Digeneans (Trematoda) Parasitic in Freshwater Fishes (Osteichthyes) of the Lake Biwa Basin in Shiga Prefecture, Central Honshu, Japan

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Abstract: The fauna of adult digeneans (Trematoda) parasitic in freshwater fishes (Osteichthyes) from the Lake Biwa basin in Shiga Prefecture, central Honshu, Japan, is studied from the literature and existing specimens. Twenty-four previously known, 2 new, and 4 unidentified species in 17 genera and 12 families are recorded. Three dubious literature records are also mentioned. All 30 confirmed species, except Sanguinicolidae gen. sp. (Aporocotylidae), are described and figured. Life cycles are discussed where known. *Philopinna kawamutsu* sp. nov. (Didymozoidae) was found in the connective tissue between the vertebrae and the air bladder near the esophagus of *Nipponocypris temminckii* (Temminck and Schlegel) (Cyprinidae). *Genarchopsis yaritanago* sp. nov. (Derogenidae) was found in the intestine of *Tanakia lanceolata* (Temminck and Schlegel) (Cyprinidae). *Asymphylodora innominata* (Faust, 1924) comb. nov. is proposed for *A. macrostoma* Ozaki, 1925 (Lissorchiidae). A key to the families, genera, and species of these digeneans is provided. Host-parasite and parasite-host lists are given.

Key words: adult digeneans, Trematoda, parasites, morphology, life cycle, *Philopinna kawamutsu* sp. nov., *Genarchopsis yaritanago* sp. nov., Lake Biwa basin, Shiga Prefecture, Japan.

Introduction

Lake Biwa located in Shiga Prefecture, central Honshu, Japan, is one of the oldest freshwater lakes in the world and the largest in Japan. This lake had its origin about 4 million years ago in the Pliocene epoch in the Tertiary period (Biwako no Shizenshi Kenkyu Kai (ed.), 1994). Some 80 species, subspecies, and types of freshwater fishes (Osteichthyes) inhabit the Lake Biwa basin, namely Lake Biwa itself and its surrounding waters (rivers, irrigation canals, ponds, etc.) (Shigaken Ikimono Sogo Chosa Iinkai (ed.), 2006). In Japan, since prehistoric time, some species of freshwater fishes have been artificially transported from water body to water body for fisheries, game fishing, or as contaminants. Those things have happened also in Lake Biwa: fish of some species have moved out, and fish of some other species have moved in. The fauna of freshwater fishes on the Japanese Islands has been formed artificially as well as naturally.

Kobayashi (1915a) was probably the first to report adult digenetic trematodes from a freshwater fish of Lake Biwa: *Leptolecithum eurytremum* gen. nov., sp. nov., and *Exorchis oviformis* gen. nov., sp. nov., both from *Parasilurus asotus* (Linnaeus). The occurrence of the latter digenean in the lake is considered questionable (this paper). Since then, Kobayashi (1921), Ozaki (1926), Goto and Ozaki (1930), Yamaguti (1934, 1938, 1939, 1942), Takeuti (1936), and Shi-

mazu (1979, 1988a–b, 1990a–c, 1992, 1995a, 2000, 2007) have made taxonomic studies of adult digeneans found in freshwater fishes from the Lake Biwa basin. An abundant literature on metacercariae of medical importance in fish also exists for Lake Biwa, but this topic is outside of the scope of the present paper.

The purpose of this paper is to present the current fauna of adult digeneans (Trematoda) parasitic in freshwater fishes in the Lake Biwa basin on the basis of the literature and existing specimens. The fauna itself is interesting and should be useful for understanding the fish parasite faunas and their formation on the Japanese Islands and East Asia.

Materials and Methods

Adult digeneans found in freshwater fishes of the Lake Biwa basin were studied from the literature and the specimens collected up to 2007. A few specimens from outside of Shiga Prefecture also were studied for morphological comparison.

The adult digenean specimens examined included those borrowed from Dr. Satyu Yamaguti's Collection (Yamaguti's Collection) and Dr. Yoshimasa Ozaki's Collection (Ozaki's Collection), both deposited in Meguro Parasitological Museum, Tokyo (MPM); from the National Museum of Nature and Science, formerly the National Science Museum, Tokyo (NSMT); and from the Lake Biwa Museum, Shiga (LBM). All the LBM specimens have been given numbers: either their permanent registration numbers (e.g., LBM 1340000023) or provisional parasite slide numbers (e.g., LBM 1-4). In addition, Urabe's and Shimazu's unpublished specimens including some collected by Dr. Kazuya Nagasawa (Department of Bioresouce Science, Graduate School of Biosphere Science, Hiroshima University) were examined.

The specimens examined had been prepared by various methods. Most of them were flattened, stained whole-mounts in Canada balsam unless stated otherwise. Some had been fixed in hot formalin, stained, and mounted in Canada balsam. Some others were serial sections stained with hematoxylin and eosin.

The family, species, and Japanese names of host fishes are based on Nakabo (ed.) (2002) with some exceptions following Takahashi and Okazaki (2002), Froese and Pauly (eds.) (2009), and Ichthyological Society of Japan (2009).

In the synonym lists, only the references for the original descriptions, redescriptions of taxonomic importance, and establishments of new combinations are given. The previous record(s) of the digenean species from the Lake Biwa basin is mentioned in the subheading "*Previous record*(*s*)". In the subheading "*Collecting locality* (*localities*)", "Lake Biwa" is given where the exact collecting locality (localities) cannot be determined for the present. The fish and locality names written in Japanese on the slide labels of the specimens examined and in the literature cited are Romanized or translated into English in brackets ([ ]) where they are quoted.

Measurements (length by width) are given in millimeters unless otherwise stated. Drawings were made with the aid of a drawing tube. All of Shimazu's and part of Urabe's unpublished specimens have been deposited in the National Museum of Nature and Science, Tokyo under the name abbreviation (or the registration code) NSMT-Pl. The rest of Urabe's unpublished specimens have been deposited in her personal collection.

As regards some old specimens related to the present paper, it seems worth mentioning the following here. The holotype (No. P. 231) of *Allocreadium hasu* Ozaki, 1926 was deposited by the author in the collection of the Zoological Institute, Science Faculty, Tokyo Imperial University, Tokyo (Ozaki, 1926). This collection has been transferred to the Department of Zoology, The

University Museum, The University of Tokyo, Tokyo; but the latter collection today does not include any holotypes of helminth parasites (Shimazu and Araki, 2006). It is believed that all the holotypes of helminth parasites including *A. hasu* deposited in the Zoological Institute were lost. In addition, none of the original specimens of some other species dealt with in the present paper (e.g., *Leptolecithum eurytremum* Kobayashi, 1915, *Steganoderma kamatukae* Takeuti, 1936, etc.) were made available to us for reexamination. They also must have been lost.

Results

Figure 1 shows the collecting localities where the host fishes were found infected with the adult digeneans studied in the present paper. The addresses of the place names are indicated by their current addresses in 2008. Many former addresses have been changed owing to recent mergers of cities, towns, and villages. The digenean species obtained are shown in Appendixes 1 and 2. Appendix 2 also indicates new parasite and host records from the Lake Biwa basin and Japan, respectively. For some of the LBM specimens, the exact site of infection was not determined.

Class **Trematoda** Rudolphi, 1808
Subclass **Digenea** Carus, 1863
Family **Azygiidae** Lühe, 1909

Azygia gotoi (Ariake, 1922) (Figs. 2–5)

Cercaria gotoi Ariake, 1922: 236–238, figs. 2–5, tables 12; Shimazu, 1979: 228, figs. 3–5.
Azygia anguillae Ozaki, 1924: 426–430, plate figs. 1–3, text fig. 2; Yamaguti, 1934: 360; Shimazu, 2007: 10–11, figs. 14–15.
Azygia gotoi: Shimazu, 1979: 229–230, figs. 6–11.

Previous record. From *Anguilla japonica* of Lake Biwa (Shimazu, 1979).

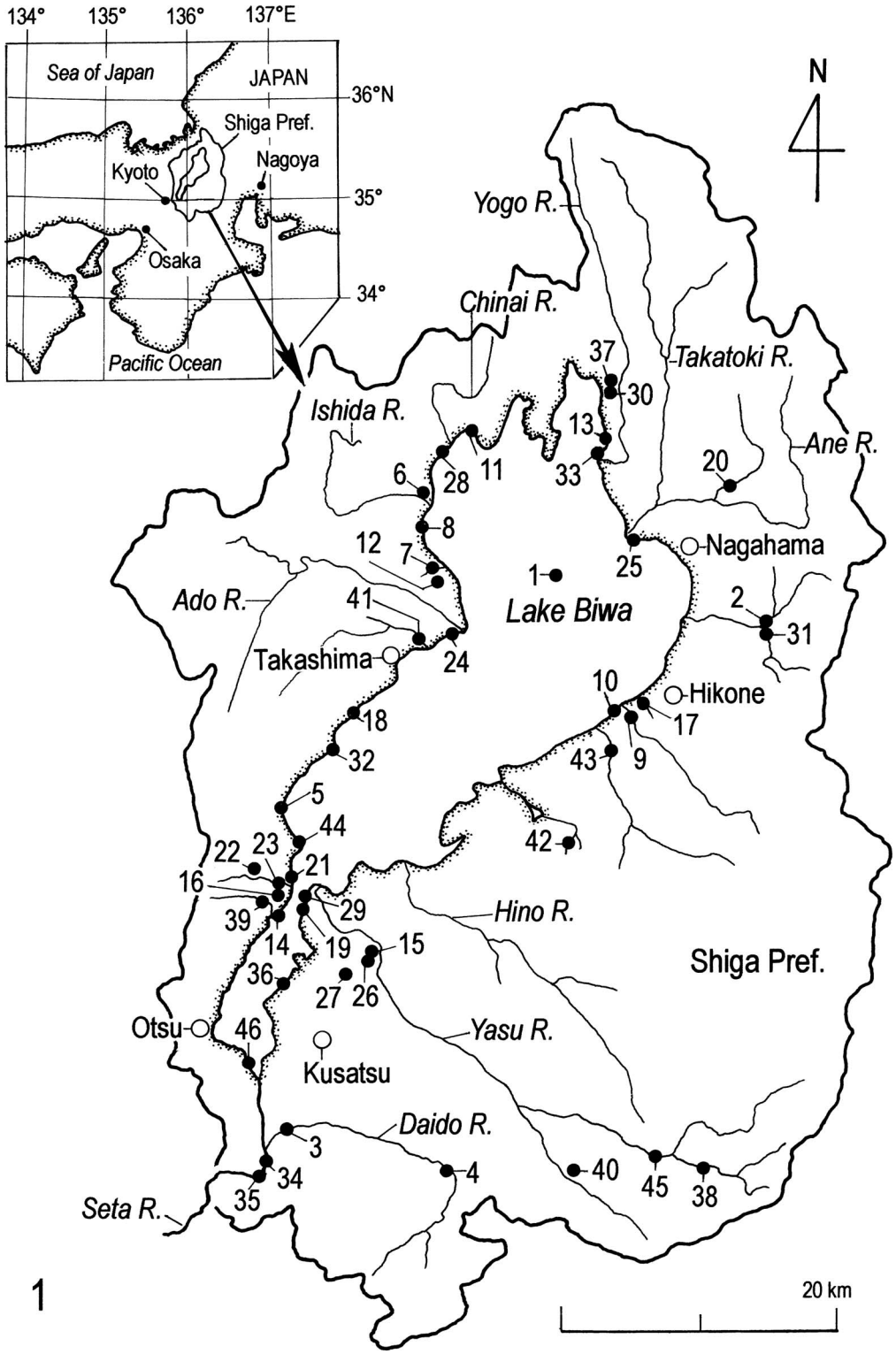
Host. *Anguilla japonica*.

Site of infection. Stomach.

Collecting localities. Lake Biwa and Uso River.

Materials examined. (1) One mature specimen (Yamaguti's Collection, MPM Coll. No. 22354, unidentified, unpublished) found in the stomach of *Anguilla japonica* from Lake Biwa on 1 July 1939 (Shimazu, 1979). (2) Two immature and seven mature (NSMT-Pl 5739, collected by Urabe), and 47 immature and 12 mature specimens (Urabe's personal collection) found in the stomach of *An. japonica* from the Uso River on 16 May 2006.

Description. Based on 20 mature whole-mounts; ten of them measured. Body elongate, slightly dorsoventrally flattened, with bluntly pointed ends, fairly large, 7.12–14.40 by 1.28–2.40; forebody 1.84–2.96 long, occupying 19–26% of total body length. Tegument smooth. Oral sucker subglobular, 0.57–1.02 by 0.60–0.96, almost ventral, close to anterior end of body. Prepharynx absent. Pharynx barrel-shaped, 0.17–0.32 by 0.17–0.29, posterodorsal to oral sucker. Esophagus short, inverted T- or Y-shaped, 0.16–0.49 long, with well-developed sphincter at either distal end of arms. Intestines almost straight, posteriorly terminating blindly near posterior end of body, lined by epithelium with numerous long, microvillous processes; Drüsenmagen may be differentiated as small, globular expansion in proximal shoulder region of intestine, separated from rest of intestine by weak constriction, with microvillous luminal lining thicker than that of rest of intestine. Ventral sucker subglobular, slightly smaller than oral sucker, 0.51–0.78 by 0.51–0.86, lo-


134°
135°
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137°E
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JAPAN
36°N
Shiga Pref.
Nagoya
Kyoto
35°
Osaka
34°
Pacific Ocean
N
Yogo R.
Chinai R.
Takatoki R.
Ishida R.
Ane R.
Nagahama
Ado R.
Lake Biwa
Takashima
Hikone
Hino R.
Shiga Pref.
Otsu
Yasu R.
Kusatsu
Daido R.
Seta R.
20 km
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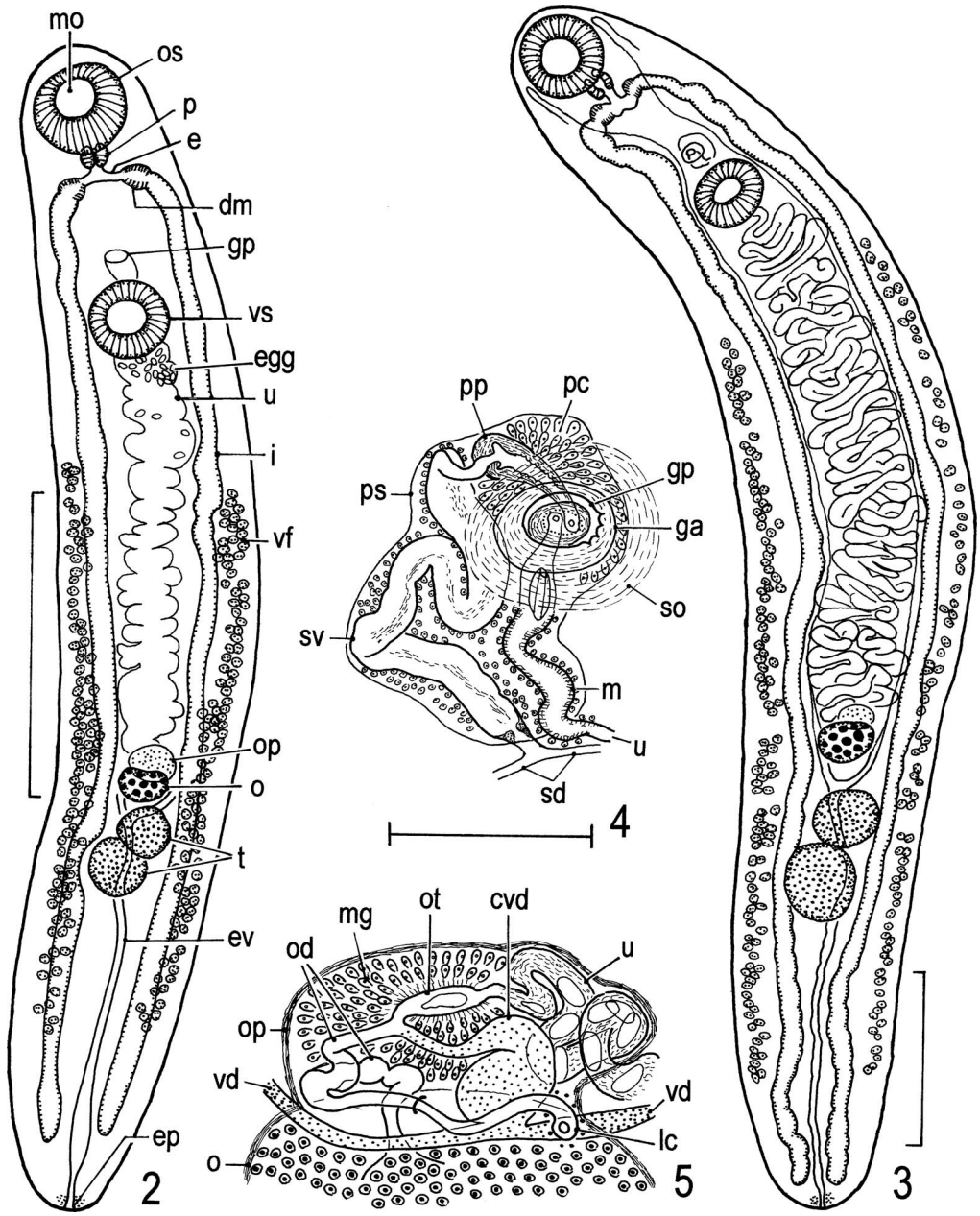
cated at about junction between anterior and second fourths of body; sucker width ratio 1 : 0.85–0.91. Gonads (two testes and one ovary) massing in hindbody; distance from anterior end of body to ovary 4.72–10.40, occupying 62–74% of total body length. Testes globular to elliptical, slightly diagonal, contiguous, between intestines, immediately postovarian; anterior (or left) testis 0.31–0.80 by 0.34–0.80, posterior (or right) 0.34–0.80 by 0.37–0.80. Sperm ducts long; common sperm duct very short. Seminal vesicle tubular, thin, thick-walled, long, convoluted, may be surrounded by small gland cells. Pars prostatica club-shaped, thick-walled, with well-developed sphincter around opening of seminal vesicle at a short distance from base. Prostatic cells well developed. Prostatic sac thin-walled, 0.22–0.48 by 0.16–0.40, median, immediately in front of ventral sucker, enclosing seminal vesicle, pars prostatica, and prostatic cells. Ejaculatory duct in sinus organ, opening side by side with metraterm into very small common depression (rather than pore) on tip of sinus organ; hermaphroditic duct absent. Sinus organ permanent, weakly muscular, slightly protruded in center of bottom of genital atrium, ventral to prostatic sac. Genital atrium large, shallow. Genital pore large, median, slightly anterior to ventral sucker. Ovary transversely reniform, 0.31–0.61 by 0.24–0.37, median, with fairly thick-walled capsule. Ovarian complex immediately preovarian. Laurer's canal fairly long, opening dorsally through single pore. Seminal receptacle absent. Ootype vesicular, large; Mehlis' gland well developed. Ootype pouch (our terminology) fairly thick-walled, transversely elliptical, 0.27–0.59 by 0.19–0.32, immediately anterodorsal to ovary, connected to capsule of ovary, enclosing distal part of oviduct, distal part of common vitelline duct, ovovitelline duct, vesicular ootype, Mehlis' gland, and proximal coils of uterus; proximal part of oviduct, proximal part of Laurer's canal, distal parts of vitelline ducts, and proximal part of common vitelline duct (or vitelline reservoir) seemingly lying in connection (or thick, dense connective tissue) between capsule of ovary and

