Bull. Natl. Mus. Nat. Sci., Ser. A, 41(2), pp. 77–103, May 22, 2015

Digeneans Parasitic in Freshwater Fishes (Osteichthyes) of Japan. IV. Derogenidae

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(Received 20 March 2015; accepted 1 May 2015)

Abstract Digeneans of the family Derogenidae Nicoll, 1910 (Trematoda) parasitic in freshwater fishes of Japan are reviewed: *Allogenarchopsis problematica* (Faust, 1924), *Genarchopsis goppo* Ozaki, 1925, *Genarchopsis anguillae* Yamaguti, 1938, *Genarchopsis gigi* Yamaguti, 1939, *Genarchopsis fellicola* Shimazu, 1995, *Genarchopsis chubuensis* sp. nov. and *Genarchopsis* spp. 1 and 2 of Shimazu, 1995. The new species *G. chubuensis* is proposed on the basis of specimens found in the stomach of *Gymnogobius urotaenia* (Hilgendorf, 1879) (Gobiidae) (type host) and several other species from the central part of Honshu, Japan (type locality: Lake Suwa in Nagano Prefecture). Each species is described and figured with a summarized life cycle where known. The life cycle of *Genarchopsis* Ozaki, 1925 in the present paper is discussed. A key to the genera and species of the Derogenidae in the present paper is given.

Key words: Digeneans, *Allogenarchopsis*, *Genarchopsis*, *Genarchopsis chubuensis* sp. nov., freshwater fishes, Japan, review.

Introduction

This is the fourth paper of a series that reviews adult digeneans (Trematoda) parasitic in freshwater fishes (Osteichthyes) of Japan (Shimazu, 2013). This contribution deals with the family Derogenidae Nicoll, 1910 *sensu* Gibson (2002b) in the superfamily Hemiuroidea Looss, 1899 *sensu* Gibson (2002a). The Introduction and Materials and Methods for the review were given by Shimazu (2013).

Abbreviations used in the figures. bp, birth pore; c, cercaria; cbp, cercarial body proper; ccc, cercarial caudal cavity; cc, cyclocoel; ct, cercarial (cystophorous) tail; cvd, common vitelline duct; Dm, Drüsenmagen; e, esophagus; ec, epithelial cell of excretory vesicle; ed, ejaculatory duct; egg, egg in uterus and metraterm; ep, excretory pore; esp, esophageal pouch; ev, excretory vesicle; fc, flame cell; ga, genital atrium; gp, genital pore; hd, hermaphroditic duct; i, intestine; Jo, Juel's organ; Lc, Laurer's canal; m, metraterm; Mg, Mehlis' gland; o, ovary; od, oviduct; op, ootype pouch; os, oral sucker; ot, ootype; p, pharynx; pc, prostatic cells; pcec, primary caudal excretory canal; pep, primary excretory pore; pp, pars prostatica; s, sphincter; scec, secondary caudal excretory canal; sd, sperm duct; so, sinus organ; ss, sinus sac; sv, seminal vesicle; t, testis; tnc, transverse nerve commissure; u, uterus; usr, uterine seminal receptacle; v, vitellarium; vd, vitelline duct; vs, ventral sucker.

Superfamily Hemiuroidea Looss, 1899

Family Derogenidae Nicoll, 1910

Genus *Allogenarchopsis* Urabe and Shimazu, 2013

Allogenarchopsis problematica (Faust, 1924)

(Figs. 1–8)

[*Cercaria cystophora* cercaria]: Kobayashi, 1915: 52–54, pl. 2, fig. 5.
[*Cercaria cystophora* C]: Kobayashi, 1922: 268.
Cercaria problematica Faust, 1924: 294, table 1;

Ito, 1964: 479, fig. 98.
Cercaria manei Ito, 1960: 70–71, figs. 16–17.
Genarchopsis yaritanago Shimazu, Urabe and Grygier, 2011: 21–23, figs. 25–29.
Allogenarchopsis yaritanago: Urabe and Shimazu, 2013: 128.
Allogenarchopsis problematica: Urabe and Shimazu, 2013: 122, 124, figs. 1–6.

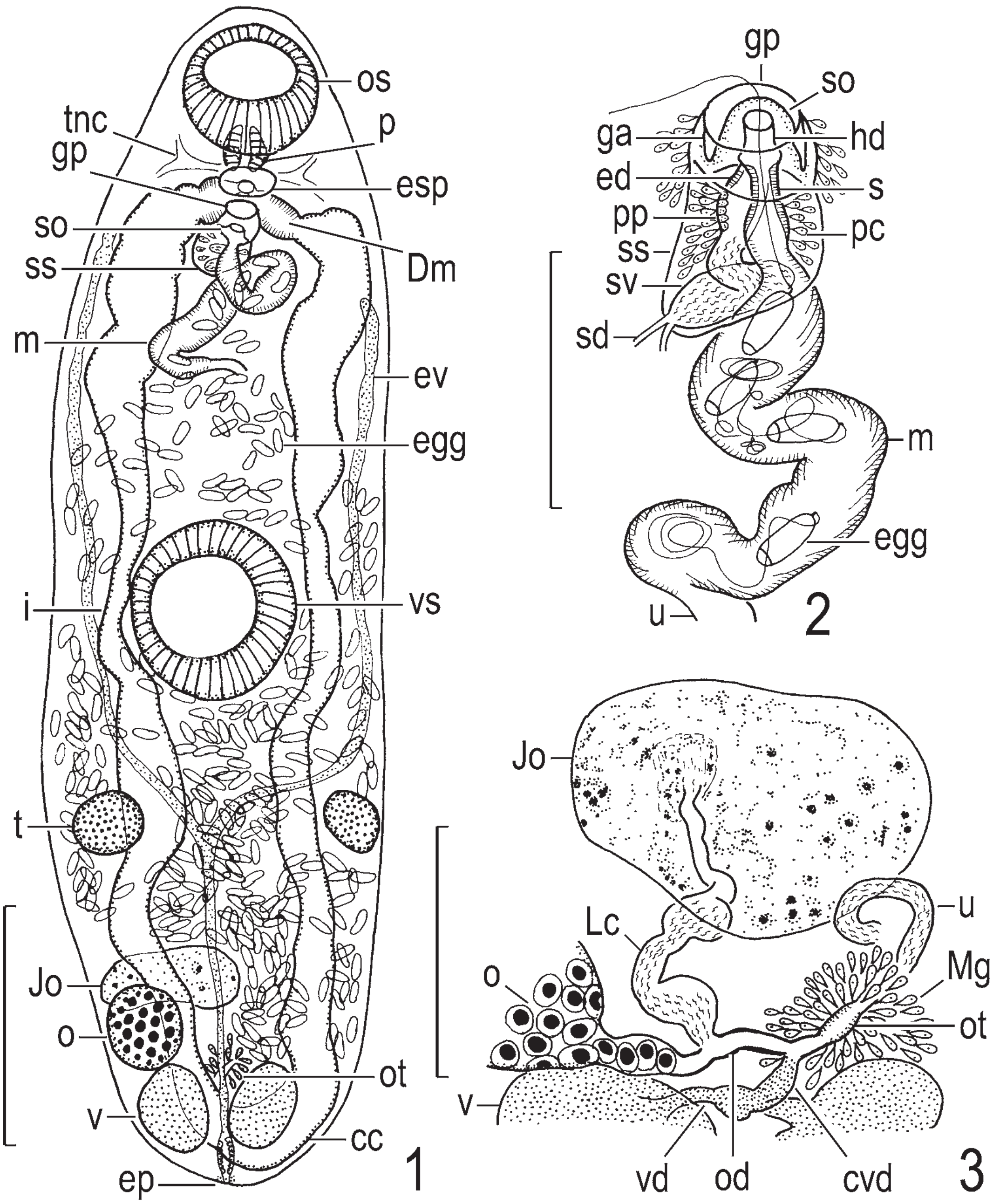
Hosts in Japan. *Tanakia lanceolata* (Temminck and Schlegel, 1846) (type host), *Tanakia limbata* (Temminck and Schlegel, 1846), *Rhodeus ocellatus ocellatus* (Kner, 1866) and *Acheilognathus rhombeus* (Temminck and Schlegel, 1846) (Cyprinidae, Acheilognathinae) (Shimazu *et al.*, 2011; Urabe and Shimazu, 2013).

Site of infection. Intestine.

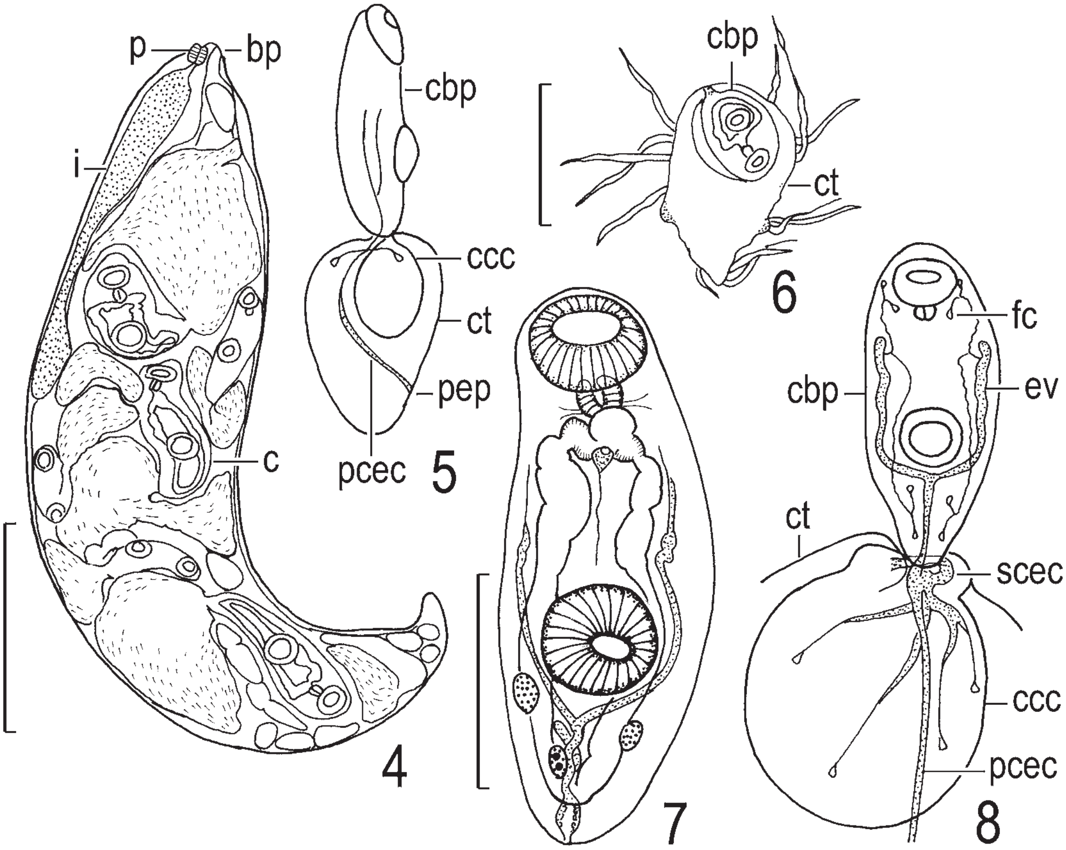
Geographical distribution. Shiga Prefecture: irrigation canal (type locality) closely connected to Yogo River at Nishiyama, Kinomoto-cho, Nagahama City; irrigation canal at Miyake-cho, Moriyama City; and agricultural irrigation canal connected to Hino River at Kominami, Yasu City (Shimazu *et al.*, 2011; Urabe and Shimazu, 2013).

Material examined. (1) Type specimens of *Genarchopsis yaritanago*: holotype (LBM 1340000079) and 1 paratype (LBM 1340000080), adult, whole-mounted, ex intestine of *Tanakia lanceolata*, Nishiyama, 27 November 2007; and 1 paratype (LBM 1340000078), adult, whole-mounted, ex intestine of *T. lanceolata*, Miyake-cho, 27 October 2000 (Shimazu *et al.*, 2011; Urabe and Shimazu, 2013). (2) 1 specimen (NSMT-Pl 5854), adult, whole-mounted, ex intestine of *T. lanceolata*, Nishiyama, 27 May 2009 (Urabe and Shimazu, 2013). (3) 1 (NSMT-Pl 5855), adult, whole-mounted, ex intestine of *T. limbata*, Nishiyama, 29 July 2012 (Urabe and Shimazu, 2013). (4) Many (NSMT-Pl 5851, 5853; Urabe's personal collection), immature, adult, whole-mounted, ex intestine of *Rhodeus ocellatus ocellatus*, Kominami, 2 May 2011, 28 October 2011, 11 September 2012 (Urabe and Shimazu, 2013). (5) Several (NSMT-Pl 5852), immature, adult, hot formalin-fixed, serially sectioned, whole-mounted, ex intestine of *Acheilognathus rhombeus*, Kominami, 11 September 2012 (Urabe and Shimazu, 2013).

Description. After Urabe and Shimazu (2013), modified from the present study (Figs. 1–3). Body spindle-shaped, anterior extremity slightly more attenuated than posterior extremity, slightly flattened dorsoventrally, anoculate, small, 1.62–3.47 by 0.52–0.97; forebody 0.84–1.84 long, occupying 51–56% of body length. Ecsoma absent. Tegument smooth. Preoral lobe not prominent. Transverse nerve commissure dorsal to esophagus. Oral sucker almost globular, 0.20–0.37 by 0.23–0.35, almost ventral, close to anterior extremity; sphincter at mouth aperture not developed. Prepharynx absent. Pharynx barrel-shaped, 0.08–0.12 by 0.07–0.11, posterodorsal to oral sucker. Esophagus inverted Y-shaped, small, 0.06–0.13 by 0.06–0.10, surrounded by small gland cells; esophageal pouch oval, small, ventral to esophagus. Drüsenmagen small, between esophageal arm and intestine on either side of body, 0.05–0.09 by 0.06–0.13. Intestines slightly undulating, distally uniting with each other to form cyclocoel; cyclocoel overlapping vitellaria. Ventral sucker almost globular, 0.23–0.39 by 0.26–0.45, a little postequatorial; sphincter at aperture of ventral sucker not developed; sucker width ratio 1 : 1.1–1.2. Testes two, elliptical to globular, sometimes slightly irregular in outline, small, 0.11–0.22 by 0.07–0.18, symmetrical or slightly diagonal, lateral to or slightly overlapping intestines, posterolateral to ventral sucker, at about junction of anterior and middle thirds of hindbody. Sperm ducts long; common sperm duct absent. Sinus sac thin-walled, membranous, small, 0.06–0.11 by 0.09 [not 0.109]–0.14, median, posterior to esophagus, enclosing seminal vesicle, prostatic complex, ejaculatory duct and distal part of metraterm. Seminal vesicle retort-shaped, small, coiled once at neck portion. Pars prostatica vesicular, large; prostatic cells well developed. Ejaculatory duct very short, like sphincter, joining metraterm dorsally at base of genital atrium to form hermaphroditic duct; hermaphroditic duct running only in sinus organ, opening on apex of it. Sinus organ permanent,



Figs. 1–3. *Allogenarchopsis problematica*, adults. — 1, specimen (NSMT-Pl 5851) found in intestine of *Rhodeus ocellatus ocellatus*, entire body, ventral view; 2, specimen (LBM 1340000079) (holotype of *Genarchopsis yaritanago*) found in intestine of *Tanakia laceolata*, terminal genitalia, ventral view; 3, specimen (NSMT-Pl 5851), ovarian complex and Juel's organ, ventral view. Redrawn from Urabe and Shimazu (2013). Scale bars: 0.5 mm in Fig. 1; 0.2 mm in Figs. 2–3.



