukuoka Prefecture: Naka River at Terase Bridge, Narutake, Nakagawa Town (Urabe and Higa, 2006; this paper). (7) Oita Prefecture: Chikugo River at Kobuchi Bridge, Miyoshikobuchi-machi, Hita City (Yoshida and Urabe, 2005; this paper).

In China (*e.g.*, Wang, 1984; Wang *et al.*, 1985).

Material examined. (1) 75 specimens (Ozaki's Collection, MPM Coll. No. 30024, labeled "*Lebouria* HIGAI," other data not given, syntypes of *L. elongata*) of *Neoplagioporus elongatus*, adult, ex "*Sarcocheilichthys variegatus* (Temminck et Schlegel)" (Shimazu, 1990b; Shimazu *et al.*, 2011). (2) 2 (Yamaguti's Collection, MPM Coll. No. 22631, labeled "*Caudotestis*," site of infection not given) of *N. elongatus*, immature, adult, ex "*S. variegatus*," Lake Biwa (exact collecting locality not indicated), 3 December 1938 (Shimazu, 1990b; Shimazu *et al.*, 2011). (3) 2 (Yamaguti's Collection, MPM Coll. No. 22219, holotype and 1 paratype of *Caudotestis orientalis*) of *N. elongatus*, adult, ex intestine of "*Sarcocheilichthys variegatus* (Temm. et Schl.)," Lake Ogura (not Yodo River), 26 October 1931 (Yamaguti, 1934; Shimazu, 1990b). (4) 1 (Yamaguti's Collection, MPM Coll. No. 22180, 1 paratype of *C. orientalis*), adult, ex

intestine of *Pseudogobio esocinus esocinus* (syn. *Ps. esocinus*), Yodo River (exact collecting locality not indicated, Osaka Prefecture (?)), 27 March 1928 (Yamaguti, 1934; Shimazu, 1990b). (5) 1 (Yamaguti's Collection, MPM Coll. No. 22220, holotype of *C. gnathopogonis*) of *N. elongatus*, adult, ex intestine of *Gnathopogon elongatus elongatus* (syn. *Gn. elongatus*), Lake Biwa (exact collecting locality not indicated), 13 March 1932 (Yamaguti, 1934; Shimazu, 1990b; Shimazu *et al.*, 2011). (6) 1 (Yamaguti's Collection, MPM Coll. No. 22625) of *N. elongatus*, adult, ex stomach of *Odontobutis obscura*, Lake Ogura, 4 May 1932 (Shimazu, 1990b). (7) Specimens of *N. elongatus*, Lake Biwa basin: 180 (NSMT-Pl 3628–3629, 3630 (from formalin-fixed fish), 5731, 5732, LBM 3-24, -27, -46, 8-37 to -39), immature, adult, ex intestine of *S. variegatus microoculus*, Onoe (Kohoku Town, now Kohoku-cho, Nagahama City), Imazu-cho, Harie River, Momose, Moriyama City, 4 May 1980, 3 June 1980, 29 November 1983, 1 and 2 May 1992, 5 May 2000, 19 October 2000, 24 November 2007; about 490 (NSMT-Pl 3631, 5733 (hot formalin-fixed), 3976, 5734, LBM 1-51, 7-26 to -30), immature, adult, ex intestine of *Hemibarbus barbus*, Onoe, Moriyama City, Hachiyadohama, Momose, Imazu-cho, 3 June 1980, 2 and 4 May 1992, 14 May 1998, 1 May 2001; 5 (LBM 5-43 to -47, hot formalin-fixed), adult, ex intestine of *He. labeo*, Seta River-1, 1 May 2001; 1 (NSMT-Pl 3632), adult, ex intestine of *Tribolodon hakonensis*, Onoe, 3 June 1980; 2 (LBM 1-75), adult, ex intestine of *Biwia zezera*, Hachiyadohama, 14 May 1998; 3 (LBM 1-30, -31), adult, ex intestine of *Ps. esocinus esocinus*, Yasu River, Hachiyadohama, 18 October 1997, 14 May 1998; 3 (LBM 3-42, -43, -45), adult, ex intestine of *Pungtungia herzi*, Yasu River, 14 October 2000; 1 (NSMT-Pl 5735), adult, ex intestine of *Squalidus chankaensis biwae*, Omatsu, 1 May 1992; 5 (LBM 1-14), immature, adult, ex intestine of *Sq. japonicus japonicus*, Hachiyadohama, 14 May 1998; 1 (NSMT-Pl 3977), adult, ex intestine of *Gymnogobius isaza*, Omatsu, 30 April 1992; 11 (LBM 3-18, -20 to -23), immature, ex intestine of *Rhinogobius flumineus*, Daido River-2, 1 May 2000; 7 (LBM 1-7 to -9), adult, ex "gut" (intestine (?)) of *Rhinogobius* sp. BW, Imazu-cho, 19 May 1998; and 3 (NSMT-Pl 3978, LBM 3-38, 1340000023), adult, ex intestine and "gut" (intestine (?)) of *Tridentiger brevispinis*, Omatsu, Mano, Imazu-cho, 5 May 1992, 10 June 1999, 10 July 2002 (Shimazu, 1990b; Shimazu *et al.*, 2011). (8) 2 (Yamaguti's Collection, MPM Coll. No. 22181, labeled "*Caudotestis orientalis*") of *N. elongatus*, adult, ex intestine of *S. variegatus microoculus*, Lake Suwa (exact collecting locality not indicated), 30 March 1936 (Shimazu, 1990b). (9) Specimens of *N. elongatus*, Lake Suwa at Suwa City: 25 (NSMT-Pl 5465–5469), adult, ex intestine of *S. variegatus microoculus*, 13 September 1991, 5 October 1991, 14 November 1991, 16 and 30 October 1993; 32 (NSMT-Pl 5470–5473), immature, adult, ex intestine of *Pseudorasbora parva*, 13 September 1991, 30 October 1993, 21 July 1994, 29 May 1999; 47 (NSMT-Pl 5474–5476), immature, adult, ex intestine of *Ps. esocinus esocinus*, 14 November 1991, 14 September 1992, 29 May 1999; 1 (NSMT-Pl 5477), adult, ex intestine of *Gn. elongatus elongatus*, 2 July 1992; 1 (NSMT-Pl 5478), adult, ex intestine of *H. barbus*, 18 September 1999; 1 (NSMT-Pl 5479), adult, ex intestine of *Carassius auratus* subsp. 1, 19 May 1992; and 9 (NSMT-Pl 5480), immature, ex intestine of *Gy. urotaenia*, 16 October 1993 (Shimazu, 2007). (10) 2 (Yamaguti's Collection, MPM Coll. No. 22742) of *N. elongatus*, adult, ex intestine of *Pseudorasbora parva*, Kowata Pond [not Lake Kohata], 14 May 1928 (Shimazu, 1992). (11) Specimens of *N. elongatus*, Uji River: 35 (NSMT-Pl 5261), immature, adult, ex intestine of *S. variegatus variegatus*, 30 April 1998, 2 May 1998; 212 (NSMT-Pl 55262–55263), immature, adult, ex intestine of *H. barbus*, 30 April 1998, 2 May 1998; 9 (NSMT-Pl 5264), adult, ex intestine of *Sq. chankaensis biwae*, 2 May 1998; 5 (NSMT-Pl 5265), immature, adult, ex intestine of *Gy. urotaenia*, 30 April 1998; 3 (NSMT-Pl 5266), adult, ex rectum (accidental (?)) of *Rhinogobius* sp. OR, 2 May 1998;

and 38 (NSMT-Pl 5267), adult, ex intestine and rectum of *Tr. brevispinis*, 30 April 1998, 2 May 1998 (Shimazu and Urabe, 2005). (The measurements given are erroneous. Correct measurements will be obtained by multiplying them by 0.8.) (12) 4 (NSMT-Pl 5481), adult, ex intestine of *Coreoperca kawamebari*, Seki River, 25 July 1991. (13) 6 (NSMT-Pl 5792), adult, ex intestine of "*Rhinogobius* sp.," Kozu River, 25 July 1991. (14) Specimens of *N. elongatus*, Naka River: 23 (NSMT-Pl 5461, Urabe's unpublished specimens), adult, ex intestine of *Ps. esocinus esocinus*, 25 November 2003, 23 December 2003, 18 October 2004; 2 (NSMT-Pl 5462, Urabe's unpublished specimens), adult, ex intestine of *Pu. herzi*, 8 October 2003, 31 March 2004; 2 (NSMT-Pl 5460), adult, ex intestine of *Co. kawamebari*, 8 October 2003, 25 May 2004 (Urabe and Higa, 2006). (15) 5 (Urabe's personal collection) of *N. elongatus*, immature, adult, ex intestine of *Pu. herzi*, Chikugo River, 22 and 23 January 2003, 21 October 2003 (Yoshida and Urabe, 2005).

Description. 1) Based on Ozaki's specimens (MPM Coll. No. 30024), after Shimazu *et al.* (2011), altered from the present study (Figs. 6–7). Body fusiform, widest at ventral sucker, or elongate-ovate, small, 0.96–1.45 by 0.29–0.61; forebody 0.40–0.61 long, occupying 40–45% of body length. Oral sucker 0.10–0.13 by 0.12–0.16. Prepharynx very short. Pharynx 0.05–0.06 by 0.06–0.08. Esophagus undulating, bifurcating midway between pharynx and ventral sucker. Intestines ending (1) in post-testicular region (ovary 2- or 3-lobed, eggs 92–113 by 39–63 μm (collapsed), vitelline follicles entering post-testicular region and confluent there, Fig. 6) in 3 of 75 specimens; (2) in testicular region (ovary globular or 2-lobed or 3-lobed, eggs 79–113 by 36–63 μm (collapsed), vitelline follicles entering post-testicular region and separate there, Fig. 7) in 70; or (3) in testicular region (ovary 2-lobed or 3-lobed, eggs 71–87 by 36–54 μm, vitelline follicles ending in testicular region and separate there, as in Figs. 8–9) in 2. Ventral sucker 0.16–0.22 by 0.19–0.21; sucker width ratio 1 : 1.3–1.6. Testes globular to elliptical, 0.09–0.19 by 0.09–0.16, slightly diagonal, contiguous or slightly separate, in posterior half of hindbody. Cirrus pouch 0.16–0.25 by 0.05–0.06, lateral or anterolateral to ventral sucker, sometimes slightly overlapping ventral sucker. Seminal vesicle occupying posterior two-thirds of cirrus pouch. Ejaculatory duct short. Genital atrium small. Genital pore at about midlevel of esophagus. Ovary globular, 2-lobed, or 3-lobed, 0.09–0.12 by 0.12–0.16, dextrally submedian, usually between intestines or slightly overlapping right intestine, anterolateral to anterior testis. Seminal receptacle clavate, 0.16–0.19 by 0.05–0.07, lying obliquely anterior to anterior testis. Laurer's canal fairly long. Uterus coiled a few times between anterior testis and ventral sucker, overlapping intestines; metraterm about half as long as cirrus pouch. Eggs few, light brown, 71–113 by 36–63 μm (collapsed). Vitelline follicles distributed from midlevel of esophagus to post-testicular region or testicular region as described above, almost confluent anteriorly, confluent or separate posteriorly. Excretory vesicle extending usually to posterior testis but rarely to anterior testis; excretory pore posteroterminal.