Fig. 1. Map showing the collecting localities of the host fishes in the Lake Biwa basin in Shiga Prefecture, central Honshu, Japan, where the freshwater fishes were found infected with the adult digeneans studied in this paper. 1, North Lake (North Basin of Lake Biwa, collecting localities not specified); 2, Amano River (Samegai, Maibara City); 3, Daido River-1 (Ishizue, Otsu City); 4, Daido River-2 (Kinose, Shigaraki-cho, Koka City); 5, Hachiyadohama* (Hachiyadohama Beach, Hachiyado, Otsu City); 6, Hamabun (irrigation canal near the Ishida River at Hamabun, Imazu-cho, Takashima City); 7, Harie River (Harie, Shin'asahi-cho, Takashima City); 8, Imazu* (Imazu-cho, Takashima City); 9, Inukami River (either the Inukami River or the Ezura River in Hikone City); 10, Isoda* (Isoda, now in Hassaka-cho, Hikone City); 11, Kaizu* (Kaizu, Makino-cho, Takashima City); 12, Kame-ga-ike Pond (Shodenji Temple, Asahi, Shin'asahi-cho, Takashima City); 13, Katayama* (Katayama, Takatsuki Town); 14, Katata* (Katata, Otsu City); 15, Kawata (irrigation canal at Kawata-cho, Moriyama City); 16, Kaya-ike Pond (Imakatata and Honkatata, Otsu City); 17, Kita River (Oyabu-cho, Hikone City); 18, Komatsu* (most likely referring to Kitakomatsu, Otsu City); 19, Konohama* (Konohama-gyoko Fishing Port, Konohama-cho, Moriyama City); 20, Kusano River (Nagahama City); 21, Mano* (Mano, Otsu City); 22, Mano-ono (Mano-ono, Otsu City); 23, Mano River (Imakatata, Otsu City); 24, Minamifunaki* (Minamifunaki-gyoko Fishing Port, Minamifunaki, Adogawa-cho, Takashima City); 25, Minamihama* (Minamihama-cho, Nagahama City); 26, Miyakawa-ike Pond (Kojima-cho, Moriyama City); 27, Miyake (irrigation canal at Miyake-cho, Moriyama City); 28, Momose* (Momose-gyoko Fishing Port, Chinai, Makino-cho, Takashima City); 29, Moriyama* (Moriyama City); 30, Nishiyama (irrigation canal closely connected to the Yogo River at Nishiyama, Kinomoto Town); 31, Nyuu River (Shiori, Maibara City); 32, Omatsu* (Omatsuzaki Point, Minamikomatsu, Otsu City); 33, Onoe* (Onoe, Kohoku Town); 34, Seta River-1 (Sekinotsu, Otsu City); 35, Seta River-2 (Ishiyamanango-cho, Otsu City); 36, Shina* (Shina-cho, Kusatsu City); 37, Tai (irrigation canal at Tai, Kinomoto Town); 38, Tamura River (Minamitsuchiyama, Tsuchiyama-cho, Koka City); 39, Tenjin River (Kinugawa, Otsu City); 40, Terasho (Terasho, Konan-cho, Koka City); 41, Ukawa River (Takashima City); 42, Uryuu River (Gokashoshichiri-cho, Higashiomi City); 43, Uso River (Hinatsu-cho, Hikone City); 44, Wani* (Wani-gyoko Fishing Port, Otsu City); 45, Yasu River (Maeno, Tsuchiyama-cho, Koka City); 46, Zeze* (Zeze, Otsu City). The collecting localities marked with an asterisk (*) are located on the coast of Lake Biwa. Most of the host fishes landed there had been collected in Lake Biwa nearby off shore, but some may have been transported from other unknown parts of the lake.



Figs. 2–5. *Azygia gotoi*. Adult specimens found in the stomach of *Anguilla japonica*. 2, Yamaguti's specimen (MPM Coll. No. 22354), entire body, eggs omitted except in uterine coils behind ventral sucker, ventral view; 3, specimen (NSMT-Pl 5739), entire body, uterine eggs omitted, ventral view; 4, specimen (NSMT-Pl 5739), terminal genitalia, ventral view; 5, specimen (NSMT-Pl 5739), ovarian complex, dorsal view. Scale bars: 2 mm in Figs. 2–3; 0.5 mm in Figs. 4–5.

ootype pouch. Uterus forming close transverse folds in field encircled by intestines, ootype pouch, and ventral sucker; uterine seminal receptacle well developed in proximal coils of uterus; metraterm well developed, surrounded by small gland cells, entering sinus organ. Eggs numer-

ous, elongate-oval, yellow, 61–78 by 32–48 μm, with domed small operculum on attenuated pole, fully embryonated. In Yamaguti's specimen, the label says that eggs 75–81 by 42–51 μm in life; but they were slightly larger than those in balsam (65–78 by 41–48 μm). Vitellaria follicular, follicles numerous, small, arranged in narrow band lateral to and slightly overlapping intestine on either side of body; distance from middle level of ventral sucker to anterior beginning of them 0.64–1.68, occupying 12–15% of hindbody length; distance from middle level of ventral sucker to posterior end of them 4.72–10.59, occupying 89–93% of hindbody length (usually some distance in front of or rarely at intestinal ends). Excretory vesicle Y-shaped, bifurcating between anterior testis and ovary; main collecting canals of stenostomate type, turning backward laterally to oral sucker; excretory pore posterodorsal.

Discussion. *Azygia anguillae* was described as a new species by Ozaki (1924) on the basis of adult specimens found in the stomach of *Anguilla japonica* from near Tokyo. Ozaki's original material has not been reexamined. This species was redescribed as *A. gotoi* (see below) by Shimazu (1979) from his adult specimens.

Shimazu (1979) experimentally proved that cercariae of *Cercaria gotoi* Ariake, 1922 developed into adults of *Azygia anguillae* Ozaki, 1924. He then proposed a new combination, *Azygia gotoi* (Ariake, 1922), for *A. anguillae*. Later, Shimazu (2007) withdrew this combination, misinterpreting the Article 23.7.1 of the International Code of Zoological Nomenclature (ICZN) (International Commission on Zoological Nomenclature, 1999) as pertaining to species included in collective groups whereas it only concerns the names of collective groups themselves. Since *C. gotoi* was found to be based on the larva of *A. anguillae*, *C. gotoi* must be a synonym of *A. anguillae*. The specific name *gotoi* has priority over the junior specific name *anguillae* (Article 23.3.2.2), as has been pointed out by Shimazu (1979). The generic name *Cercaria*, nevertheless, does not have priority over the generic name *Azygia* Looss, 1899, because the collective-group name *Cercaria* Müller, 1773 (Article 67.14, Example) does not compete in priority with other generic names (Article 23.7.1). Consequently, *Azygia gotoi* (Ariake, 1922) Shimazu, 1979 continues to be the valid species name of the present taxon.

The late Mr. Shunya Kamegai (MPM) labeled Yamaguti's specimen *Azygia* on 19 April 1972. Shimazu (1979) stated that it was most likely *A. gotoi*. We regard Yamaguti's specimen and those from the Uso River as *A. gotoi*, because they are identical in morphology and host with *A. anguillae* (now *A. gotoi*) as described by Ozaki (1924) and as redescribed by Yamaguti (1934) and Shimazu (1979, 2007).

A bag-like structure, which is connected to the capsule of the ovary, encloses the distal part of the oviduct, the distal part of the common vitelline duct, the ovovitelline duct, the ootype, Mehlis' gland, and proximal coils of the uterus (Ozaki, 1924; Shimazu, 1979; this paper, Fig. 5). We term this structure the "ootype pouch" that primarily encloses the ootype complex (or the ootype and Mehlis' gland).

The present study suggests that the Drüsenmagen is differentiated as a small, globular expansion in the proximal shoulder region of each of the intestines (Figs. 2–3) and that the seminal vesicle is surrounded by small gland cells (Fig. 4). Gibson and Bray (1979) and Gibson (2002a) said that the Drüsenmagen is absent in the family Azygiidae. The present observations need to be confirmed through the study of additional material.

Life cycle. First intermediate hosts are viviparid snails, *Cipangopaludina japonica* (Martens) (Japanese name: Oo-tanishi) (natural) in Japan (Ariake, 1922; Shimazu, 1979, 2007) and *Viviparus quadrata* Benson (experimental) in China (Tang and Tang, 1964). Large furcocystocercous cercariae (*Cercaria gotoi*) are produced in sausage- to spindle-shaped sporocysts (Ari-

ake, 1922; Tang and Tang, 1964; Shimazu, 1979, 2007). When or soon after leaving the host snail, the body proper of a fully formed cercaria sinks (or may become withdrawn) into the anterior part of the tail. The tail containing the body proper swims around like a mosquito larva in water (Ariake, 1922; Shimazu, 1979). Although *Ci. japonica* lives in the Lake Biwa basin (Kihira *et al.*, 2003), *C. gotoi* has not yet been recorded from there.

Final hosts are *An. japonica* in Japan (Ozaki, 1924; Yamaguti, 1934; Shimazu, 1979, 2007; Iwashita *et al.*, 2003; this paper) and China (Wang, 1991a), and *Monopterus albus* (Zuiew) (Japanese name: Taunagi) (Synbranchidae) in China (Tang and Tang, 1964; Institute of Hydrobiology, Hubei Province, China (chief ed.), 1973; Liang *et al.*, 1987; Wang, 1991a).

Since the above-mentioned final hosts usually feed on small fish, shrimps, etc., it seems improbable that they acquire infection with the digenean by ingesting free-living swimming cercariae. Small fish that directly ingest cercariae are essential as second intermediate hosts, as was experimentally demonstrated by Shimazu (1979). Furthermore, fish or other animals that eat these small fish may be involved as paratenic hosts. The second intermediate and paratenic hosts retain metacercariae or small juvenile worms in the alimental canal and carry the worms into the final host when it swallows them (Tang and Tang, 1964; Shimazu, 1979, 2007). No juvenile of *A. anguillae* has been found in fishes of any species besides *An. japonica* in the Lake Biwa basin.

Family **Didymozoidae** Monticelli, 1888

Philopinna higai Yamaguti, 1936 (Figs. 6–8)

Philopinna higai Yamaguti, 1936b: 1–2, figs. 1–7.

Previous records. From *Sarcocheilichthys variegatus microoculus* of Minamihama and Onoe, and from *S. biwaensis* of Minamihama (Shimazu, 2007).

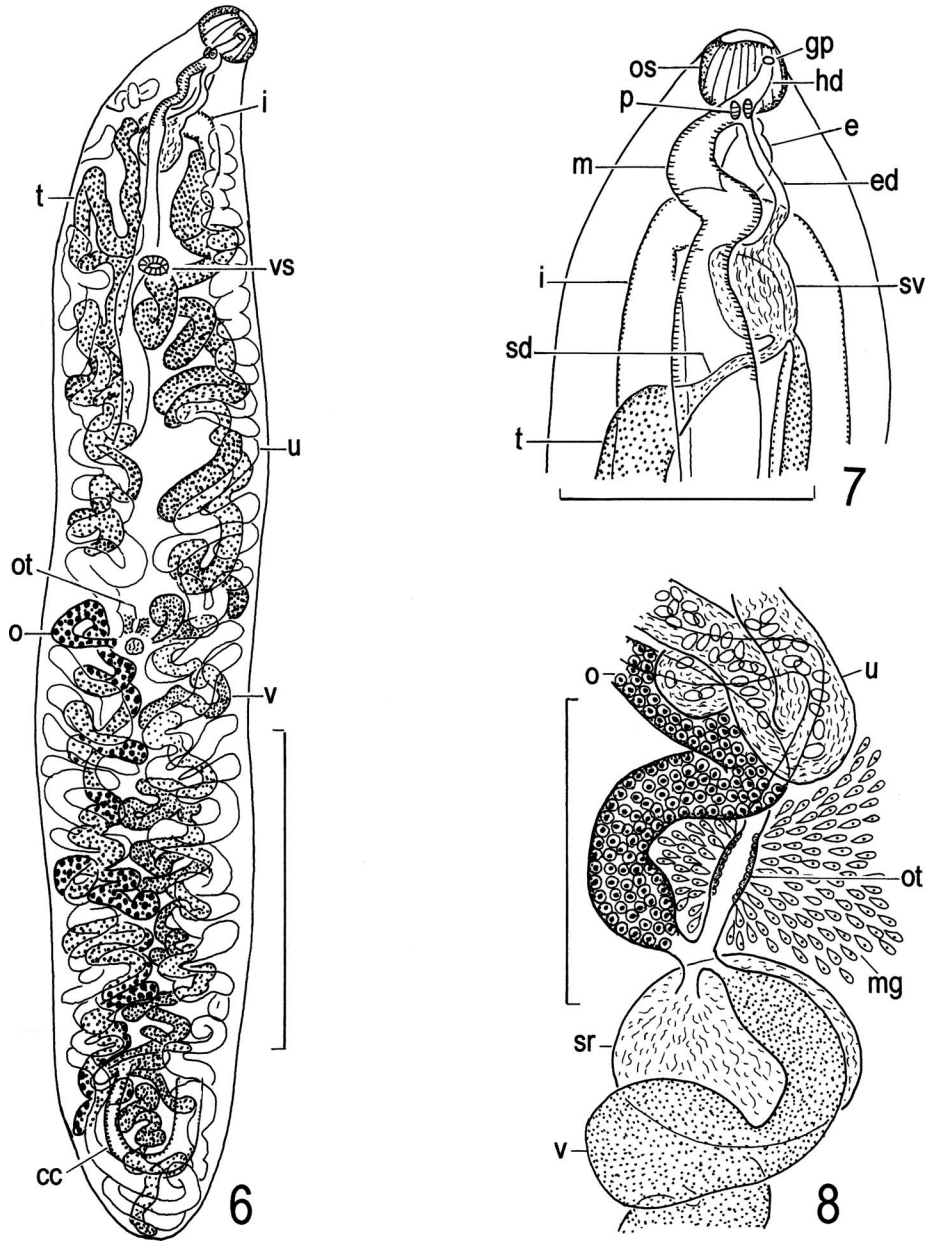
Hosts. *Sarcocheilichthys biwaensis* and *S. variegatus microoculus*.

Site of infection. Fins.

Collecting localities. Harie River, Imazu, Minamihama, and Onoe.

Materials examined. (1) [Five and five mature] specimens (NSMT-Pl 5389 and 5390, respectively) found in the soft tissue of the fins of *Sarcocheilichthys variegatus microoculus* from Onoe on [28 October 1976] and from Minamihama, Nagahama City [not in Shiga Town] on [15 June 1982], respectively (Shimazu, 2007). (2) Two and one mature specimens (LBM 3-25 and 3-26, and 3-47) found in the fins of *S. variegatus microoculus* from Imazu on 5 May 2000 and from the Harie River on 19 October 2000, respectively. (3) [Two mature] specimens (NSMT-Pl 5392) found in the soft tissue of the fins of *S. biwaensis* from Minamihama on [15 June 1982] (Shimazu, 2007).

Description. Of the 15 specimens examined, two lacked the anterior and posterior part of the body, respectively. Twelve mature whole-mounts were measured. Body hermaphroditic, narrow-elongate, tapering anteriorly, rounded posteriorly, slightly flattened dorsoventrally, fairly small, 2.24–4.80 by 0.45–0.86, not oculate; forebody 0.56–0.96 long, occupying 18–25% of total body length. Tegument smooth. Oral sucker anteroterminal, 0.10–0.18 by 0.10–0.16. Prepharynx absent. Pharynx subglobular, very small, 0.02–0.04 by 0.03–0.05. Esophagus straight or curved, 0.09–0.17 long. Intestines thin, undulating, posteriorly uniting with each other to form cyclocoel near posterior end of body. Ventral sucker feeble, flat, small, 0.07–0.09 by 0.05–0.11, located at about middle of anterior third of body; sucker width ratio 1 : 0.56–0.89. Testes two, tubular, long, symmetrical, submedian on either side of body, winding and convoluted irregularly, ascending



Figs. 6–8. *Philopinna higai*. Adult specimens found in fins of *Sarchocheilichthys variegatus microoculus*. 6, specimen (NSMT-Pl 5389), entire body, greater part of the intestines obscured by genital organs, uterus in dorsal parenchyma and eggs in uterus omitted, ventral view; 7, specimen (LBM 3-26), anterior part of body, ventral view; 8, specimen (LBM 3-26), ovarian complex, dorsal view. Scale bars: 1 mm in Fig. 6; 0.5 mm in Fig. 7; 0.3 mm in Fig. 8.

from a little behind of ovarian complex to behind intestinal bifurcation. Sperm ducts short, arising from anterior ends of their respective testes; common sperm duct absent. Seminal vesicle pyriform, 0.08–0.20 by 0.06–0.17, almost median, immediately behind and slightly overlapping intestinal bifurcation ventrally. Ejaculatory duct long, running forward to join metraterm ventral-

ly to pharynx. Cirrus pouch absent. Pars prostatica absent. Genital atrium (or hermaphroditic duct) tubular, long. Genital pore ventral to oral sucker, sinistrally submedian, slightly anterior to middle level of oral sucker. Ovary single, tubular, long, dextrally or sinistrally submedian, dorsal to intestine, winding and convoluted irregularly, extending from near cyclocoel to a little in front of ovarian complex, then turning back to ootype; oviduct very short. Ovarian complex median, greatly posterior to ventral sucker, almost equatorial (lying at distance of 41–55% of body length from anterior end of body). Seminal receptacle almost spherical, large, 0.06–0.17 by 0.06–0.23. Laurer's canal absent. Ovovitelline duct short. Ootype median, in front of seminal receptacle. Mehlis' gland well developed. Uterus highly folded transversely in dorsal parenchyma of all available space on either side of body except in prebifurcal region, transverse folds moving around in lateral field of body into ventral parenchyma considerably, possibly running anterolaterally to right side of body from ootype, backward to posterior end of body on right side of body, across to left side of body there, forward to bifurcal level on left side of body, backward slightly, across to right side of body again, forward slightly to bifurcal level, then backward to level of ovarian complex, and finally forward along median line of body in ventral parenchyma, acting as uterine seminal receptacle in proximal folds; metraterm long, almost median, in ventral parenchyma, beginning behind seminal vesicle. Eggs numerous, filling up uterus, rounded rectangular, thin-shelled, light brown, small, 21–25 by 14–17 μm, with small operculum, fully embryonated. Vitellarium single, tubular, long, submedian, opposite ovary, dorsal to intestine, winding and convoluted irregularly, ascending from posterior end of body to ovarian complex; vitelline duct very short. Excretory vesicle not clearly observed; excretory pore posteroterminal.