Figs. 4–8. *Allogenarchopsis problematica*, life cycle, daughter redia and cercariae (*Cercaria problematica*) found in *Semisulcospira reiniana*. — 4, daughter redia, lateral view; 5, weakly developed cercaria, lateral view (scale unknown); 6, fully developed cercaria; 7, body proper of fully developed cercaria, ventral view; 8, fully developed cercaria, showing excretory system, ventral view (scale unknown). Redrawn from Urabe and Shimazu (2013). Scale bars: 0.5 mm in Figs. 4 and 6; 0.2 mm in Fig. 7.

muscular, cone-shaped, small, 0.02–0.05 by 0.03–0.06, projecting into genital atrium. Genital atrium cylindrical, thick-walled, 0.05–0.10 by 0.06–0.10, surrounded by small gland cells. Genital pore wide, median, slightly posterior or ventral to esophagus. Ovary almost globular, larger than testes, 0.16–0.26 by 0.14–0.22, dextrally or sinistrally lateral, post-testicular, usually anterior to vitellaria or slightly overlapping them. Oviduct fairly long; ovovitelline duct short. Seminal receptacle absent. Laurer's canal dilated, sinuous, including sperm, running forward, leading into Juel's organ, may be connected to inner vesicle of Juel's organ. Juel's organ large, 0.14–0.16 by 0.14–0.31 in 3 specimens (not clearly observed in others), in dorsal parenchyma, anteromedial to ovary and ootype. Ootype usually submedian but rarely median, opposite to ovary, anterior to or overlapping vitellaria; Mehlis' gland well developed, free in parenchyma. Uterus much coiled in all available space of body between vitellaria and metraterm or sinus sac; metraterm well developed, much longer than sinus sac, folded between middle of forebody and sinus sac, leading into sinus sac, with well-developed sphincter at its anterior end; uterine seminal receptacle well developed in proximal coils of uterus. Eggs numerous, elongate-oblong, slightly curved, operculate, brown, fully embryonated, 56–64 by 25–32 μm; anopercular filament present, long.

Vitellaria consisting of two glands, elliptical, large, 0.16–0.30 by 0.10–0.20, symmetrical or diagonal, separate, close to posterior extremity. Vitelline ducts very short; common vitelline duct short. Excretory vesicle Y-shaped, in ventral parenchyma, bifurcating at about testicular level; stem having small dilatation lined with epithelial cells near excretory pore; arms lateral, running forward, terminating at near intestinal shoulders, well separated there; excretory pore posteroterminal.

Remarks. Urabe and Shimazu (2013) established a new genus, *Allogenarchopsis*, with *Genarchopsis yaritanago* Shimazu *et al.*, 2011, or now *Allogenarchopsis yaritanago* (Shimazu *et al.*, 2011), as the type species on the basis of the type specimens of *G. yaritanago* and their new adult specimens. Moreover, they indicated that *Cercaria problematica* Faust 1924 and *A. yaritanago* are the same species in morphology and DNA sequences (partial sequences of the cytochrome *c* oxidase subunit I gene of the mitochondrial DNA (COI mtDNA)) and that *Cercaria manei* Ito, 1960 is synonymous with *C. problematica*. Consequently, they changed the species name from *A. yaritanago* to *Allogenarchopsis problematica* (Faust, 1924).

The adult of this species has been recorded from the intestine of acheilognathine fishes of the Lake Biwa basin (Shimazu *et al.*, 2011; Urabe and Shimazu, 2013). Kobayashi (1922) said that *Cercaria cystophora* C was common in Okayama Prefecture. Ito (1960) reported *C. manei* from Shizuoka Prefecture.

Life cycle. Natural first intermediate hosts are *Semisulcospira libertina* (Gould, 1859) (Gastropoda, Pleuroceridae) [Japanese name: Kawanina] (Kobayashi, 1915, 1922; Ito, 1960) and *Semisulcospira reiniana* (Brot, 1874) [Japanese name: Chirimen-kawanina] (Urabe and Shimazu, 2013). Cercariae (*Cercaria problematica*) of the cystophorous type (Figs. 5–8) are produced in daughter rediae (Fig. 4). The flame cell formula is $2[(2)+(2)+(2)]=12$. Neither sporocysts nor mother rediae are known. No second intermediate hosts are known. Natural final hosts are acheilognathine fishes, *Tanakia lanceolata*, *T. limbata*, *Rhodeus ocellatus ocellatus* and *Acheilognathus rhombeus*, in the intestine of which adults live (Shimazu *et al.*, 2011; Urabe and Shimazu, 2013).

Genus ***Genarchopsis*** Ozaki, 1925

Genarchopsis goppo Ozaki, 1925

(Figs. 9–11)

Genarchopsis goppo Ozaki, 1925: 101–103, figs. 1–3; (?) Takahashi, 1929: 1928–1929, pl. 3, fig. 12; (?) Shimazu, 2008: 43, fig. 2.

Progonus goppo: Srivastava, 1933: 55.

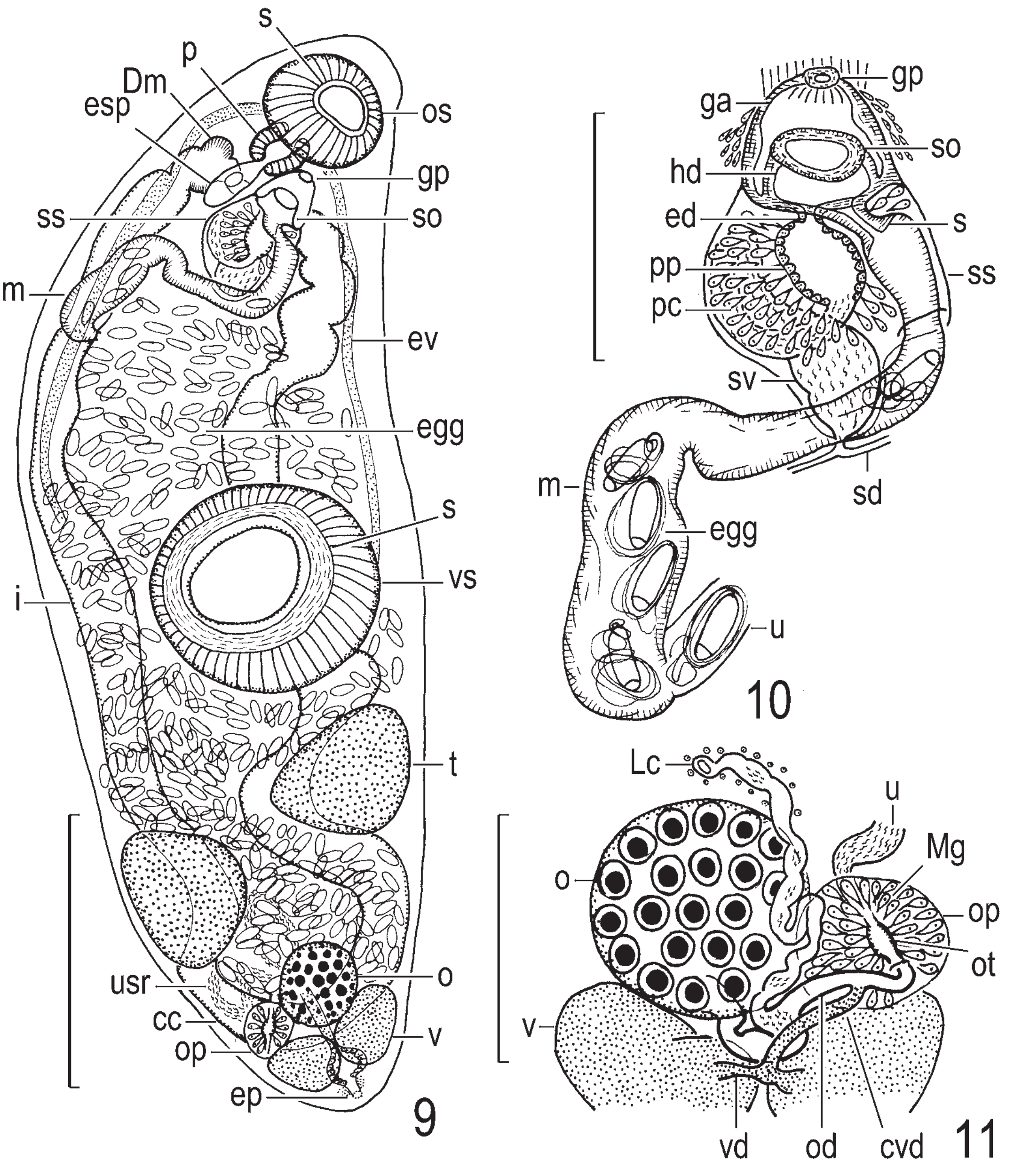
Genarches goppo: Skryabin and Guschanskaya, 1955: 685–686, 689, fig. 201.

Genarchapsis goppo [*sic*, misspelling of *Genarchopsis*] (not of Ozaki, 1925): Shimazu, 1995a, in part: 6–8, figs. 1–4.

Hosts in Japan. *Odontobutis obscura* (Temminck and Schlegel, 1845) (Odontobutidae) (type host), *Coreoperca kawamebari* (Temminck and Schlegel, 1843) (Percichthyidae) and “[Gori]” (most likely referring to *O. obscura*); *Silurus asotus* Linnaeus, 1758 (Siluridae) (presumably accidental host as discussed below) (Ozaki, 1925; Takahashi, 1929; Shimazu, 1995a; Lin *et al.*, 2006; Urabe *et al.*, 2013; this paper); and (?) *Rhinogobius flumineus* (Mizuno, 1960), (?) *Rhinogobius giurinus* (Rutter, 1897), (?) *Rhinogobius nagoyae* Jordan and Seale, 1906, (?) *Gymnogobius petschiliensis* (Rendal, 1924) and (?) *Tridentiger brevispinis* Katsuyama, Arai and Nakamura, 1972 (Gobiidae) (Shimazu, 2008; this paper).

Sites of infection. Primarily stomach, and intestine (possibly erroneous record as discussed below).

Geographical distribution. (1) Hiroshima Prefecture: a brook near Saijo-cho; Nukui River at Hara, Hachihonmatsu-cho; Matsuita River at Umaki, Saijo-cho; Kurose River at Nomio, Kurose-cho; Takeyasu River at Munechika-yanakuni, Kurose-cho; Karei River at Maruyama, Kurose-cho; and Irasuke River at Kanesawa, Kurose-cho, all Higashihiroshima City (Ozaki,



Figs. 9–11. *Genarchopsis goppo*, adult (NSMT-Pl 3998) found in stomach of *Odontobutis obscura*. — 9, entire body, middle part of excretory vesicle obscured, ventral view; 10, terminal genitalia, ventral view; 11, ovarian complex, dorsal view. Scale bars: 0.5 mm in Fig. 9; 0.2 mm in Figs. 10–11.

1925; Shimazu, 1995a; Urabe *et al.*, 2013; this paper). (2) (?) Okayama Prefecture: Okayama City (Takahashi, 1929). (3) (?) Tokushima Prefecture: Kaifu River at Yoshino, Kaiyo Town; and Fukui River at Kono, Fukui, Anan City (Shimazu, 2008). (4) (?) Kochi: Okuura River at Uranouchihaigata, Susaki City; Oshioka River at Oshioka, Susaki City; Sakura River at Koda, Susaki City; and Matsuda River at Nakatsuno, Ninomiya and Wada, Sukumo City (Shimazu, 2008). (5) Fukuoka Prefecture: Futatsu River at Takahatake, Mitsuhashi-machi, Yanagawa City;

Sakuta Creek, Nakagawa Town; and Naka River at Terase Bridge, Narutake, Nakagawa Town (Lin *et al.*, 2006; Urabe *et al.*, 2013; this paper).

In Primorsky Region, Russia (e.g., Besprozvannykh and Ermolenko, 1988; Ermolenko, 1992; Besprozvannykh, 2000), China (*e.g.*, Wang, 1991; Moravec *et al.*, 2003), Laos (*e.g.*, Scholz, 1991) and India (*e.g.*, Pandey, [1975]; Madhavi, 1978).

Material examined. (1) 1 specimen (Ozaki's Collection, MPM Coll. No. 30028, labeled "[Gori]," other data not given) of *G. goppo*, adult, whole-mounted (Shimazu, 1995a, b). (2) Many specimens (NSMT-Pl 3996–3998) of *G. goppo*, immature, adult, whole-mounted, serially sectioned, ex stomach of *Odontobutis obscura*, Kurose River at Nomio, now in Kurose-cho, 13 April 1991; Takeyasu River, 30 April 1991; and Nukui River at Babadai, now Hara, Hachihonmatsu-cho, 26 July 1991 (Shimazu, 1995a). (3) 4 (NSMT-Pl 4016) of *G. goppo*, adult, whole-mounted, ex stomach of *Silurus asotus*, Nukui River, 26 July 1991 (Shimazu, 1995a). (4) 1 (NSMT-Pl 5764), adult, whole-mounted, ex stomach of *O. obscura*, Nukui River, 30 October 2008. (5) 8 (NSMT-Pl 5765–5766), adult, whole-mounted, ex stomach of *O. obscura*, Matsuita River, 30 October 2008, 18 June 2009. (6) 1 (NSMT-Pl 5767), adult, whole-mounted, ex stomach of *O. obscura*, Karei River, 18 June 2009. (7) 7 (NSMT-Pl 5768), adult, whole-mounted, ex stomach of *O. obscura*, Irasuke River, 18 June 2009. (8) 31 (Urabe's personal collection), immature, adult, whole-mounted, ex *O. obscura* (site of infection not given), Futatsu River, 22 and 23 May 2003, 5 and 21 June 2003. (9) 3 (Urabe's personal collection), adult, whole-mounted, ex *Coreoperca kawamebari* (site of infection not given), Futatsu River, 20 and 26 August 2002. (10) 6 (Urabe's personal collection), adult, whole-mounted, ex *O. obscura* (site of infection not given), Naka River, 8 October 2003.

Description. 1) Based on Ozaki's specimen (MPM Coll. No. 30028), after Shimazu (1995a, fig. 1), modified from the present study. Body mounted laterally, 1.17 long. Oral sucker 0.14 in diameter; sphincter at aperture of oral sucker fairly well developed. Pharynx 0.06 by 0.05. Intestines undulating, distally uniting with each other to form cyclocoel dorsal to vitellaria. Ventral sucker 0.25 by 0.21; sphincter at aperture of ventral sucker well developed; radial muscle bundles connected to ventral sucker well developed. Testes 0.19 by 0.14. Sinus sac 0.11 by 0.12. Ovary 0.09 by 0.07. Eggs 40–45 by 18–19 μm (collapsed). Vitellaria 0.12 by 0.05.