2) For the holotype and two paratypes (MPM Coll. Nos. 22219 and 22180) of *Caudotestis orientalis*, see Yamaguti (1934) and Shimazu (1990b, fig. 12). Holotype (MPM Coll. Nos. 22219, body 1.49 by 0.47, eggs 89–92 by 52–58 μm, operculum domed) (Fig. 8).

3) For the holotype (MPM Coll. No. 22220) of *C. gnathopogonis*, see Yamaguti (1934), Shimazu (1990b, fig. 13), and Shimazu *et al.* (2011, figs. 56–57). Holotype (body 1.42 by 0.40, eggs 88–98 by 40–54 μm, operculum domed or truncated) (Fig. 9).

4) In most of the present other specimens from the Lake Biwa basin, both intestines and vitelline follicles terminating in testicular region, and eggs 67–86 by 37–51 μm. In flattened adult specimens (NSMT-Pl 3629) from *Sa. variegatus microoculus*, intestines terminating in testicular region, vitelline follicles entering post-testicular region, eggs 88–94 by 43–64 μm, and operculum

domed or truncated (Shimazu *et al.*, 2011). In flattened adult specimens (NSMT-Pl 5465–5469) found in *Sa. variegatus microoculus* from Lake Suwa, both intestines and vitelline follicles terminating in testicular region, and eggs 78–89 by 46–52 μm.

Remarks. Goto and Ozaki (1930) described *Lebouria elongata* as a new species based on adult specimens found in the intestine of "*Sarcocheilichthys variegatus* (Temminck et Schlegel)" (Japanese name: Higai) from Lake Biwa. They did not designate the holotype for this species. Shimazu *et al.* (2011) considered Ozaki's specimens (MPM Coll. No. 30024) syntypes of *L. elongata*. In Lake Biwa of today, two species, *S. variegatus microoculus* and *Sarcocheilichthys biwaensis* Hosoya, 1982, are distributed. It cannot be determined at present which of them is Goto and Ozaki's "*Sarcocheilichthys variegatus* (Temminck et Schlegel)," or the type host of *L. elangata* (Shimazu *et al.*, 2011). Likewise, the current scientific names of "*Sarcocheilichthys variegatus* (Temm. et Schl.)" (host of *C. orientalis*, MPM Coll. 22219, Lake Ogura) and "*S. variegatus*" (host of "*Caudotestis*," MPM Coll. Nos. 22631, Lake Biwa) are uncertain. On the other hand, "*Sarcocheilichthys variegatus*" (host of *C. orientalis*, MPM Coll. No. 22181, Lake Suwa) (Shimazu, 1990b; this paper) should have been *S. variegatus microoculus* (Shimazu *et al.*, 2011; Shimazu, 2015).

Goto and Ozaki (1930, fig. 2) described both of the intestines and vitelline follicles as extending to the posterior extremity of the body in *L. elongata*. In the above-described 75 syntypes, (1) both intestines and vitelline follicles entered the post-testicular region in 3 of them (Fig. 6); (2) the intestines ended in the testicular region, and the vitelline follicles entered the post-testicular region in 70 (Fig. 7); and both ended in the testicular region in 2 (as in Figs. 8–9) (see also Shimazu, 1990b; Shimazu *et al.*, 2011). Goto and Ozaki (1930) seem to have used only a few morphologically exceptional specimens with the intestines and vitelline follicles entering the post-testicular region for their description of *L. elongata* (Shimazu *et al.*, 2011).

Yamaguti (1934) described two new species, *C. orientalis* and *C. gnathopogonis*: *C. orientalis* found in the intestine of "*Sarcocheilichthys variegatus* (Temm. et Schl.)" from Lake Ogura (not the Yodo River) and in the intestine of *Ps. esocinus* from the Yodo River; and *C. gnathopogonis* found in the intestine of *Gn. elongatus* from Lake Biwa (see *Material examined* above). Yamaguti (1934) distinguished *C. orientalis* from *L. elongata* by that both of the intestines and vitelline follicles extended to the midlevel of the posterior testis (Fig. 8); and *C. gnathopogonis* (Fig. 9) from *C. orientalis* (Fig. 8) by that the testes were contiguous instead of separate; and eggs were smaller, 0.0815 by 0.05 mm instead of 0.0894–0.0921 by 0.0526–0.0578 mm, with a truncated (or collapsed) operculum instead of a domed operculum. As described above, however, these three species cannot be separated from one another by the posterior extent of the intestines and vitelline follicles, egg size, and nature (domed or truncated) of the operculum. Therefore, I agree with Skryabin and Koval (1958), Shimazu (1990b), and Shimazu *et al.* (2011) that *C. gnathopogonis* is a junior synonym of *C. orientalis*, and *C. orientalis* is a junior synonym of *L. elongata*, or now *N. elongatus*.

Shimazu *et al.* (2011) tentatively classified *N. elongatus* into two types on the basis of the posterior extent of the vitelline follicles, regardless of that of the intestines, as follows: (1) *elongatus* type (Figs. 6–7), in which the vitelline follicles extend into the post-testicular region, and eggs are 88–112 by 43–67 μm; and (2) *orientalis* type (Figs. 8–9), in which the vitelline follicles end in the testicular region, and eggs are 67–98 by 34–54 μm. It is uncertain at present whether this classification is of taxonomic significance.

As mentioned above, *N. elongatus* has been recoreded from cyprinids (12 identified and 3 unidentified species), gobiids (6 identified and 1 unidentified), an odontobutid (1 identified), and a percichthyid (1 identified) in rivers and lakes in Chubu Region (Nagano Prefecture), Kinki Region (Shiga, Kyoto, and Osaka (?) Prefec-

tures), Chugoku Region (Hiroshima Prefecture), and Kyushu Region (Fukuoka and Oita Prefectures). It seems that the host specificity is considerably low, because the specimens found in all of these fishes but 11 specimens found in *Rhinogobius flumineus* were sexually matured.

Life cycle. According to unpublished data (Misako Urabe, personal communication, 20 April 2016), the first intermediate host of *N. elongatus* in the Uji River is *Semisulcospira* (*Biwamelania*) *nakasekoae* Kuroda, 1929 (Gastropoda, Pleuroceridae) (Japanese name: Nakaseko-kawanina). Cotylomicrocercous cercariae easily invaded *Tubifex tubifex* (Müller, 1774) (Annelida, Oligochaeta) (Japanese name: Itomimizu) to encyst in them in experimental infection.

Neoplagioporus kajika Urabe and Higa, 2006

(Fig. 10)

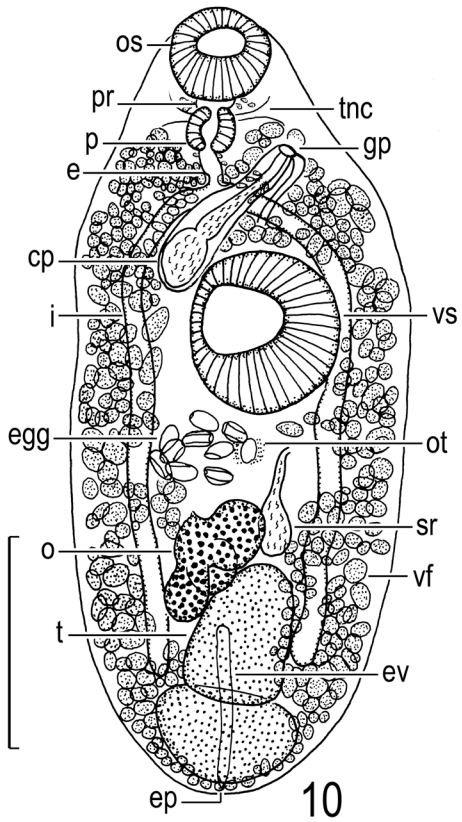
Neoplagioporus kajika Urabe and Higa, 2006: 208–210, figs. 1A–E.

Hosts in Japan. *Cottus pollux* Günther, 1873 (Cottidae) (type host), *Nipponocypris temminckii* (Cyprinidae), and *Pseudogobio esocinus esocinus* (Cyprinidae) (Urabe and Higa, 2006; this paper).

Site of infection. Intestine.

Geographical distribution. Fukuoka Prefecture: Naka River at Terase Bridge (type locality), Narutake, Nakagawa Town; and Sakuta channel at Yamada, Nakagawa Town (Urabe and Higa, 2006).

Material examined. (1) 12 specimens



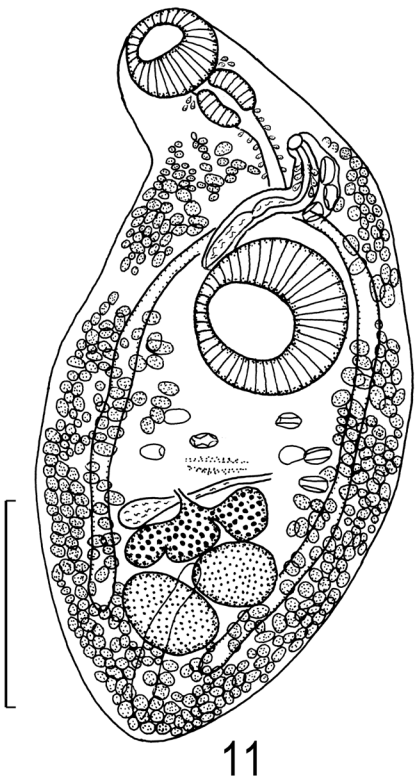


Fig. 10. *Neoplagioporus kajika*, holotype (NSMT-Pl 5445), adult specimen found in intestine of *Cottus pollux*, entire body, ventral view. Scale bar: 0.5 mm.

Fig. 11. *Neoplagioporus* sp., adult specimen (LBM 3-28) found in rectum of *Odontobutis obscura*, entire body, ventral view. Scale bar: 0.5 mm.

(NSMT-Pl 5445, holotype; 5446–5455, 11 paratypes) of *Neoplagioporus kajika*, adult, ex intestine of *Cottus pollux*, Naka River, 5 March 2005 (Urabe and Higa, 2006). (2) 2 (NSMT-Pl 5456, 5457) of *N. kajika*, immature, adult, ex intestine of *Nipponocypris temminckii* (syn. *Zacco temminckii*) and *Pseudogobio esocinus esocinus* (syn. *Ps. esocinus*), Sakuta channel, 23 April 2004, 28 March 2004 (Urabe and Higa, 2006). (3) 3 (Urabe's personal collection) of *N. kajika*, adult, ex intestine of *Cottus pollux*, Naka River, 25 November 2003, 5 March 2005 (Urabe and Higa, 2006).

Description. After Urabe and Higa (2006), altered from the present study (Fig. 10). Body broad-ovate, small, 1.42–2.08 by 0.59–0.86 (holotype 1.84 by 0.78); forebody 0.63–0.87 long, occupying 41–50% of body length. Oral sucker 0.19–0.23 by 0.19–0.27. Prepharynx very short. Pharynx 0.08–0.11 by 0.09–0.13. Esophagus bifurcating about halfway between pharynx and ventral sucker. Intestines extending to mid-level of testicular region. Ventral sucker 0.28–0.38 by 0.27–0.36; sucker width ratio 1 : 1.2–1.7. Testes globular to elliptical, 0.17–0.39 by 0.20–0.42, almost tandem, contiguous, close to posterior extremity of body. Cirrus pouch anterior to or slightly overlapping ventral sucker, 0.32–0.55 by 0.06–0.12. Seminal vesicle occupying about posterior three-fourths of cirrus pouch. Pars prostatica small; prostatic cells well developed. Ejaculatory duct short. Genital atrium small. Genital pore slightly posterior to pharyngeal level. Ovary 3-lobed, 0.16–0.28 by 0.22–0.33, median, immediately pretesticular, or dextrally submedian, anterolateral to anterior testis. Seminal receptacle clavate, 0.16–0.25 by 0.06–0.08. Laurer's canal running anteriorly. Uterus coiled a few times between ovary, ventral sucker, and intestines; metraterm short. Eggs few, light brown, 61–83 by 34–49 μm. Vitelline follicles distributed between pharynx and posterior extremity on left side of body, testicular region on right side, but rarely to posterior border of posterior testis on both sides, confluent anteriorly and posteriorly, present in lateral and posterior peripheral fields of body. Excretory vesicle reaching to about posterior part (middle in Fig. 10) of anterior testis; excretory pore postero-dorsal or -terminal.