Discussion. *Philopinna higai* was described as a new genus and species by Yamaguti (1936b) from adult specimens found in the fins and orbits of *Sarchocheilichthys variegatus* from Lake Suwa in Nagano Prefecture. This host fish should have been *S. variegatus microoculus* (Shimazu, 1999, 2003b, 2007). The present specimens are identical in morphology with Yamaguti's original description and figure for *P. higai*.

Life cycle. The life cycle is not known.

Philopinna kawamutsu sp. nov. (Figs. 9–13)

Previous record. None.

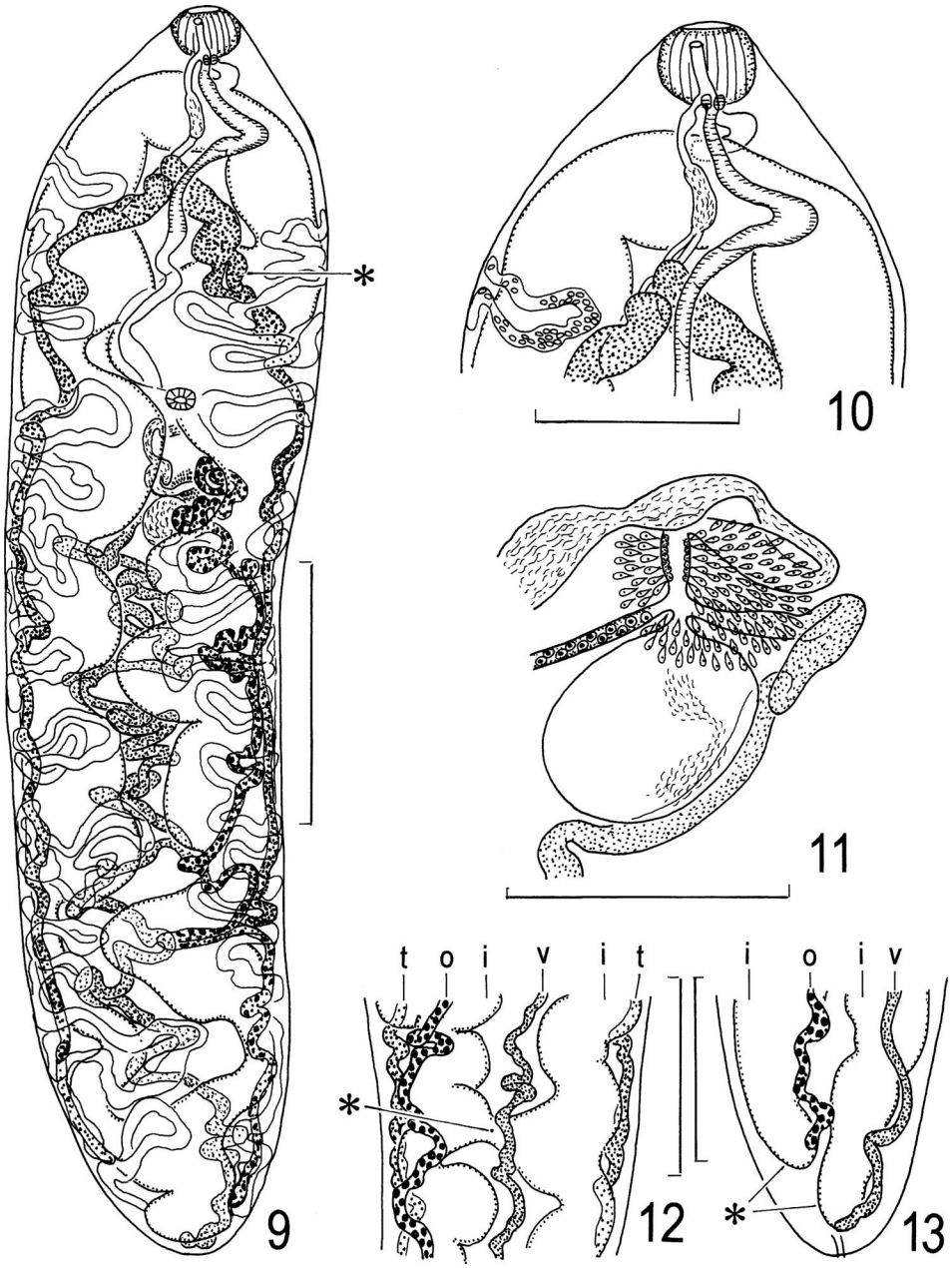
Host. *Nipponocypris temminckii* (Temminck and Schlegel) (Japanese name: Kawamutsu) (Cyprinidae) (type host).

Site of infection. Connective tissue between the vertebrae and the air bladder near the esophagus.

Collecting locality. Yasu River (type locality) at Maeno (34°56′E, 136°15′N), Tsuchiyama-cho, Koka City, Shiga Prefecture.

Materials examined. Holotype (LBM 1340000066, mature), eight paratypes (LBM 1340000067, 1340000069, 1340000070, and 1340000072, mature), two paratypes and four vouchers (NSMT-Pl 5740, mature), 18 vouchers (LBM 1340000068, 1340000071, and 1340000073–1340000075, immature), five vouchers (LBM 1340000076, mature, serial sections), and several vouchers (LBM 1340000077, immature, serially-sectioned *in situ* in an infected host fish), all found in the connective tissue of *Nipponocypris temminckii* collected on 18 October 1997.

Description. Based on 11 mature specimens (holotype and ten paratypes). Similar to *Philopinna higai* (this paper) in general morphology. Body hermaphroditic, elongate, slightly ta-



Figs. 9–13. *Philopinna kawamutsu* sp. nov. Specimens found in connective tissue of *Nipponocypris temminckii* (type host). 9, holotype (LBM 1340000066), entire body, uterus in dorsal parenchyma and eggs in uterus omitted, abnormality in testis (*), ventral view; 10, holotype, anterior part of body, ventral view; 11, paratype (LBM 1340000067), ovarian complex, ventral view; 12, immature voucher (LBM 1340000074), abnormality in intestines (fused halfway) (*), dorsal view; 13, immature voucher (LBM 1340000073), abnormality in intestines (separate posteriorly) (*), dorsal view. Scale bars: 1 mm in Fig. 9; 0.5 mm in Figs. 10 and 12; 0.3 mm in Figs. 11 and 13.

pering anteriorly, rounded posteriorly, slightly dorsoventrally flattened, fairly small, 2.96–5.16 by 0.77–1.15 (holotype 4.92 by 1.16), not oculate; forebody 1.04–1.52 long, occupying 22–36% of total body length. Tegument smooth. Oral sucker anteroterminal, subglobular, 0.16–0.21 by 0.16–0.23. Prepharynx absent. Pharynx subglobular, very small, 0.02–0.03 by 0.02–0.04. Esophagus straight or curved, 0.14–0.16 long. Intestines thick, undulating, distally uniting to form cyclocoel near posterior end of body. Ventral sucker feeble, flat, small, 0.05–0.07 by 0.05–0.11, located median at junction between anterior and second fourths of body or in front of it; sucker width ratio 1 : 0.30–0.46. Testes two, tubular, long, one longer than the other, symmetrical, in lateral field and ventral to intestine on either side of body, winding and convoluted irregularly; one ascending from near posterior end of body (at distance of 8–19% of body length from posterior end of body), and the other ascending from about junction between middle and posterior thirds of hindbody, both to near intestinal bifurcation. Sperm ducts short, arising from anterior ends of their respective testes; common sperm duct absent. Seminal vesicle spindle-shaped, almost median, ventral to intestinal bifurcation, 0.09–0.14 by 0.02–0.05. Ejaculatory duct long, running forward to join metraterm anteroventrally to pharynx. Cirrus pouch absent. Pars prostatica absent. Genital atrium (or hermaphroditic duct) tubular, long. Genital pore ventral to oral sucker, submedian, slightly anterior to middle level of oral sucker. Ovary single, tubular, long, sinistrally lateral and submedian, dorsal to intestine, winding and convoluted irregularly, extending from near posterior end of body to a little in front of ootype, then turning back to ootype; oviduct very short. Ovarian complex median, located slightly posterior to ventral sucker or at about junction between anterior and middle thirds of body (laying 28–39% of body length from anterior end). Seminal receptacle spherical, large, 0.12–0.16 in diameter. Laurer's canal absent. Ovovitelline duct short. Ootype median, anterior or anteroventral to seminal receptacle. Mehlis' gland well developed. Uterus highly folded transversely in dorsal parenchyma of all available space on either side of body except in prebifurcal region, transverse folds moving around in lateral field of body into ventral parenchyma considerably; metraterm long, almost median, in ventral parenchyma, beginning behind seminal vesicle. Eggs fairly numerous, scattered in uterus, elliptical, thin-shelled, yellow, small, 13–22 by 9–14 μm, with small operculum; miracidia in them not clearly observed. Vitellarium single, tubular, long, almost median, dorsal to intestines, winding and convoluted irregularly from posterior end of body to ovarian complex; vitelline duct very short. Excretory vesicle not clearly observed; excretory pore posteroterminal.

Abnormality. Morphological abnormalities (or malformations) were observed, as follows: (1) One of the testes partially formed a pair of tubes in the holotype (Fig. 9, ∗); (2) the intestines were fused twice, behind the ovarian complex (Fig. 12, ∗) and at the posterior ends in an immature voucher; and (3) the intestines were posteriorly separate (or ended blindly) in another immature voucher (Fig. 13, ∗).

Serial sections of infected fish. In the serial sections of the infected fish, (1) worms were found free in elongate, wide spaces lined with a simple squamous endothelium in the connective tissue around small muscles between the vertebrae and the air bladder near the esophagus; (2) the worms contained blood cells of the host in the intestine; (3) some blood cells were seen in the spaces; (4) no hemorrhagic lesion was seen around or near the worms; and (5) no eggs were detected within the spaces.

Etymology. The specific name *kawamutsu*, a noun in apposition, is derived from the Japanese name of the type host fish.

Discussion. The genus *Philopinna* Yamaguti, 1936 has so far comprised two species: *P. higai* Yamaguti, 1936 (Yamaguti, 1936b; this paper); and *P. aegyptica* Yamaguti, 1971 nom. nov.

(syn. *Nematobothrium labeonis* of Fischthal and Kuntz, 1963, not McClelland, 1955) that was found in the small intestine of *Labeo forskalii* Rüppell (Cyprinidae) from the Giza Fish Market, Giza Province, Egypt (Fischthal and Kuntz, 1963; Yamaguti, 1971).

This new species *Philopinna kawamutsu* sp. nov. morphologically differs from *P. higai* as described by Yamaguti (1936b) and in this paper in that the ventral sucker is situated more posteriorly (the forebody occupying 22–36%, instead of 18–25%, of the total body length); the testes are much longer, beginning from near the posterior end of the body instead of the ovarian complex; the seminal vesicle is spindle-shaped and bifurcal instead of pyriform and postbifurcal; the ovarian complex is located slightly instead of greatly posterior to the ventral sucker; and eggs are smaller, 13–22 by 9–14 μm instead of 21–25 by 14–17 μm. Furthermore, the new species is morphologically different from *P. aegyptica* as briefly redescribed and figured by Yamaguti (1971, fig. 654) in that the long testes ascend to near the bifurcal level instead of only to near the ventral sucker; the vas deferens (seminal vesicle of this paper) is spindle-shaped, bifurcal, and much smaller instead of tubular and long (beginning a short distance behind the ventral sucker); the uterine folds are distributed anteriorly to near the bifurcal level instead of only to some distance behind the anterior ends of the testes; and eggs are smaller, 13–22 by 9–14 μm instead of 29–34 by 20–23 μm.

In the serial sections of the infected fish, the worms were found in the wide spaces lined with the simple squamous endothelium, and blood cells of the host were present in the spaces and the intestines of the worms. This indicates that the worms were found in the blood or lymphatic vessels or both of the connective tissue. The space is considered not to be a lymph capillary but to be a capillary, which suggests that the site of infection is the capillary of the connective tissue. The site of infection needs definitely determining by further critical studies.

The abnormalities observed in the intestines of the worms suggest that the intestines tend to unite to each other anywhere; that, in organogenesis, distally separated intestines (or intestinal ceca) are more primitive and distally united intestines are more advanced; and that the separated intestines, which are initially formed in earlier stages of development (possibly in the cercarial stage), become distally united to each other to form a cyclocoel either in metacercariae in the second intermediate host or in smaller juveniles in the final host.

Life cycle. The life cycle is not known.

Family **Derogenidae** Nicoll, 1910

Genarchopsis goppo Ozaki, 1925 (Figs. 14–24)

Genarchopsis goppo Ozaki, 1925: 101–103, figs. 1–3; Yamaguti, 1934: 500–501, fig. 128; Yamaguti, 1942: 388–389; Urabe, 2001b: 1407, fig. 3E; Shimazu and Urabe, 2005: 2-3, figs. 1-3; Shimazu, 2008: 43, fig. 2.
Progonus goppo: Srivastava, 1933; 55.
(?) *Genarchopsis anguillae* Yamaguti, 1938: 132–133, fig. 81; Shimazu, 1995a: 11, fig. 6.
Genarchopsis gigi Yamaguti, 1939: 227, pl. 29, fig. 6; Shimazu, 1995a; 9, fig. 5.
(?) *Genarches anguillae*: Skryabin and Guschanskaya, 1955: 680, fig. 199.
Genarches gigi: Skryabin and Guschanskaya, 1955: 680, 685, fig. 200.
Genarches goppo: Skryabin and Guschanskaya, 1955: 685–686, 689, fig. 201.
Genarchapsis goppo [sic; misspelling of *Genarchopsis*]: Shimazu, 1995a: 6–9, figs. 1–5.

Previous records. From *Pelteobagrus nudiceps* of Lake Biwa, as *Genarchopsis gigi* (Yamaguti, 1939), and of Onoe, as *G. goppo* (Shimazu, 1995a); from *Gymnogobius isaza* (syn. *Chaenogobius isaza* Tanaka) of Katata [not Katada], as *G. goppo* (Yamaguti, 1942; Shimazu, 1995a), and of Isoda, Omatsu, and Onoe, as *G. goppo* (Shimazu, 1995a); from *Gy. urotaenia*

(syn. *Chaenogobius urotaenia* Hilgendorf) of Onoe, as *G. goppo* (Shimazu, 1995a); *Rhinogobius brunneus* [most likely referring to *Rhinogobius* sp. OR] of Omatsu and Onoe, as *G. goppo* (Shimazu, 1995a); from *Tridentiger brevispinis* of Omatsu, as *G. goppo* (Shimazu, 1995a); from *Anguilla japonica* of Omatsu, as *G. goppo* (Shimazu, 1995a); from *Cottus reinii* of Omatsu and Onoe, as *G. goppo* (Shimazu, 1995a); and from *Lepomis macrochirus* of Omatsu, as *G. goppo* (Shimazu, 1995a).

Hosts. *Anguilla japonica*, *Gambusia affinis*, *Cottus reinii*, *Gymnogobius isaza*, *Gy. urotaenia*, *Lepomis macrochirus*, *Odontobutis obscura*, *Pelteobagrus nudiceps*, *Rhinogobius flumineus*, *R. brunneus* [most likely referring to *Rhinogobius* sp. OR], *Rhinogobius* sp. BW, *Rhinogobius* sp. OR, and *Tridentiger brevispinis*.

Sites of infection. Primarily stomach, and also fins and gills [sic; most presumably postmortem migration] and intestine [sic; accidental (?)].

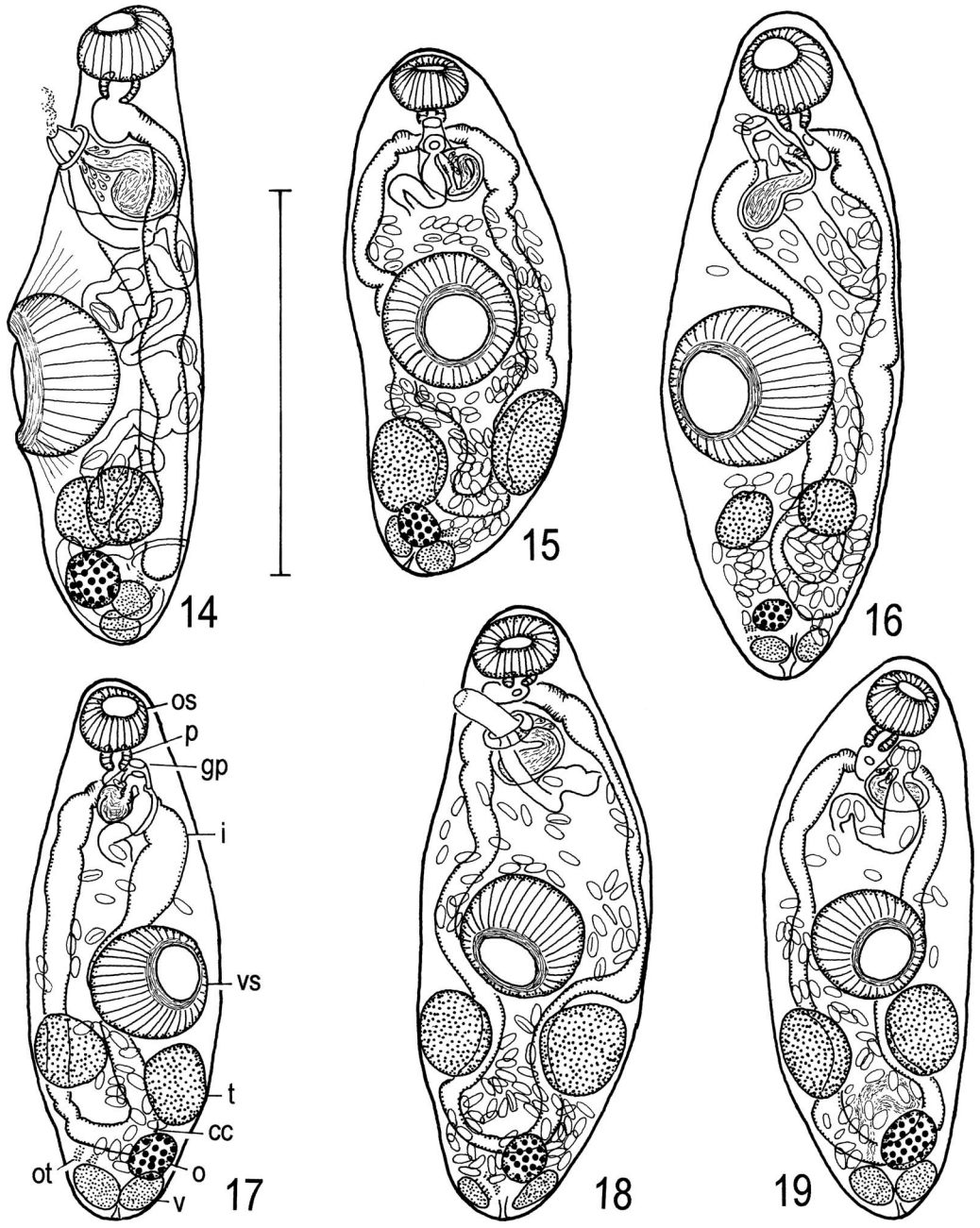
Collecting localities. Lake Biwa, Daido River-2, Hachiyadohama, Hamabun, Harie River, Imazu, Isoda, Kame-ga-ike Pond, Katata, Kaya-ike Pond, Mano-ono, Momose, Nishiyama, Omatsu, Onoe, Tamura River, and Ukawa River.