2) Based on specimens (NSMT-Pl 3998) from *Odontobutis obscura*, after Shimazu (1995a), modified from the present study (Figs. 9–11). Body spindle-shaped, with bluntly pointed ends, small, 1.09–2.16 by 0.37–0.72; forebody 0.54–1.04 long, occupying 48–54% of body length. Transverse nerve commissure dorsal to pharynx or esophagus. Tegument smooth. Preoral lobe prominent. Oral sucker subglobular, 0.14–0.21 by 0.16–0.26, anteroventral; sphincter around mouth aperture fairly well developed. Radial muscle bundles connected to mouth aperture well developed, lateral ones better developed (not illustrated). Prepharynx absent. Pharynx almost round, 0.06–0.10 in diameter. Esophagus inverted Y- or T-shaped, short, surrounded by small gland cells; esophageal pouch present, oval, small, posteroventral to esophagus. Drüsenmagen small, between esophageal arm and intestine on either side of body. Intestines undulating, distally uniting with each other to form cyclocoel just anterior to vitellaria, overlapping dorsally to ovary. Ventral sucker subglobular, large, 0.30–0.45 by 0.28–0.45, posterior to esophagus, at about middle of body; sphincter around aperture well developed; sucker width ratio 1 : 1.7–2.2. Radial muscle bundles connected to aperture of ventral sucker well developed, anterior and posterior ones better developed (not illustrated). Testes two, elliptical, 0.14–0.35 by 0.13–0.28, diagonal to symmetrical, lateral, overlapping intestines, posterolateral to ventral sucker, separated greatly from ventral sucker by uterus, at about midlevel of hindbody. Sperm ducts long; common sperm duct absent. Sinus sac thin-walled, 0.10–0.19 by 0.11–0.22, posterior to

esophagus, including seminal vesicle, prostatic complex, ejaculatory duct and distal part of metraterm. Seminal vesicle retort-shaped, looped once in long neck portion. Pars prostatica vesicular, oval, fairly large; prostatic cells large, well developed. Ejaculatory duct thick-walled, like sphincter, very short, joining metraterm dorsally at base of genital atrium to form hermaphroditic duct; hermaphroditic duct present only in sinus organ. Sinus organ muscular, cylindrical, thick, stumpy, 0.05–0.09 by 0.07–0.09, projecting into genital atrium. Genital atrium thick-walled, dome-shaped, surrounded by small gland cells; longitudinal muscle fibers present in its wall, those on dorsal side running forward farther into parenchyma. Genital pore median, usually closed and puckered, sometimes opening wide, ventral to pharynx. Ovary globular to elliptical, smaller than testes, 0.06–0.14 by 0.06–0.18, dextrally or sinistrally submedian, between testis and vitellarium. Oviduct fairly long, leaving ovary posteriorly, giving off Laurer's canal, usually dilated at its base to store sperm, receiving common vitelline duct, and then leading to ootype. Juel's organ absent. Laurer's canal fairly long, median, running forward, opening dorsally between ovary and testes or sometimes at testicular level, usually forming small rudimentary seminal vesicle to store sperm in it. Ootype pouch (terminology of Shimazu *et al.*, 2011; membranous sheath in Shimazu, 1995a) thin-walled, 0.09–0.15 by 0.06–0.10, submedian, between ovary and right or left vitellarium, enveloping ootype, massive Mehlis' gland and proximal coils of uterus. Uterus much folded transversely between vitellaria and sinus sac (seven to nine times in forebody) (see also Shimazu *et al.*, 2011), mostly between intestines and cyclocoel, overlapping intestines; metraterm well differentiated, muscular, thick, much longer than (about three times as long as) sinus sac, leading into sinus sac, with well-developed sphincter at anterior end; uterine seminal receptacle present. Eggs numerous (100–177 in forebody) (see also Shimazu *et al.*, 2011), elongate-oval, somewhat reniform, yellowish brown, fully embryonated, unembryonated eggs (before cleavage) 48–67 by 25–28 μm, fully embryonated eggs 51–72 by 27–29 μm; anopercular filament present, 1.26–1.76 long. Vitellaria two, each elliptical, 0.09–0.16 by 0.07–0.14, diagonal or symmetrical, contiguous or a little separate, near posterior extremity of body; vitelline ducts short; common vitelline duct or vitelline reservoir small, anterior to vitellaria. Excretory vesicle Y-shaped, running anteriorly in ventral parenchyma, bifurcating between testes and ventral sucker (middle part obscured in figured specimen, Fig. 9); stem having small dilatation lined with epithelial cells near excretory pore; arms uniting with each other dorsally to pharynx; excretory pore posterodorsal.

Remarks. Ozaki (1925) established a new genus and species, *Genarchopsis goppo*, on the basis of adult specimens found in the intestine [*sic*, see below] of *Mogurnda obscura* (now in *Odontobutis*) [Japanese name: Donko, but Goppo in Ozaki] collected in a brook near Saijo, now Saijo-cho, Higashihiroshima City. He did not designate a holotype for this species. His specimen (MPM Coll. No. 30028) is labeled "[Gori]" only. This host fish "[Gori]" most likely refers to *O. obscura* from Saijo, and so the specimen is possibly the only existent syntype of *G. goppo* (Shimazu, 1992, 2000). The name of the brook has remained undetermined.

The site of infection of adult worms is primarily the stomach of fish as shown in most of the above-mentioned cases. Ozaki (1925) and Takahashi (1929) reported adult worms from the intestine of *O. obscura* and *S. asotus*, respectively. Ozaki claimed to have found worms frequently in the intestine. However, I obtained worms only from the stomach of these two fishes as mentioned above. It is possible that Ozaki and Takahashi may have erroneously recorded the site of infection.

In the adult stage, *Genarchopsis* differs from the foregoing *Allogenarchopsis* in that Juel's organ is absent, Lauer's canal opens outside dorsally, the ootype pouch is present, and the excretory arms are united anteriorly (Urabe and Shimazu, 2013).

Allogenarchopsis and *Genarchopsis* have an inverted Y- or T-shaped esophagus and a posteroventral esophageal pouch. It appears that the esophageal pouch is a posteroventral outgrowth of the ventral wall of the stem of the esophagus, with a dorsal aperture surrounded by a sphincter into the two arms (Shimazu, 1995a, fig. 9; Figs. 9, 15, 16 and 18).

Urabe *et al.* (2013) carried out a molecular study of adult specimens of *Genarchopsis* and rediae from Japan. The first internal transcribed spacer region of the ribosomal DNA (ITS-1 rDNA) and the cytochrome *c* oxidase subunit I gene of the mitochondrial DNA (COI mtDNA) were partially sequenced. Their molecular phylogenetic analyses of the partial sequences separated the adult and redial forms into four groups: (1) West Japan Group of *G. goppo*, or *Genarchopsis goppo* Ozaki, 1925 (*sensu stricto*), in Hiroshima, Tottori, Fukuoka and Oita Prefectures; (2) Central Japan Group of *G. goppo*, or a cryptic species of *G. goppo*, in Shiga (waters around Lake Biwa and rivers flowing into it), Nara, Gifu, Fukui, Nagano and Saitama Prefectures; (3) Lake Biwa Group, or *Genarchopsis gigi* Yamaguti, 1939, in Lake Biwa itself; and *Genarchposis fellicola* Shimazu, 1995 in Nagano and Ibaraki Prefectures. The first group included the samples found in *O. obscura* from the Nukui, Matsuita, Irasuke and Karei rivers in Higashihiroshima City; and Sakuta Creek, Nakagawa Town, and the Futatsu River both in Fukuoka Prefecture. Therefore, the present specimens are assigned to *G. goppo* (*sensu stricto*).

Takahashi (1929) described the ovarian complex of *G. goppo* found in the intestine [*sic*, see above] of *Parasilurus asotus* (now in *Silurus*) from Okayama City, Okayama Prefecture. He overlooked the presence of the ootype pouch. It seems likely from the occurrence in Okayama that he had *G. goppo* (*sensu stricto*) at that time. Shimazu (2008) reported specimens under the species name *G. goppo* found in the stomach of gobiids, *Rhinogobius flumineus*, *R. giurinus*, *R. nagoyae* [syn. *Rhinogobius* sp. CB], *Gymnogobius petschiliensis* and *Tridentiger brevispinis*, from Tokushima and Kochi Prefectures (see *Hosts in Japan* and *Geographical distribution*). Eggs were 48–73 [not 70] by 24–35 μm. It is considered from adult morphology (Shimazu, 2008, fig. 2) that they belong to *G. goppo* (*sensu stricto*), though no molecular data on them are available at present.

In addition, *G. goppo* (or as *Genarches goppo*) has been reported from Primorsky Region, Russia (*e.g.*, Besprozvannykh and Ermolenko, 1988; Ermolenko, 1992; Besprozvannykh, 2000), China (*e.g.*, Wang, 1991; Moravec *et al.*, 2003), Laos (*e.g.*, Scholz, 1991) and India (*e.g.*, Pandey, [1975]; Madhavi, 1978). Although the species in their descriptions certainly belong to *Genarchopsis*, they need further morphological and molecular studies for definitive identification. Madhavi (1978) studied the life cycle of *G. goppo* in India. Urabe (2001) was the opinion that Madhavi's species differed from her *G. goppo* [Central Japan Group]. Besprozvannykh and Ermolenko (1988), Ermolenko (1992) and Besprozvannykh (2000) also studied the life cycle of *Genarches goppo* in Primorsky Resion, Russia. First intermediate hosts were snails, *Juga* spp. (Pachychilidae). A second intermediate host was a mayfly, *Ecdyonurus aurarius* (Heptageniidae). Final hosts were *Rhinogobius similis* and *Chaenogobius annuralis urotaenia*. I do not consider that their species is *G. goppo* (*sensu stricto*), because the cercaria resembles *Cercaria longicerca* Ito, 1953; and the adult has smaller eggs (45–47 by 23–25 μm) and much fewer uterine transverse folds.

Life cycle. A natural first intermediate host is *Semisulcospira libertina* in Oita, Hiroshima and Tottori Prefectures (Urabe *et al.*, 2013). Cercariae similar to *Cercaria yoshidae* Cort and Nichols, 1920 are produced in daughter rediae, but they have not yet been described. No natural second intermediate hosts are known. Natural final hosts are at least *Odontobutis obscura*, *Coreoperca kawamebari* and *Silurus asotus* (this paper). These fishes are predatory. It is unknown whether the former two are true final hosts to become infected with worms by eating the second intermediate host. At least *S. asotus* is considered to be an accidental host to become infected with worms by ingesting infected fish.

Genarchopsis anguillae Yamaguti, 1938

(Fig. 12)

Genarchopsis anguillae Yamaguti, 1938: 132–133, fig. 81; Yamaguti, 1942: 388; Shimazu, 1995a: 11, fig. 6.
Genarches anguillae: Skryabin and Guschanskaya, 1955: 680, fig. 199.

Hosts in Japan. *Anguilla japonica* Temminck and Schlegel, 1846 (Anguillidae) (type host) and *Gymnogobius urotaenia* (Hilgendorf, 1879) (Gobiidae) (Yamaguti, 1938, 1942; this paper).

Site of infection. Intestine.

Geographical distribution. Ibaraki Prefecture: Tsuchiura (type locality) (Yamaguti, 1938, 1942).

Material examined. 1 specimen (Yamaguti's Collection, MPM Coll. No. 22005, holotype) of *Genarchopsis anguillae*, adult, whole-mounted, ex intestine of *Anguilla japonica* (wild), Tsuchiura, 16 April 1929 (Yamaguti, 1938; Shimazu, 1995a).

Description. After Shimazu (1995a), modified from the present study (Fig. 12). Similar to *G. goppo* (this paper) in general morphology. Body small, 1.48 by 0.51; forebody 0.70 long, occupying 47% of body length. Oral sucker 0.12 by 0.13; sphincter fairly well developed. Pharynx 0.05 by 0.07. Cyclocoel dorsal to ovary and vitellaria. Ventral sucker 0.23 by 0.24; sucker width ratio 1 : 1.8; sphincter fairly well developed. Testes 0.12 by 0.10, fairly separated from ventral sucker by uterus, at junction of middle and posterior thirds of body. Sinus sac 0.12 by 0.10. Sinus organ cylindrical, stumpy, 0.05 by 0.04. Genital atrium dome-shaped, slightly longer than sinus organ. Genital pore fairly wide, ventral to posterior border of pharynx. Ovary larger than testes, 0.17 by 0.13, dextrally submedian, immediately anterior to right vitellarium. Ootype pouch 0.15 by 0.09. Uterus folded transversely about ten times in forebody; metraterm may be about three times as long as sinus sac; uterine seminal receptacle not seen. Eggs numerous, 67–80 by 28–34 μm (slightly collapsed). Vitellaria 0.17 by 0.12–0.13, oblique. Excretory vesicle bifurcating between testes.

Remarks. Yamaguti (1938) described this specie based on the holotype found in the intestine of *Anguilla japonica* (wild) from Tsuchiura. Later, Yamaguti (1942) found an additional adult specimen, associated with two adult specimens of *G. goppo*, in the small intestine [*sic*, possibly either erroneous record or accidental site of infection] of *Gymnogobius urotaenia* (syn. *Chaenogobius annularis urotaenia*) from Tsuchiura. He stated that, in *G. anguillae*, the testes were small for the body size and constantly smaller than the ovary, and eggs were larger than those of *G. goppo*. None of these three specimens was found in Yamaguti's Collection.

Shimazu (1995a) said that *G. anguillae* and *G. goppo* were very similar in morphology except in the egg size. Shimazu and Urabe (2005) concluded that the two species were the same species, using the wrong egg size (60–84 by 32–42 μm) in *G. goppo* for comparison. The correct egg size of their material of *G. goppo* (Central Japan Group) (see below) should have been 48–67 by 26–34 μm (see Shimazu, 2013), obviously smaller than that of *G. anguillae*. I attempted to obtain additional specimens of *G. anguillae* in the Lake Kasumigaura basin several times without success.

Life cycle. Not known.

Genarchopsis gigi Yamaguti, 1939

(Figs. 13–16)

Genarchopsis gigi Yamaguti, 1939: 227, pl. 29, fig. 6.
Genarchopsis goppo (not of Ozaki, 1925): Yamaguti, 1942: 389; Shimazu *et al.*, 2011, in part: 15, 18–19, figs. 14–16, 18, 20, 22–24.
Genarches gigi: Skryabin and Guschanskaya, 1955: 680, 685, fig. 200.
Genarchapsis goppo [*sic*, misspelling of *Genarchopsis*] (not of Ozaki, 1925): Shimazu, 1995a, in part: 9, fig. 5.