Remarks. This species resembles *N. zacconis* (see above) in that the body is broad-ovate, the intestines end in the testicular region, the testes are close to the posterior extremity of the body, and the ovary is 3-lobed. Urabe and Higa (2006) distinguished the species from the latter by the vitelline follicles being present in the lateral and posterior peripheral fields of the body instead of absent. However, some of the specimens (NSMT-Pl 5270) of *N. zacconis* from the Takami River also had the vitelline follicles in the lateral and posterior peripheral fields (this paper, Fig. 4). The difference between these two species is open to further comparative studies.

Life cycle. Not known.

Neoplagioporus sp. of Shimazu, Urabe, and Grygier (2011)

(Fig. 11)

Neoplagioporus sp.: Shimazu, Urabe, and Grygier, 2011: 50–52, figs. 65–67.

Host in Japan. *Odontobutis obscura* (Odontobutidae) (Shimazu *et al.*, 2011).

Site of infection. Rectum.

Geographical distribution. Shiga Prefecture: Lake Biwa basin (Mano-ono, Otsu City) (Shimazu *et al.*, 2011).

Material examined. 1 specimen (LBM 3-28) of *Neoplagioporus* sp., adult, ex rectum of *Odontobutis obscura*, Mano-ono, 3 May 2000 (Shimazu *et al.*, 2011).

Description. After Shimazu *et al.* (2011), altered from the present study (Fig. 11). Body broad-ovate, 1.84 by 0.88; forebody 0.80 long, occupying 43% of body length. Oral sucker 0.20 by 0.22. Prepharynx very short. Pharynx 0.16 by 0.12. Esophagus bifurcating between pharynx and ventral sucker. Intestines extending to posterior border of posterior testis. Ventral sucker 0.39 by 0.37; sucker width ratio 1 : 1.7. Testes elliptical, small, 0.16–0.17 by 0.20–0.27, diagonal,

contiguous, in third fourth of hindbody. Cirrus pouch 0.41 by 0.06. Seminal vesicle occupying posterior four-fifths of cirrus pouch. Genital pore at midlevel of esophagus. Ovary large, 3-lobed, 0.17 by 0.38, almost median. Seminal receptacle clavate, 0.44 by 0.06. Laurer's canal fairly long. Uterus coiled a few times between ovary, ventral sucker, and intestines; metraterm about half as long as cirrus pouch. Eggs few, brown, 58–69 by 38–45 μm (collapsed). Vitelline follicles distributed from pharynx to posterior extremity of body, filling up lateral and posterior peripheral fields of body, anteriorly slightly separate, posteriorly confluent. Excretory vesicle extending to middle of anterior testis; excretory pore posterodorsal.

Remarks. This unidentified specimen differs from *N. zacconis* (see above) in having the vitelline follicles filling up even the lateral and posterior peripheral spaces (Shimazu *et al.*, 2011) and from *N. kajika* (see above) in having smaller testes in the third fourth of the hindbody instead of being close to the posterior extremity of the body. Since *N. zacconis* has not been found in *Od. obscura* from the Lake Biwa basin (see above), it is possible that this specimen represents an unidentified species of *Neoplagioporus*.

Life cycle. Not known.

A key to species of *Neoplagioporus* in this paper

1.1. Body elongate-ovate, more than 2.5 times longer than wide 2
1.2. Body broad-ovate, less than 2.5 times longer than wide 3
2.1. Intestines and vitelline follicles extending into post-testicular region; ovary 3-lobed; eggs 67–78 by 39–48 μm ..... *N. ayu*
2.2. Intestines and vitelline follicles terminating usually in testicular region; ovary globular, 2-lobed, or 3-lobed; eggs 71–113 by 36–63 μm ..... *N. elongatus*
3.1. Testes large, close to posterior extremity of body 4
3.2. Testes small, in third fourth of hindbody; vitelline follicles present in lateral and posterior peripheral fields of body ..... *Neoplagioporus* sp.
4.1. Vitelline follicles present in lateral and posterior peripheral fields of body ..... *N. kajika*
4.2. Vitelline follicles absent in lateral and posterior peripheral fields of body ..... *N. zacconis*

Genus ***Urorchis*** Ozaki, 1927

Urorchis goro Ozaki, 1927

(Figs. 12–16)

Urorchis goro Ozaki, 1927: 160–163, figs. 5–7; Shimazu, 1990a: 205–207, figs. 1–8; Shimazu, 2005: 141, fig. 5; Shimazu *et al.*, 2011: 55, figs. 74–77.

Hosts in Japan. *Tridentiger brevispinis* (Gobiidae) (type host) (Shimazu, 1990a, 2005; Shimazu *et al.*, 2011; this paper), *Barbatula toni* (Dybowski, 1869) (Nemacheilidae) (this paper), *Cottus pollux* (Cottidae) (Shimazu, 2007), *Cottus reinii* (Shimazu *et al.*, 2011), *Gnathopogon elongatus elongatus* (Cyprinidae) (Shimazu, 1990a; this paper), *Gymnogobius urotaenia* (Gobiidae) (Shimazu *et al.*, 2011), *Lefua echigonia* Jordan and Richardson, 1907 (Nemacheilidae) (Shimazu, 1990a), *Rhinogobius flumineus* (Gobiidae) (Shimazu and Urabe, 2005; Shimazu *et al.*, 2011; this paper), *Rhinogobius kurodai* (Tanaka, 1908) (this paper), *Rhinogobius* sp. OR (Shimazu, 1990a, 2007; Shimazu *et al.*, 2011; this paper), and "*Tridentiger obscurus* (Temminck & Schlegel)" (Ozaki, 1927; Shimazu, 1990a; this paper).

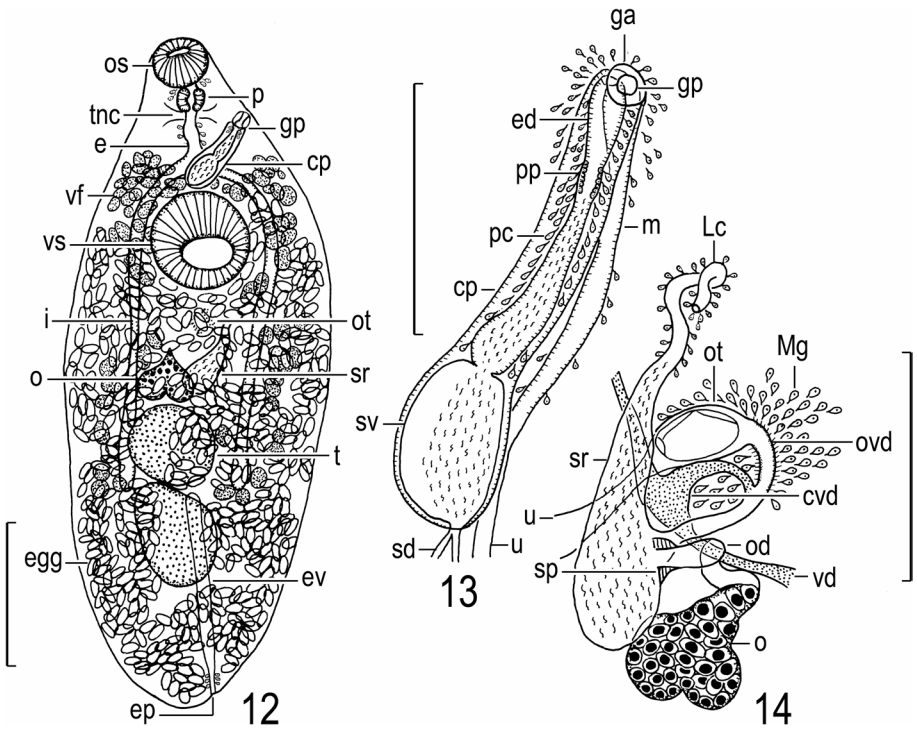
Sites of infection. Intestine, and also stomach and rectum (accidental (?)).

Geographical distribution. (1) Aomori Prefecture: Lake Ogawara at Asahikita, Tohoku Town (Shimazu, 2005; this paper). (2) Miyagi Prefecture: a swamp near Sendai City (Ozaki, 1927). (3) Yamagata Prefecture: Tanjo River at

Shimokosuge, Yonezawa City (this paper). (4) Ibaraki Prefecture: Lake Kasumigaura (Ozaki, 1927); Kamihinuma River at Ibaraki Town (this paper); Tsuchiura City (Shimazu, 1990a); Gantsu River at Yabata (type locality), Namegata City (this paper); and irrigation canals at Oou, Itako City (this paper). (5) Nagano Prefecture: Hiroi River at Kotobuki, Iiyama City (Shimazu, 2007); a small river at Midori, Iiyama City (Shimazu, 1990a; this paper); small rivers at Okada-machi and Oomura, and Metoba River at Asahi 3-chome, Matsumoto City (Shimazu, 1990a, 2007; this paper); Lake Suwa (Shimazu, 1990a), and Lake Suwa at Suwa City (Shimazu, 2007) and Okaya City (this paper). (5) Shiga Prefecture: Lake Biwa basin (Daido River-2 at Kinose, Shigaraki-cho, Koka City; Harie River at Harie, Shin'asahi-cho, Takashima City; Imazu-cho, Takashima City; Kame-ga-ike Pond at Shodenji Temple, Asahi, Shin'asahi-cho; Yasu River at Maeno, Tsuchiyama-cho, Koka City) (Shimazu *et al.*, 2011). (6) Nara Prefecture: Takami River at Kotsugawa, Higashiyoshino Village (Shimazu and Urabe, 2005).

In China (*e.g.*, Wang *et al.*, 1985).