Materials examined. (1) One mature specimen (Yamaguti's Collection, MPM Coll. No. 22004, holotype of *Genarchopsis gigi*) found in the small intestine [sic] of *Pelteobagrus nudiceps* from Lake Biwa on 7 December 1938 (Yamaguti, 1939; Shimazu, 1995a). (2) Twelve immature and 68 mature specimens (NSMT-Pl 4017–4018) of *G. goppo* found in the stomach of *P. nudiceps* from Onoe on [6 June 1980 and 4 May 1992] (Shimazu, 1995a). (3) One mature specimen (NSMT-Pl 4013) found in the stomach of *Anguilla japonica* from Omatsu on 4 May 1992 (Shimazu, 1995a). (4) One immature and 16 mature specimens (NSMT-Pl 4028) found in the stomach of *Lepomis macrochirus* from Omatsu on 29 April 1992 (Shimazu, 1995a). (5) One mature specimen (LBM 1-13) found on either a gill or a fin of *L. macrochirus* from Kaya-ike Pond on 21 May 1998. (6) [Two immature and 15 mature] (NSMT-Pl 4019–4020) and [two immature and 19 mature] specimens (NSMT-Pl 4021–4024) found in the stomach of *Cottus reinii* from Onoe on [4 February 1980 and 6 June 1980] and from Omatsu on [30 April 1992 and 1, 2, and 4 May 1992], respectively (Shimazu, 1995a). (7) Specimens found in the stomach and intestine of *C. reinii*: four mature (LBM 1-68 from stomach) from Hachiyadohama on 14 May 1998, four immature and 25 mature (LBM 1-70 from stomach and 3-39 from intestine) from Imazu on 19 May 1998 and 5 May 2000, one immature and 13 mature (LBM 1-72 to -74 from stomach) from the Ukawa River on 22 October 1997, three mature (LBM 8-32 from stomach) from Wani on 25 April 2007, and one immature and nine mature (LBM 8-34 and 35 from stomach) from Momose on 24 November 2007. (8) Four mature (LBM 3-29), and eight immature and seven mature specimens (LBM 3-30 to -31) found in the stomach of *Odontobutis obscura* from Mano-ono on 4 May 2000 and from the Daido River-2 on 1 May 2000, respectively. (9) Two mature specimens (Yamaguti's Collection, MPM Coll. No. 22016) found in a variety of *Chaenogobius annularis urotaenia*) (now *Gy. isaza*) (site of infection not given) from Katata [not Katada] on 22 November 1939 (Yamaguti, 1942; Shimazu, 1995a). (10) Specimens found in the stomach of *Gy. isaza* (syn. *Ch. isaza*): [two immature and 19 mature] (NSMT-Pl 4006) from Onoe on [6 June 1980], [three mature] (NSMT-Pl 4007) from Isoda on [11 November 1980], and [11 mature] (NSMT-Pl 4008) from Omatsu on [1 May 1992] (Shimazu, 1995a). (11) Specimens found in the stomach and intestine of *Gy. isaza*: one immature and 31 mature (LBM 1-22 and -23 from stomach) from North Lake on 31 October 1997, one immature and 39 mature (LBM 1-24 and -25 from stomach) from Hachiyadohama on 14 May 1998, ten immature and 28 mature (LBM 1-27 and 28, and 3-33 to -35 from stomach) from Imazu on 19 May 1998 and 5 May 2000, and 15 mature (LBM

6-8 to LBM 6-14 from intestine, hot formalin-fixed, collected and identified as *G. goppo* by Tomáš Scholz) from Momose on 1 May 2001. (12) Twenty-nine mature specimens (NSMT-Pl 3990–3992) found in the stomach and intestine of *Gy. urotaenia* (syn. *Ch. urotaenia*) from Onoe on [4 February, 6 June, and 11 November 1980] (Shimazu, 1995a). (13) Specimens found in the stomach and intestine of *Gy. urotaenia*: 28 mature (LBM 1-57 and 8-33 from stomach) from the Ukawa River on 22 October 1997 and 25 April 2007, one immature and seven mature (LBM 1-60–62 from stomach) from Imazu on 19 May 1998, five immature and 55 mature (LBM 1-58 and 59 from stomach) from Hamabun on 24 October 1997, four mature (LBM 1-64 from stomach) from the Mano River on 17 October 1997, two mature (LBM 1-66 from stomach) from Kamega-ike Pond on 17 May 1998, and 12 mature (LBM 3-48 from intestine and LBM 3-56 from [stomach (?)]) from the Harie River on 19 October 2000. (14) Three mature specimens (LBM 7-32) found in the stomach of *Rhinogobius flumineus* from the Tamura River on 30 April 2001. (15) [Nineteen mature] (NSMT-Pl 3999 from gill, stomach, and intestine) and [five immature and eight mature] specimens (NSMT-Pl 4000–4001 from stomach) found on the gills and in the stomach and intestine of *R. brunneus* [most likely referring to *Rhinogobius* sp. OR] from Onoe on [6 June 1980] and from Omatsu on [29 April and 4 May 1992], respectively (Shimazu, 1995a). (16) One immature and 14 mature specimens (LBM 3-54 from [stomach (?)], -57 from stomach, and -58 from [stomach (?)]) found in the gut of *Rhinogobius* sp. OR from the Harie River on 19 October 2000. (17) Sixteen mature specimens (LBM 1-5) and two mature (LBM 1-6 and -7) found in the stomach of *Rhinogobius* sp. BW from Hachiyadohama on 14 May 1998 and from Imazu on 19 May 1998, respectively. (18) Two immature and seven mature specimens (NSMT-Pl 4012) found in the stomach of *Tridentiger brevispinis* from Omatsu on 5 May 1992 (Shimazu, 1995a). (19) Specimens found in the gut of *T. brevispinis:* six mature (LBM 1-52 from stomach) from Hamabun on 24 October 1997, one mature (LBM 1340000026 from "gut", collected by Urabe) from Imazu on 7 October 2002, and two mature (LBM 8-36 from stomach) from Nishiyama on 28 November 2007. (20) Two immature specimens (LBM 3-52) found in either the stomach or the gills of *Gambusia affinis* from Kawata on 26 October 2000.

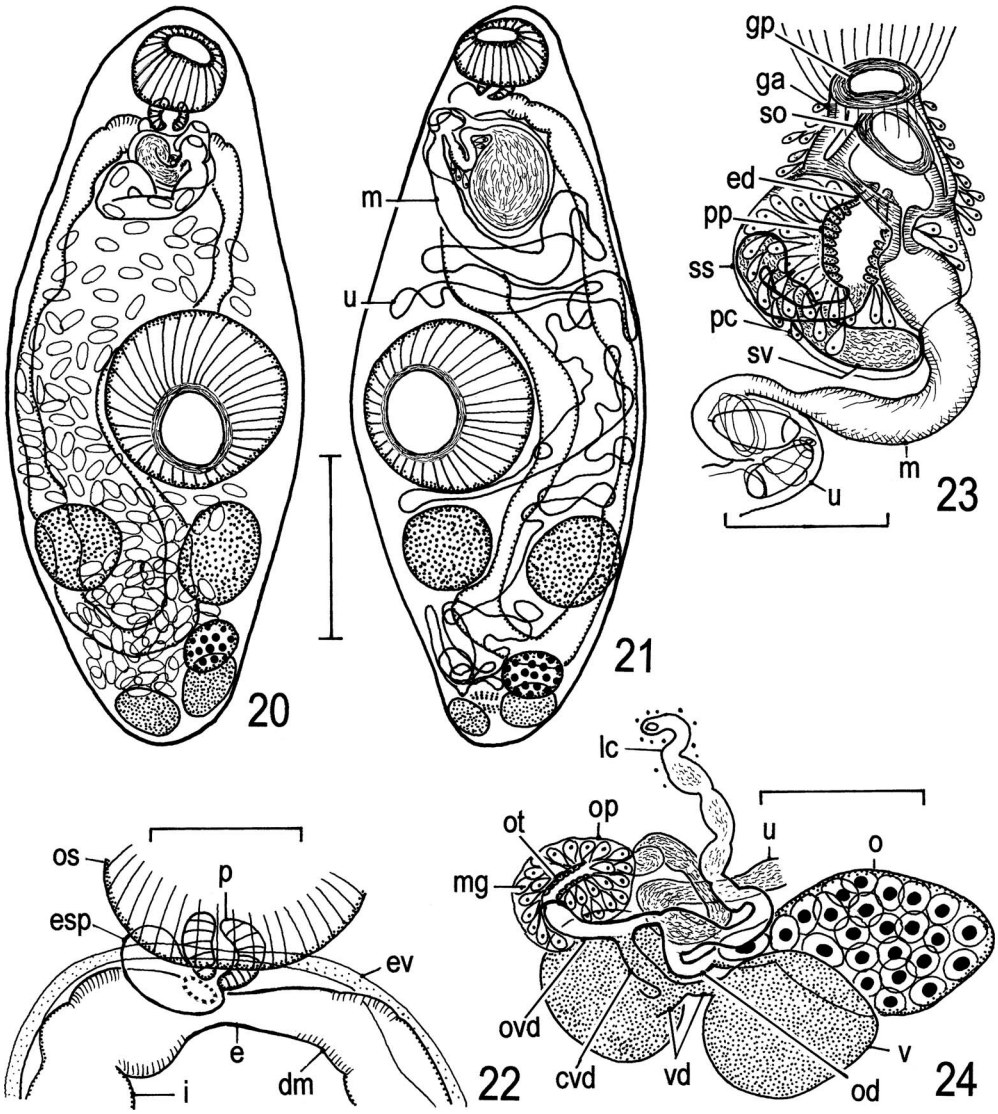
Description. 1) The holotype (MPM Coll. No. 22004) of *G. gigi* was described by Yamaguti (1939) and later redescribed by Shimazu (1995a). Similar to the next description in general morphology. Body barely mature, laterally mounted, very small, 0.80 long; forebody 0.47 long, occupying 59% of total body length (Fig. 14). 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. Testes 0.10 in diameter. Ovary 0.06 in diameter. Uterus folded in forebody (four transverse folds) as well as in hindbody. Uterine eggs seven, unsegmented, 40–48 by 17–22 μm (collapsed). Vitellaria 0.05 in diameter.

2) Based on Shimazu's (1995a) specimens (NSMT-Pl 4017–4018) from *P. nudiceps*; ten large, mature specimens measured (Figs. 15 and 22–24). Body spindle-shaped, slightly dorsoventrally flattened, with bluntly pointed ends, small, 0.99–1.68 by 0.38–0.61; not oculate; forebody 0.50–0.91 long, occupying 47–55% of total body length. Preoral lobe present. Tegument smooth. Oral sucker, 0.10–0.17 by 0.12–0.21, almost ventral, close to anterior end of body; sphincter at mouth aperture weakly developed. Prepharynx absent. Pharynx subglobular, 0.05–0.06 by 0.05–0.07. Esophagus short, inverted Y- or T-shaped, with small, oval posteroventral pouch. Drüsenmagen small, present between esophageal arm and intestine on either side of body. Intestines thick, slightly undulating, united with each other to form cyclocoel in front of or dorsally to ovary. Ventral sucker subglobular, large, larger than oral sucker, 0.23–0.42 by 0.22–0.42, median, usually slightly postequatorial; sucker width ratio 1 : 1.70–2.06. Sphincter at aperture of



Figs. 14–19. *Genarchopsis goppo*. Adult specimens. 14, holotype (MPM Coll. No. 22004) of *G. gigi* found in the small intestine [sic] of *Pelteobagrus nudiceps*, entire body, lateral view; 15, specimen (NSMT-Pl 4017) found in the stomach of *P. nudiceps*, entire body, ventral view; 16, specimen (LBM 1-74) found in the stomach of *Cottus reinii*, entire body, ventral view; 17, specimen (LBM 3-30) found in the stomach of *Odontobutis obscura*, entire body, ventral view; 18, specimen (NSMT-Pl 4008) found in the stomach of *Gymnogobius isaza*, entire body, ventral view; 19, specimen (LBM 7-32) found in the stomach of *Rhinogobius flumineus*, entire body, ventral view. Scale bars: 0.5 mm in Figs. 14–19.

ventral sucker well developed; radial muscle bundles attached to aperture well developed, anterior and posterior ones of them more developed (as in Fig. 14). Testes two, elliptical, large, 0.22–0.30 by 0.12–0.23, symmetrical or slightly diagonal, lateral to or overlapping intestine on either side of body, immediately posterolateral to ventral sucker or separated from it by uterus. Sperm ducts long; common sperm duct absent. Seminal vesicle internal, retort-shaped, convoluted. Pars prostatica vesicular; prostatic cells well developed. Ejaculatory duct very short, opening into base of sinus organ dorsally, with weakly developed sphincter at anterior end. Sinus sac thin-



Figs. 20–24. *Genarchopsis goppo* (continued). Adult specimens. 20, specimen (LBM 3-58) found in the stomach of *Rhinogobius* sp. BW, entire body, ventral view; 21, specimen (NSMT-Pl 4001) found in the stomach of *R. brunneus* (most likely referring to *Rhinogobius* sp. OR), entire body, showing uterus, ventral view; 22, specimen (NSMT-Pl 4017) found in the stomach of *Pelteobagrus nudiceps*, showing esophageal pouch and excretory vesicle fused dorsally to pharynx, ventral view; 23, specimen (NSMT-Pl 4018) found in the stomach of *P. nudiceps*, terminal genitalia, ventral view; 24, specimen (NSMT-Pl 4017), ovarian complex, dorsal view. Scale bars: 0.5 mm in Figs. 20–22; 0.1 mm in Figs. 23–24.

walled, median, posterior to esophagus, 0.08–0.16 by 0.11–0.19, enclosing seminal vesicle, prostatic complex, ejaculatory duct, and distal part of metraterm. Hermaphroditic duct thick, present only in sinus organ. Sinus organ permanent, weakly muscular, thick-walled, cylindrical, stumpy, 0.04–0.06 by 0.04–0.08, projecting into genital atrium, rarely protruded outside through genital pore. Genital atrium cylindrical, thick-walled, slightly longer than sinus organ, surrounded by small gland cells; longitudinal muscle fibers present in its wall, those on dorsal half side running forward farther into parenchyma. Genital pore usually opening wide but rarely puckered, median to submedian, ventral to pharynx. Ovary single, globular to elliptical, usually much or rarely slightly smaller than testes, 0.05–0.15 by 0.05–0.11, usually sinistrally or dextrally submedian, but rarely median, post-testicular, in front of or slightly overlapping vitellaria. Oviduct fairly long; ovovitelline duct short. Laurer's canal fairly long, storing a small number of sperm, opening dorsally to exterior between ovary and testes, often dilated at its junction with oviduct to store sperm as small seminal receptacle. Ovarian complex usually submedian, usually opposite ovary or rarely between ovary and vitellaria, anterior to or overlapping vitellaria. Ootype possibly vesicular, fairly large; Mehlis' gland well developed. Ootype pouch membranous, enclosing ootype and Mehlis' gland. Uterus folded several times in all available space from vitellaria to sinus sac, rarely extending posteriorly to vitellaria; metraterm well differentiated, much longer than sinus sac, opening into base of sinus organ ventrally to ejaculatory duct, with well-developed sphincter at its anterior end, may be surrounded by small gland cells; uterine seminal receptacle well developed in proximal coils. Eggs fairly numerous, elongate-oblong, somewhat curved, operculate, embryonated; unsegmented eggs 40–64 by 18–30 μm, considerably embryonated eggs yellowish brown, 51–65 by 24–30 μm; anopercular filament present, long, measuring up to 1.20 long. Vitellaria two compact masses, elliptical to globular, 0.08–0.16 by 0.04–0.09, symmetrical or diagonal, separate or contiguous, postovarian, near posterior end of body. Vitelline ducts very short; common vitelline duct short, joining oviduct. Excretory vesicle Y-shaped, ascending in ventral parenchyma, bifurcating between testes and ventral sucker (not illustrated); arms running forward in either lateral field of body, fused dorsally to pharynx or oral sucker; excretory pore posteroterminal.

Uterus slightly winding from ovarian complex to metraterm along median line of body even in immature specimens, as in the holotype (Fig. 14). With further growth of mature worms, uterine eggs increasing in number, uterus becoming more largely folded, and accordingly uterine field enlarging, especially in forebody. Of mature specimens, ten (0.59–0.89 long) of the smallest ones contained only 2–12 unsegmented uterine eggs; and four of the largest ones, 10–40 uterine eggs in forebody. Uterus in hindbody tightly folded, containing more numerous eggs. Eggs considerably embryonated, but no miracidium found in them even in large, mature specimens.

3) Based on the specimens found in the fishes other than *P. nudiceps*; ten large, mature specimens measured (Figs. 16–21). General morphology as in the foregoing description. Body 0.91–1.73 by 0.36–0.88; forebody 0.45–0.96 long, occupying 48–55% of total body length. Oral sucker 0.11–0.22 by 0.13–0.22. Pharynx 0.05–0.08 by 0.05–0.09. Ventral sucker 0.21–0.41 by 0.21–0.38; sucker width ratio 1 : 1.58–2.08. Testes 0.12–0.31 by 0.11–0.22. Sinus sac 0.06–0.16 by 0.07–0.19. Sinus organ 0.03–0.07 by 0.02–0.07. Ovary 0.08–0.15 by 0.07–0.13. Uterus folded several times. Fully embryonated eggs 53–70 by 24–35 μm. Vitellaria 0.08–0.17 by 0.04–0.10.

