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

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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 Hemiuroidae 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; Le, 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.


*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).


**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.
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.

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.
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* 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)


*Progonus goppo*: Srivastava, 1933: 55.


**Hosts in Japan.** *Odontobutis obscura* (Temminck and Schlegel, 1845) (Odontobutidae) (type host), *Coreoperca kawamebari* (Temminck and Schlegel, 1843) (Percichthyidae) (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 Munechikayakuni, Kurose-cho; Karei River at Maruyama, Kurose-cho; and Irasuke River at Kanesawa, Kurose-cho, all Higashihiroshima City (Ozaki,
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;

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.
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).


**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-PI 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. Tegmentum 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, posterovertral to esophagus. Drüsemagen 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, Laurer’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, Fukagawa and Saitama Prefectures; (3) Lake Biwa Group, or Genarchopsis gigi Yamaguti, 1939, in Lake Biwa itself; and Genarchopsis 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 Higashihoshima 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 gobids, Rhinogobius flumineus, R. giurinus, R. nagoyae [syn. Rhinogobius sp. CB], Gymnogobius petchiliensis 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 Region, Russia. First intermediate hosts were snails, Juga spp. (Pachychilidae). A second intermediate host was a mayfly, Ecdyomurus 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. *Chae nogobius 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 gigi* [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 reinitii* 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-PI 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; 4 (LBM 1-68 from stomach), adult, stomach and intestine, Hachi-yadohama, 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-yadokyo 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), Hachi-yadohama, 14 May 1998; and 2 (LBM 1-6 to -7), Imazu-cho, 19 May 1998 (Shimazu et al., 2011). (6) 1 (NSMT-PI 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 protruded outside through genital pore; sinus 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). 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). 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). 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). 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). 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). 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). 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). 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). Pharynx 0.05–0.06 by 0.05–0.07.

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.


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).

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.
Takeshi Shimazu


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).

**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.


**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; Omatu (Omatuzaki 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,
Gymnogobius urotaenia (Hilgendorf, 1879) (Gobiidae).

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


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 0.11–0.16 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; and 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-PI 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.
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 25–32μm. Vitellaria 0.25–0.48 by 0.24–32.

Remarks. It is possible that these specimens may have been obtained from the stomach of Tridendiger 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 25–32μm) 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.


Material examined. 31 specimens (Ozaki’s Collection, MPM Coll. No. 30209, unidentifed, 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 sac. 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 26–30μm. 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 26–30μm instead of 67–80 by 28–34μm and 56–80 by 25–32μm, 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 cercar-
iae are known to develop in freshwater snails of
Semisulcospira spp. (Ito, 1964): Cercaria yoshi-
dae Cort and Nichols, 1920, Cercaria longicerca
Ito, 1953, Cercaria introverta Faust, 1924 and
Cercaria problematica Faust, 1924 (syn. Cer-
caria 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
the intestinal ceca develop fully to form a cyclo-
coel in the metacercarial stage in G. goppo (now
G. chubuensis). 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. Accord-
ing to Yoshida (1917) and Ito (1952, 1953), Cerc-
caria yoshidae develops in S. libertina, S. rein-
iana and S. japonica in various areas in Japan.
The cercariae of the three species are thus mor-
phologically similar to one another, and the mor-
phological 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 spe-
cies. Urabe (2001) avoided definitively identify-
ing her cercaria as C. yoshidae (see also Shimazu
et al., 2011). Her daughter redia (fig. 2A) is dif-
ferent 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. longi-
cerca 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. longi-
cerca is distinct from the Lake Biwa Group (G.
gigi), West Japan Group (G. goppo (sensu stricto)), Central Japan Group (now G. chubuen-
sis) and G. fellicola. Cercaria problematica is the
cercaria of Allogenarchopsis problematica
(Urabe and Shimazu, 2013; this paper). Cercaria
introverta is the cercaria of Isoparorchis eurytre-
mum (Kobayashi, 1915) (Hemiuroidea, Isoparor-
chiidae) (Shimazu et al., 2014).

Urabe (2001) experimentally showed that copepods of three species served as second inter-
mediate hosts for G. goppo (now G. chubuensis).
Shimazu et al. (2011) recorded unencysted meta-
cercariae 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 ingest-
ing 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 .................................................. 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 .......... G. goppo

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.

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