Material examined. (1) 3 specimens (Ozaki's Collection, MPM Coll. No. 30022, labeled "GORO," other data not given) of *Urorchis goro*, adult, ex "*Tridentiger obscurus* (Temminck & Schlegel)" (Shimazu, 1990a; this paper). (2) 5 (NSMT-Pl 5241) of *U. goro*, adult, ex rectum of *Tr. brevispinis*, Lake Ogawara at Kamikita Town, now Asahikita, Tohoku Town, 5 September 1997 (Shimazu, 2005). (3) 4 (MPM Coll. No. 21202), adult, ex intestine of *Barbatula toni*, Tanjo River, 8 October 2011. (4) 1 (Yamaguti's Collection, MPM Coll. No. 22628) of *U. goro*, adult, ex intestine of *Tr. brevispinis* (not *Tr. obscurus*), Tsuchiura City, 16 April 1929 (Yamaguti, 1934; Shimazu, 1990a). (5) 4 (NSMT-Pl 5847), adult, ex intestine of *Tr. brevispinis*, Gantsu River, 3 June 2011. (6) 2 (MPM Coll. No. 21203), adult, ex intestine of *Tr. brevispinis*, Kamihinuma River, 27 September 2012. (7) 4 (NSMT-Pl 5492), adult, ex intestine of *Rhinogobius kurodai*, irrigation canals at Oou, 8 August 1994. (8) 1 (NSMT-Pl 5848), adult, ex intestine of *R. kurodai*, Gantsu River, 3 June 2011. (9) 1 (Yamaguti's Collection, MPM Coll. No. 22015) of *U. goro*, adult, ex intestine of *Gnathopogon elongatus elongatus* (syn. *Gn. elongatus*), Lake Suwa (exact collecting locality not indicated), 19 May 1935 (Shimazu, 1990a). (10) 4 (NSMT-Pl 5301) of *U. goro*, adult, ex intestine of *Rhinogobius* sp. OR [*Rhinogobius* sp. of Shimazu (2007), probably *R. kurodai*], Lake Suwa at Suwa City, 30 October 1993 (Shimazu, 2007). (11) 1 (NSMT-Pl 5491) of *U. goro*, adult, ex intestine of *Cottus pollux*, Lake Suwa at Okaya City [not Suwa City], 5 October 1996 (Shimazu, 2007). (12) 67 and several serially sectioned specimens (NSMT-Pl 3605–3611) of *U. goro*, immature, adult, ex intestine of *Lefua echigonia*, Midori, 14 November 1982, 15 May 1983, 5 May 1986, 14 September 1986, 3 May 1988, 9 July 1989 (Shimazu, 1990a). (13) 2 (NSMT-Pl 5490) of *U. goro*, adult, ex intestine of *Rhinogobius* sp. OR [*Rhinogobius* sp. of Shimazu (2007), probably *R. kurodai*], Hiroi River, 13 August 1999 (Shimazu, 2007). (14) 27 (NSMT-Pl 3612, 5489) of *U. goro*, immature, adult, ex intestine of *Rhinogobius* sp. OR [*R. brunneus* of Shimazu (1990a), *Rhinogobius* sp. of Shimazu (2007), probably *R. kurodai*], Okada-machi [not Matsuoka] and Oomura, 3 November 1982, 23 August 1995 (Shimazu, 1990a, 2007). (15) 1 (MPM Coll. No. 21204), adult, ex intestine of *Rhinogobius* sp. OR (probably *R. kurodai*), Metoba River, 25 August 2015. (16) Specimens of *U. goro*, Lake Biwa basin: 4 (LBM 1-4, 3-53), adult, ex intestine and rectum of *Rhinogobius* sp. OR, Yasu and Harie rivers, 18 October 1997, 19 October 2000; 3 (LBM 1-66, 3-56), immature, adult, ex intestine and "gut" (intestine (?)) of *Gymnogobius urotaenia*, Kame-ga-ike Pond, Harie River, 17 May 1998, 19 October 2000; 2 (LBM 3-17 and -19), immature, adult, ex intestine of *R. flumineus*, Daido River-2, 1 May 2000; 3 (LBM 3-37, 1340000024, 1340000025), adult, ex intestine (?) of *Tr. brevispinis*, Imazu-cho, 1 August 2002; and 7 (LBM 3-39), adult, ex intestine of *Cottus reinii*, Imazu-cho, 5 May 2000 (Shimazu *et al.*, 2011).



Figs. 12–14. *Urorchis goro*, adult specimens. 12, neotype (NSMT-Pl 5847) found in intestine of *Tridentiger brevispinis*, entire body, ventral view; 13, specimen (NSMT-Pl 3606) found in intestine of *Lefua echigonia*, terminal genitalia, ventral view; 14, specimen (NSMT-Pl 3606), ovarian complex, dorsal view. Scale bars: 0.5 mm in Fig. 12; 0.2 mm in Figs. 13–14.

(19) 1 (NSMT-Pl 5272) of *Urorchis* sp., adult, ex intestine of *R. flumineus*, Takami River, 15 August 2000 (Shimazu and Urabe, 2005). (The measurements given are erroneous. Correct measurements will be obtained by multiplying them by 0.8.)

Description. 1) Based on specimens (NSMT-Pl 4847) found in *Tr. brevispinis* from Gantsu River (Fig. 12). Body fairly broad, tapering anteriorly, small, 1.98–2.66 by 0.82–0.98; forebody 0.66–0.82 long, occupying 31–34% of body length. Oral sucker 0.16–0.18 by 0.19–0.20. Prepharynx very short. Pharynx 0.07–0.10 by 0.07–0.10. Esophagus bifurcating anterior to ventral sucker. Intestines ending usually in testicular region. Ventral sucker 0.29–0.34 by 0.34–0.37; sucker width ratio 1 : 1.7–1.8. Testes entire or slightly indented, large, 0.28–0.41 by 0.19–0.38, almost tandem, usually contiguous but rarely slightly separated by uterus, in middle third of hindbody. Cirrus pouch entire, fairly thick-walled, 0.25–0.35 by 0.09–0.11, anterior to ventral sucker. Seminal vesicle occupying about posterior four-fifths of cirrus pouch; anterior portion clavate, fairly thick-walled; posterior portion elliptical, thin-walled. Pars prostatica small; prostatic cells well developed. Ejaculatory duct short, fifth as long as cirrus pouch, sometimes everted slightly. Genital atrium small. Genital pore at about midlevel of esophagus or slightly anterior to it. Ovary globular or 2-lobed, 0.13–0.18 by 0.10–0.16, sinistrally submedian or almost median, immediately pretesticular. Seminal receptacle clavate, 0.30–0.32 by 0.07–0.19, almost median, opposite or anterior to ovary (see *Remarks* of *Neoplagioporus zacconis* above). Laurer's canal fairly long, extending anteriorly. Uterus occupying all available space of hindbody; metraterm about half as long as cirrus pouch. Eggs numerous, light brown, 64–76 by

35–41 μm (collapsed), fully embryonated. Vitelline follicles rather sparse, surrounding whole intestines or almost so, distributed between midlevel of esophagus and slightly posterior to intestinal ends, separate anteriorly and posteriorly. Excretory vesicle reaching to testicular region; excretory pore posterodorsal.

2) Based on specimens (NSMT-Pl 3605–3611) found in *Lefua echigonia*, after Shimazu (1990a), altered from the present study (Figs. 13–14). Body ovate, 0.95–2.37 by 0.33–0.67; forebody 0.43–0.63 long, occupying 30–45% of body length. Oral sucker 0.11–0.20 by 0.12–0.21. Pharynx 0.06–0.08 in diameter. Intestines short, ending at various levels between ventral sucker and posterior testis. Ventral sucker 0.19–0.33 by 0.20–0.38; sucker width ratio 1 : 1.6–1.8. Testes 0.12–0.40 by 0.12–0.28, usually contiguous but rarely slightly separated by uterus, in middle third of hindbody in fully matured adult specimens, more posterior or near posterior extremity of body in immature and barely matured adult specimens (see Shimazu, 1990a, figs. 4 and 8). Cirrus pouch 0.16–0.35 by 0.06–0.09, extending posteriorly to midlevel of ventral sucker. Ovary globular, 2-lobed, or 3-lobed, 0.09–0.13 by 0.10–0.13, sinistrally [not dextrally] submedian, immediately pretesticular. Seminal receptacle 0.08–0.16 by 0.07–0.08. Laurer's canal straight or coiled [figured incorrectly by Shimazu (1990a, fig. 7)]. Uterus occupying all available space of hindbody in fully matured adult specimens. Eggs 70–84 by 30–42 μm (collapsed in balsam) (75–92 by 40–45 μm in life), fully embryonated. Excretory vesicle rarely reaching to middle of anterior testis.

Remarks. Ozaki (1927) erected a new genus and species, *Urorchis goro*, on the basis of adult specimens found in the intestine of "*Tridentiger obscurus* Temminck & Schlegel" (Japanese name: Chichibu; but Goro of Ozaki) from Lake Kasumigaura in Ibaraki Prefecture and a swamp near Sendai City, Miyagi Prefecture, in August, 1925. The holotype (No. P. 260) of this species was lost (Shimazu, 2013). Ozaki did not indicate which locality the holotype was from (Shimazu *et al.*, 2011). The host fish from the Lake Kasumigaura basin should have been *Tr. brevispinis* (Japanese name: Numa-chichibu), not *Tr. obscurus* (Shimazu, 1995). Shimazu (1990a) treated one adult specimen (MPM Coll. No. 22628) of *U. goro* of Yamaguti as unpublished, but Yamaguti (1934) had referred to this specimen in the Discussion on *Urorchis acheilognathi* Yamaguti, 1934.

Ozaki' Collection includes three adult specimens (MPM Coll. No. 30022), one of which Shimazu (1990a) dealt with. The letters written in ink on the labels of the two slides have been considerably faded away, but the first word barely read "GORO." Accordingly, the host is "*Tridentiger obscurus* (Temminck & Schlegel)" of Ozaki. These three specimens are likely to be part of the type series, or paratypes (see also Shimazu, 1990a). However, the collecting locality and current scientific name of the host remain undetermined.

As mentioned above, *U. goro* has been recorded from gobiids (six species), nemacheilids (two), cottids (two), and a cyprinid in a swamp, irrigation canals, rivers, and lakes in Tohoku Region (Aomori, Miyagi, and Yamagata Prefectures), Kanto Region (Ibaraki Prefecture), Chubu Region (Nagano Prefecture), and Kinki Region (Shiga and Nara Prefectures). *Barbatula toni*, one of the present final hosts, has recently been artificially introduced into the Tanjo River in Yamagata Prefecture (its origin unknown).

The present study clearly indicates that *U. goro* occurs in *Tr. brevispinis* in the Lake Kasumigaura basin. The type host and type locality of *U. goro* have previously been ambiguous (Shimazu *et al.*, 2011). In order to show them distinctly, a neotype is designated for *U. goro*, as follows.

Designation of a neotype of Urorchis goro *Ozaki*, *1927*. Neotype: a whole-mounted adult specimen (NSMT-Pl 5847), slightly flattened, 2.30 by 0.89 mm, Fig. 12, 3 June 2011.