Of the specimens from *O. obscura*, seven contained 4–22 uterine eggs (Fig. 17). Of the specimens from *Rhinogobius* sp. BW, which had the most widely enlarged uterine field in the forebody (Fig. 20), three contained 39–90 uterine eggs in the forebody. One of the mature specimens (NSMT-Pl 4001) from *R. brunneus* [most likely referring to *Rhinogobius* sp. OR] had the uterus

that was transversely folded about four times in the forebody (Fig. 21).

4) Uterine eggs. Fully embryonated eggs containing a fully formed miracidium were found in large, mature specimens from *C. reinii*, *Gy. isaza*, *Gy. urotaenia*, *O. obscura*, *R. brunneus* [most likely referring to *Rhinogobius* sp. OR], *R. flumineus*, *Rhinogobius* sp. BW, and *T. obscura*. However, even large, mature specimens from *A. japonica*, *L. macrochirus*, and *P. nudiceps* did not possess any fully embryonated eggs. Malformed eggs with no ovum were often found, especially in the specimens from *Gy. isaza*, *Gy. urotaenia*, *L. macrochirus*, *O. obscura*, and *P. nudiceps*. The eggshell of such eggs was much thicker, much smaller, and largely distorted.

Discussion. *Genarchopsis goppo* was described as a new genus and species by Ozaki (1925) on the basis of adults found in the intestine [sic] of *Odontobutis obscura* (syn. *Mogurnda obscura* Temminck and Schlegel) (Japanese name: Donko, "[Goppo]" of Ozaki) collected in a brook in the vicinity of Saijo, now Saijo-cho, Higashihiroshima City, Hiroshima Prefecture. Ozaki's original material has not yet been reexamined. *Genarchopsis gigi* was described as a new species by Yamaguti (1939) based on a single specimen (or the holotype) found in the small intestine [sic] of *Pelteobagrus nudiceps* from Lake Biwa (locality not specified). We reexamined the holotype, a barely mature specimen (see also Shimazu, 1995a).

We provisionally classified the present specimens into three groups and described them group by group: (1) the holotype of *G. gigi* from *P. nudiceps*, (2) Shimazu's (1995a) specimens from *P. nudiceps*, and (3) the remaining specimens from the fishes other than *P. nudiceps*. The last included Yamaguti's (1942) specimens (MPM Coll. No. 22016) from *Gy. isaza* and the present specimens from *O. obscura*. As described above (Figs. 14–21), the three groups are very similar to one another in morphology and measurements. By morphology, we regard all the present specimens as belonging to a single species.

Since none of Ozaki's (1925) original specimens of *G. goppo* have yet been reexamined, and *G. gigi* was based on a single, barely mature specimen, we carefully compared two lots of Shimazu's (1995a) specimens of *G. goppo* in considering whether these two nominal species are synonyms: (1) specimens (NSMT-Pl 4017–4018) found in the stomach of *P. nudiceps* from Lake Biwa at Onoe; and (2) specimens (NSMT-Pl 3998) found in the stomach of *O. obscura* from the Nukui River at Babadai [now in Hara], Hachihonmatsu-cho, Higashihiroshima City.

Yamaguti (1939) merely stated that *G. gigi* was distinguished from two known species of *Genarchopsis* by smaller egg size, but he did not mention the species names of the two known species nor did he cite any related literature. Because *G. goppo* and *G. anguillae* Yamaguti, 1938 were known in the genus at that time, he seems to have compared *G. gigi* with these two species in egg size: 43–51 by 19–21 μm (Yamaguti, 1939) in *G. gigi*, 46–50 by 25–26 μm (Ozaki, 1925) and 48–66 by 24–33 μm (Yamaguti, 1938) in *G. goppo*, and 69–78 by 33–36 μm (Yamaguti, 1938) in *G. anguillae*. His egg size for *G. goppo* was taken from the seven specimens of two different species: two of *G. goppo* and five of *G. fellicola* Shimazu, 1995 (Shimazu, 1995a). Yamaguti (1939) said that the eggs in the holotype of *G. gigi* were embryonated and 43–51 by 19–21 μm. However, the seven uterine eggs in the holotype are actually unsegmented and measured 40–48 by 19–22 μm (Shimazu, 1995a) and 40–48 by 17–22 μm (collapsed) (this paper). In Shimazu's (1995a) specimens from *P. nudiceps*, unsegmented eggs are 40–52 by 19–21 μm (Shimazu, 1995a) and 40–64 by 18–30 μm (this paper), and partially [not fully] embryonated eggs are 53–64 by 24–29 μm (Shimazu, 1995a) and 51–65 by 24–30 μm (this paper). On the other hand, fully embryonated eggs in Shimazu's (1995a) specimens from *O. obscura* are 51–72 by 27–29 μm (Shimazu, 1995a). Although eggs are likely to increase somewhat in size with development of embryos (Shimazu, 1995a; this paper), it does not seem that *G. gigi* can be separated

from *G. goppo* by egg size alone, which supports Shimazu's (1995a) conclusion that the two species are synonymous. In fact, Yamaguti (1942) identified the two mature specimens (MPM Coll. No. 22016) from *Gy. isaza* of Katata as *G. goppo*. Consequently, we consider it preferable at present to assign all the present specimens to *G. goppo*.

Nevertheless, slight differences can be noted in number of the uterine eggs in the forebody, in number of the transverse uterine folds in the forebody, and in size of the genital pore between the present specimens from the Lake Biwa basin and the specimens found in *O. obscura* from Higashihiroshima. With further growth of adult worms in the final host, the uterine eggs increase in number, and accordingly the uterus becomes more widely folded, especially in the forebody (Shimazu, 2008; this paper, Figs. 14, 20, and 21), but the transverse uterine folds in the forebody do not seem to increase in number. Among the present specimens, the mature specimens (LBM 3-58 and NSMT-Pl 4000–4001) found in *Rhinogobius* sp. BW and *R. brunneus* had the most enlarged uterine field in the forebody (Figs. 20 and 21). The former specimens (LBM 3-58) contained 39–90 uterine eggs in the forebody. The barely mature holotype of *G. gigi* and the fully mature specimens (NSMT-Pl 4001) had about four transverse uterine folds in the forebody (Figs. 14 and 21). The genital pore was wide open (Fig. 23). On the other hand, the specimens from Higashihiroshima had 100–177 uterine eggs (see also Shimazu, 1995a, fig. 2), seven to nine transverse uterine folds, and a closed, puckered genital pore (see also Shimazu, 1995a, fig. 3). The specimen of *G. goppo* figured by Ozaki (1925, fig, 1) has about 43 uterine eggs and about six transverse uterine folds in the forebody. Species of *Genarchopsis* need to be further critically studied.

Yoshida (1917) described *Cercaria* F from three species of pleurocerid snails, *Semisulcospira* (syn. *Melania*), collected in six places in Japan. Cort and Nichols (1920) named this cercaria *Cercaria yoshidae* sp. nov. Urabe (2001b) experimentally indicated that cystophorous cercariae found in *S. libertina* (Gould) (Japanese name: Kawanina) developed into adults of *G. goppo* (see *Life cycle*). She stated that the cercaria morphologically matched *Ce. yoshidae*, but she avoided definitely identifying her cercaria as *Ce. yoshidae*. If her cercaria is certainly *Ce. yoshidae*, *Ce. yoshidae* is the cercaria of *G. goppo*, and accordingly the specific name *yoshidae* Cort and Nichols, 1920 has priority over the specific name *goppo* Ozaki, 1925 (ICZN, Article 23.3.2.2). However, we refrain at present from proposing a new combination for *G. goppo*, because *Genarchopsis* in Japan contains several different species, because even the species that has been regarded as *G. goppo* may include two or more different species, and because *Ce. yoshidae* also may be composed of two or more different cercariae of *Genarchopsis* (Shimazu, 1999, 2003b; Urabe, 2001a; this paper). Cystophorous cercariae that develop in *Semisulcospira* spp. in Japan need to be further carefully studied.

Shimazu and Urabe (2005) synonymized *G. anguillae* with *G. goppo*. *G. anguillae* also was based on a single adult specimen found in the intestine of *Anguilla japonica* from Lake Kasumigaura in Ibaraki Prefecture (Yamaguti, 1938). Shimazu and Urabe's treatment is still open to further studies from additional specimens from Lake Kasumigaura.

Life cycle. Urabe (2001b) experimentally elucidated the life cycle of *G. goppo* in Nara, Nara Prefecture. A natural first intermediate host was *S. libertina*, in which small cystophorous cercariae, which were closely resembled *Ce. yoshidae*, were produced in daughter rediae. Experimental second intermediate hosts were cyclopid copepods, *Mesocyclops leuckarti* (Claus) (Japanese name: Asagao-kenmijinko), *Thermocyclops hyalinus* (Rehberg) (Japanese name not given), and *Eucyclops serrulatus* (Fischer) (Japanese name: Nokogiri-kenmijinko). Unencysted metacercariae grew in the hemocoel of these hosts. During this growth, the intestines were formed completely, and subsequently they became fused distally to form a cyclocoel. An experimental final

host was *Rhinogobius* sp. OR. Natural final hosts in Nara were *Rhinogobius* sp. OR and *O. obscura*.

Madhavi (1978) worked out the life cycle of a digenean under the name *G. goppo* in India, but Urabe (2001b) doubts whether Madhavi's digenean was really *G. goppo*.

In the Lake Biwa basin, the cercaria was recorded as *Ce. yoshidae* from many species of pleurocerid snails: *Semisulcospira* (*Biwamelania*) *habei* Davis (Japanese name: Habe-kawanina); *S.* (*B.*) *niponica* (Smith) (Japanese name: Yamato-kawanina); *S.* (*B.*) *fuscata* Watanabe and Nishino (Japanese name: Kuro-kawanina); *S.* (*B.*) *decipiens* (Westerlund) (Japanese name: Tatehida-kawanina); *S.* (*B.*) *multigranosa* Böttger (Japanese name: Ibo-kawanina); *S.* (*B.*) *reticulata* Kajiyama and Habe (Japanese name: Kagome-kawanina); *S.* (*B.*) *nakasekoae* Kuroda (Japanese name: Nakaseko-kawanina); *S.* (*S.*) *reiniana* (Brot) (Japanese name: Chirimen-kawanina); and *S.* (*S.*) *libertina*. A similar cercaria also was found in *S.* (*B.*) *reticulata* (Urabe, 2003).

Unencysted metacercariae of *Genarchopsis* were found in the hemocoel of copepods collected in Lake Biwa off Take Island, Hikone City: one (NSMT-Pl 5741) in a diaptomid, *Eodiaptomus japonicus* (Burckhardt) (Japanese name: Yamato-higenaga-kenmijinko), at a site of 30 m depth (the exact collection depth is unknown because the plankton net was trawled vertically from the bottom to the surface of the water column) on 26 August 2005; and two (NSMT-Pl 5742) in unidentified copepods at a depth of 60 m on 8 September 2005 (Urabe, unpublished data). In these three metacercariae, the body was 0.25–0.36 by 0.09–0.12 in balsam; the ventral sucker had a well-developed sphincter; and the sucker width ratio was high, 1 : 1.39–1.43. The collecting localities were located in Lake Biwa, quite distant from those (Nishiyama and Miyake in the inland area) of the next new species. From the morphology and collecting locality, we regard them as *G. goppo*.

Various species of fishes serve as natural final hosts in the Lake Biwa basin (this paper). The status of each of them as a final host is not necessarily clear. Based on food habits, at least, *Gy. isaza*, *R. flumineus*, *Rhinogobius* sp. BW, and *Rhinogobius* sp. OR (including *R. brunneus*) are considered true final hosts; but *A. japonica*, *O. obscura*, and *P. nudiceps* are most likely accidental final hosts.

Genarchopsis yaritanago sp. nov. (Figs. 25–29)

Previous record. None.

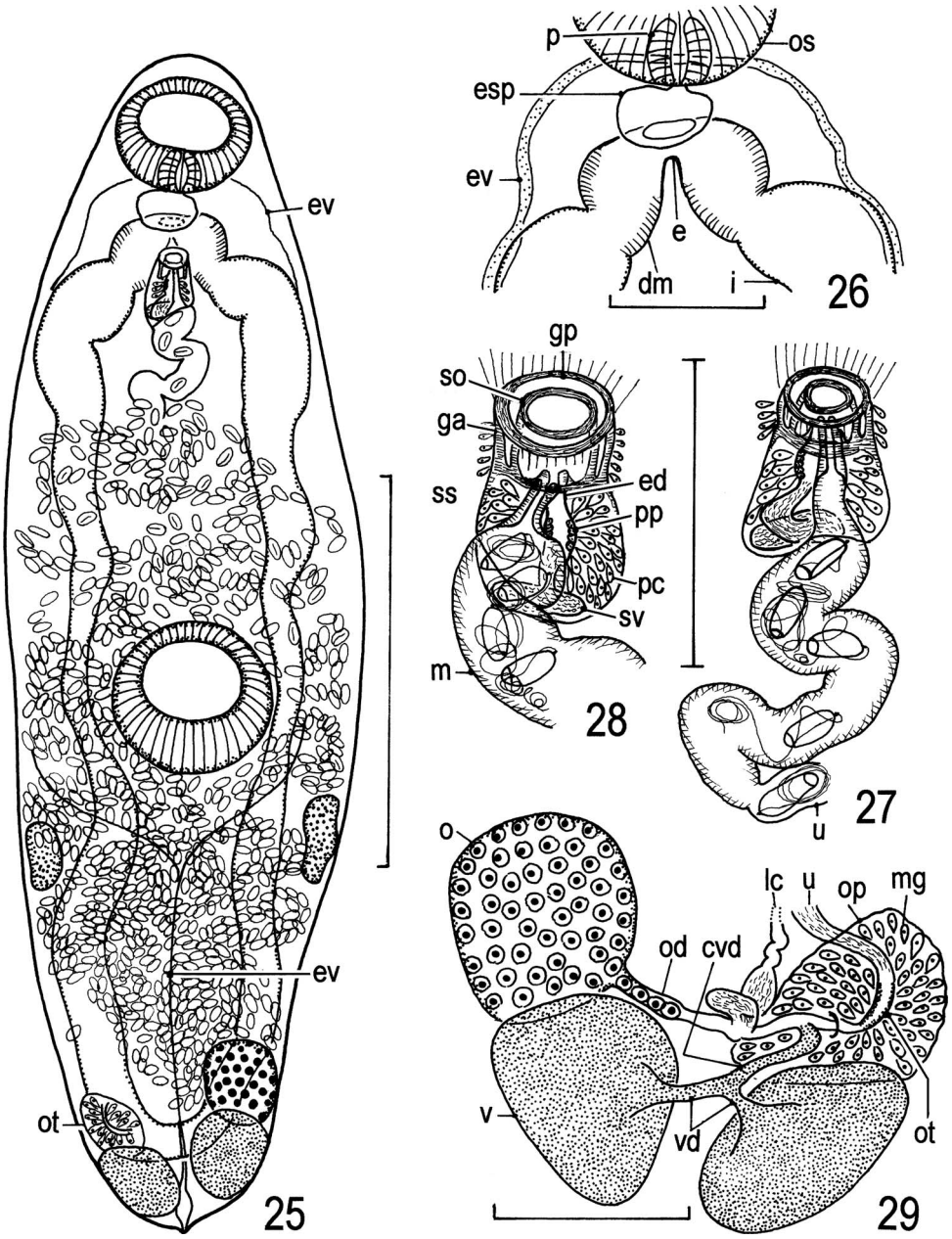
Host. Tanakia lanceolata (Temminck and Schlegel) (Japanese name: Yari-tanago) (Cyprinidae) (type host).

Site of infection. Intestine.

Collecting localities. Irrigation canal (type locality) closely connected to the Yogo River at Nishiyama (35°29′E, 136°12′N), Kinomoto Town; and irrigation canal at Miyake-cho (35°03′E, 135°58′N), Moriyama City, both in Shiga Prefecture.

Materials examined. Specimens found in the intestine of *Tanakia lanceolata*: holotype (LBM 1340000079, mature) and one paratype (LBM 1340000080, mature) from Nishiyama on 27 November 2007, and one paratype (LBM 1340000078, mature) from Miyake on 27 October 2000.

Description. Based on three mature specimens. Similar to *Genarchopsis goppo* (this paper) in general morphology. Body spindle-shaped, slightly flattened dorsoventrally, with bluntly pointed ends, 2.56–3.47 by 0.83–0.97 (holotype 2.98 by 0.89), not oculate; forebody 1.44–1.84 long, occupying 52–56% of total body length. Tegument smooth. Preoral lobe present. Oral sucker



Figs. 25–29. *Genarchopsis yaritanago* sp. nov. Adult specimens found in the intestine of *Tanakia lanceolata* (type host). 25, holotype (LBM 1340000079), entire body, ventral view; 26, holotype, showing esophageal pouch and arms of excretory vesicle fused dorsally to pharynx; 27, holotype, terminal genitalia, ventral view; 28, paratype (LBM 1340000078), terminal genitalia, ventral view; 29, holotype, ovarian complex, distal part of Laurer's canal obscured by uterine eggs, dorsal view. Scale bars: 1 mm in Fig. 25; 0.5 mm in Fig. 26; 0.3 mm in Figs. 27–28; 0.2 mm in Fig. 29.

subglobular, 0.30–0.37 by 0.33–0.35, almost ventral, close to anterior end of body; sphincter at mouth aperture weakly developed. Prepharynx absent. Pharynx barrel-shaped, 0.09–0.12 by 0.09–0.11. Esophagus small, inverted Y- or T-shaped; esophageal pouch small, oval, posteroven-

tral to esophagus. Drüsenmagen small, present between esophageal arm and intestine on either side of body. Intestines slightly undulating, distally uniting with each other to form cyclocoel anteriorly to vitellaria or overlapping them. Ventral sucker spherical, slightly larger than oral sucker, 0.37–0.45 in diameter, median, slightly postequatorial; sucker width ratio 1 : 1.14–1.16. Sphincter at aperture of ventral sucker weakly developed; radial muscle bundles attached to aperture weakly developed (not illustrated). Testes two, elliptical or irregular in outline, small, 0.11–0.22 by 0.08–0.17, symmetrical or slightly diagonal, lateral to or overlapping intestine on either side of body, posterolateral to ventral sucker, widely separated from it by uterus. Sperm ducts long; common sperm duct absent. Sinus sac thin-walled, median, posterior to esophagus, 0.10–0.11 by 0.11–0.14, enclosing seminal vesicle, pars prostatica complex, ejaculatory duct, and distal part of uterus. Seminal vesicle retort-shaped, convoluted; prostatic complex well developed; ejaculatory duct very short, opening into base of sinus organ dorsally to metraterm. Hermaphroditic duct thick, present only in sinus organ. Sinus organ permanent, muscular, cylindrical, stumpy, thick, short, 0.05 by 0.05–0.06, projecting into genital atrium. Genital atrium usually cylindrical, thick-walled, surrounded by small gland cells, with many longitudinal muscle fibers, those on dorsal half side running forward farther into parenchyma. Genital pore opening wide, median to submedian, ventral to esophagus. Ovary single, globular to subglobular, larger than testes, 0.20–0.26 by 0.19–0.22, dextrally or sinistrally lateral, post-testicular, in front of vitellaria or slightly overlapping them. Oviduct fairly long; ovovitelline duct short. Laurer's canal storing a small number of sperm, its distal part obscured by uterine eggs, dilated at its junction with oviduct to store sperm as small seminal receptacle. Ovarian complex usually submedian, opposite ovary or between ovary and vitellaria, anterior to or overlapping vitellaria. Ootype and Mehlis' gland enclosed by membranous ootype pouch. Uterus much folded in all available space of body from vitellaria to sinus sac; metraterm well developed, much longer than sinus sac, with well-developed sphincter at its anterior end, opening into base of sinus organ ventrally to ejaculatory duct, surrounded by small gland cells; uterine seminal receptacle well developed. Eggs numerous, elongate-oblong, somewhat curved, brown, operculate, fully embryonated; unsegmented eggs 53–56 by 24–27 μm, embryonated eggs 56–64 by 25–32 μm; anopercular filament measuring up to 1.16 long. Vitellaria two compact masses, elliptical, large, 0.22–0.29 by 0.12–0.20, symmetrical or diagonal, separate, postovarian, near posterior end of body. Vitelline ducts very short; common vitelline duct short. Excretory vesicle Y-shaped, ascending in ventral parenchyma, bifurcating between testes and ventral sucker; arm running forward in either lateral field of body, fused dorsally to pharynx or oral sucker; excretory pore posteroterminal.