Hosts in Japan. *Gymnogobius isaza* (Tanaka, 1916), *Tridentiger brevispinis*, *Rhinogobius* sp. BW (Gobiidae) and *Cottus reinii* Hilgendorf, 1879 (Cottidae); and *Tachysurus nudiceps*

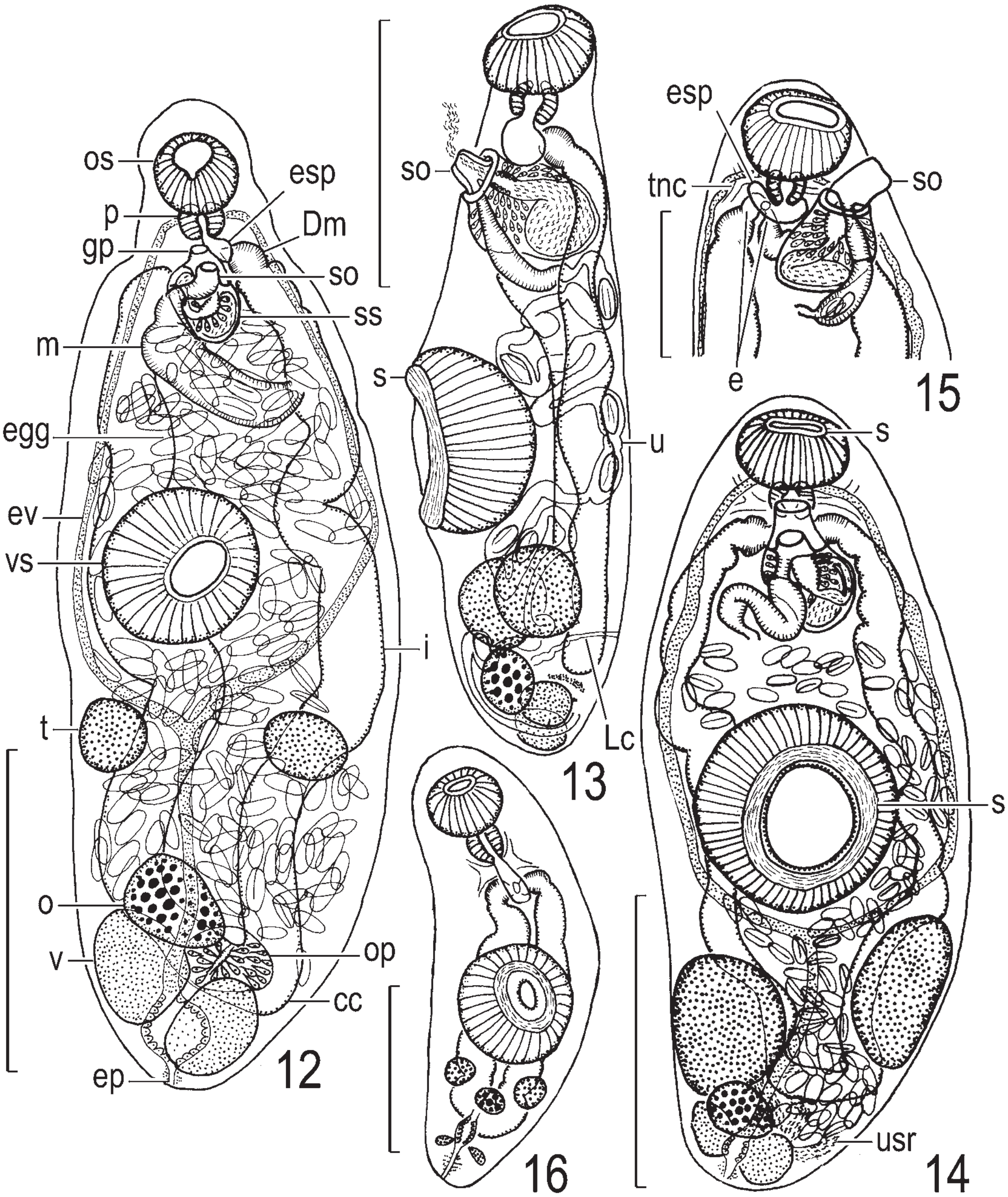


Fig. 12. *Genarchopsis anguillae*, adult, holotype (MPM Coll. No. 22005) found in intestine of *Anguilla japonica*, entire body, ventral view. Scale bar: 0.5 mm.

Figs. 13–16. *Genarchopsis gigi*, adults and life cycle. — 13, holotype (MPM Coll. No. 22004) of *G. gigi* found in small intestine [*sic*] of *Tachysurus nudiceps*, entire body, lateral view; 14, specimen (NSMT-Pl 4017) found in stomach of *T. nudiceps*, entire body, ventral view; 15, specimen (NSMT-Pl 4006) found in stomach of *Gymnogobius isaza*, anterior part of body, showing sinus organ protruded through genital pore; 16, possible metacercaria (NSMT-Pl 5742, 0.26 mm long by 0.09 mm wide) found in hemocoel of unidentified copepod. Scale bars: 0.5 mm in Fig. 14; 0.3 mm in Fig. 13; 0.2 mm in Fig. 15; 0.1 mm in Fig. 16.

(Sauvage, 1883) (Bagridae) (type host), *Anguilla japonica* (Anguillidae) and *Opsariichthys uncirostris uncirostris* (Temminck and Schlegel, 1846) (Cyprinidae) (presumably accidental hosts) (Yamaguti, 1939, 1942; Shimazu, 1995a; Shimazu *et al.*, 2011; Urabe *et al.*, 2013; this paper).

Sites of infection. Primarily stomach, and intestine (see below).

Geographical distribution. Shiga Prefecture: Lake Biwa itself (Yamaguti, 1939, 1942; Shimazu, 1995a; Shimazu *et al.*, 2011; Urabe *et al.*, 2013; this paper).

Material examined. (1) 1 specimen (Yamaguti's Collection, MPM Coll. No. 22004, holotype) of *G. gigi*, barely matured adult, whole-mounted, ex small intestine [*sic*, possibly either erroneous record or accidental site of infection] of *Tachysurus nudiceps* (syn. *Pelteobagrus nudiceps* (Sauvage, 1883)), Lake Biwa (locality not specified), 7 December 1938 (Yamaguti, 1939; Shimazu, 1995a; Shimazu *et al.*, 2011). (2) 80 (NSMT-Pl 4017–4018) of *G. goppo*, immature, adult, whole-mounted, ex stomach of *T. nudiceps*, Lake Biwa off Onoe, Kohoku Town, now Kohoku-cho, Nagahama City, 6 June 1980, 4 May 1992 (Shimazu, 1995a; Shimazu *et al.*, 2011). (3) Specimens, whole-mounted, ex *Gymnogobius isaza*, Lake Biwa: 2 (Yamaguti's Collection, MPM Coll. No. 22016) of *G. goppo*, adult, site of infection not given, Katata, Otsu City, 22 November 1939; 21 (NSMT-Pl 4006) of *G. goppo*, immature, adult, stomach, Onoe, 6 June 1980; 3 (NSMT-Pl 4007) of *G. goppo*, adult, stomach, Isoda, Hassaka-cho, Hikone City, 11 November 1980; 11 (NSMT-Pl 4008) of *G. goppo*, adult, stomach, Lake Biwa, Omatsu (Omatsuzaki Point), Minamikomatsu, Otsu City, 1 May 1992; 32 (LBM 1-22 to -23) of *G. goppo*, immature, adult, stomach, North Lake, 31 October 1997; 40 (LBM 1-24 to -25) of *G. goppo*, immature, adult, stomach, Hachiyadohama, Otsu City, 14 May 1998; 38 (LBM 1-27 to -28, 3-33 to -35) of *G. goppo*, immature, adult, stomach, Imazu-cho, Takashima City, 19 May 1998, 5 May 2000; 15 (LBM 6-8 to -14) of *G. goppo*, adult, intestine, Lake Biwa, Momose (Momose-gyoko Fishing Port), Chinai, Makino-cho, Takashima City, 1 May 2001 (Yamaguti, 1942; Shimazu, 1995a; Shimazu *et al.*, 2011); and 2 (NSMT-Pl 5905), adult, whole-mounted, Momose, 14 May 2009. (4) Specimens of *G. goppo*, whole-mounted, ex *Cottus reinii*, Lake Biwa: 17 (NSMT-Pl 4019–4020), immature, adult, stomach, Onoe, 4 February 1980, 6 June 1980; 21 (NSMT-Pl 4021–4024), immature, adult, stomach, Omatsu, 30 April 1992, 1, 2 and 4 May 1992; 4 (LBM 1-68 from stomach), adult, stomach and intestine, Hachiyadohama, 14 May 1998; 29 (LBM 1-70, 3-39), immature, adult, stomach, Imazu-cho, 19 May 1998, 5 May 2000; 3 (LBM 8-32), adult, stomach, Wani-gyoko Fishing Port, Otsu City, 25 April 2007; and 10 (LBM 8-34 to -35), immature, adult, stomach, Momose, 24 November 2007 (Shimazu, 1995a; Shimazu *et al.*, 2011). (5) Specimens of *G. goppo*, adult, whole-mounted, ex stomach of *Rhinogobius* sp. BW: 17 (LBM 1-5), Hachiyadohama, 14 May 1998; and 2 (LBM 1-6 to -7), Imazu-cho, 19 May 1998 (Shimazu *et al.*, 2011). (6) 1 (NSMT-Pl 4013) of *G. goppo*, adult, whole-mounted, ex stomach of *Anguilla japonica* (raised on small lake fish in a fish preserve), Omatsu, 4 May 1992 (Shimazu, 1995a; Shimazu *et al.*, 2011). (7) 1 (NSMT-Pl 5906), adult, whole-mounted, ex intestine of *Opsariichthys uncirostris uncirostris*, Momose, 14 May 2009.

Description. 1) Based on holotype (MPM Coll. No. 22004) from *Tachysurus nudiceps*, after Shimazu *et al.* (2011), altered from the present study (Fig. 13). Body barely matured, laterally mounted, very small, 0.80 long; forebody 0.47 long, occupying 59% of body length. Oral sucker 0.09 by 0.11. Pharynx 0.04 by 0.05. Ventral sucker 0.21 long. Sinus organ 0.03 by 0.04, protruded outside through genital pore; sinus sac 0.13 by 0.11. Genital atrium short. Testes 0.10 in diameter. Ovary 0.06 in diameter. Uterus folded several times (four times transversely in forebody), extending posteriorly to vitellaria. Uterine eggs 7, unembryonated (before cleavage), 40–48 by 17–22 μm (collapsed). Vitellaria 0.05 in diameter.

2) Based on specimens (NSMT-Pl 4017–4018) from *T. nudiceps*, after Shimazu *et al.* (2011), altered from the present study (Fig. 14). Similar to *G. goppo* (this paper) in general morphology. Body small, 0.99–1.68 by 0.38–0.61; forebody 0.50–0.91 long, occupying 47–55% of body length. Oral sucker 0.10–0.17 by 0.12–0.21; sphincter well developed; radial muscle fibers well developed (not illustrated). Pharynx 0.05–0.06 by 0.05–0.07. Cyclocoel anterior or dorsal to ovary. Ventral sucker large, 0.23–0.42 by 0.22–0.42; sucker width ratio 1 : 1.7–2.1; sphincter well developed; radial muscle fibers well developed (not illustrated). Testes 0.22–0.30 by 0.12–0.23, slightly separated from ventral sucker by uterus. Sinus sac 0.08–0.16 by 0.11–0.19. Sinus organ cylindrical, stumpy, 0.04–0.06 by 0.04–0.08. Genital atrium cylindrical, slightly longer than sinus organ. Genital pore usually opening wide but rarely puckered, median to submedian, ventral to pharynx. Ovary smaller than testes, 0.05–0.15 by 0.05–0.11, usually submedian or rarely median, immediately anterior to or slightly overlapping vitellaria. Ovarian complex usually submedian. Uterus folded a few times (four times transversely in forebody), extending posteriorly beyond cyclocoel to vitellaria; metraterm about two times as long as sinus sac. Eggs fairly numerous (10–40 in large specimens); considerably embryonated eggs 51–65 by 24–30 μm; fully embryonated eggs not seen. Vitellaria 0.08–0.16 by 0.04–0.09. Excretory vesicle bifurcating between testes and ventral sucker.

3) Based on specimens (NSMT-Pl 4006–4008, 5905) from *Gy. isaza*. Sinus organ rarely protruded outside through genital pore (Fig. 15). Uterus extending posteriorly to vitellaria. Uterine eggs not numerous, including malformed eggs, not fully embryonated, except for those of one specimen (NSMT-Pl 4008). Fully embryonated eggs of this specimen 56–67 by 24–29 μm.

Remarks. When Yamaguti (1939) proposed this species based on the holotype found in the intestine of *Tachysurus nudiceps* (syn. *Pelteobagrus nudiceps*) from Lake Biwa, he described uterine eggs as 43–51 by 19–21 μm and embryonated. He stated that the species was distinguished from the two known members (species names not given) of *Genarchopsis* by smaller egg size. He seems to have compared *G. gigi* in egg size with *G. goppo* as described by Ozaki (1925) and Yamaguti (1934, 1938) and *G. anguillae* as described by Yamaguti (1938) (Shimazu *et al.*, 2011). The seven uterine eggs in the holotype were, in fact, unembryonated (before cleavage) and 40–48 by 17–22 μm (collapsed) (Shimazu *et al.*, 2011). Uterine eggs of *G. gigi* are distinctly smaller than those of *G. anguillae* (67–80 by 28–34 μm in this paper) but slightly smaller than those of *G. goppo*. Fully embryonated eggs were 56–67 by 24–29 μm in the specimens (NSMT-Pl 4008) of *G. gigi* from *Gymnogobius isaza* (this paper) and 51–72 by 27–29 μm in *G. goppo* (*sensu stricto*) (this paper). Therefore, *G. gigi* cannot be separated from *G. goppo* by egg size alone as observed by Shimazu *et al.* (2011).

Shimazu *et al.* (2011) pointed out other morphological differences between *G. gigi* and *G. goppo* (*sensu stricto*): in number of uterine eggs in the forebody, at the most 39–90 instead of 100–177; in number of the transverse uterine folds in the forebody, about four instead of seven to nine; and in size of the genital pore, wide open instead of closed and puckered. Moreover, *G. gigi* differs from *G. goppo* (*sensu stricto*) in that the testes are slightly, instead of greatly, separated from the ventral sucker by the uterus; the cyclocoel is located anterior or dorsal, instead of posterior or dorsal, to the ovary; and the uterus extends posteriorly beyond the cyclocoel to the vitellaria instead of to the cyclocoel. Consequently, I consider that *G. gigi* differs from *G. goppo* (*sensu stricto*) in adult morphology as well as in the molecular data obtained by Urabe *et al.* (2013).

Urabe *et al.* (2013) demonstrated that the samples obtained from *T. nudiceps*, *Tridentiger brevispinis*, *Gy. isaza* and *Rhinogobius kurodai* (Tanaka, 1908) [most likely referring to

Rhinogobius sp. BW] collected in Lake Biwa itself belonged to the Lake Biwa Group, or *G. gigi*. Shimazu *et al.* (2011) reported a large number of specimens under the species name *G. goppo* from fishes of various species collected in the Lake Biwa basin. I here assign the specimens found in, at least, *T. nudiceps*, *Gy. isaza*, *Cottus reinii*, *Rhinogobius* sp. BW and *Anguilla japonica* (raised on small lake fish) to *G. gigi*. Close reexamination of the remainder is required. *Opsariichthys uncirostris uncirostris* from Lake Biwa itself is added as an accidental final host. This cyprinid fish lacks the stomach. The infected fish seems to have recently become infected by ingesting infected small fish.