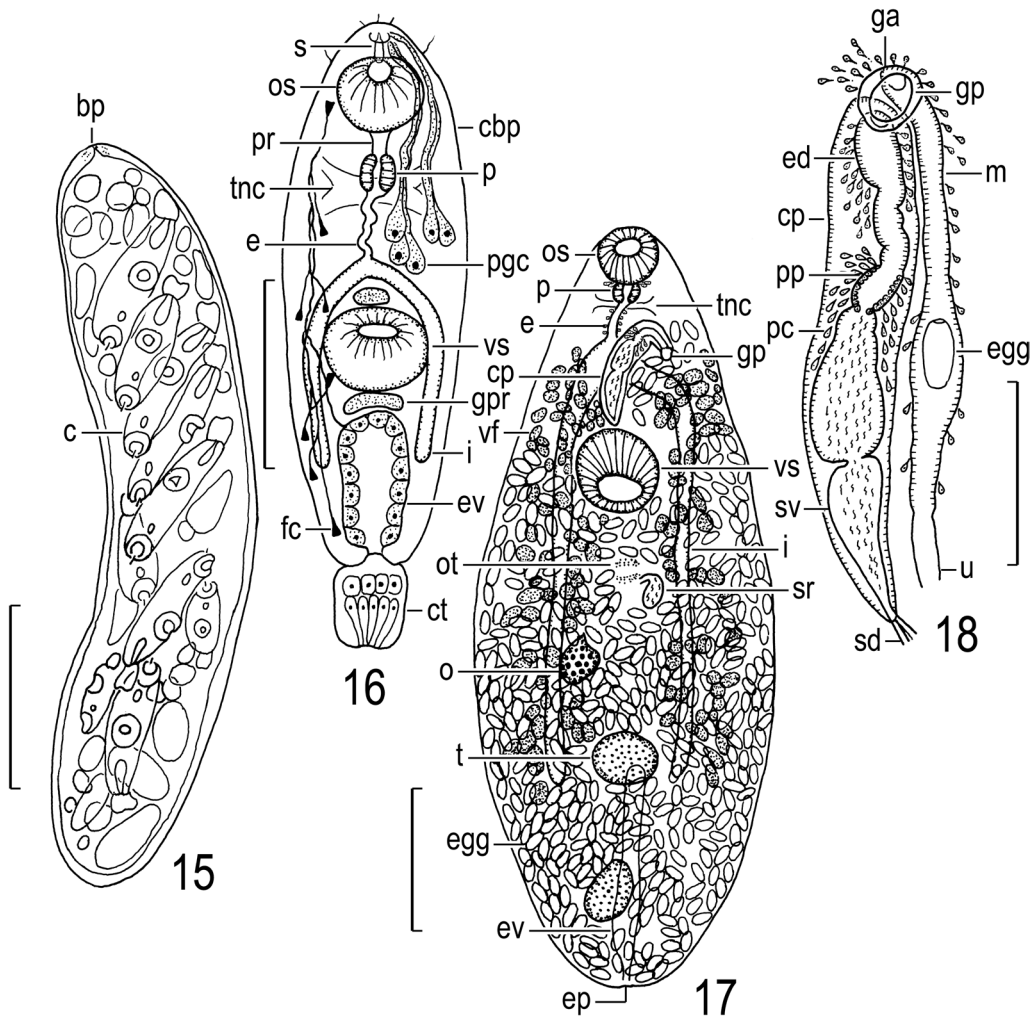
Type host. *Tridentiger brevispinis* Katsuyama, Arai, and Nakamura (Gobiidae).

Site of infection. Intestine.

Type locality. Gantsu River at Yabata (36°0′N, 140°31′E), Namegata City, Ibaraki Prefecture, Japan.

Life cycle. Cercariae of the cotylomicrocercous type were found produced in daughter sporocysts in the pleurocerid snail *Semisulcospira libertina* (Gould, 1859) (Japanese name: Kawanina) in the small river at Midori, Iiyama City, on 6 May 1989; the small river at Oomura, Matsumoto City, on 9 October 2013 (MPM Coll. No. 21206) and 16 November 2016 (MPM Coll. No. 21300); and the Metoba River at Asahi 3-chome, Matsumoto City, on 25 August 2015 (MPM Coll. No. 21205) and 16 November 2016 (MPM Coll. No. 21299). Adults were also collected in these three places (see *Material examined* above). Daughter sporocysts were found in the midgut gland (and possibly the testis) and rectum of *Se. libertina*. No mother sporocysts were obtained.

Morphology of the daughter sporocysts (Fig.



Figs. 15–16. *Urorchis goro* (continued), life cycle. 15, daughter sporocyst (MPM Coll. No. 21205) found in *Semisulcospira libertina*, relatively small specimen, entire body; 16, cercaria (MPM Coll. No. 21205), slightly flattened, entire body, ventral view. Scale bars: 0.3 mm in Fig. 15; 0.1 mm in Fig. 16.

Figs. 17–18. *Urorchis acheilognathi*, adult specimens found in intestine of *Tanakia lanceolata*. 17, specimen (NSMT-Pl 3622), entire body, ventral view; 18, specimen (NSMT-Pl 3622), terminal genitalia, ventral view. Scale bars: 0.5 mm in Fig. 17; 0.2 mm in Fig. 18.

15) and cercariae (Fig. 16) in them were briefly as follows. Hot 10% formalin-fixed specimens measured (in μm). Daughter sporocysts cylindrical, 1666–2570 by 206–285, including numerous developing cercariae in body cavity. Cercarial body proper 329–364 by 65–91; forebody 206–230 long, occupying 60–65% of body length; tail 44–49 by 38–43. Stylet oblong, 1-pointed, 11 by 5. Penetration gland cells 5 pairs (inner 3 and outer 2). Oral sucker 48–51 by 41–48. Prepharynx fairly long. Pharynx 16–17 by 17–20. Esophagus long, undulating, bifurcating anterior to ventral sucker. Intestines ending blindly at near midlevel of hindbody. Ventral sucker 46–55 by 43–51; sucker width ratio 1 : 1.1–1.2. Genital primordium seen anterior and posterior to ventral sucker. Excretory vesicle epithelial, oblong, large, 63–97 by 36–70. Flame cell formula [(2 + 2) + (2 + 2)] = 16 (see also Shimazu, 1990a, fig. 8). No encysted metacercariae seen in daughter sporocysts.

The cercariae were molecularly identified as *U. goro*. Misako Urabe sequenced the large subunit region (28S) and second internal transcribed spacer region (ITS-2) of the ribosomal RNA gene (rDNA) of the daughter sporocysts (plus cercariae) (ex *Se. libertina*, Metoba River, 24 September 2015) and the adults (ex intestine of *Rhinogobius* sp. OR, the same locality, 25 August 2015). The partial sequences determined (28S, 1274 bp; ITS-2, 408 bp) were identical between them, which proved the present cercaria to be the larva of *U. goro*. Their GenBank accession numbers deposited by her are: the 28S rDNA sequences of the daughter sporocyst and adult LC149879 and LC149880, respectively; and the ITS-2 rDNA sequences of the daughter sporocyst and adult LC149881 and LC149882, respectively.

The present daughter sporocyst and cercaria are somewhat similar to those of *Cercaria incerta* Faust, 1924 as described by Ito (1953) from the rectum of *Se. libertina* in Tokyo and Kanagawa, Shizuoka, Yamanashi, and Kochi Prefectures. This cercaria was originally described briefly by Kobayashi (1922) as [Microcercous cercaria E] from *Se. libertina* of Okayama. However, the present cercaria is different from *Ce. incerta* in that it has five pairs of penetration gland cells (three inner and two outer) instead of three (two inner and one outer); and the intestines are shorter, ending at near the midlvevel of the hindbody instead of the posterior extremity of the body. Ito's specimens of *Ce. incerta* need reexamination. Although the late Prof. Jiro Ito studied cercariae of many species from Japan (Ito, 1964, 1988), none of his specimens have been deposited anywhere (Hideto Kino, personal communication, 21 October 2015). It is desired that the present cercaria and *Ce. incerta* be further comparatively studied, because *U. goro* was named after *Ce. incerta*, which may thus be the senior synonym.

The absence of any encysted metacercariae in the present daughter sporocysts suggests that the life cycle involves a second intermediate host, perhaps a benthic animal, which remains unknown.

Urorchis acheilognathi Yamaguti, 1934

(Figs. 17–18)

Urorchis acheilognathi Yamaguti, 1934: 415–417, figs. 81–82; Yamaguti, 1942: 359; Shimazu, 1990a: 208–209, figs. 9–15; Shimazu *et al.*, 2011: 52, 54, figs. 68–73.

Hosts in Japan. *Tanakia lanceolata* (Temminck and Schlegel, 1846) (Cyprinidae) (type host) (Yamaguti, 1934; Shimazu, 1990a; Shimazu *et al.*, 2011; this paper), *Tanakia limbata* (Temminck and Schlegel, 1846) (this paper), *Acheilognathus cyanostigma* Jordan and Fowler, 1903 (Cyprinidae) (Yamaguti, 1934; Shimazu, 1990a), *Acheilognathus rhombeus* (Temminck and Schlegel, 1846) (Shimazu *et al.*, 2011; this paper), *Acheilognathus tabira tabira* Jordan and Thompson, 1914 (this paper), *Gnathopogon caerulescens* (Sauvage, 1883) (Cyprinidae) (Shimazu, 1990a; Shimazu *et al.*, 2011), *Phoxinus steindachneri* Sauvage, 1883 (Cyprinidae) (Shimazu, 1990a; this paper), *Pseudorasbora parva* (Cyprinidae) (Yamaguti, 1942;

Shimazu, 1990a, 1992, 2007), *Sarcocheilichthys variegatus microoculus* (Cyprinidae) (Shimazu, 1990a, 2007), and *Oncorhynchus masou* subsp. (Salmonidae) (Japanese name: Kizaki-masu) (Shimazu, 1990a, 2007; this paper).

Site of infection. Intestine.

Geographical distribution. (1) Nagano Prefecture: Lake Kizaki in Oomachi City (Shimazu, 1990a, 2007) and Lake Suwa at Suwa City (Shimazu, 2007). (2) Shiga Prefecture: Lake Biwa; and Lake Biwa basin (Kame-ga-ike Pond at Shodenji Temple, Asahi, Shin'asahi-cho, Takashima City; irrigation canal at Miyake-cho, Moriyama City; Momose, Chinai, Makino-cho, Takashima City; and irrigation canal at Nishiyama, Kinomoto-cho, Nagahama City) (Shimazu, 1990a; Shimazu *et al.*, 2011; this paper). (3) Kyoto Prefecture: Lake Ogura (type locality) (Yamaguti, 1934; Shimazu, 1990a), near Kyoto (Yamaguti, 1942), and Kowata Pond in Uji City (Shimazu, 1990a, 1992; this paper).

In China (*e.g.*, Wang *et al.*, 1985).

Material examined. (1) 24 specimens (Yamaguti's Collection, MPM Coll. No. 22629, holotype, 21 adult (paratypes (?)), and 2 immature) of *Urorchis acheilognathi*, ex intestine of *Tanakia lanceolata* (syn. *Acheilognathus intermedia* (Temminck and Schlegel, 1846), *A. lanceolatus*), Lake Ogura, 3 and 31 (not 23) May 1932; and 2 (MPM Coll. No. 22630, paratypes (?)), adult, ex intestine of *A. cyanostigma*, Kowata Pond [not Lake Kohata] (not from Lake Ogura), 14 May 1928 (Yamaguti, 1934; Shimazu, 1990a). (2) 1 (Yamaguti's Collection, MPM Coll. No. 22742) of *U. acheilognathi*, adult, ex intestine of *Pseudorasbora parva*, Kowata Pond, 14 May 1928 (Shimazu, 1992). (3) 1 (Yamaguti's Collection, MPM Coll. No. 22627) of *U. acheilognathi*, adult, ex intestine of "experimental" *Pseudorasbora parva*, near Kyoto (exact collecting locality not indicated), 22 June 1937 (Yamaguti, 1942; Shimazu, 1990b). (4) 1 (Yamaguti's Collection, MPM Coll. No. 22014, labeled "*Urorchis goro*") of *U. acheilognathi*, adult, ex intestine of *Gnathopogon caerulescens*, Lake Biwa (exact collecting locality not given), 26 May 1936 (Shimazu, 1990a; Shimazu *et al.*, 2011). (5) Specimens of *U. acheilognathi*, Lake Biwa basin: 2 (LBM 3-49, -50), adult, ex intestine of *T. lanceolata*, irrigation canal at Miyake-cho, 27 October 2000; 13 (LBM 7-31, 8-26, -52, -53), immature, adult, ex intestine of *T. lanceolata*, irrigation canal at Nishiyama, 26 April 2001, 27 November 2007; 2 (LBM 1-38), adult, ex intestine of *A. rhombeus*, Kame-ga-ike Pond, 17 May 1998; and 2 (LBM 3-49, -50), adult, ex intestine of *T. lanceolata*, irrigation canal at Miyake-cho, 27 October 2000 (Shimazu *et al.*, 2011). (6) Other specimens of *U. acheilognathi*, Lake Biwa basin: 7 (MPM Coll. No. 21199), immature, adult, ex intestine of *T. lanceolata*, irrigation canal at Nishiyama, 27 May 2009; 1 (MPM Coll. No. 21198), adult, ex intestine of *T. limbata*, irrigation canal at Nishiyama, 27 May 2009; 2 (MPM Coll. No. 21201), adult, ex intestine of *A. rhombeus*, Momose, 14 May 2009; and 3 (MPM Coll. No. 21200), adult, ex intestine of *A. tabira tabira*, Momose, 14 May 2009. (7) Specimens of *U. acheilognathi*, Lake Kizaki: 62 (NSMT-Pl 3618–3622), immature, adult, ex intestine of *T. lanceolata*, 1 and 21 October 1980, 5 November 1980, 16 May 1981, 30 June 1981; 13 (NSMT-Pl 3614–3615) of *U. acheilognathi*, immature, adult, ex intestine of *Pseudorasbora parva*, 28 August 1981, 5 July 1983; 8 (NSMT-Pl 3617), adult, ex intestine of *Phoxinus steindachneri* (syn. *Moroco steindachneri*), 21 September 1979; 1 (NSMT-Pl 3613), adult, ex intestine of *Sarcocheilichthys variegatus microoculus*, 18 July 1981; and 3 (NSMT-Pl 3616), adult, ex intestine of *Oncorhynchus masou* subsp., 27 September 1977 (Shimazu, 1990a). (8) 1 (NSMT-Pl 5470) of *U. acheilognathi*, adult, ex intestine of *Pseudorasbora parva*, Lake Suwa, 13 September 1991 (Shimazu, 2007).