Etymology. The specific name *yaritanago*, a noun in apposition, is derived from the Japanese name of the type host fish.

Discussion. This new species *Genarchopsis yaritanago* sp. nov. most closely resembles *G. elongatum* Wang, 1984 [sic; should be *elongata*], which Wang (1984) originally described from three adults found in the intestine of *Zacco platypus* from Chong'an, Fujian Province, China. However, the new species differs from the latter in having the ventral sucker located more posteriorly (or slightly postequatorial) instead of at the junction between the anterior and middle thirds of the body; a lower sucker width ratio, 1 : 1.14–1.16 instead of 1 : 1.5; and a smaller sinus sac (cirrus pouch of Wang), 0.10–0.11 by 0.11–0.14 instead of 0.18–0.19 by 0.11–0.12.

Besides, the new species is somewhat similar to *G. fellicola* Shimazu, 1995, which Shimazu (1995a) originally described from adult specimens found in the gall bladder of *Gymnogobius urotaenia* (syn. *Chaenogobius urotaenia*) (type host) and *Rhinogobius brunneus* [*Rhinogobius* sp. OR] from Lake Suwa (type locality) at Suwa City, Nagano Prefecture; *Gy. urotaenia* and *R.*

brunneus [*Rhinogobius* sp. OR] collected in the irrigation canals in Itako City; and *Tridentiger brevispinis* from the Gantsu River in Aso, now in Namegata City, both latter localities in Ibaraki Prefecture. However, the new species is separated from the latter by that the oral sucker is larger, 0.30–0.37 by 0.33–0.35 instead of 0.11–0.26 by 0.12–0.31; the ventral sucker is larger, 0.37–0.45 in diameter instead of 0.14–0.39 by 0.16–0.40; the sucker width ratio is lower, 1 : 1.14–1.16 instead of 1 : 1.1–1.6; the testes are smaller than, instead of almost as large as, the ovary; the sinus sac is smaller, 0.10–0.11 by 0.11–0.14 instead of 0.08–0.33 by 0.06–0.18; and eggs are smaller, 56–64 by 25–32 μm instead of 57–76 by 26–32 μm. Furthermore, the new species is possibly different also in host fish (a cyprinid instead of gobiids) and in site of infection (the intestine instead of the gall bladder).

The new species is readily distinguished from *G. goppo* (this paper) by that the ventral sucker is smaller; the sucker width ratio is lower, 1 : 1.14–1.16 instead of 1 : 1.58–2.08 (combined); uterine eggs are much more numerous; and possibly the primary site of infection is the intestine of a cyprinid instead of the stomach of gobiids.

Life cycle. The life cycle is not known.

Family **Isoparorchiidae** Travassos, 1922

Isoparorchis hypselobagri (Billet, 1898) (Figs. 30–33)

Distomum hypselobagri Billet, 1898: 289–290, pl. 13, fig. 8.
Isoparorchis trisimilitubis Southwell, 1913: 92–94, pls. 8–9, figs. 9–12; Yamaguti, 1934: 502, fig. 129.
Leptolecithum eurytremum Kobayashi, 1915a: 50–52, pl. 2, figs. 1–3; Kobayashi, 1921: 397–399, pl. 26, fig. 1.
Isoparorchis euritrema [sic; should be *eurytremum*]: Travassos, 1922a: 20.
Isoparorchis eurytrema [sic; should be *eurytremum*]: Travassos, 1922b: 230.
Isoparorchis tandani Johnston, 1927: 129, 131–132, text fig. A, figs. 1–4.
Isoparorchis hypselobagri: Ejsmont, 1932: 456.
Isoparorchis pakistani Bilqees and Khatton, 1972: 49–50, figs. 1–5.

Previous records. From *Silurus asotus* (syn. *Parasilurus asotus*) of Lake Biwa, as *Leptolecithum eurytremum* (Kobayashi, 1915a, 1921) and *Isoparorchis hypselobagri* (Shimazu, 2007); and from *Pseudobagrus aurantiacus* (Temminck and Schlegel) [sic; should be *Pelteobagrus nudiceps*] of Lake Biwa [(?); vague] as *L. eurytremum* (Kobayashi, 1915a, 1921).

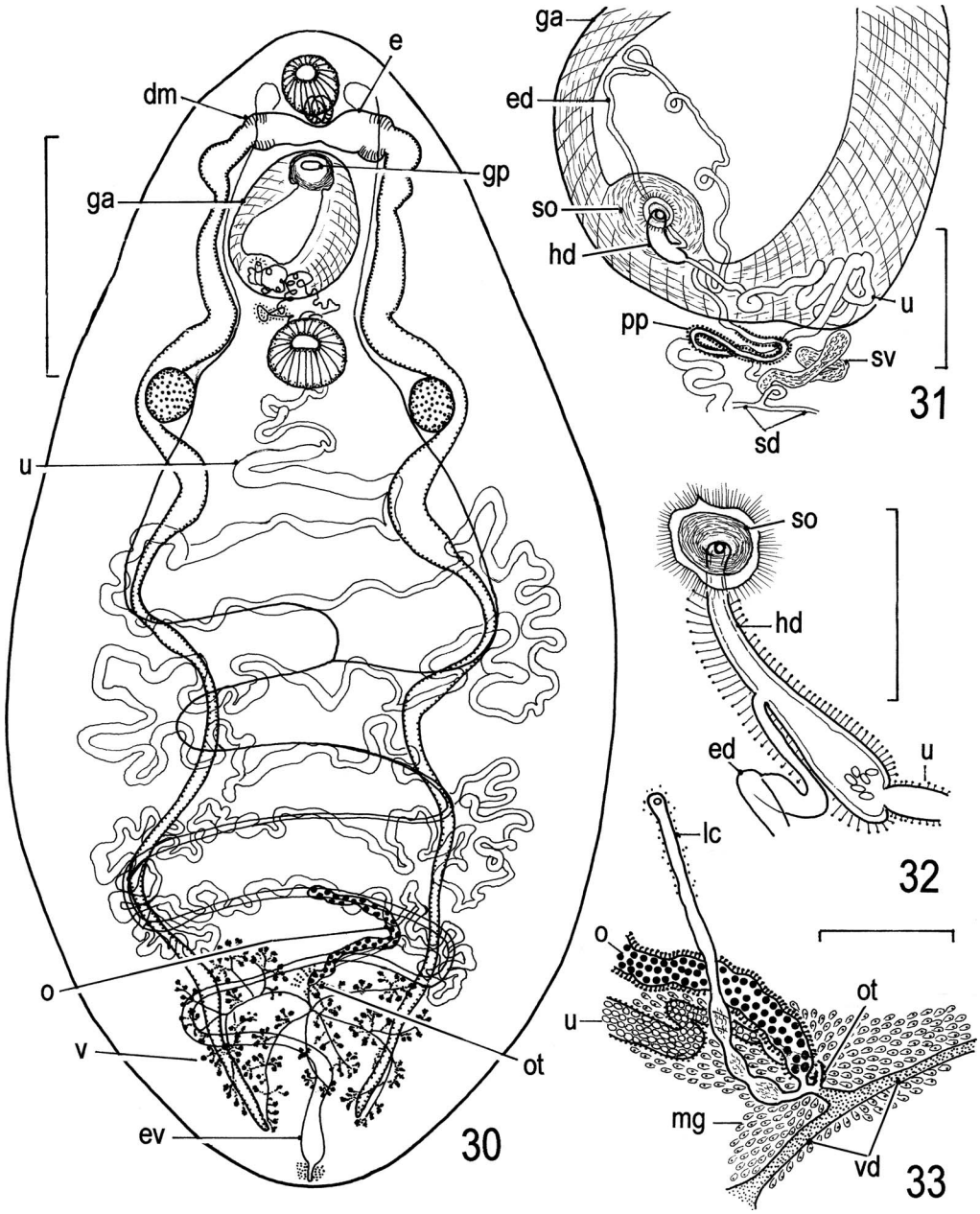
Hosts. *Silurus asotus* and *S. biwaensis*, and also *Pelteobagrus nudiceps* (?).

Site of infection. Air bladder.

Collecting localities. Lake Biwa, Daido River-1, Katayama, Kita River, Minamifunaki, Momose, and Onoe.

Materials examined. (1) Three immature and two mature specimens (Yamaguti's collection, MPM Coll. No. 22009, labeled "*I. trisimilitubis*", unpublished (?)) found in the air bladder of *Silurus asotus* from Lake Biwa on 9 July 1927 (Yamaguti, 1934 [(?); vague]; Shimazu, 2007). (2) Specimens found in the air bladder of *S. asotus*: one mature (NSMT-Pl 5561, collected by Shimazu) from Onoe on 4 May 1992, one mature (LBM 3-36) from the Daido River-1 on 1 May 2000, one mature (Urabe's personal collection) from the Kita River on 12 November 2005, one immature and 14 mature (LBM 8-59 to -73) from Momose on 24 April 2007 and 24 November 2007, and four mature (LBM 8-74 to -77) from Minamifunaki on 24 April 2007. (3) One immature and one mature specimens (Urabe's personal collection) found in the air bladder of *S. biwaensis* from Katayama on 20 July 2006.

Description. Based on 22 flattened, mature specimens from *S. asotus*; ten of them meas-



Figs. 30–33. *Isoparorchis hypselobagri*. Adult specimens found in the air bladder of *Silurus asotus*. 30, specimen (LBM 8-74), entire body, ventral view; 31, specimen (LBM 8-69), posterior part of terminal genitalia, ventral view; 32, specimen (LBM 8-64), hermaphroditic duct, ventral view; 33, specimen (LBM 8-67), ovarian complex, dorsal view. Scale bars: 5 mm in Fig. 30; 1 mm in Fig. 31; 0.5 mm in Figs. 32–33.

ured. Body broad-ovate large, 20–40 by 10–18, not oculate; forebody 6–14 long, occupying 26–37% of total body length. Tegument smooth. Preoral lobe present. Tegument smooth. Oral sucker subglobular, 1.20–2.08 by 1.12–2.08, ventral, near anterior end of body. Prepharynx absent. Pharynx barrel-shaped, 0.56–0.96 by 0.56–1.04, posterodorsal to oral sucker. Esophagus in-

verted T- or Y-shaped, short, 0.40–0.64 long. Drüsenmagen globular, small, with several internal, longitudinal grooves, differentiated in proximal shoulder region of intestine on either side of body. Intestines symmetrically undulating about five times, distally ending blindly near posterior end of body. Ventral sucker subglobular, larger than oral sucker, 1.40–2.72 by 1.52–2.88, median, located usually in front of junction between anterior and middle thirds of body; sucker width ratio 1 : 1.05–1.63. Testes two, globular to elliptical, 1.12–3.20 by 0.96–2.88, symmetrical, immediately medial to intestines, posterolateral to ventral sucker. Sperm ducts long; common sperm duct short, in front of ventral sucker. Seminal vesicle tubular, thin, long, convoluted in front of or overlapping ventral sucker, connected to pars prostatica with short, thin duct. Pars prostatica tubular, thin, long, convoluted, surrounded by prostatic cells, free in parenchyma, between ventral sucker and genital atrium. Ejaculatory duct thin, very long, highly convoluted in sinus sac and wall of genital atrium, opening into middle of hermaphroditic duct. Hermaphroditic duct clavate, thick-walled, 0.37–0.81 by 0.09–0.19, lying in sinus organ, surrounded by tall gland cells, opening in center of small, shallow depression of tip of sinus organ. Sinus organ muscular, conical, small. Sinus sac very weakly differentiated, with diffuse musculature, boundary between sinus sac and genital atrium not seen. Genital atrium oval, thick-walled with diffuse musculature, large, 1.60–7.84 by 1.60–7.04, median, between esophagus and ventral sucker, divided into two portions; anterior portion small, thin-walled; posterior large, thick-walled, including spiral muscle fibers, with spiral groove, its anterior edge anteriorly protruded like valve running obliquely posteriorly from dorsal to ventral. Genital pore large, median, behind esophagus, with sphincter. Ovary single, tubular, long, straight or folded once or twice, 3.52–5.76, surrounded by tall gland cells, dextral or sinistral to ootype, located at about junction between third and posterior quarters of body. Oviduct and ovovitelline duct very short. Laurer's canal fairly long, storing sperm, opening dorsally, making spherical dilatation 0.11–0.15 in diameter to store sperm as seminal receptacle near its proximal end. Ootype not vesicular, small, median. Mehlis' gland well developed. Uterus dorsal, surrounded by small gland cells, forming about seven large, transverse turns across intestines and then about five small, transverse turns in field between intestines and ventral sucker; metraterm tubular, thin, long, surrounded by small gland cells, convoluted in front of ventral sucker and then in sinus sac, leading to base of hermaphroditic duct; uterine seminal receptacle not seen. Eggs numerous, elliptical, light brown, 43–53 by 24–27 μm, fully embryonated, with small operculum. Vitellaria apparently two, each dendritic, diagonal, dorsal, median; vitelline area overlapping intestines, between ovary and intestinal ends, 3.52–5.60 by 4.80–8.00. Vitelline ducts two, very short; common vitelline duct (or vitelline reservoir) very short. Excretory vesicle Y-shaped, ventral; stem transversely folded five times between intestines, bifurcating a little in front of middle of hindbody; arm running forward on either side of body, turning backward laterally to pharynx, not fused there; excretory pore posteroventral.

Immature specimen found in air bladder of *S. asotus* measuring 8 by 6.

Discussion. Kobayashi (1915a) described a new genus and species, *Leptolecithum eurytremum*, on the basis of adult specimens found in the air bladder of *Silurus asotus* (syn. *Parasilurus asotus*) and *Pseudobagrus aurantiacus* (Japanese name: "[Gigi]" of Kobayashi) (see also Kobayashi, 1921) caught at several places including Lake Biwa in Japan. The scientific name of the fish Gigi in Lake Biwa is *Pelteobagrus nudiceps* (Shimazu, 1990c). It is unclear from Kobayashi (1915a, 1921) whether *P. nudiceps* was really found infected also in Lake Biwa. Kobayashi did not designate the holotype, nor the type host, nor the type locality for *L. eurytremum*. It is believed that Kobayashi's original specimens were lost (see Materials and Methods).

Travassos (1922a) synonymized *Leptolecithum* Kobayashi, 1915 with *Isoparorchis* South-

well, 1913 and made a new combination, *I. euritrema* (Kobayashi, 1915) comb. nov. Travassos (1922b) changed "*euritrema*" to "*eurytrema*". This specific name *eurytrema* raises a nomenclatural problem. The specific name *eurytremum* was most likely derived from a Greek compound noun, eury-trema. Kobayashi (1915) did not indicate whether he regarded *eurytremum* as a noun or as an adjective. Since *Isoparorchis* is a masculine noun, Travassos' (1922b) *eurytrema* (feminine) is not acceptable even though *eurytremum* (neuter) is an adjective. Odhner (1927) and Bovien (1927) used the species name *I. eurytremum* (Kobayashi). Ejsmont (1932) used *I. eurytremus*. We are the opinion that *eurytremum* may be regarded either a noun or an adjective, and so it is treated as a noun in apposition to *Leptolecithum* in accordace with Article 31.2.2 (ICZN). The species name of Kobayashi's species is *I. eurytremum* (Kobayashi, 1915) Travassos, 1922.

Bhalerao (1926) considered *L. eurytremum* from Japan to be a synonym of *I. trisimilitubis* Southwell, 1913 from India. Ejsmont (1932) designated *Distomum hypselobagri* Billet, 1898 from Vietnam as the type species of *Isoparorchis* and synonymized *D. hypselobagri*, *I. trisimilitubis*, *L. eurytremum*, *I. eurytremus* (Kobayashi, 1915) Travassos, 1923 [sic; should be *euritrema,* Travassos, 1922a; *eurytrema*, Travassos, 1922b [not 1923]], and *I. tandani* Johnston, 1927 from Australia with *I. hypselobagri* (Billet, 1898) Ejsmont, 1932 [not Odhner, 1927]. Yamaguti (1934) summarized the history of taxonomic studies of this digenean, and he retained *I. trisimilitubis* as the type species, because *D. hypselobagri* was not fully known at that time. Southwell (1913) established the new genus *Isoparorchis* and included the only new species *I. trisimilitubis* in it. Although this species is now a junior subjective synonym of *I. hypselobagri* (Ejsmont, 1932), the type species of *Isoparorchis* is originally *I. trisimilitubis* Southwell, 1913 (Article 68.3, ICZN), or now *I. hypselobagri* (Billet, 1898) Ejsmont, 1932 (Recommendation 67B, ICZN) (see also Gibson, 2002b). Bilqees and Khatoon (1972) proposed a new species, *I. pakistani*, from West Pakistan. Bhutta and Khan (1975) reduced this species to a synonym of *I. hypselobagri*.

Yamaguti (1934) gave measurements and described the ovarian complex in adult specimens of *I. trisimilitubis* found in *S. asotus* (syn. *P. asotus*). Since he mentioned nothing about the locality, it is unknown whether he actually used his adult specimens (MPM Coll. No. 22009) from Lake Biwa for his description.