Life cycle. A cystophorous cercaria was recorded under the species name *Cercaria yoshidae* Cort and Nichols, 1920 from several species of snails of *Semisulcospira* (natural first intermediate hosts) in the Lake Biwa basin (Urabe, 2003). Urabe *et al.* (2013) showed that the redia from *Semisulcospira* (*Biwamelania*) *niponica* (Smith, 1876) [Japanese name: Yamato-kawanina] belonged to *G. gigi*. According to them, *G. gigi* is highly infectious to *S.* (*B.*) *niponica* and *Semisulcospira* (*Biwamelania*) *habei* Davis, 1969 [Japanese name: Habe-kawanina], both endemic to Lake Biwa. Neither mother and daughter rediae nor cercariae have been described.

Shimazu *et al.* (2011) reported unencysted metacercariae under the species name *G. goppo* from the hemocoel of copepods (natural second intermediate hosts) collected in Lake Biwa off Take Island, Hikone City: one (NSMT-Pl 5741) in a diaptomid, *Eodiaptomus japonicus* (Burckhardt, 1913) [Japanese name: Yamato-higenaga-kenmijinko]; and two (NSMT-Pl 5742; this paper, Fig. 16) in unidentified copepods. These three metacercariae probably belong to *G. gigi*.

Tachysurus nudiceps, *Anguilla japonica* and *Opsariichthys uncirostris uncirostris* are predatory, and so they are considered to be accidental final hosts to become infected with worms by ingesting infected small fish. Since none of the adult specimens from *T. nudiceps* contained fully embryonated eggs, it seems likely that *T. nudiceps* is unsuitable for *G. gigi*.

Genarchopsis fellicola Shimazu, 1995

(Figs. 17–18)

Genarchopsis goppo (not of Ozaki, 1925): Yamaguti, 1938, in part: 133.

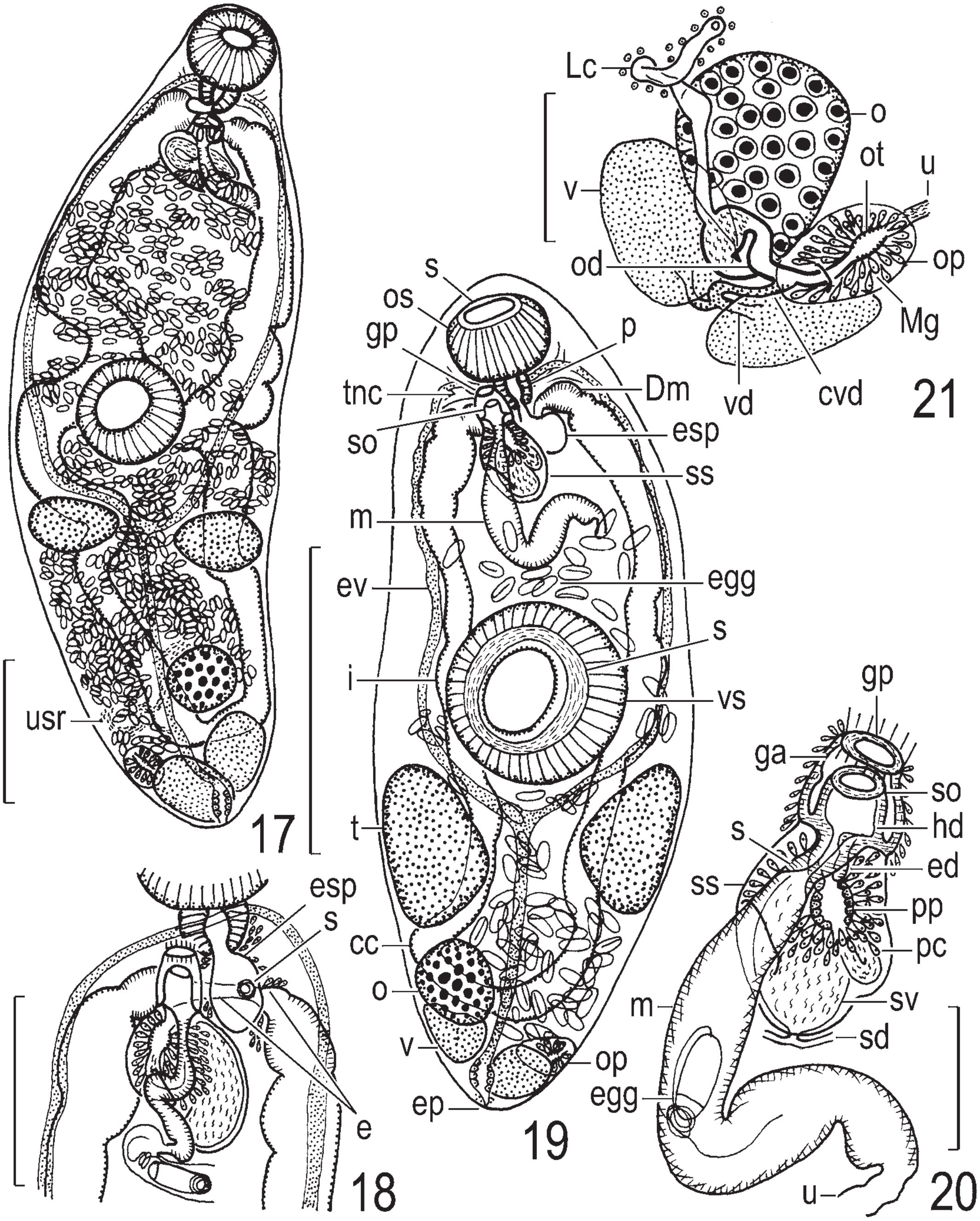
Genarchopsis fellicola Shimazu, 1995a: 13–14, figs. 7–11.

Hosts in Japan. *Gymnogobius urotaenia* (type host), *Rhinogobius kurodai* (Tanaka, 1908), *Rhinogobius* sp. OR and *Tridentiger brevispinis* (Gobiidae); and *Silurus asotus* (Siluridae) (presumably accidental host) (Yamaguti, 1938; Shimazu, 1995a, 2007; Urabe *et al.*, 2013; this paper).

Sites of infection. Primarily gall bladder, and intestine (presumably accidental).

Geographical distribution. (1) Ibaraki Prefecture: irrigation canals at Oou, Itako City; Gantsu River at Yabata, Namegata City; and Kamihinumagawa and Hinumamaekawa rivers at Ibaraki Town (Shimazu, 1995a; Urabe *et al.*, 2013; this paper). (2) Nagano Prefecture: Lake Suwa (type locality) at Suwa City (Yamaguti, 1938; Shimazu, 1995a, 2007; Urabe *et al.*, 2013; this paper).

Material examined. (1) 6 specimens (Yamaguti's Collection, MPM Coll. Nos. 22808–22809, 6 paratypes) of *G. fellicola*, adult, whole-mounted, ex gall bladder of *Gymnogobius urotaenia* (syn. *Chaenogobius annularis urotaenia*, *Chaenogobius urotaenia*), Lake Suwa, 31 March 1936, 21 May 1939 (Yamaguti, 1938; Shimazu, 1995a). (2) 7 (NSMT-Pl 4536, holotype; 4029–4030, 4528, 6 paratypes) of *G. fellicola*, adult, whole-mounted, ex gall bladder of *Gy. urotaenia*, Lake Suwa, 14 November 1991, 19 May 1992, 14 September 1992, 16 June 1994 (Shimazu, 1995a). (3) 3 (NSMT-Pl 4531, 1 paratype; 4530 (unpublished), 5398) of *G. fellicola*, adult, whole-mounted, ex gall bladder of *Rhinogobius brunneus* (Temminck and Schlegel, 1845) [correctly *Rhinogobius* sp. OR], Lake Suwa, 30 October 1993, 20 November 1993, 4 August 1998 (Shimazu, 1995a, 2007). (4) 30 (NSMT-Pl



Figs. 17–18. *Genarchopsis fellicola*, adults found in gall bladder of *Gymnogobius urotaenia*. — 17, holotype (NSMT-Pl 4536), entire body, 1 and 4 eggs present in hermaphroditic duct and genital atrium, respectively, ventral view; 18, paratype (NSMT-Pl 4528), anterior part of body, showing digestive organs and terminal genitalia. Scale bars: 0.5 mm.

Figs. 19–21. *Genarchopsis chubuensis* sp. nov., adults found in stomach of *Gy. urotaenia*. — 19, holotype (NSMT-Pl 3995), entire body, ventral view; 20, holotype, terminal genitalia, ventral view; 21, voucher (NSMT-Pl 3994), ovarian complex, dorsal view. Scale bars: 0.5 mm in Fig. 19; 0.1 mm in Figs. 20–21.

5761–5762), immature, adult, whole-mounted, ex gall bladder of *Tridentiger brevispinis*, Lake Suwa, 13 and 18 November 2008. (5) 4 (NSMT-Pl 4529, 3 paratypes, adult, 1 voucher, immature) of *G. fellicola*, whole-mounted, ex gall bladder of *Gy. urotaenia*, Oou, Itako Town, now Itako City, 10 August 1994 (Shimazu, 1995a). (6) 3 (NSMT-Pl 5758–5759), adult, whole-mounted, ex gall bladder of *Gy. urotaenia*, Oou, 22 and 23 October 2008. (7) 24 [not 20] (NSMT-Pl 4532, 1 paratype, adult, 5 vouchers, immature; 4533, 4 paratypes, adult, 7 vouchers, immature; 4534, 7 paratypes, adult) of *G. fellicola*, whole-mounted, ex gall bladder of *R. brunneus* [now *R. kurodai*], Oou, 7, 8 and 10 August 1994 (Shimazu, 1995a). (8) 1 (NSMT-Pl 5760), adult, whole-mounted, ex ball bladder of *R. kurodai*, Oou, 22 October 2008. (9) 2 (NSMT-Pl 4535, 1 paratype, adult, 1 voucher, immature) of *G. fellicola*, whole-mounted, ex gall bladder of *Tr. brevispinis*, Gantsu River at Yabata, Aso Town, now Yabata, Namegata City, Ibaraki Prefecture, 9 August 1994 (Shimazu, 1995a). (10) 1 (NSMT-Pl 5845), adult, whole-mounted, ex gall bladder of *Gy. urotaenia*, Gantsu River, 3 June 2011. (11) 1 (NSMT-Pl 5763), adult, whole-mounted, ex intestine of *Silurus asotus*, Lake Suwa, 26 June 2007. (12) 1 (NSMT-Pl 5903), adult, whole-mounted, ex gall bladder of *R. kurodai*, Kami-hinumagawa River, 27 September 2012. (13) 1 (NSMT-Pl 5904), adult, whole-mounted, ex gall bladder of *R. kurodai*, Hinumamaekawa River, 27 September 2012.

Description. 1) After Shimazu (1995a), modified from the present study (Figs. 17–18). Similar to *G. goppo* (this paper) in general morphology. Body 0.60–3.20 by 0.25–1.17 (holotype 2.92 by 0.94); forebody 0.31–1.56 long, occupying 45–57% of body length. Preoral lobe indistinct. Oral sucker 0.11–0.26 by 0.12–0.31; sphincter weakly developed; radial muscle bundles weakly developed (not illustrated). Pharynx 0.04–0.12 by 0.04–0.13. Cyclocoel usually anterodorsal but rarely posterior to ovary. Ventral sucker 0.14–0.39 by 0.16–0.40; sphincter weakly developed; sucker width ratio 1 : 1.1–1.6; radial muscle bundles weakly developed (not illustrated). Testes 0.08–0.33 by 0.08–0.31 (usually larger than ovary but rarely almost as large as it in new specimens from Lake Suwa, and usually smaller than ovary but rarely almost as large as it in new specimens from Ibaraki Prefecture), separated greatly from ventral sucker by uterus, at about junction of middle and posterior thirds of body. Sinus sac 0.11–0.31 by 0.09–0.19. Sinus organ cylindrical, stumpy, 0.04–0.07 by 0.03–0.07. Genital atrium cylindrical, slightly longer than sinus organ. Genital pore fairly wide, ventral to esophagus or slightly anterior or posterior to it. Ovary 0.08–0.31 in diameter, dextrally or sinistrally submedian, greatly posterior to testes, anterior to vitellaria. Ootype pouch 0.08–0.19 by 0.04–0.16. Uterus folded transversely about ten times in forebody, extending posteriorly beyond cyclocoel to vitellaria; metraterm about twice as long as sinus sac. Eggs numerous, 57–76 by 26–32 μm. Vitellaria 0.06–0.35 by 0.06–0.22. Excretory vesicle bifurcating between testes.

Remarks. Shimazu (1995a) described this species on the basis of the type specimens (1 holotype and 29 [not 39] paratypes), which included six paratypes (Yamaguti's Collection, MPM Coll. Nos. 22808–22809) that Yamaguti (1938) had reported as *G. goppo* from the gall bladder of *Gymnogobius urotaenia* of Lake Suwa.

Urabe *et al.* (2013) used samples of *G. fellicola* found in *Gymnogobius urotaenia* and *Tridentiger brevispinis* from Lake Suwa and *Gy. urotaenia* and *Rhinogobius kurodai* from the Lake Kasumigaura basin for their molecular study (see *Remarks* of *G. goppo*). They showed that *G. fellicola* is closely related to the West and Central Japan Groups of *G. goppo*. However, it is easily distinguishable from the other *Genarchopsis* species by adult morphology and especially by its site of infection (gall bladder) in fish hosts; and, accordingly, *G. fellicola* is a valid species (Urabe *et al.*, 2013).

Morphologically, *G. fellicola* differs from *G. anguillae* in smaller eggs, 57–76 by 26–32 μm instead of 67–80 by 28–34 μm (this paper) and from *G. goppo* (*sensu stricto*) (West Japan Group) and *G. gigi* by having a lower sucker width ratio, 1 : 1.1–1.6 instead of 1 : 1.7–2.2 in *G. goppo*, 1 : 1.7–2.1 in *G. gigi* and 1 : 1.4–1.9 in the Central Japan Group (see blow); less developed sphincters of the oral and ventral suckers; and less developed radial muscle fibers connected to the oral and ventral suckers (see also Shimazu, 1995a). Furthermore, *G. fellicola* is different from *G. goppo* in the posterior extent of the uterus, beyond the cyclocoel to the vitellaria instead of to the cyclocoel; and from *G. gigi* and the Central Japan Group in having more numerous eggs and more transverse uterine folds in the forebody.

Genarchopsis fellicola lives in the gall bladder of *Gy. urotaenia*, *R. kurodai*, *Rhinogobius* sp. OR and *Tr. brevispinis* in Lake Suwa and Ibaraki Prefecture (this paper). It is possible that *G. fellicola* may have been artificially introduced from Lake Kasumigaura (possibly original distribution area) into Lake Suwa together with *Gy. urotaenia* probably in 1931 (Kumakawa, 2001; Takei, 2007; Urabe *et al.*, 2013).

Life cycle. Not known.

Genarchopsis chubuensis sp. nov.

(Figs. 19–26)

(?) *Cercaria* F: Yoshida, 1917: 114–115, figs. 9–10, pl. 2, fig. 18, 1 table (p. 115).

(?) *Cercaria yoshidae* Cort and Nichols, 1920: a footnote (p. 12); Ito, 1952: 449–450, figs. 1–4; Shimazu and Shimizu, 1984: 15, fig. 1.