Description. 1) For the type series, see Yamaguti (1934) and Shimazu (1990a). Holotype 1.45 by 0.42 (measured by Takashi Iwaki at the MPM, Tokyo).

2) Based on specimens (NSMT-Pl 3613–3622) from Lake Kizaki, after Shimazu (1990a), altered from the present study (Figs. 17–18). Body elon-

gate-ovate, fairly broad, small, 0.95–3.16 by 0.51–1.30; forebody 0.47–1.00 long, occupying 31–60% of body length. Oral sucker 0.13–0.25 by 0.15–0.26. Prepharynx very short. Pharynx 0.06–0.12 by 0.07–0.12. Esophagus bifurcating about midway between two suckers. Intestines terminating in testicular region. Ventral sucker 0.21–0.35 by 0.20–0.40, located at about junction between anterior and middle thirds of body in fully matured adult specimens; sucker width ratio 1 : 1.3–1.6. Testes globular or elliptical, sometimes slightly indented irregularly, small, 0.16–0.31 by 0.12–0.34, tandem or slightly oblique, contiguous or separated by uterus, in posterior half of hindbody in fully matured adult specimens (Fig. 30), close to posterior extremity of body in barely matured adult specimens (see Shimazu, 1990a, figs. 11–12). Cirrus pouch 0.24–0.51 by 0.04–0.12, anterior to ventral sucker or slightly overlapping it. Seminal vesicle occupying about posterior half of cirrus pouch. Pars prostatica small; prostatic cells well developed. Ejaculatory duct fairly long, fourth as long as cirrus pouch, sometimes slightly everted. Genital atrium small. Genital pore at esophageal level. Ovary globular, 2-lobed, or 3-lobed, 0.08–0.27 by 0.09–0.20. Seminal receptacle clavate, 0.10–0.14 by 0.05–0.08. Laurer's canal fairly long. Uterus occupying all available space of hindbody; metraterm about two-thirds as long as cirrus pouch. Eggs numerous, asymmetric longitudinally, light brown, 70–90 by 38–46 μm (collapsed in balsam) (72–79 by 37–42 μm in life), fully embryonated. Vitellaria follicles sparse, surrounding intestines between bifurcal level and intestinal ends, separate anteriorly and posteriorly. Excretory vesicle extending to anterior testis; excretory pore posterodorsal.

Remarks. Yamaguti (1934) merely stated that *Urorchis acheilognathi* very closely resembled *U. goro* but differed distinctly from it in the characters of the eggs. Eggs are "0.084–0.09 by 0.051–0.054 mm" in *U. acheilognathi* (Yamaguti, 1934) but "0.063–0.072 by 0.038–0.042 mm," each bearing "a small knob-like projection at the antiopecular pole" in *U. goro* (Ozaki, 1927).

According to the above descriptions, *U. acheilognathi* is distinguished from *U. goro* by that eggs are larger, 70–90 by 38–46 μm instead of 64–84 by 30–42 μm; the body is larger, 0.95–3.16 by 0.51–1.30 instead of 1.98–2.66 by 0.82–0.98; the intestines are longer, usually terminating in the testicular region instead of scarcely entering the testicular region; the sucker width ratio is lower, 1 : 1.3–1.6 instead of 1 : 1.6–1.8; the testes are smaller, 0.16–0.31 by 0.12–0.34 instead of 0.28–0.41 by 0.19–0.38; and the ejaculatory duct is longer, fourth as long as the cirrus pouch instead of fifth.

As mentioned above, *U. acheilognathi* has been recorded from cyprinids (nine species) and a salmonid in lakes, ponds, and irrigation canals in Chubu Regin (Nagano Prefecture) and Kinki Region (Shiga and Kyoto Prefectures).

Life cycle. Not known.

Urorchis imba Ishii, 1935

(Fig. 19)

Urorchis imba Ishii, 1935: 547–548, figs. 1–2.

Host in Japan. *Pseudorasbora parva* (Cyprinidae) (type host) (Ishii, 1935).

Site of infection. Intestine.

Geographical distribution. Chiba Prefecture: Lakes Inbanuma and Teganuma (type localities) (Ishii, 1935).

In China: Sichuan Province (Wang, 1985).

Material examined. None.

Description. After Ishii (1935), altered (Fig. 19). Body [elongate-ovate], 1.64–1.83 by 0.59–0.60. Oral sucker 0.16–0.18 in diameter. Pharynx 0.064–0.079 [in diameter]. Esophagus bifurcating about midway between pharynx and ventral sucker. Intestines ending at midlevel of posterior testis. Ventral sucker 0.22–0.24 in diameter. Testes multilobed [*sic*, deeply indented irregularly], 0.143–0.223 by 0.175–0.270, contiguous, tandem, in posterior third of body. Cirrus pouch conical [*sic*, elongate-clavate], anterior to ventral sucker, 0.318 by 0.048–0.056. [Seminal vesicle bipartite; posterior portion globular], 0.318 by

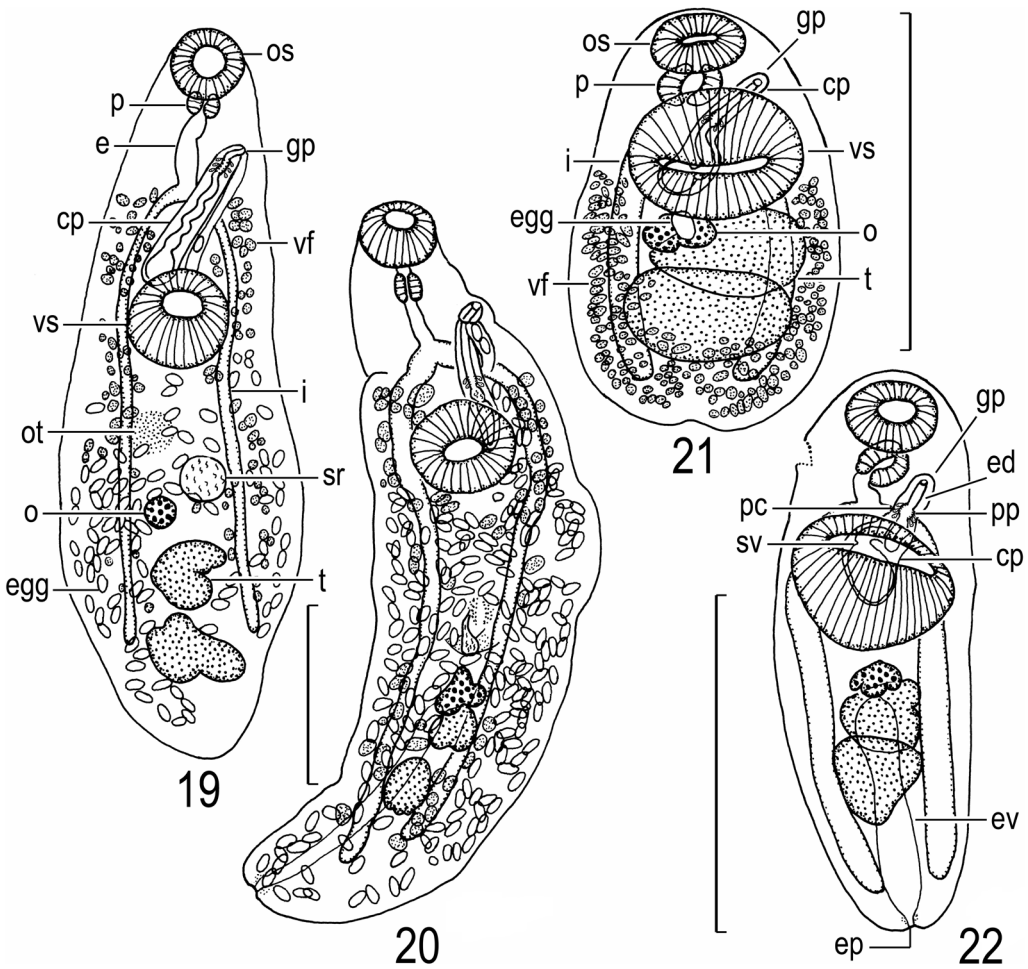


Fig. 19. *Urorchis imba*, adult specimen found in intestine of *Pseudorasbora parva*, entire body, ventral view. Redrawn from Ishii (1935), modified. Scale unknown.

Fig. 20. *Urorchis* sp., adult specimen (MPM Coll. No. 30023) found in *Odontobutis obscura*, entire body, ventral view. Site of infection unknown. Redrawn from Shimazu *et al.* (2011). Scale bar: 0.5 mm.

Figs. 21–22. Opecoelidae gen. sp., specimens (NSMT-Pl 3100, 3101) found in intestine of *Oncorhynchus keta* (smolts). 21, barely matured adult specimen, entire body, ventral view; 22, immature specimen, entire body, ventral view. Scale bars: 0.5 mm.

0.048–0.056 [*sic*]. Ejaculatory duct [*sic*, should be anterior portion of seminal vesicle] [long], [more than three times as long as posterior portion] (calculated from fig. 1), winding. Pars prostatica not differentiated [*sic*]. Prostatic cells present around pars prostatica [*sic*] and ejaculatory duct [*sic*, should be anterior part of anterior portion of seminal vesicle] in anterior third of cirrus pouch. [Ejaculatory duct very short, about eighth as long as cirrus pouch] (calculated from fig. 2). Genital pore [sinistrally submedian], a little anterior to intestinal bifurcation. Ovary dextrally submedian, nearly round, 0.072–0.095 in diameter. Seminal receptacle [sinistrally submedian], 0.095–0.127 by 0.048–0.064. Mehlis' gland [dextrally submedian.] Uterus running down to posterior extremity of body. Eggs 66–75 by 28–33 μm. [Vitelline follicles scattered along intestines (fig. 1).] [Excretory vesicle not described.]