Gibson and Bray (1979) and Gibson (2002b) said that the Drüsenmagen is absent in the family Isoparorchiidae. However, the organ was seen in the present specimens (see also Kobayashi, 1915a, 1915d, 1921). Kobayashi (1915a) described that the semial vesicle enters the "cirrus-pouch-like muscular organ" (Kobayashi, 1921) (genital atrium of this paper) and continues to the pars prostatica, which leads to the ejaculatory duct; but Kobayashi (1921) mentioned nothing about the pars prostatica. However, the pars prostatica is actually located outside the genital atrium (this paper, Fig. 31). Kobayashi (1915a, 1921) said the seminal receptacle as absent, but a small seminal receptacle is formed as a spherical dilatation in the proximal part of Laurer's canal (Yamaguti, 1934; this paper, Fig. 33).

The genital atrium is large, and the sinus organ is small in the present specimens. None of them had either such a large (long) "Genitalpapille" (sinus organ of this paper) as illustrated for *Isoparorchis eurytremum* (Kobayashi) by Odhner (1927, fig. 1) or such a protruded sinus organ as illustrated for *Isoparorchis* by Gibson and Bray (1979, fig. 2).

Life cycle. Besprozvannykh and Ermolenko (1989) experimentally studied the life cycle of *I. hypselobagri* in southern Primorye, Russia. Natural first intermediate hosts were snails of the genus *Juga*, in which cystophorous cercariae were produced in sporocysts. Cercariae were infective to second intermediate hosts, a mayfly, an amphipod, and cyclopid copepods, in which unencysted metacercariae grew. Metacercariae were infective to small fishes. Third intermediate hosts

[sic; transport or paratenic hosts (?)] were various species of benthophagous fishes. The final host was *Silurus asotus*. According to Shimazu (1999, 2003b), their cystophorous cercaria (fig. 3) resembles *Cercaria introverta* Faust, 1924, which has been reported from *Semisulcospira* spp. at various places in Japan (Ito, 1964). Urabe (2003) recorded *C. introverta* from *S.* (*Biwamelania*) *nakasekoae* of the Uji River downstream from Lake Biwa through the Seta River.

Yamaguti (1934) fed two juveniles obtained from the body cavity of *Odontobutis obscura* (syn. *Mogurnda obscura*) from Lake Ogura in Kyoto Prefecture to an individual of *Silurus asotus* (syn. *Parasilurus asotus*) and subsequently recovered the two, still immature worms (MPM Coll. No. 22010) from the air bladder of the fish seven and 17 days later (Experiment V). He considered that, in *S. asotus*, juveniles in the intestine are capable of migrating through the intestinal wall into the body cavity, where they wander about till they find their way into the air bladder. The infection route in the final host by way of the pneumatic duct as postulated by Kobayashi (1915a) is untenable (Yamaguti, 1934).

In addition to the specimens from the air bladder of *S. asotus* and *S. biwaensis*, some worms have been found in the body cavity, internal organs, and musculature of fishes of various species, and even in the air bladder of *O. obscura* (see Yamaguti, 1934), in Japan (Komiya, 1965; Shimazu, 1999, 2003a). Some are immature, but some others are mature. We examined the following materials: (1) Specimens found in the body muscles of *Micropterus salmoides*: one mature (NSMT-Pl 5562, collected by Shimazu) from Lake Biwa (other data unknown) and one mature (LBM 2-67) from Konohama on 10 January 1999. (2) One mature specimen (NSMT-Pl 5707, collected by Shimazu) found in the body muscles of *Lepomis macrochirus* from Lake Biwa (other data unknown). (3) One mature specimen (NSMT-Pl 5708, collected by Shimazu) found in the body cavity of *S. biwaensis* from Onoe on 4 May 1992. (4) Two mature specimens (LBM 1340000054) found in the body cavity of *Channa argus* from the mouth of the Yasu River in Moriyama in April 2001. (5) Four immature specimens (NSMT-Pl 5709, collected by Nagasawa) found in the stomach wall and the liver of *Cottus reinii* from Lake Biwa on 4 February 1980. (6) One immature specimen (NSMT-Pl 5710, collected by Shimazu) found in the intestine of *S. asotus* from Onoe on 4 May 1992. (7) Specimens found in the body cavity of *Pungtungia herzi*: two immature (LBM 1-49) from Tai on 25 October 1997, and one immature (LBM 3-44) from the Yasu River on 14 October 2000. (8) Specimens found in the body cavity of *Gnathopogon elongatus elongatus*: six immature (LBM 1-56) from Tai on 25 October 1997, and one immature (LBM 3-41) from Miyakawa-ike Pond on 26 October 2000. (9) One immature specimen (LBM 1-32) found in the body cavity of *Pseudogobio esocinus esocinus* from Hachiyadohama on 15 May 1998. (10) One immature specimen (LBM 3-51) found in the body cavity of *Nipponocypris sieboldii* from Miyake on 1 November 2000. (11) One immature specimen (LBM 8-55) found in the body cavity of *Tanakia lanceolata* from Nishiyama on 27 November 2007. (12) One immature specimen (LBM 1-65) found in the body cavity of *Gymnogobius urotaenia* from the Mano River on 17 October 1997. (13) Nine immature specimens (Urabe's personal collection) found in the body cavity of *Tridentiger brevispinis* from either the Inukami River or the Ezura River on 22 August 2006. (14) One immature specimen (LBM 1-7) found in the gut of *Rhinogobius* sp. BW from Imazu on 19 May 1998.

It still remains to be explained why worms are capable of attaining sexual maturity also in the body cavity and others, instead of in the air bladder, of some of these fishes.

Family **Allocreadiidae** Looss, 1902

Allocreadium gotoi (Hasegawa and Ozaki, 1926) (Figs. 34–35)

Macrolecithus gotoi Hasegawa and Ozaki, 1926: 225–227, fig. 1, 1 table; Yamaguti, 1934: 333–334, fig. 38.
Allocreadium gotoi: Shimazu, 1988a: 6–7, figs. 1–3.

Previous records. From *Misgurnus anguillicaudatus* of Koga [sic; should be Koka, namely Terasho, Koka-gun, now in Koka City] and Zeze, and from *Gnathopogon elongatus elongatus* of Lake Biwa (Shimazu, 1988a).

Hosts. *Gnathopogon elongatus elongatus* and *Misgurnus anguillicaudatus*.

Site of infection. Intestine.

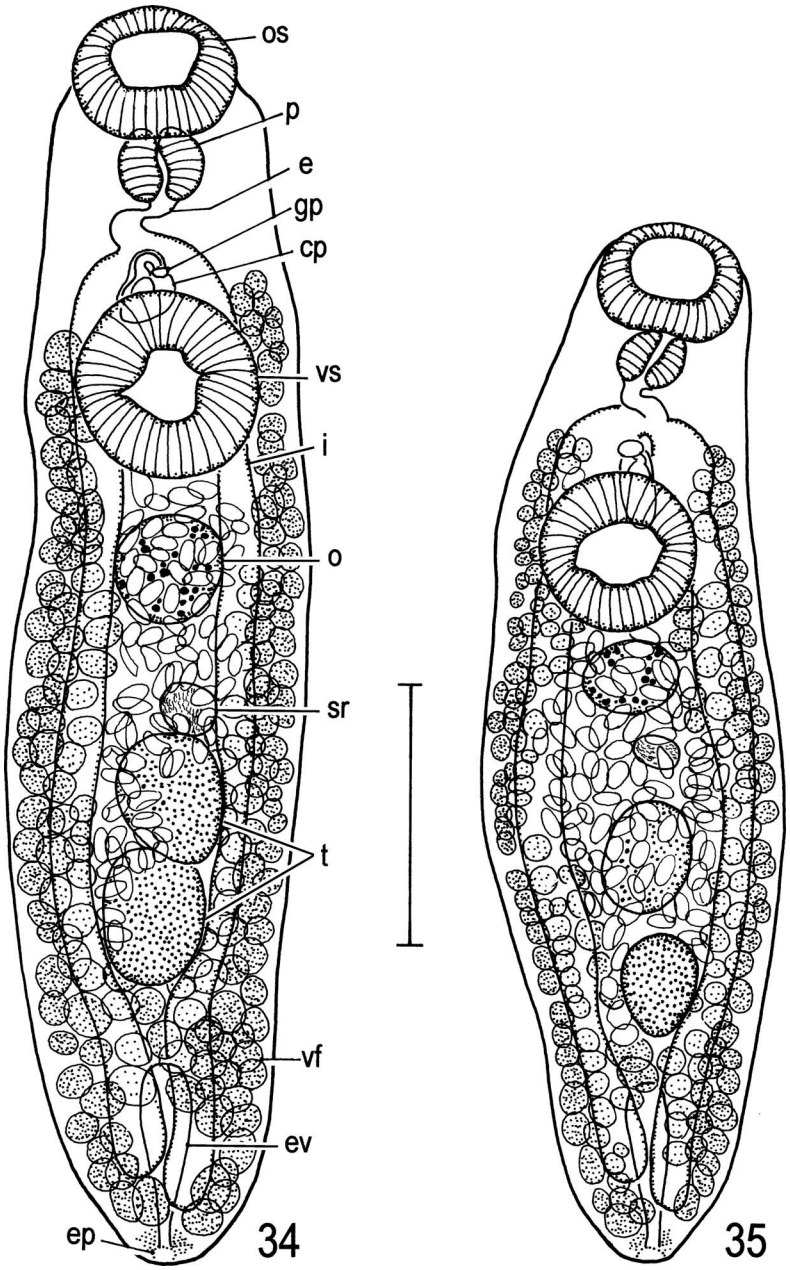
Collecting localities. Lake Biwa, Terasho, and Zeze.

Materials examined. (1) Specimens found in the intestine of *Misgurnus anguillicaudatus*: one mature (Yamaguti's Collection, MPM Coll. No. 22571, labeled "*Macrolec. gotoi*", unpublished (?)) from Terasho, Koka-gun, now in Koka City on 8 July 1927, and one serially-sectioned mature (Yamaguti's Collection, MPM Coll. No. 22568, unidentified, unpublished (?)) from Zeze on 16 July 1928 (Shimazu, 1988a). (2) Specimens found in the intestine of *Gnathopogon elongatus elongatus* from Lake Biwa: one mature (Yamaguti's Collection, MPM Coll. No. 22572, labeled "*Macrolecithus gotoi* [Moroko]", unpublished (?)) on 9 July 1927, and one mature (Yamaguti's Collection, MPM Coll. No. 22569, labeled "*Allocread*. [Moroko]", unpublished (?)) on 29 July 1927 (Shimazu, 1988a).

Description. Three mature specimens measured. Body elongate, slightly flat dorsoventrally, 2.00–2.48 by 0.59–0.72; forebody 0.72–0.75 long, occupying 29–37% of body length. Tegument smooth. Eyespot pigment not seen. Gland cells present in forebody. Oral sucker broad elliptical, 0.19–0.25 by 0.24–0.29, subterminal. Prepharynx very short. Pharynx globular, 0.10–0.14 by 0.11–0.17. Esophagus straight or S-shaped, 0.09–0.12 long, bifurcating in front of ventral sucker. Intestines terminating blindly near posterior end of body. Ventral sucker globular, 0.31–0.35 by 0.29–0.33, located at about junction between anterior and second thirds of body; sucker width ratio 1 : 1.04–1.23. Testes two, elliptical, tandem, contiguous, in middle third of hindbody; anterior testis 0.22–0.25 by 0.15–0.31; posterior 0.22–0.28 by 0.15–0.33. Cirrus pouch claviform, small, 0.12–0.22 by 0.06–0.09, postbifurcal, slightly overlapping ventral sucker posteriorly. Male terminal genitalia in cirrus pouch not clearly observed. Genital pore median, at bifurcal level or slightly behind it. Ovary single, globular, 0.15–0.23 by 0.17–0.20, median, pretesticular, slightly posterior to ventral sucker, well anterior to anterior testis. Seminal receptacle elliptical, 0.08–0.14 by 0.07–0.15, submedian, between ovary and anterior testis. Ovarian complex postovarian (not clearly observed due to uterine eggs). Uterus almost between intestines, coiled between posterior margin of posterior testis and ventral sucker. Eggs numerous, oval, brown, 77–86 by 48–53 μm (slightly collapsed), not embryonated, with small operculum at attenuated pole. Vitellaria follicular, follicles large, mostly dorsal to intestines, distributed from bifurcal level to posterior end of body, separate anteriorly, confluent post-testicularly. Excretory vesicle I-shaped, short, thick-walled, ending anteriorly some distance behind posterior testis; excretory pore subterminal.

Discussion. The Japanese name of the host fish written on the labels of Yamaguti's specimens (MPM Coll. Nos. 22569 and 22572) is "[Moroko]". Yamaguti (1934, p. 290; 1938, p. 137) applied the scientific names *Gnathopogon elongatus* and *G. elongatus elongatus* (current Japanese name: Tamoroko), respectively, to the fish "Moroko".

Hasegawa and Ozaki (1926) created a new genus and species, *Macrolecithus gotoi*, based on



Figs. 34–35. *Allocreadium gotoi*. Adult specimens. 34, specimen (MPM Coll. No. 22571) found in the intestine of *Misgurnus anguillicaudatus*, entire body, ventral view; 35, specimen (MPM Coll. No. 22572) found in the intestine of *Gnathopogon elongatus elongatus*, entire body, ventral view. Scale bar: 0.5 mm in Figs. 34–35.

adult specimens found in the intestine of *Misgurnus anguillicaudatus*; but they did not mention the type locality. Yamaguti (1934) redescribed *M. gotoi* from seven adult specimens. Because Yamaguti did not refer to their locality, it is unclear whether the present specimens were used for his redescription and figure at that time. Shimazu (1988a) treated *Macrolecithus* as a junior synonym of *Allocreadium* Looss, 1900 and proposed a new combination, *Allocreadium gotoi*

(Hasegawa and Ozaki, 1926), for the species. He briefly described the present specimens as *A. gotoi*. This digenean has not been recorded from the Lake Biwa basin since the present specimens.

Allocreadium gotoi is different from its Japanese congeners from the Lake Biwa basin (this paper) in having a larger oral sucker; a larger pharynx; a small, postbifurcal cirrus pouch; and the uterus usually extending posteriorly into the testicular zone and sometimes farther into the post-testicular region of the body (Hasegawa and Ozaki, 1926; Shimazu, 1988a).

Life cycle. Shimazu (2002) found that ophthalmoxiphidiocercous cercariae developed in [daughter (?)] rediae in the sphaeriid bivalve *Pisidium nikkoense* Mori (Japanese name not yet given). He identified them as belonging to *A. gotoi* because of close morphological similarity in the excretory system between cercariae and adults, but this identification needs to be experimentally confirmed. The second intermediate host is not known as yet.

Allocreadium hasu Ozaki, 1926 (Figs. 36–39)

Allocreadium hasu Ozaki, 1926: 125, no figure; Yamaguti, 1934: 281–282, no figure; Shimazu, 1988a: 9, figs. 4–5.

Previous records. From *Opsariichthys uncirostris uncirostris* (syn. *O. uncirostris* (Temminck and Schlegel)) of Lake Biwa (Shimazu, 1988a) and of Omatsu (Yamaguti, 1934; Shimazu, 1988a), and from *Gnathopogon elongatus elongatus* of Lake Biwa and of Komatsu (Shimazu, 1988a).

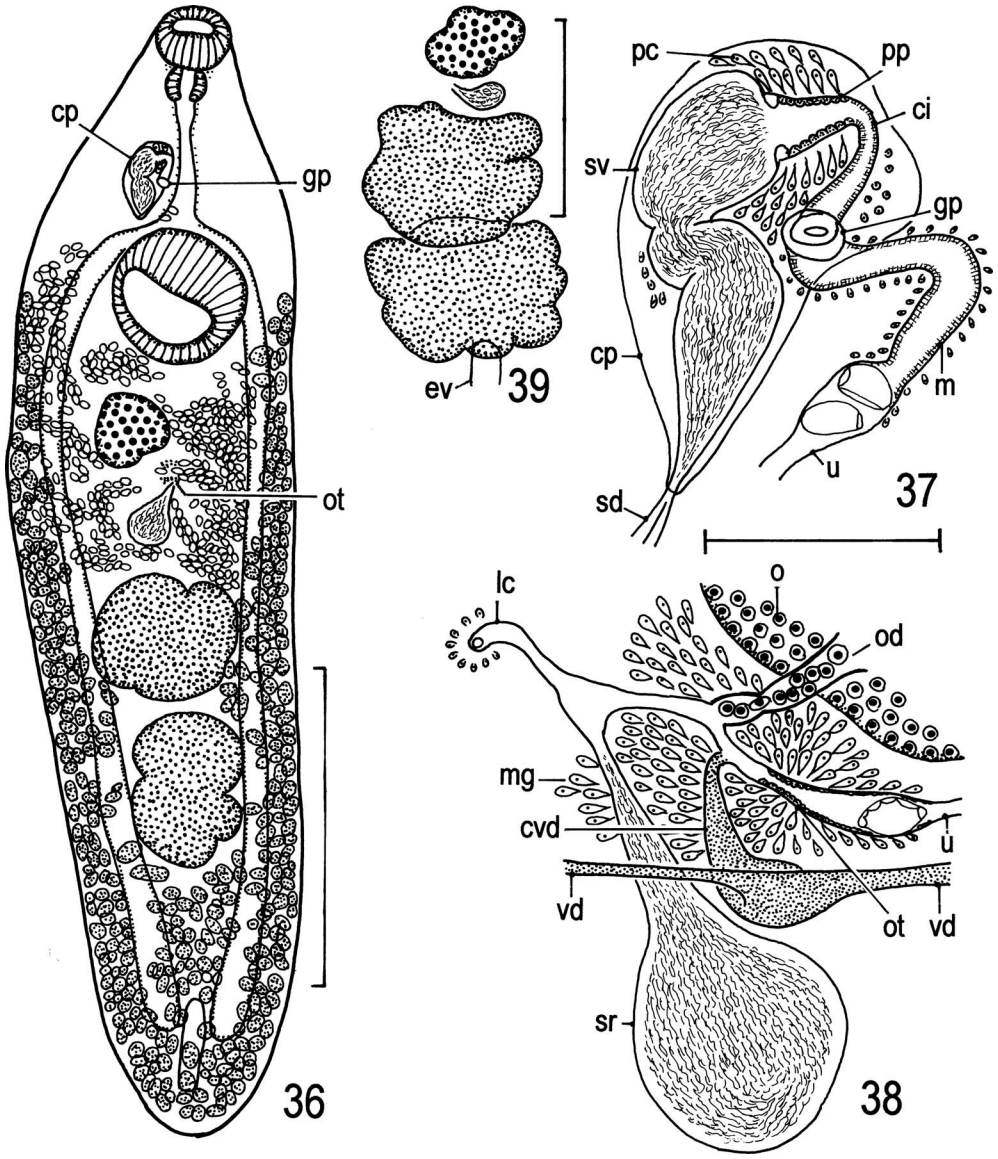
Hosts. *Gnathopogon elongatus elongatus*, *Opsariichthys uncirostris uncirostris*, and *Zacco platypus*.