(?) *Cercaria cystophora* A: Kobayashi, 1922: 267–268.

Genarchopsis goppo (not of Ozaki, 1925): Yamaguti, 1934: 500–501, fig. 128; Yamaguti, 1938, in part: 133; Yamaguti, 1942: 388; Urabe, 2001: 1407, figs. 1G, 3E; Shimazu and Urabe, 2005: 2–3, figs. 1–3; Shimazu *et al.*, 2011, in part: 18–19, (?) figs. 17, 19, 21.

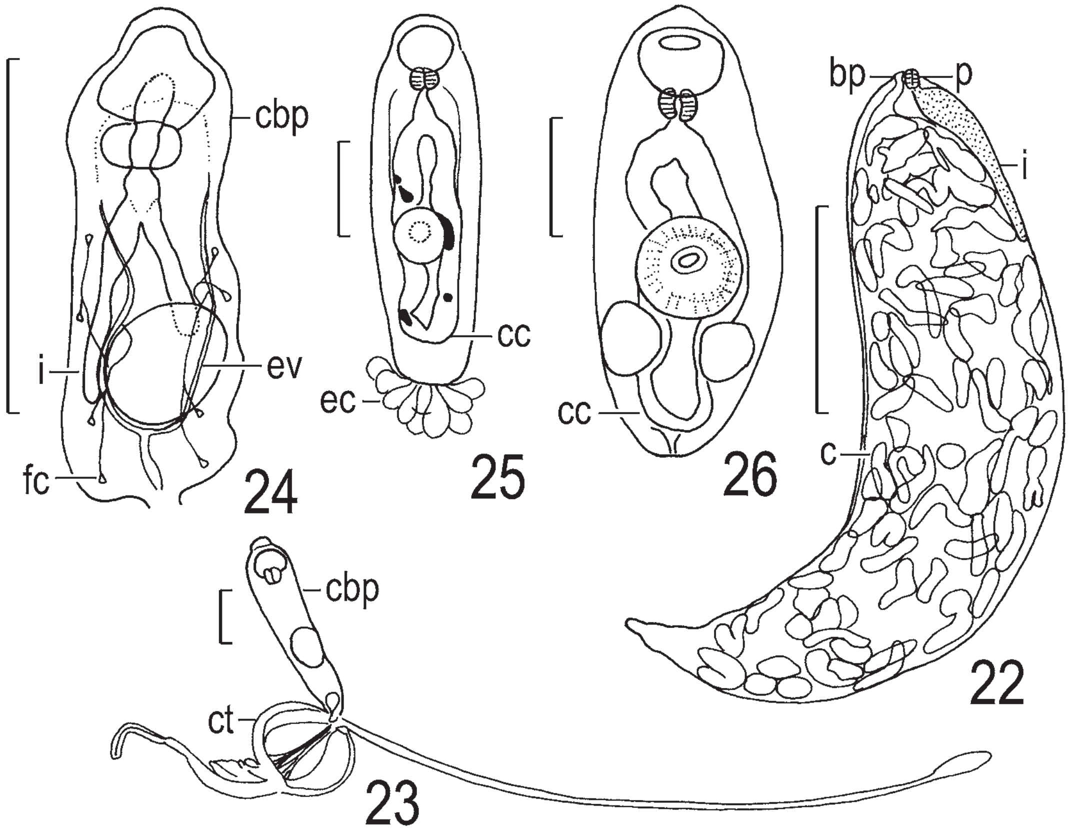
Genarchapsis goppo [*sic*, misspelling of *Genarchopsis*] (not of Ozaki, 1925): Shimazu, 1995a, in part: 6–8.

Hosts in Japan. *Gymnogobius castaneus* (O'Shaughnessy, 1875), *Gymnogobius urotaenia* (type host), *Rhinogobius flumineus*, *Rhinogobius kurodai*, *Rhinogobius* sp. OM, *Rhinogobius* sp. OR, "*Gobius similis* Gill," *Tridentiger brevispinis* (Gobiidae), *Odontobutis obscura* (Odontobutidae) and *Cottus pollux* Günther, 1873 (Cottidae); and *Silurus asotus* (Siluridae), *Anguilla japonica* (Anguillidae) and *Micropterus salmoides* (Lacepède, 1802) (Centrarchidae) (presumably accidental hosts) (Yamaguti, 1934, 1938, 1942; Nakamura *et al.*, 2000; Shimazu, 1995a, 2007; Shimazu and Urabe, 2005; Shimazu *et al.*, 2011; Urabe, 2001; Urabe *et al.*, 2013; this paper).

Sites of infection. Primarily stomach; and esophagus, gills, buccal cavity, peribuccal tissue [*sic*], intestine and gut (possibly migration after death of host fish).

Geographical distribution. (1) Ibaraki Prefecture: Himumamaekawa River at Ibaraki Town; Tsuchiura City; and irrigation canals at Oou, Itako City (Yamaguti, 1942; this paper). (2) Saitama Prefecture: Otsubata, Ranzan Town (Urabe *et al.*, 2013; this paper). (3) Nagano Prefecture: Lake Kizaki in Oomachi City and Lake Suwa (type locality) at Suwa City (Shimazu, 1995a, 2007; Urabe *et al.*, 2013; this paper). (4) Gifu Prefecture: Takarae, Mizuho City (Urabe *et al.*, 2013). (4) Fukui Prefecture: Obama City and Kannon River at Hosorogi, Awara City (Yamaguti, 1938; Shimazu, 1995a; Urabe *et al.*, 2013). (5) Shiga Prefecture: Lake Biwa basin; Onoe, Kohoku Town, now Kohoku-cho, Nagahama City; Nishikouzaka, Nagahama City; Omatsu (Omatsuzaki Point), Minamikomatsu, Otsu City; Harie River at Harie, Shin'asahi-cho, Takashima City; and Inukami River at Hikone City (Shimazu *et al.*, 2011; Urabe *et al.*, 2013; this paper). (6) Kyoto Prefecture: Lake Ogura (Yamaguti, 1934; Shimazu, 1995a); Katura [Katsura River (?)] near Kyoto City (Yamaguti, 1942). (7) Nara Prefecture: Tobihino, Nara City (Urabe, 2001; Urabe *et al.*, 2013); and Takami River at Kotsugawa, Higashiyoshino Village (Nakamura *et al.*, 2000; Shimazu and Urabe, 2005).

Material examined. (1) 2 specimens (Yamaguti's Collection, MPM Coll. No. 22585) of *G. goppo*, adult, whole-mounted, ex stomach of *Odontobutis obscura* (syn. *Mogurnda obscura*), Lake Ogura, 2 June 1932 (Yamaguti, 1934; Shimazu, 1995a). (2) 1 (Yamaguti's Collection,



Figs. 22–26. *Genarchopsis chubuensis* sp. nov., life cycle. — 22, daughter redia found in *Semisulcospira libertina* (natural first intermediate host); 23, cercaria found in crashed *S. libertina*; 24, cercarial body proper, showing digestive and excretory systems; 25, 5-day-old metacercaria found in a copepod (experimental second intermediate host); 26, 21-day-old metacercaria found in a copepod. Redrawn from Urabe (2001). Scale bars: 0.5 mm in Figs. 22 and 26; 0.1 mm in Figs. 23–25.

MPM Coll. No. 22006) of *G. goppo*, adult, whole-mounted, ex stomach of *Gymnogobius urotaenia* (syn. *Chaenogobius annularis urotaenia*), Obama, 26 March 1935 (Yamaguti, 1938; Shimazu, 1995a). (3) 2 (Yamaguti's Collection, MPM Coll. No. 23139) of *G. goppo*, adult, whole-mounted, ex stomach of "*Gobius similis* Gill" [a species of *Rhinogobius*], Katura [Katsura River (?)], 26 December 1938 (Yamaguti, 1942). (4) 2 (NSMT-Pl 5907), adult, whole-mounted, ex stomach of *Gy. urotaenia*, Hinumamaekawa River, 27 September 2012. (5) 6 (NSMT-Pl 5773–5774), adult, whole-mounted, ex stomach of *Gy*. *urotaenia*, Oou, 22 and 23 October 2008. (6) 3 (NSMT-Pl 5775–5776), adult, whole-mounted, ex stomach of *Rhinogobius kurodai*, Oou, 22 and 23 October 2008. (7) 5 (NSMT-Pl 5909), adult, whole-mounted, ex stomach of *R. kurodai*, Otsubata, 29 October 2011. (8) 32 (NSMT-Pl 4009–4011) of *G. goppo*, immature, adult, whole-mounted, serially sectioned, ex stomach of *Gymnogobius castaneus* (now not *Chaenogobius laevis*), Lake Suwa, 12 May 1989, 19 May 1992, 2 June 1992 (Shimazu, 1995a). (9) Many (NSMT-Pl 3993–3995, 4519–4520, 4526–4527, 5399–5404) of *G. goppo*, immature, adult, whole-mounted, serially sectioned, ex stomach of *Gy. urotaenia* (syn. *Ch. urotaenia*), Lake Suwa, 13 September 1991, 19 May 1992, 2 June 1992, 14 September 1992, 2 October 1992, 21 May 1994, 9 June 1994, 5 October 1996, 21 November 1998, 29 May 1999, 13 June 1999, 18

September 1999 (Shimazu, 1995a, 2007). (10) 1 (NSMT-Pl 5769), adult, whole-mounted, ex stomach of *Gy. urotaenia*, Lake Suwa, 13 November 2008. (11) Many (NSMT-Pl 4003–4005, 4521–4522, 5405) of *G. goppo*, immature, adult, whole-mounted, ex stomach of *Rhinogobius brunneus* and *Rhinogobius* sp. [correctly *Rhinogobius* sp. OR], Lake Suwa, 12 May 1989, 19 May 1992, 2 June 1992, 24 September 1992, 16 June 1994, 18 September 1999 (Shimazu, 1995a, 2007). (12) 5 (NSMT-Pl 5770) of *G. goppo*, adult, whole-mounted, ex stomach of *Rhinogobius* sp. OR, Lake Suwa, 18 November 2008. (13) 6 (NSMT-Pl 5771–5772), adult, whole-mounted, ex stomach of *Tridentiger brevispinis*, Lake Suwa, 13 and 18 November 2008. (14) 20 (NSMT-Pl 4014, 4015) of *G. goppo*, adult, whole-mounted, ex stomach of *Silurus asotus*, Lake Suwa, 27 May 1975, 9 April 1992 (Shimazu, 1995a). (15) 4 (NSMT-Pl 4524–4525) of *G. goppo*, adult, whole-mounted, ex stomach of *Anguilla japonica*, Lake Suwa, 16 June 1994 (Shimazu, 1995a). (16) 6 (NSMT-Pl 4027) of *G. goppo*, immature, adult, whole-mounted, ex stomach of *Micropterus salmoides*, Lake Suwa, 13 September 1991 (Shimazu, 1995a). (17) 1 (NSMT-Pl 5406) of *G. goppo*, adult, whole-mounted, ex stomach of *Cottus pollux*, Lake Suwa, 18 September 1999 (Shimazu, 2007). (18) 19 (NSMT-Pl 4002) of *G. goppo*, adult, whole-mounted, ex stomach of *R. brunneus* [correctly *Rhinogobius* sp. OR], Lake Kizaki, 5 June 1983 (Shimazu, 1995a). (19) 31 (NSMT-Pl 4025–4026, 4523) of *G. goppo*, adult, whole-mounted, ex stomach of *M. salmoides*, Lake Kizaki, 11 June 1989, 11 September 1989, 18 June 1994 (Shimazu, 1995a). (20) 3 (LBM 7-32) of *G. goppo*, adult, whole-mounted, ex stomach of *R. flumineus*, Tamura River, 30 April 2001 (Shimazu *et al.*, 2011). (21) Specimens of *G. goppo*, immature, adult, whole-mounted, ex *R. brunneus* and *Rhinogobius* sp. OR [most likely referring to *Rhinogobius* sp. OM]: 19 (NSMT-Pl 3999) ex gill, stomach and intestine, Onoe, 6 June 1980; 13 (NSMT-Pl 4000, 4001), ex stomach, Omatsu, 29 April 1992, 4 May 1992 (Shimazu, 1995a; Shimazu *et al.*, 2011); and 15 (LBM 3-54, -57 to -58), ex stomach (?) and gut, Harie River, 19 October 2000 (Shimazu *et al.*, 2011). (22) 2 (NSMT-Pl 5908), adult, whole-mounted, ex stomach of *Odontobutis obscura*, Inukami River, 10 May 2009. (23) 10 (NSMT-Pl 5254–5256) of *G. goppo*, adult, whole-mounted, ex stomach of *R. flumineus*, Takami River, 26 July 1999, 9 October 1999, 14 and 15 August 2000 (Shimazu and Urabe, 2005).

Type host. *Gymnogobius urotaenia* (Hilgendorf, 1879) (Gobiidae).

Type locality. Lake Suwa (36°2′N, 138°6′E) at Suwa City, Nagano Prefecture, Japan.

Type specimens. Holotype (NSMT-Pl 3995, adult, 1.33 by 0.51, slightly flattened, whole-mounted, ex stomach of *Gy. urotaenia*, Lake Suwa, 2 June 1992), 302 paratypes (adult specimens, slightly flattened, whole-mounted, ex stomach, Lake Suwa): 5 (NSMT-Pl 3993, 13 September 1991), 43 (NSMT-Pl 3994, 19 May 1992), 15 (NSMT-Pl 3995, 2 June 1992), 3 (NSMT-Pl 4519, 14 September 1992), 164 (NSMT-Pl 4520, 2 October 1992) and 22 (NSMT-Pl 4526, 21 May 1994) from *Gy. urotaenia*; 3 (NSMT-Pl 4003, 12 May 1989), 8 (NSMT-Pl 4004, 19 May 1992), 2 (NSMT-Pl 4005, 2 June 1992) and 9 (NSMT-Pl 4522, 16 June 1994) from *Rhinogobius* sp. OR; and 5 (NSMT-Pl 4009, 12 May 1989), 16 (NSMT-Pl 4010, 19 May 1992) and 7 (NSMT-Pl 4011, 2 June 1992) from *Gy. castaneus*.

Etymology. The specific name *chubuensis*, an adjective in the feminine gender, is a combining form of Japanese *chubu* and Latin *-ensis* meaning "the central part of Honshu, Japan" and "belonging to," respectively.