Remarks. Ishii (1935) found this species fre-

quently but in small numbers in the intestine of *Pseudorasbora parva* from Lakes Imbanuma [Inbanuma] and Teganuma. He distinguished the species from *U. goro* as described by Ozaki (1927) by an elongate-ovate body, multilobed [*sic*] testes, a more spiral ejaculatory duct [*sic*, should be the anterior portion of the seminal vesicle], a submedian ovary, a submedian seminal receptacle, and a submedian Mehlis' gland. Ishii seems to have been unaware of Yamaguti's (1934) description of *Urorchis acheilognathi*.

As shown above, Ishii's description is brief and includes misinterpretations and erroneous measurements of some organs, especially the male terminal genitalia (see also Shimazu, 1990a). The presence of the prostatic cells (figs. 1–2, PC) in the anterior third of the cirrus pouch suggests that the seminal vesicle is long and bipartite, with a globular posterior portion and a long winding anterior portion; and the ejaculatory duct (or penis) is very short, about eighth as long as the cirrus pouch. These features readily separate *U. imba* from *U. goro* and *U. acheilognathi*, though it is uncertain at present whether they were correctly described. Ishii's original specimens need reexamination. The parasite collection of the late Dr. Nobutaro Ishii has been deposited in the Meguro Parasitological Museum, Tokyo, since 1961. It includes none of the original specimens (Takashi Iwaki at the MPM, personal communication, 16 November 2016), which suggests that all of them were lost. I was unsuccessful in obtaining any additional specimens of *U. imba* from 172 individuals of *Pseudorasbora parva* collected in Lake Inbanuma on 29 October 2011. According to Liu (1987), Wang (1985) described *U. imba* in detail from Sichan Province, China. However, this description has not yet been available to me.

Life cycle. Not known.

Urorchis sp. of Shimazu (1990)

(Fig. 20)

Urorchis sp.: Shimazu, 1990a: 211, fig. 17; Shimazu *et al.*, 2011: 57, figs. 78–80.

Hosts in Japan. *Odontobutis obscura* (Odontobutidae), *Gnathopogon caerulescens* (Cyprinidae), and *Tanakia limbata* (Cyprinidae) (Shimazu, 1990a; Shimazu *et al.*, 2011).

Site of infection. Intestine.

Geographical distribution. Shiga Prefecture: Lake Biwa and irrigation canal at Tai, Kinomoto-cho, Nagahama City (Shimazu, 1990a; Shimazu *et al.*, 2011; this paper).

Material examined. (1) 1 specimen (Ozaki's Collection, MPM Coll. No. 30023, labeled "[Goppo] [Lake Biwa]," other data not given) of *Urorchis* sp., adult, ex *Odontobutis obscura*, Lake Biwa (exact collecting locality not indicated) (Shimazu, 1990a; Shimazu *et al.*, 2011). (2) 1 (Yamaguti's Collection, MPM Coll. No. 22626, labeled "*Urorchis*," *U. acheilognathi* of Shimazu (1990a)) of *Urorchis* sp., adult, ex intestine of *Gnathopogon caerulescens*, Lake Biwa (exact collecting locality not indicated), 9 July 1927 (Shimazu, 1990a; Shimazu *et al.*, 2011). (3) 1 (LBM 1-37) of *Urorchis* sp., adult, ex intestine of *Tanakia limbata*, Tai, 25 October 1997 (Shimazu *et al.*, 2011).

Description. Measurements of specimen from *O. obscura* given (Fig. 20). Body elongate-ovate, 2.40 by 0.61; forebody 0.80 long, occupying 33% of body length. Oral sucker 0.21 in diameter. Pharynx 0.10 by 0.09. Intestines long, extending into post-testicular region of body. Ventral sucker 0.30 by 0.31; sucker width ratio 1 : 1.5. Testes globular, elliptical, or irregular in shape, 0.17–0.19 by 0.11–0.13, tandem or diagonal, contiguous or separate. Cirrus pouch 0.37 by 0.02. Ejaculatory duct fairly long. Ovary globular, 2-lobed, or 3-lobed, 0.16 in diameter. Uterus occupying all available space of hindbody. Eggs light brown, 72–80 by 32–35 μm (collapsed). Vitelline follicles extending along intestines. Excretory vesicle extending to near anterior border of anterior testis; excretory pore posteroterminal.

Remarks. These specimens differ from *U. acheilognathi*, *U. goro*, and *U. imba* (this paper) in that the intestines are longer, extending into the post-testicular region of the body (Shimazu,

1990a; Shimazu *et al.*, 2011). Although they seem to be different from one another in egg size (Shimazu *et al.*, 2011), length of the seminal vesicle, and length of the ejaculatory duct, they are here treated as the same unidentified species. It is desired that they be further critically studied.

Life cycle. Not known.

Opecoelidae gen. sp. of Shimazu (1990)

(Figs. 21–22)

Opecoelidae gen. sp.: Shimazu, 1990b: 395, figs. 18–19.

Host in Japan. *Oncorhynchus keta* (Walbaum, 1792) (Salmonidae) (Shimazu, 1990b).

Site of infection. Intestine.

Geographical distribution. Hokkaido: Shin River at Hamanaka Town (Shimazu, 1990b).

Material examined. 6 specimens (NSMT-Pl 3100, 3101), immature, adult, ex intestine of smolts (formalin-preserved) of *Oncorhynchus keta*, Shin River, 10 and 11 June 1981 (Shimazu, 1990b).

Description. After Shimazu (1990b), altered from the present study (Figs. 21–22). Body ovate or elongate-ovate, 0.59–0.83 by 0.30–0.35; forebody 0.23–0.40, occupying 37–47% of body length. Tegument smooth. Eyespot pigment not seen. Oral sucker 0.10–0.13 by 0.10–0.15. Prepharynx very short. Pharynx 0.06–0.09 by 0.05–0.07. Esophagus bifurcating anterior to ventral sucker. Intestines ending blindly near posterior extremity of body. Ventral sucker large, 0.16–0.20 by 0.19–0.25, with no papillae; sucker width ratio 1 : 1.4–2.5. Testes 0.08–0.11 by 0.12–0.17, tandem, in middle of hindbody. Cirrus pouch entire, extending to midlevel of ventral sucker. Seminal vesicle clavate, long, sinuous, may be bipartite. Genital pore sinistrally submedian, at near level of pharynx. Ovary weakly 3-lobed, dextrally submedian or median, 0.04–0.05 by 0.06. Seminal receptacle not seen. One uterine egg 46 by 32 μm. Vitelline follicles extending from midlevel of ventral sucker to posterior extremity of body. Excretory vesicle reaching to middle of anterior testis; excretory pore posteroterminal.

Remarks. Five immature and one barely matured adult specimens were obtained from formalin-preserved smolts of *Oncorhynchus keta*. Although the seminal receptacle was not detected, it seems likely that they belong to a species of *Neoplagioporus*, because of a smooth tegument, eyespot pigment being absent, relative position of the genital glands, an entire cirrus pouch, a possible bipartite seminal vesicle, a sinistrally submedian genital pore in the forebody, the vitelline follicles extending to the posterior extremity of body, and an I-shaped excretory vesicle. It differs from *N. zacconis*, *N. kajika*, and *Neoplagioporus* sp. (this paper) in an elongate-ovate body and the vitelline follicles distributed only in the hindbody and from *N. ayu* and *N. elongatus* (this paper) in a higher sucker ratio. Further, it is different from *Neoplagioporus glomeratus* (Roitman, 1963) in *Rhodeus sericeus* (Pallas, 1776) (Cyprinidae) from Sakhalin Island, Russia (Sokolov and Frolova, 2015), in a higher sucker width ratio, 1 : 1.4–2.5 instead of 1 : 1.4 (calculated from fig. 3.1); a larger cirrus pouch, extending to the posterior border of the ventral sucker instead of the anterior border; a 3-lobed ovary instead of much more lobed (or indented); and larger entire testes instead of smaller indented. Better prepared, fully matured adult specimens, in which the male terminal genitalia and ovarian complex can be clearly observed, are necessary for definitive identification of them.

Life cycle. Not known.

Discussion on morphological differences between *Neoplagioporus* and *Urorchis*

In the present paper, I have treated *Neoplagioporus* and *Urochis* as separate genera in the subfamily Plagioporinae. They are distinguished from each other mainly by the uterine area, embryonation of uterine eggs, and posterior extent of the vitelline follicles (see the above key).

Fayton and Andres (2016) have recently carried out a phylogenetic analysis of partial

sequence data of the large subunit region of the ribosomal RNA gene (28S rDNA) of freshwater plagioporines of the Holarctic. Their material used for sequencing and morphological observation included some specimens of *N. zacconis*, *N. ayu*, *N. elongatus*, *U. goro*, and *U. acheilognathi* from Japan (Palaearctic). These five Japanese species formed a clade that differed from a clade formed by seven species of *Plagioporus* Stafford, 1904 from North America (Nearctic) in a clade of the Plagioporinae. *Neoplagioporus* and *Urorchis* were sister to each other. *Neoplagioporus zacconis* + *N. ayu* and *N. elongatus* + *U. acheilognathi* + *U. goro* were sister to each other. They could not discern a difference in the embryonation of the uterine eggs in their specimens of *Urorchis* and *Neoplagioporus*. They considered that differences in posterior extent of the uterus and embryonation of uterine eggs were not significant enough to separate *Neoplagioporus* from *Urorchis* and suggested that *Neoplagioporus* was a junior synonym of *Urorchis*.

In *Urorchis*, the uterus is coiled from the testicular region of the body to the ventral sucker in immature specimens, in which the testes are close to the posterior extremity of the body (Shimazu, 1990a, fig. 8), However, it is coiled in all available space, even in the lateral fields and post-testicular region of the hindbody, in fully gravid adult specimens, in which the testes are quite separate from the posterior extremity (Shimazu, 1990a; Shimazu *et al.*, 2011; this paper). It may be inferred from this that, after worms attain sexual maturity, as the body itself grows further as usual in other genera and the uterine area widens largely in the preovarian region of the hindbody and especially on either lateral side of the body (Ozaki, 1927, fig. 5; Shimazu, 1990a, figs. 2–5), and the post-testicular region gradually elongates posteriorly, so that the uterus comes to fill up all available space of the hindbody in fully gravid adults with the elongated post-testicular region. This posterior elongation of the post-testicular region filled up with uterine coils has not been observed in *Neoplagioporus*. Although Ozaki (1927) did not mentioned the embryonation of uterine eggs in *U. goro*, uterine eggs certainly become fully embryonated in gravid adults of *Urorchis* (Yamaguti, 1934; Shimazu, 1990a; Shimazu *et al.*, 2011; this paper). This embryonation of uterine eggs has not been observed in *Neoplagioporus*. As for morphological similarity or difference between *Urorchis* and *N. elongatus*, weakly matured specimens of *Urorchis* (Shimazu, 1990a, figs. 4 and 11–12; Shimazu *et al.*, 2011, fig. 69) are similar to adult specimens of *N. elongatus* (Shimazu, 1990b, figs. 11–14; Shimazu *et al.*, 2011, figs. 56 and 58–59; this paper, Figs. 8–9) in that both of the intestines and vitelline follicles terminate in the testicular region close to the posterior extremity, though the uterine area is wider in the weakly matured specimens of *Urorchis*. The uterus extends to the posterior border of the posterior testis or slightly more in the weakly matured specimens of *Urorchis* but only to the anterior testis in the adult specimens of *N. elongatus* (Shimazu, 1990b; Shimazu *et al.*, 2011; this paper, Fig. 6). The vitelline follicles are absent in the post-testicular region in the adult specimens of *Urorchis* but either present or absent in those of *N. elongatus*. *Neoplagioporus* and *Urorchis* thus distinctly differ from each other in adult morphology. Further morphological, life cycle, and molecular studies of *Neoplagioporus* and *Urorchis* are required.