Description. Based on type specimens; holotype and 9 paratypes measured (Figs. 19–21). Similar to *G. goppo* (this paper) in general morphology. Body spindle-shaped, with bluntly pointed ends, small, 1.11–1.59 by 0.43–0.57 (holotype 1.33 by 0.51); forebody 0.56–0.79 long, occupying 50–53% of body length. Preoral lobe present. Oral sucker 0.11–0.16 by 0.16–0.19; sphincter fairly well developed; radial muscle bundles moderately developed (not illustrated). Pharynx 0.06–0.08 by 0.05–0.07. Esophagus short; esophageal pouch small, posteroventral to esophagus. Drüsenmagen 0.06–0.09 by 0.04–0.07. Cyclocoel anterior or dorsal to ovary. Ventral sucker 0.23–0.35 by 0.22–0.34; sucker width ratio 1 : 1.4–1.9; sphincter well developed; radial muscle bundles well developed (not illustrated). Testes elliptical, large, 0.18–0.26 by 0.13–0.21, slightly separated from ventral sucker by uterus. Sinus sac 0.09–0.13 by 0.08–0.14. Seminal vesicle retort-shaped, looped once in neck portion. Pars prostatica vesicular; prostatic cells well developed. Ejaculatory duct short. Hermaphroditic duct present only in sinus organ. Sinus organ cylindrical, short, 0.04–0.06 by 0.03–0.06, rarely slightly protruded outside through genital pore. Genital atrium cylindrical, 0.07–0.09 long. Genital pore opening wide, median but usually sifted slightly sinistrally or dextrally, at posterior border of oral sucker. Ovary elliptical to globular, smaller than testes, 0.12–0.16 by 0.08–0.13, dextrally or sinistrally lateral to submedian. Laurer's canal running forward, opening dorsally. Ootype pouch 0.08–0.13 by 0.04–0.08. Uterus much folded, with about two transverse folds in forebody, extending posteriorly beyond cyclocoel to vitellaria; metraterm long, more than three times as long as sinus sac, reaching to midlevel of ventral sucker when extended; uterine seminal receptacle present. Eggs usually not numerous in forebody, 50–69 by 24–32 μm, fully embryonated. Vitellaria elliptical, 0.06–0.14 by 0.05–0.09. Excretory vesicle bifurcating between testes and ventral sucker.

Remarks. Urabe *et al.* (2013) demonstrated that the Central Japan Group (specimens from the central part of Honshu) differs specifically from the West Japan Group (or *G. goppo* (*sensu stricto*)) and Lake Biwa Group (or *G. gigi*) in their molecular data (see *Remarks* of *G. goppo*). They indicated that the samples found in *Rhinogobius kurodai* from Saitama Prefecture; *Gy. urotaenia* and *Rhinogobius* sp. OR from Nagano Prefecture; *Tr. brevispinis* from Fukui Prefecture; *R. flumineus* from Gifu Prefecture; *R. flumineus* and *Tr. brevispinis* from Shiga Prefecture; and *Rhinogobius* sp. OR from Nara Prefecture belonged to the Central Japan Group.

Close examination of the present material has shown that the Central Japan Group also differs in adult morphology from other Japanese species. It most closely resembles *G. gigi* (this paper) in that the uterus extends posteriorly beyond the cyclocoel to the vitellaria. However, it differs from *G. gigi* in that the sucker width ratio is lower, 1 : 1.4–1.9 instead of 1 : 1.7–2.1; the uterus is shorter in the forebody, about two transverse folds instead of four; and the metraterm is longer, more than three times as long as the sinus sac instead of about two times. In the long metraterm, it is similar to *G. goppo* (*sensu stricto*) (this paper). However, it is different from the latter in that the cyclocoel is anterior or dorsal to the ovary instead of between the ovary and vitellaria; the testes are separated slightly, instead of greatly, from the ventral sucker by the uterus; the uterus extends posteriorly beyond the cyclocoel to the vitellaria instead of anterior to the cyclocoel; the uterus is folded transversely much less in the forebody, two times instead of seven to nine times; and the uterine eggs are much fewer in the forebody. It is distinguished from *G. anguillae* (this paper) and *G. fellicola* (this paper) in the position of the testes and much less transverse folds of the uterus and much fewer uterine eggs in the forebody; and from *G. anguillae* in smaller uterine eggs, 50–69 by 24–32 μm instead of 67–80 by 28–34 μm. Consequently, I propose *Genarchopsis chubuensis* sp. nov. for the Central Japan Group. The present specimens from Ibaraki Prefecture refer to this new species because of close similarity in adult morphology to the other specimens, though no molecular data are available from them. The egg size (60–84 by 32–42 μm) given by Shimazu and Urabe (2005) for the specimens (NSMT-Pl 5254–5256) from Nara Prefecture was erroneous. The correct egg size is 48–67 by 26–34 μm as mentioned above (see also Shimazu, 2013).

Shimazu *et al.* (2011) reported a large number of specimens as *G. goppo* from fishes of various species collected in the Lake Biwa basin. According to Urabe *et al.* (2013), I here assign, at least, the specimens found in *Rhinogobius flumineus* from the Tamura River and *Rhinogobius* sp. OM from Onoe, Omatsu and the Harie River to the present new species. The rest of the specimens need close reexamining for definitive species identification.

Shimazu and Shimizu (1984) studied the excretory system of a cercaria under the species name *Cercaria yoshidae* in *Semisulcospira libertina* at Hoshina, Wakaho, Nagano City, Nagano Prefecture. The Y-shaped excretory vesicle had a globular small dilatation lined with large epithelial cells near the posterior end; the arms were found uniting with each other dorsally to the pharynx and had two pairs of flame cells; and the caudal excretory canal had two pairs of flame cells. The flame cell formula was thus $2[(2)+(2)+(2)]=12$ as in *Allogenarchopsis problematica* (this paper). The epithelial dilatation remains in the adult stage. Their cercaria is likely to belong *G. chubuensis*.

Genarchopsis chubuensis has previously been recorded from not only the stomach of fish but also the esophagus, gills, buccal cavity, peribuccal tissue [*sic*], intestine and gut (Yamaguti, 1942; Shimazu *et al.*, 2011). It is possible that worms migrate from the stomach (the primary site of infection) up to the esophagus, buccal cavity and gill chamber and down to the intestine after the death of host fish.

Life cycle. Urabe (2001) studied the life cycle in the field and laboratory. Cystophorous cercariae (Figs. 23–24) were found produced in daughter rediae (Fig. 22) in the pleurocerid snail *Semisulcospira libertina* (a natural first intermediate host) from Tobihino, Nara City. The cercariae were exposed to copepods, *Mesocyclops leuckarti* (Claus, 1857) [Japanese name: Asagao-kenmijinko], *Thermocyclops hyalinus* (Rehberg, 1880) [Japanese name not yet given] and *Eucyclops serrulatus* (Fischer, 1851) [Japanese name: Nokogiri-kenmijinko] (experimental second intermediate hosts), in the hemocoel of which unencysted metacercariae (Figs. 25–26) grew. During this growth, the intestinal ceca developed fully to form a cyclocoel in 5 days after infection. The experimental metacercariae were fed to *Rhinogobius* sp. OR and *O. obscura*, and subsequently gravid adults were recovered from the stomach of the former host (an experimental final host). Natural final hosts in Tobihino were *Rhinogobius* sp. OR and *O. obscura*. It should be pointed out here that Urabe's adult (96- to 108-day-old, fig. 1 G and fig. 3E) has much more eggs in the forebody than those from Lake Suwa (Fig. 19). Urabe *et al.* (2013) showed that adult specimens found in *Rhinogobius kurodai* [correctly *Rhinogobius* sp. OR] from Tobihino and rediae (cystophorous cercariae) found in *Semisulcospira reiniana* from the Hachioji River at Takashima City, Ooura River at Nagahama City, Hayama River at Kusatsu City, Lake Biwa at Kannonji, Otsu City, and Yasu, Yasu City, all in Shiga Prefecture were assigned to the Central Japan Group (or now *C. chubuensis*).

***Genarchopsis* sp. 1** of Shimazu, 1995

(Fig. 27)

Genarchopsis sp. 1: Shimazu, 1995a: 15–16.

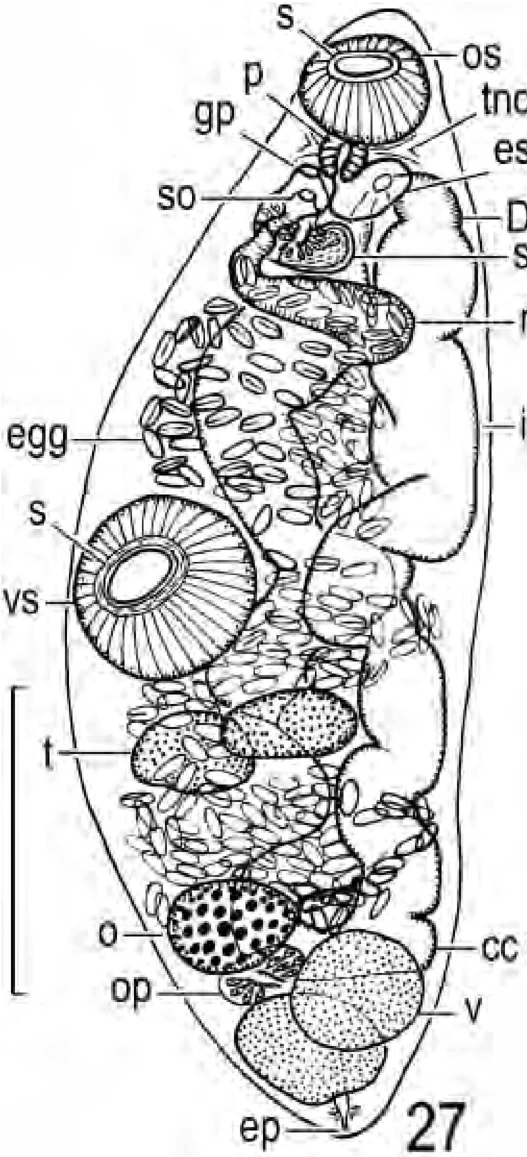
Host in Japan. *Tridentiger brevispinis* (Gobiidae) (Shimazu, 1995a).

Site of infection. Unknown [stomach (?)].

Geographical distribution. Ibaraki Prefecture: Lake Kasumigaura (Shimazu, 1995a).

Material examined. 12 [not 11] specimens (Ozaki's Collection, MPM Coll. No. 30208, unpublished, labeled "*Genarchopsis Tridentiger ob*. Goro [Kasumigaura] [Sakamoto]," other data not given) of *Genarchopsis* sp. 1, immature, adult, ex *Tridentiger brevispinis*, Lake Kasumigaura, possibly at Sakamoto, Minaminemoto, Dejima Village, now in Kasumigaura City (Shimazu, 1995a, 2014).

Description. After Shimazu (1995a), modified from the present study. Similar to *G. goppo* (this paper) in general morphology (Fig. 27). Body 1.02–1.76 by 0.32–0.56; forebody 0.51–0.85 long, occupying 48–54% of body length.



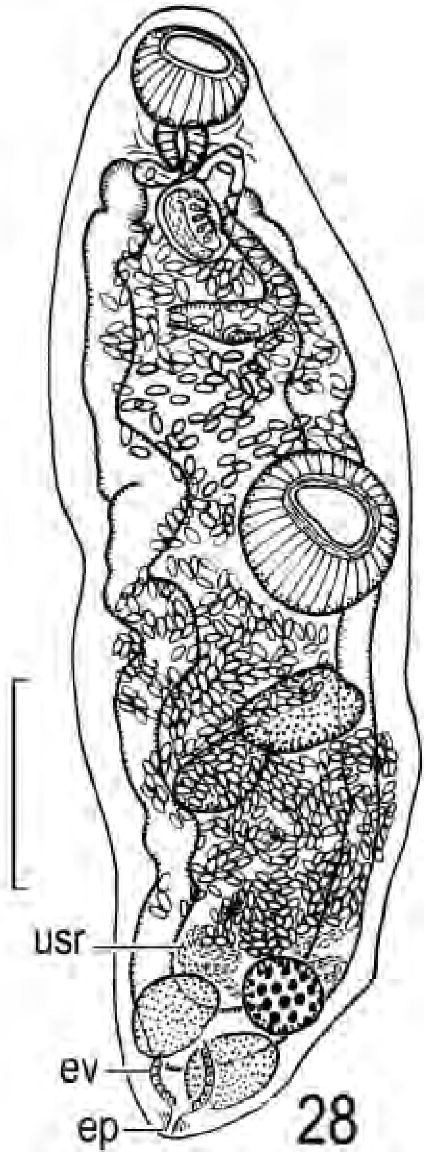


Fig. 27. *Genarchopsis* sp. 1, adult (MPM Coll. No. 30208) found in *Tridentiger brevispinis*, entire body, ventral view. Scale bar: 0.5 mm.

Fig. 28. *Genarchopsis* sp. 2, adult (MPM Coll. No. 30209) found in *Acanthogobius flavimanus*, entire body, ventral view. Scale bar: 0.5 mm.

Oral sucker 0.24–0.48 by 0.32–0.53; sphincter fairly well developed. Pharynx 0.11–0.24 by 0.11–0.26. Ventral sucker 0.48–0.88 by 0.50–0.88; sucker width ratio 1 : 1.4–1.7; sphincter well developed; radial muscle bundles well developed. Testes 0.32–0.72 by 0.24–0.53, slightly separated from ventral sucker by uterus. Sinus sac 0.10–0.16 by 0.09–0.16. Sinus organ 0.05 by 0.05–0.07. Genital atrium longer than sinus organ. Genital pore puckered. Ovary smaller than testes, 0.32–0.48 by 0.32. Ootype pouch 0.16–0.17 by 0.08–0.09. Uterus much folded, with about eight transverse folds in forebody, overlapping cyclocoel; metraterm much longer than sinus sac. Eggs 56–80 by 25–32 μm. Vitellaria 0.25–0.48 by 0.24–32.

Remarks. It is possible that these specimens may have been obtained from the stomach of *Tridentiger brevispinis*, not *T. obscura* in Lake Kasumigaura, because an immature specimen of *Azygia rhinogobii* Shimazu, 2007 (a stomach parasite) was found mounted among them (Shimazu, 1995a, 2014).

The specimens are somewhat similar to *G. anguillae* (this paper) in having about eight transverse uterine folds in the forebody and large eggs (56–80 by 25–32 μm) and in the position of the cyclocoel. They remain to be identified to species until new specimens are obtained for morphological and molecular studies.

Life cycle. Not known.

***Genarchopsis* sp. 2** of Shimazu, 1995

(Fig. 28)

Genarchopsis sp. 2: Shimazu, 1995a: 15–16.

Host in Japan. *Acanthogobius flavimanus* (Temminck and Schlegel, 1845) (Gobiidae) (Shimazu, 1995a).

Site of infection. Unknown.

Geographical distribution. Tokyo: Senju (Shimazu, 1995a).

Material examined. 31 specimens (Ozaki's Collection, MPM Coll. No. 30209, unidentified, unpublished, labeled "MAHAZE Senju]," other data not given) of *Genarchopsis* sp. 2, immature, adult, ex *Acanthogobius flavimanus*, Senju (Shimazu, 1995a).

Description. After Shimazu (1995a), modified from the present study (Fig. 28). Similar to *G. goppo* (this paper) in general morphology. Body 0.97–2.69 by 0.31–0.82; forebody 0.47–1.29 long, occupying 48–57% of body length. Oral sucker 0.12–0.24 by 0.12–0.27; sphincter fairly well developed. Pharynx 0.05–0.13 by 0.05–0.12. Cyclocoel overlapping ovary and vitellaria. Ventral sucker 0.19–0.43 by 0.20–0.39; sucker width ratio 1:1.4–1.7; sphincter well developed; radial muscle bundles well developed. Testes 0.14–0.33 by 0.10–0.27, greatly separated from ventral sucker by uterus. Sinus sac 0.12–0.23 by 0.06–0.16. Sinus organ 0.05–0.08 by 0.04–0.07. Genital atrium longer than sinus organ. Genital pore puckered. Ovary smaller than testes, 0.08–0.19 in diameter. Ootype pouch not clearly observed. Uterus much folded, with about nine transverse folds in forebody, anterior to cyclocoel; metraterm much longer than sinus sac. Eggs 52–70 by 26–30 μm. Vitellaria globular, elliptical or slightly lobed, 0.11–0.23 by 0.08–0.15.