Acknowledgments

I am grateful to Mr. Makoto Mizumoto (Okayama), Dr. Kouki Kanou and Mr. Seiya Kaneko (Center for Water Environment Studies, Ibaraki University, Itako), Mr. Ken'ichi Hashimoto (Saitama), and Dr. Koji Tojo (Shinshu University, Matsumoto) for collecting some of the fish examined; Dr. Ryoji Nakazato (Center for Water Environment Studies, Ibaraki University, Itako) for laboratory facilities; Prof. Misako Urabe (The University of Shiga Prefecture, Hikone) for sequencing some samples of *Urorchis goro*; Dr. Takashi Iwaki (MPM, Tokyo) for measuring the body size of the holotype of *U.*

acheilognathi; Dr. Hideto Kino (formerly Hamamatsu University School of Medicine, Hamamatsu) for searching for cercarial specimens of the late Prof. Jiro Ito; Dr. Toshiki Aji (Okayama University Graduate School of Medicine, Okayama) for searching for specimens of *Podocotyle ayu* of the late Dr. Shozo Takahashi; and Dr. Thomas H. Cribb (School of Biological Sciences, The University of Queensland, Brisbane, Australia) for reviewing a draft of the manuscript.

References

Cribb, T. H. 2005a. Superfamily Allocreadioidea Looss, 1902. In Jones, A., R. A. Bray and D. I. Gibson (eds.), Keys to the Trematoda, 2: 413–416. CAB International and The Natural History Museum, Wallingford.

Cribb, T. H. 2005b. Family Opecoelidae Ozaki, 1925. In Jones, A., R. A. Bray and D. I. Gibson (eds.), Keys to the Trematoda, 2: 443–531. CAB International and The Natural History Museum, Wallingford.

Fayton, T. J. and M. J. Andres 2016. New species of *Plagioporus* Stafford, 1904 (Digenea: Opecoelidae) from California, with an amendment of the genus and a phylogeny of freshwater plagioporines of the Holarctic. Systematic Parasitology, 93: 731–748.

Gibson, D. I. 1976. Monogenea and Digenea from fishes. Discovery Reports, 36: 179–266, pl. 18.

Goto, S. and Y. Ozaki 1930. Brief notes on new trematodes III. Japanese Journal of Zoology, 3: 73–82.

Ishii, N. 1935. Brief note on a new species of fish trematodes, *Urorchis imba*. Japanese Journal of Zoology, 6: 547–549.

Ito, J. 1953. Redescription of *Cercaria incerta* Faust, 1924 a cotylomicrocercous cercaria in snail host *Semisulcospira* spp. in Japan, (Trematoda). Japanese Journal of Medical Science & Biology, 6: 289–297.

Ito, J. 1964. A monograph of cercariae in Japan and adjacent territories. In Morishita, K., Y. Komiya and H. Matsubayashi (eds.), Progress of Medical Parasitology in Japan, 1: 395–550. Meguro Parasitological Museum, Tokyo.

Ito, J. 1988. A subsequent monograph of cercariae in Japan (1962–1988). Japanese Journal of Parasitology, 37: 269–322.

Kim, K. H., J. B. Cho and H.-J. Rim 1998. *Neoplagioporus zacconis* (Trematoda: Opecoelidae) from the intestine of the pale chub, *Zacco platypus*, in Korea. Korean Journal of Parasitology, 36: 199–202.

Kobayashi, H. 1922. [A review of Japanese cercariae.] Dobutsugaku Zasshi, 34: 252–270. (In Japanese.)

Koval, V. P. 1959. [Critical survey of the aggregate of species of the genus *Plagioporus* Stafford, 1904 (Trematoda: Digenea).] Trudy Gel'mintologicheskoy Laboratorii, 9: 129. (In Russian.)

Liu, C.-W. 1987. A new species of the genus *Urorchis* from Anhui Province, China. Acta Zootaxonomica Sinica, 12: 337–339. (In Chinese with English abstract.)

Manter, H. W. 1954. Some digenetic trematodes from fishes of New Zealand. Transactions of the Royal Society of New Zealand. 82: 475–568

Nakamura, S., M. Urabe and M. Nagoshi 2000. Seasonal change of prevalence and distribution of parasites in freshwater fishes at Higashi-yoshino, Nara Prefecture. Biology of Inland Waters, (15): 12–19. (In Japanese with English abstract.)

Ozaki, Y. 1927. Two new genera of fish trematodes. Japanese Journal of Zoology, 1: 157–164.

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

Shimazu, T. 1990a. Trematodes of the genus *Urorchis* (Digenea: Opecoelidae: Urorchiinae) from freshwater fishes of Japan. Japanese Journal of Parasitology, 39: 204–212.

Shimazu, T. 1990b. Trematodes of a new genus, *Neoplagioporus* gen. n. (Digenea: Opecoelidae: Plagioporinae), and an unidentified opecoelid from freshwater fishes of Japan. Japanese Journal of Parasitology, 39: 384–396.

Shimazu, T. 1992. Trematodes of the genera *Asymphylodora*, *Anapalaeorchis* and *Palaeorchis* (Digenea: Lissorchiidae) from freshwater fishes of Japan. Journal of Nagano Prefectural College, (47): 1–19.

Shimazu, T. 1995. Trematodes of the genus *Genarchopsis* (Digenea, Derogenidae, Halipeginae) from freshwater fishes of Japan. Proceedings of the Japanese Society of Systematic Zoology, (54): 1–18.

Shimazu, T. 2005. Digeneans found in fresh- and brackish-water fishes of Lake Ogawara in Aomori Prefecture, Japan. Bulletin of the National Science Museum, Tokyo, Series A (Zoology), 31: 137–150.

Shimazu, T. 2007. Digeneans (Trematoda) of freshwater fishes from Nagano Prefecture, central Japan. Bulletin of the National Museum of Nature and Science, Series A (Zoology), 33: 1–30.

Shimazu, T. 2008. Digeneans (Trematoda) found in freshwater fishes of Wakayama, Tokushima, and Kochi Prefectures, Japan. Bulletin of the National Museum of Nature and Science, Series A (Zoology), 34: 41–61.

Shimazu, T. 2013. Digeneans parasitic in freshwater fishes (Osteichthyes) of Japan. I. Aporocotylidae, Bivesiculidae and Haploporidae. Bulletin of the National Museum of Nature and Science, Series A (Zoology), 39: 167–184.

Shimazu, T. 2015. Digeneans parasitic in freshwater fishes (Osteichthyes) of Japan. V. Didymozoidae and Isoparorchiidae. Bulletin of the National Museum of Nature and Science, Series A (Zoology), 41: 201–216.

Shimazu, T. 2016. Digeneans Parasitic in Freshwater Fishes (Osteichthyes) of Japan. IX. Opecoelidae, Opecoelinae. Bulletin of the National Museum of Nature and Science, Series A (Zoology), 42: 163–180.

Shimazu, T. and M. Urabe 2005. Digeneans found in freshwater fishes of the Uji River at Uji, Kyoto Prefecture, and the Takami River at Higashiyoshino, Nara Prefecture, Japan. Journal of Nagano Prefectural College, (60): 1–14.

Shimazu, T., M. Urabe and M. J. Grygier 2011. Digeneans (Trematoda) parasitic in freshwater fishes (Osteichthyes) of the Lake Biwa basin in Shiga Prefecture, central Honshu, Japan. National Museum of Nature and Science Monographs, (43): 1–105.

Skryabin, K. I. and V. P. Koval 1958. [Subfamily Plagioporinae Manter, 1947.] In K. I. Skryabin (ed.), [Trematodes of Animals and Man.] Osnovy Trematodologii, 15: 424–811. Izdatel'stvo Academii Nauk SSSR, Moskva. (In Russian.)

Sokolov, S. G. and S. E. Frolova 2015. Data of the parasite fauna of the Sakhalin fishes. Bulletin of the North-East Scientific Center, Russia Academy of Sciences Far East Branch, (2): 90–97. (In Russian with English abstract.)

Takahashi, S. 1928. On a new trematode *Podocotyle ayu* n. sp. from the intestine of *Plecoglossus altivelis* (T. and S.). Arbeiten aus der Medizinischen Universität zu Okayama, 1: 51–56.

Takahashi, S. 1929. A contribution to the structure of the female genital organs in some digenetic trematodes in Japan. Okayama Igakkai Zasshi, 41: 1924–1933, pls. 1–4. (In Japanese with English abstract.)

Urabe, M. and E. Higa 2006. A new trematode species *Neoplagioporus kajika* sp. n. (Digenea: Opecoelidae), parasitic in the Japanese fluvial sculpin, *Cottus pollux* (Osteichthyes: Scorpaeniformes: Cottidae), from Japan. Folia Parasitologica, 53: 208–210.

Wang, P.-Q. 1984. Some digenetic trematodes from fishes in Fujian Province, China. Acta Zootaxonomica Sinica, 9: 122–131. (In Chinese with English abstract.)

Wang, P.-Q. 1985. [Parasitic helminths of vertebrates from Sichuan Province—parasitic trematodes of fishes.] Sichuan Dongwu, 4: 1–5. (In Chinese.) Cited by Liu (1987).

Wang, P.-Q., Y.-L. Sun, Y.-R. Zhao, W.-H. Zhang and Y.-L. Wang 1985. Notes on some digenetic trematodes of vertebrates from Wuyishan, Fujian. Wuyi Science Journal, 5: 129–139. (In Chinese with English abstract.)

Yamaguti, S. 1934. Studies on the helminth fauna of Japan. Part 2. Trematodes of fishes, I. Japanese Journal of Zoology, 5: 249–541.

Yamaguti, S. 1938. Studies on the Helminth Fauna of Japan. Part 21. Trematodes of Fishes, IV. 139 pp., 1 pl. Author's publication, Kyoto.

Yamaguti, S. 1942. Studies on the helminth fauna of Japan. Part 39. Trematodes of fishes mainly from Naha. Transactions of the Biogeographical Society of Japan, 3: 329–398, pl. 24.

Yamaguti, S. 1953 [issued 1954]. Systema Helminthum. Part I. Digenetic trematodes of fishes. 405 pp. Maruzen Co., Ltd., Tokyo.

Yamaguti, S. 1958. Systema Helminthum. Volume I. The digenetic trematodes of vertebrates. 1575 pp. Interscience Publishers, Inc., New York.

Yamaguti, S. 1971. Synopsis of Digenetic Trematodes of Vertebrates. Volume I: 1074 pp.; Volume II: 349 pls. Keigaku Publishing Co., Tokyo.

Yanagi, S., Y. Kuribayashi, M. Okamoto, Y. Mori and M. Urabe 2010. Seasonal dynamics of the fish parasite *Neoplagioporus ayu* (Digenea) in its definitive host, *Plecoglossus altivelis*, in the Chikugo River, Kyushu, Japan. Limnology, 11: 167–170.

Yoshida, R. and M. Urabe 2005. Life cycle of *Coitocoecum plagiorchis* (Trematoda: Digenea: Opecoelidae). Parasitology International, 54: 237–242.