Remarks. The specimens somewhat resemble *G. goppo* (*sensu stricto*) (this paper), but they differ from the latter in having a lower sucker width ratio, 1:1.4–1.7 instead of 1:1.7–2.2. They differ from *G. anguillae* and *Genarchopsis* sp. 1 in having smaller eggs, 52–70 by 26–30 μm instead of 67–80 by 28–34 μm and 56–80 by 25–32 μm, respectively. They are distinguished from *G. gigi* and *G. chubuensis* (this paper) in having more transverse uterine folds in the forebody, about nine instead of four and two, respectively. They differ from *G. fellicola* in that the sphincters of the oral and ventral suckers are much less developed. They also remain to be identified to species until new specimens are obtained for morphological and molecular studies.

It is interesting that Ozaki collected *Genarchopsis* spp. 1 and 2 in the distribution area of *G. chubuensis* many years ago. Further field studies of species composition of *Genarchopsis* should be made in Ibaraki Prefecture and Tokyo.

Life cycle. Not known.

Discussion on the life cycle of *Genarchopsis* in the present paper

It is desirable that the entire life cycle and geographical distribution of each species of *Genarchopsis* should be further studied in the field. Since it is not always easy to identify worms (cercariae, metacercariae, adults, *etc*.) to species, it would be necessary to apply not only morphological but also molecular methods for species identification. These studies would also result in discovering some undescribed species.

The Hemiuroidea produces cercariae of the cystophorous type or modified therefrom (La Rue, 1957). In Japan, four cystophorous cercariae are known to develop in freshwater snails of *Semisulcospira* spp. (Ito, 1964): *Cercaria yoshidae* Cort and Nichols, 1920, *Cercaria longicerca* Ito, 1953, *Cercaria introverta* Faust, 1924 and *Cercaria problematica* Faust, 1924 (syn. *Cercaria manei* Ito, 1960). The former two have two intestinal ceca and anteriorly fused arms of the Y-shaped excretory vesicle, but they differ from each other in morphology of the cystophorous tail (Ito, 1952, 1953). Urabe (2001) indicated that the intestinal ceca develop fully to form a cyclocoel in the metacercarial stage in *G. goppo* (now *G. chubuensis*). Cercariae of *G. chubuensis*, *G. goppo* (sensu stricto) and *G. gigi* resemble *C. yoshidae* (Urabe, 2001; Urabe *et al.*, 2013; this paper), though the cercariae of *G. goppo* and *G. gigi* have not yet been fully described. Cort and Nichols (1920) gave the name *Cercaria yoshidae* to *Cercaria* F of Yoshida, 1917, which Yoshida (1917) had described from *S. libertina*. According to Yoshida (1917) and Ito (1952, 1964), *Cercaria yoshidae* develops in *S. libertina*, *S. reiniana* and *S. japonica* in various areas in Japan. The cercariae of the three species are thus morphologically similar to one another, and the morphological characteristics that may differentiate them remain uncertain at present. It is still unknown which species of *Genarchopsis C. yoshidae* really belongs to. It is possible that *C. yoshidae* may be larvae of more than one species. Urabe (2001) avoided definitively identifying her cercaria as *C. yoshidae* (see also Shimazu *et al.*, 2011). Her daughter redia (fig. 2A) is different from Yoshida's (1917, pl. 2 fig. 17) redia (locality not specified) in having a much shorter intestine, about one-fourth of the body length instead of about three-fourths. Besprozvannykh and Ermolenko (1988), Ermolenko (1992) and Besprozvannykh (2000) considered that *C. longicerca* is the cercaria of *G. goppo* in Primorsky Region, Russia. However, I do not agree with them as mentioned above. The molecular work by Urabe *et al.* (2012) has indicated that *C. longicerca* is distinct from the Lake Biwa Group (*G. gigi*), West Japan Group (*G. goppo* (*sensu stricto*)), Central Japan Group (now *G. chubuensis*) and *G. fellicola*. *Cercaria problematica* is the cercaria of *Allogenarchopsis problematica* (Urabe and Shimazu, 2013; this paper). *Cercaria introverta* is the cercaria of *Isoparorchis eurytremum* (Kobayashi, 1915) (Hemiuroidea, Isoparorchiidae) (Shimazu *et al.*, 2014).

Urabe (2001) experimentally showed that copepods of three species served as second intermediate hosts for *G. goppo* (now *G. chubuensis*). Shimazu *et al.* (2011) recorded unencysted metacercariae under the species name *G. goppo* from copepods of Lake Biwa. They probably belong to *G. gigi* (this paper).

Fishes of many species have been recorded as final hosts for *Genarchopsis*, especially for *G. goppo* (*sensu stricto*) and *G. gigi*. It is almost certain that some of them are really true final hosts to become infected with worms by ingesting the second intermediate host, and others are accidental final hosts to become infected with worms by ingesting infected small fish. Even accidental final hosts will do for completion of the life cycle as long as gravid worms lay fully embryonated eggs in them. It seems likely that small fish harboring immature worms soon after eating copepod second intermediate hosts are involved as transport (or third intermediate) hosts between the second intermediate and final hosts.

Key to the genera and species of the Derogenidae in the present paper*

1.1. Juel's organ present; Laurer's canal leading into Juel's organ; excretory arms separate anteriorly .... *Allogenarchopsis*
.... *A. problematica*

1.2. Juel's organ absent; Laurer's canal opening dorsally; excretory arms united anteriorly .... *Genarchopsis*....2
2.1. Parasitic primarily in stomach; sphincters of oral and ventral suckers developed well 3
2.2. Parasitic in gall bladder; sphincters of oral and ventral suckers developed weakly........*G. fellicola*
3.1. Cyclocoel anterior or dorsal to ovary; uterus extending posteriorly beyond cyclocoel to vitellaria 4
3.2. Cyclocoel between ovary and vitellaria; uterus not extending posteriorly beyond cyclocoel.........5
4.1. Metraterm more than three times as long as sinus sac..................................*G. chubuensis* sp. nov.
4.2. Metraterm about two times as long as sinus sac...*G. gigi*
5.1. Ovary smaller than testes; eggs 51–72 by 27–29 μm..*G. goppo*
5.2. Ovary larger than testes; eggs 67–80 by 28–34 μm ....*G. anguillae*

*This key excludes *Genarchopsis* spp. 1 and 2.

Acknowledgments

I am grateful to Dr. Norio Shimizu (Hiroshima University Museum, Hiroshima University, Higashihiroshima) and Dr. Kouki Kanou and Mr. Seiya Kaneko (Center for Water Environment Studies, Ibaraki University, Itako) for collecting some fishes for the present study; and Dr. Thomas H. Cribb (School of Biological Sciences, The University of Queensland, Brisbane, Australia) for reviewing a draft of the manuscript.

References

Besprozvannykh, V. V. 2000. Fauna, Biology, and Ecology [of] Part[h]enitae and Cercariae [of] Trematodes [in] Mollusks of Genus *Juga* (Pachychilidae) from River [in] Primorye Territory. 120 pp. Dalnauka, Vladivostok. (In Russian with English title.)

Besprozvannykh, V. V. and A. V. Ermolenko 1988. [Biology of *Genarches goppo* (Ozaki, 1925) (Trematoda. Halipegidae). In [Fauna, Systematics and Biology of Freshwater Invertebrate Animals,] pp. 67–69. DVNY AN SSSR, Vladivostok. (In Russian.)

Cort, W. W. and E. B. Nichols 1920. A new cystophorous cercaria from California. Journal of Parasitology, 7: 8–15.

Ermolenko, A. V. 1992. [Parasites of Freshwater Fishes of the Continental Part of the Basin, Sea of Japan.] 238 pp. FEB RAS, Vladivostok. (In Russian.)

Faust, E. C. 1924. Notes on larval flukes from China. II. Studies on some larval flukes from the central and south coast provinces of China. American Journal of Hygiene, 4: 241–301.

Gibson, D. I. 2002a. Superfamily Hemiuroidea Looss, 1899. In Gibson, D. I., A. Jones and R. A. Bray (eds.): Keys to the Trematoda, 1: 299–304. CAB International and The Natural History Museum, Wallingford.

Gibson, D. I. 2002b. Family Derogenidae Nicoll, 1910. In Gibson, D. I., A. Jones and R. A. Bray (eds.): Keys to the Trematoda, 1: 351–368. CAB International and The Natural History Museum, Wallingford.

Ito, J. 1952. Redescription of *Cercaria yoshidae* Cort et Nichols, 1920, a cystophorous cercaria in the snail *Semisulcospira* spp. in Japan. Japanese Journal of Medical Science & Biology, 5: 447–454.

Ito, J. 1953. Two cystophorous cercariae, *C. introverta* Faust, 1942, and *C. longicerca* n. sp. from fresh water snail, *Semisulcospira* spp. in Japan, with a list of cystophorous cercariae. Japanese Journal of Medical Science & Biology, 6: 487–492.

Ito, J. 1960. Contributions to the morphology of cercariae obtained from a snail host, *Semisulcospira libertina* in Japan. Japanese Journal of Medical Science & Biology, 13: 59–72.

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, pp. 395–550. Meguro Parasitological Museum, Tokyo.

Kobayashi, H. 1915. [Studies of endoparasitic trematodes from Japan (2).] Dobutsugaku Zasshi, 27: 50–57, pl. 2. (In Japanese.)

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

Kumakawa, S. 2001. Sexual maturity of the gobid [sic] fishes named "Tonko" in Lake Suwa and its inflow and outflow rivers and planktonic behavior of its larvae and juveniles in Lake Suwa. Bulletion of Nagano Prefectural Fisheries Experimental Station, (5): 25–30. (In Japanese.)

La Rue, G. R. 1957. The classification of digenetic Trematoda: a review and a new system. Experimental Parasitology, 6: 306–349.

Lin, C., M. Urabe and K. Yoshizuka 2006. Test of toxicity of heavy metals to intestinal parasites of freshwater fish. Journal of Japan Society on Water Environment, 29: 333–337. (In Japanese with English abstract.)

Madhavi, R. 1978. Life history of *Genarchopsis goppo* Ozaki, 1925 (Trematoda: Hemiuridae) from the freshwater fish *Channa punctata*. Journal of Helminthology, 52: 251–259.

Moravec, F., P. Nie, T. Scholz and G.-T. Wang 2003. Some trematodes and cestodes of fishes mainly from Hubei Province, central China. Acta Societatis Zoologicae Bohemicae, 67: 161–174.

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. 1925. On a new genus of fish trematodes, *Genarchopsis*, and a new species of *Asymphylodora*. Japanese Journal of Zoology, 1: 101–108.

Pandey, K. G. 1973 [issued 1975]. A restudy of *Genarchpsis goppo* (Tubangui) [sic] Ozaki, 1925 with a note on validity of certain species. Indian Journal of Zootomy, 14: 167–174.

Scholz, T. 1991. Observations on trematode fauna of freshwater fish in Laos. Helminthologia, 28: 125–130.

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. 1995a. 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. 1995b. A revised checklist and bibliography of the platyhelminth parasites reported by Dr. Yoshimasa Ozaki, 1923–1966, and their specimens deposited in the Meguro Parasitological Museum, Tokyo. Journal of Nagano Prefectural College, (50): 33–50.

Shimazu, T. 2000. A revised and enlarged version of Shimazu's (1988) paper entitled "Trematodes of the genera *Coitocaecum*, *Dimerosaccus* and *Opecoelus* (Opecoelidae: Opecoelinae) from freshwater fishes of Japan." Journal of Nagano Prefectural College, (55): 15–29.

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. 2014. Digeneans parasitic in freshwater fishes (Osteichthyes) of Japan. III. Azygiidae and Bucephalidae. Bulletin of the National Museum of Nature and Science, Series A (Zoology), 40: 167–190.

Shimazu, T., T. H. Cribb, T. L. Miller, M. Urabe, Nguyen Van Ha, Tran Thi Binh and M. B. Shed'ko 2014. Revision of *Isoparorchis* Southwell, 1913 (Digenea, Hemiuroidea, Isoparorchiidae), parasites of the air bladder of freshwater catfishes: a molecular and morphological study. Bulletin of the National Museum of Nature and Science, Series A (Zoology), 40: 15–51.

Shimazu, T. and C. Shimizu 1984. Flame-cell formula of a cystophorous cercaria, *Cercaria yoshidae* (Trematoda: Hemiuridae). Journal of Nagano-ken Junior College, (39): 15–16.

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 L. Kh. Guschanskaya 1955. [Suborder Hemiurata (Markevitsch, 1951) Skrjabin et Guschanskaja, 1954. Part 3.] In Skryabin, K. I. (ed.): [Trematodes of Animals and Man.] Osnovy Trematodologii, 11: 465–748. Izdatel'stvo Akademii Nauk SSSR, Moskva. (In Russian.)

Srivastava, H. D. 1933. On new trematodes of frogs and fishes of the United Provinces, India. Part I.—New distomes of the family Hemiuridae Luhe [sic] 1901 from North Indian fishes and frogs with a systematic discussion on the family Halipegidae Poche 1925 and the genera *Vitellotrema* Guberlet 1928 and *Genarchopsis* Ozaki 1925. Bulletin of the Academy of Sciences, United Provinces, Allahabad, 3: 41–60.

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.)

Takei, K. 2007. Verified the list of the fishes of Lake Suwa. Bulletion of Nagano Prefectural Fisheries Experimental Station, (9): 7–21. (In Japanese.)

Urabe, M. 2001. Life cycle of *Genarchopsis goppo* (Trematoda: Derogenidae) from Nara, Japan. Journal of Parasitology, 87: 1404–1408.

Urabe, M. 2003. Trematode fauna of prosobranch snails of the genus *Semisulcospira* in Lake Biwa and the connected drainage system. Parasitology International, 52: 21–34.

Urabe, M., T. Nishimura and T. Shimazu 2013. Taxonomic revision of three species of the genus *Genarchopsis* (Digenea: Hemiuroidea: Derogenidae) in Japan by molecular phylogenetic analyses. International Parasitology, 61: 554–560.

Urabe, M. and T. Shimazu 2013. *Allogenarchopsis* gen. nov. (Digenea, Derogenidae, Halipeginae) parasitic in the intestine of freshwater fishes: a molecular and morphological study of adult and cercarial forms. Bulletin of the National Museum of Nature and Science, Series A (Zoology), 39: 119–130.

Wang, S.-X. 1991. [Family Halipegidae.] In Wu, B.-H. (chief ed.): Fauna of Zhejiang. Trematoda, pp. 288–289. Zhejiang Science and Technology Publishing House, Hangzhou. (In Chinese.)

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. 1939. Studies of the helminth fauna of Japan. Part 26. Trematodes of fishes, VI. Japanese Journal of Zoology, 8: 211–230, pls. 29–30.

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.

Yoshida, S. 1917. [On the cercariae in *Melania*.] Dobutsugaku Zasshi, 29: 103–119, pl. 2. (In Japanese.)