Site of infection. Intestine.

Collecting localities. Lake Biwa, Imazu, Komatsu, Moriyama, Omatsu, and Onoe.

Materials examined. (1) Six serially sectioned and 11 whole-mounted mature specimens (Ozaki's Collection, MPM Coll. No. 30006, labeled "*A. hasu* HASU [Lake Biwa]") found in *Opsariichthys uncirostris uncirostris* (syn. *O. uncirostris*) from Lake Biwa (other data not given) (Shimazu, 1988a). (2) Specimens found in the intestine of *O. u. uncirostris*: six mature (Yamaguti's Collection, MPM Coll. No. 22287) from Omatsu on 10 and 17 July 1927 (Yamaguti, 1934; Shimazu, 1988a), and one immature (Yamaguti's Collection, MPM Coll. No. 22576, labeled "*Allocread. hasu*", unpublished) from Lake Biwa in December, 1926 (other data not given) (Shimazu, 1988a). (3) One mature specimen (NSMT-Pl 2934) found in the intestine of *O. u. uncirostris* from [Onoe] on 6 June 1980 (Shimazu, 1988a). (4) Specimens found in the intestine of *O. u. uncirostris*: two immature and six mature (NSMT-Pl 5711–5712, collected by Shimazu) from Omatsu on 30 April and 1 May 1992, 12 mature (NSMT-Pl 5713, collected by Shimazu) from Moriyama on 2 May 1992, and two mature (LBM 3-55) from Imazu on 5 May 2000. (5) Specimens found in the intestine of *Gnathopogon elongatus elongatus*: one mature (Yamaguti's Collection, MPM Coll. No. 22569, labeled "*Allocread.*", unpublished) from Lake Biwa on 29 July 1927 (Shimazu, 1988a), and one immature (Yamaguti's Collection, MPM Coll. No. 22576, labeled "*Allocread. hasu*", unpublished) from Komatsu in December, 1926 (other data not given) (Shimazu, 1988a). (6) One mature specimen (NSMT-Pl 5714, collected by Shimazu) found in the intestine of *Zacco platypus* from Omatsu on 30 April 1992.

Description. Based on mature specimens, ten of them measured (Figs. 36–38). Similar to *Allocreadium gotoi* (this paper) in general morphology. Body elongate, rapidly attenuated anteriorly in forebody, fairly small, 3.92–7.20 by 1.52–2.08; forebody 1.12–1.92 long, occupying 20–28% of total body length. Eyespot pigment fine, scattered in forebody. Gland cells present in



Figs. 36–39. *Allocreadium hasu*. 36, adult specimen (NSMT-Pl 5711) found in the intestine of *Opsariichthys uncirostris uncirostris,* entire body, ventral view; 37, specimen (NSMT-Pl 5711), terminal genitalia, ventral view; 38, specimen (NSMT-Pl 5711), ovarian complex, dorsal view; 39, immature specimen (MPM Coll. No. 22576) (2.48 by 0.81) found in the intestine of *O. u. uncirostris*, showing ovary, seminal receptacle, and testes, ventral view. Scale bars: 2 mm in Fig. 36; 0.5 mm in Fig. 39; 0.3 mm in Figs. 37–38.

forebody. Oral sucker globular, 0.34–0.43 by 0.39–0.47, subterminal. Prepharynx almost absent. Pharynx globular, 0.15–0.23 by 0.16–0.24. Esophagus bifurcating immediately anteriorly or dorsally to ventral sucker. Intestines terminating some distance in front of posterior end of body. Ventral sucker globular, 0.57–0.88 by 0.56–0.88, located at about junction between anterior and second fifths of body; sucker width ratio 1 : 1.34–2.01. Testes large, deeply indented irregularly, almost contiguous, in middle third of hindbody; anterior testis 0.41–0.81 by 0.78–1.06, posterior 0.69–1.19 by 0.66–1.06. Cirrus pouch spherical to oboval, 0.33–0.66 by 0.19–0.50, overlapping

ventral sucker, rarely extending to posterior border of ventral sucker in serially-sectioned specimens, and artificially shifted more anteriorly in whole-mounted specimens. Seminal vesicle large, S-shaped, possibly weakly constricted once. Pars prostatica ovate; prostatic cells small, well developed. Cirrus (or ejaculatory duct) fairly long. Genital atrium small. Genital pore at about middle level of esophagus. Ovary globular to three-lobed, sometimes transversely elongated, 0.25–0.50 by 0.25–0.65, almost median, slightly posterior to ventral sucker, some distance in front of anterior testis. Seminal receptacle retort-shaped, 0.18–0.56 by 0.14–0.28, usually submedian but rarely median, between ovary and anterior testis. Laurer's canal short, sinistrally submedian. Ootype vesicular, large, surrounded by well-developed Mehlis' gland. Uterus coiled in field encircled by intestines, anterior testis, and ventral sucker, slightly overlapping intestines; metraterm slightly shorter than cirrus pouch. Eggs numerous, broad-oval, brown, 69–91 by 53–64 μm. Vitelline follicles fairly small, extending from bifurcal level to posterior end of body, mostly dorsal to intestines, separate anteriorly, confluent post-testicularly. Excretory vesicle short, extending anteriorly slightly beyond intestinal ends but not to posterior testis; excretory pore dorsal near posterior end of body.

In small, immature specimens, testes large, deeply indented irregularly; ovary entire to weakly three-lobed; and excretory vesicle rarely reaching to posterior testis (Fig. 39).

Discussion. Ozaki (1926) briefly described a new species, *Allocreadium hasu*, with no figure, from adult specimens found in the intestine of *Opsariichthys uncirostris uncirostris* (syn. *O. uncirostris*). He did obtain the host fish in Japan, but he did not specify the locality. It is believed that the holotype (No. P. 231) was lost (see Materials and Methods). Ozaki's specimens reexamined here are most likely paratypes (Shimazu, 1988a), but there is no conclusive evidence to prove this.

Yamaguti (1934) redescribed *A. hasu*, with no figure, from his own specimens found in *O. uncirostris* from Lake Biwa. It seems certain that he used the six adult specimens (MPM Coll. No. 22287) at least at that time.

Shimazu (1988a, figs. 4–5 [not 1–2]) redescribed and figured *A. hasu* from Ozaki's and Yamaguti's specimens and his own specimen. He also determined Yamaguti's specimens (MPM Coll. Nos. 22569 and 22576) as *A. hasu*. He found one mature specimen (NSMT-Pl 2934) of *A. hasu* in the intestine of *O. u. uncirostris* from [Onoe] on 6 June 1980. We could not reexamine this specimen, because it was out on loan to some parasitologist. All of the present new specimens are regarded as *A. hasu*.

Neither Ozaki (1926) nor Yamaguti (1934) compared *A. hasu* with other Japanese congeners then known in morphology. *Allocreadium hasu* differs from *Allocreadium japonicum* Ozaki, 1926 (see the next species) in that the body is larger, 3.92–7.20 long instead of 1.60–5.20 long, and more rapidly tapers anteriorly; the oral sucker is smaller; and uterine eggs are more numerous. It is different from *Allocreadium* sp. (this paper) in that the body is larger, 3.92–7.20 long instead of 1.60–3.44 long, and more rapidly tapers anteriorly; the oral sucker is smaller; uterine eggs are more numerous; and the excretory vesicle is shorter, not reaching to the posterior testis.

Life cycle. The life cycle is not known.

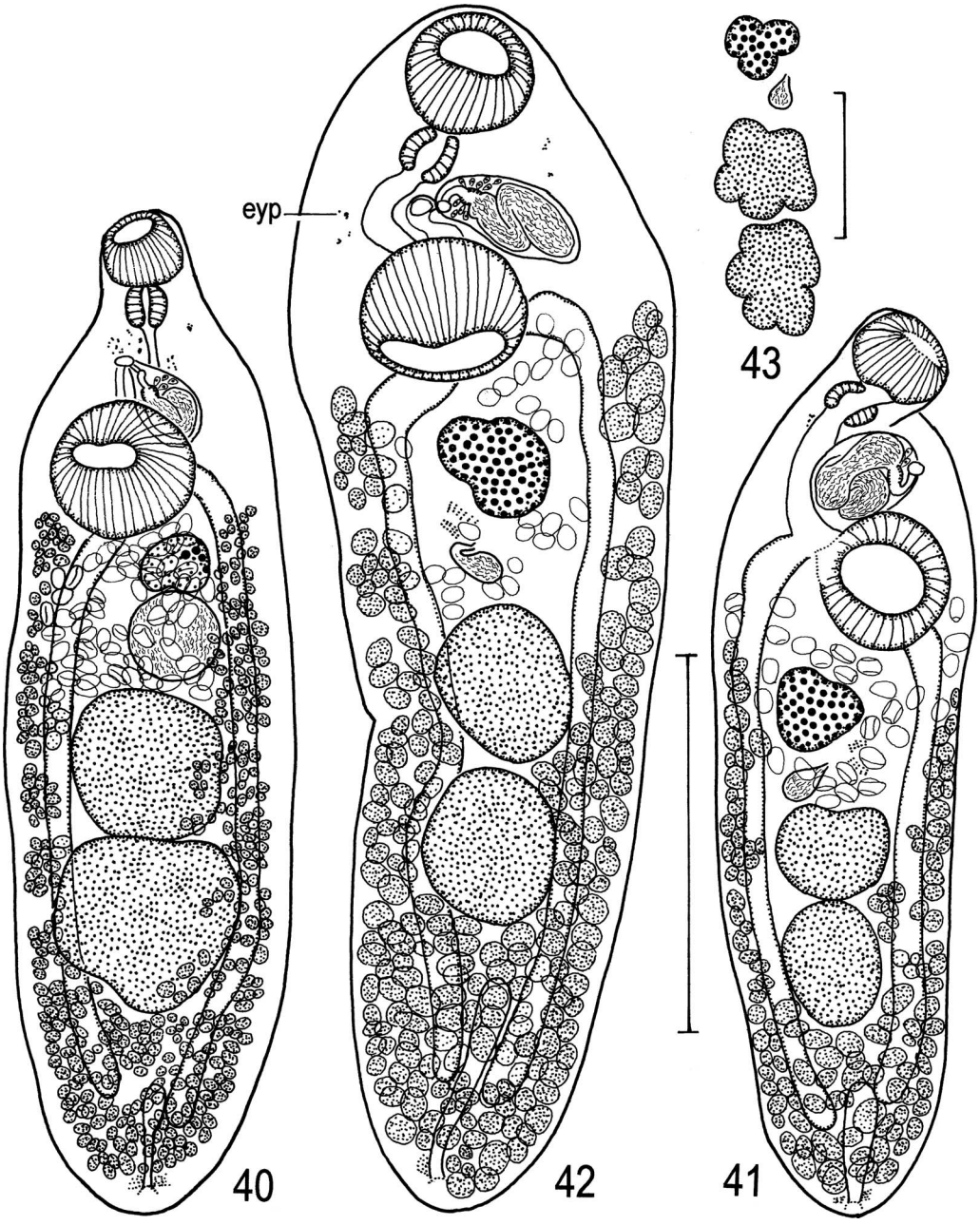
Allocreadium japonicum Ozaki, 1926 (Figs. 40–43)

Allocreadum japonicum Ozaki, 1926 [sic; misspelling of *Allocreadium*]: 124–125, no figure.
Allocreadium japonicum: Yamaguti, 1934: 282, no figure; Shimazu, 1988a: 13–14, figs. 10–11.

Previous records. From *Zacco platypus* and *Nipponocypris temminckii* (syn. *Z. temminckii*

(Temminck and Schlegel)) of Lake Biwa (Yamaguti, 1934; Shimazu, 1988a).

Hosts. *Gasterosteus aculeatus leiurus*, *Nipponocypris temminckii*, *Rhynchocypris oxycephalus*, and *Zacco platypus*.



Figs. 40–43. *Allocreadium japonicum*. Adult specimens. 40, specimen (MPM Coll. No. 22285) found in the intestine of *Zacco platypus*, entire body, ventral view; 41, specimen (LBM 8-18) found in the intestine of *Gasterosteus aculeatus leiurus*, entire body, ventral view; 42, specimen (LBM 8-25) found in the intestine of *Rhynchocypris oxycephalus*, entire body, ventral view; 43, specimen (LBM 8-25), showing ovary, seminal receptacle, and testes, ventral view. Scale bars: 1 mm in Figs. 40–43.

Site of infection. Intestine.

Collecting localities. Lake Biwa, Amano River, Momose, and Nyuu River.

Materials examined. (1) Specimens found in the intestine of *Zacco platypus*: two mature (Yamaguti's Collection, MPM Coll. No. 22285) from Lake Biwa on 7 July 1927 (Yamaguti, 1934; Shimazu, 1988a), and two immature and one barely mature (Yamaguti's Collection, MPM Coll. No. 22285, labeled "*Allocead.*", unpublished) from Lake Biwa on 10 July 1927 (Shimazu, 1988a). (2) One mature specimen (LBM 8-54) found in the intestine of *Z. platypus* from Momose on 24 November 2007. (3) One mature specimen (Yamaguti's Collection, MPM Coll. No. 22577) found in the intestine of *Nipponocypris temminckii* (syn. *Z. temminckii*) from Lake Biwa on 7 July 1927 (Yamaguti, 1934; Shimazu, 1988a). (4) One mature specimen (LBM 8-18) found in the intestine of *Gasterosteus aculeatus leiurus* (syn. *G. microcephalus* Girard) from the Amano River on 10 May 1998. (5) Five mature specimens (LBM 8-25) found in the intestine of *Rhynchocypris oxycephalus* from the Nyuu River on 26 April 2001.

Description. 1) Based on five mature specimens from *Z. platypus* and *N. temminckii* (Fig. 40). Similar to *Allocreadium gotoi* (this paper) in general morphology. Body elongate, 1.60–3.44 by 0.59–0.80; forebody 0.53–0.83 long, occupying 24–33% of total body length. Eyespot pigment fine, scattered in forebody. Oral sucker subglobular, 0.17–0.26 by 0.19–0.27. Prepharynx not seen. Pharynx globular, 0.09–0.12 in diameter. Esophagus 0.19–0.43 long, bifurcating dorsally to ventral sucker. Intestines terminating some distance in front of posterior end of body. Ventral sucker nearly globular, 0.32–0.44 by 0.34–0.44, located at about junction between anterior and second fifths of body; sucker width ratio 1 : 1.59–1.87. Testes large (but small and seemingly atrophied in LBM 8-54), smooth or only slightly irregular in outline, almost contiguous, in middle third of hindbody; anterior testis 0.22–0.44 by 0.32–0.44, posterior 0.30–0.56 by 0.34–0.45. Cirrus pouch spherical, oboval, or elliptical, 0.14–0.41 by 0.07–0.19, in front of or overlapping ventral sucker. Seminal vesicle large, S-shaped, occupying posterior two-thirds of cirrus pouch. Pars prostatica ovate; prostatic cells small, well developed. Cirrus fairly long. Genital atrium small. Genital pore at about middle level of esophagus. Ovary elliptical, globular or transversely elonagate or weakly bilobed, 0.12–0.28 by 0.17–0.31, slightly posterior to ventral sucker, some distance in front of anterior testis. Seminal receptacle 0.06–0.25 by 0.11–0.24. Laurer's canal short. Ootype and Mehlis' gland well developed. Uterus coiled between anterior testis and ventral sucker, between intestines and slightly overlapping intestines; metraterm slightly shorter than cirrus pouch. Eggs fairly numerous, broad ovate, light brown, 64–80 by 43–56 μm. Vitelline follicles fairly small, distributed from near bifurcal level to posterior end of body, mostly dorsal to intestinal ceca, separate anteriorly, confluent post-testicularly. Excretory vesicle short, extending anteriorly slightly beyond intestinal ends but not to posterior testis; excretory pore dorsal near posterior end of body. In small immature specimens, testes and ovary almost entire as in the above-described mature specimens.

2) Based on six mature specimens (LBM 8-18 and -25) from *G. aculeatus leiurus* and *R. oxycephalus* (Figs. 41–42). Body 2.45–5.20 by 0.69–1.28; forebody 0.75–1.28 long, occupying 23–31% of total body length. Oral sucker 0.23–0.44 by 0.26–0.44. Pharynx 0.11–0.19 by 0.12–0.20. Esophagus 0.31–0.56 long. Ventral sucker 0.36–0.54 by 0.34–0.59; sucker width ratio 1 : 1.19–1.46. Testes large; anterior testis 0.25–0.75 by 0.29–0.69, posterior 0.34–0.94 by 0.28–0.63. Cirrus pouch 0.29–0.59 by 0.19–0.37. Ovary 0.22–0.41 by 0.22–0.45. Seminal receptacle 0.15–0.28 by 0.09–0.22. Eggs 65–83 by 48–59 μm.

Ventral sucker and genital pore shifted to left in the specimen (LBM 8-18) (Fig. 41) due to flattening during fixation. One of the specimens (LBM 8-25) having irregularly indented testes, a

trilobed ovary, and uterine eggs measuring 67–75 by 48–56 μm (Fig. 43).

Discussion. Ozaki (1926) briefly described a new species, *Allocreadium japonicum*, with no figure, based on adult specimens found in the intestine of *Zacco platypus*. He certainly obtained the host fish in Japan, but he did not specify the locality. It is believed that the holotype (No. P. 226) was lost (see Materials and Methods). None of Ozaki's other original specimens have been reexamined. Yamaguti (1934) identified three mature specimens from Lake Biwa as *A. japonicum*: two (MPM Coll. No. 22285) from *Z. platypus* and one (MPM Coll. No. 22577) from *N. temminckii* (syn. *Z. temminckii*), but he merely gave their measurements. Therefore, *A. japonicum* is problematic in morphology.

We tentatively regard, as *A. japonocum*, also the present new specimens from *G. aculeatus leiurus* and *R. oxycephalus*. However, they are slightly different from those found in *Z. platypus* and *N. temminckii* of the Lake Biwa basin (Yamaguti, 1934; Shimazu, 1988a; this paper) in having a larger body, larger oral and ventral suckers, and a lower sucker width ratio. Furthermore, one of them had irregularly indented testes and a trilobed ovary (Fig. 43). They need to be carefully studied from additional specimens.

Life cycle. The life cycle is not known.

Allocreadium sp. (Figs. 44–46)

Previous record. None.

Host. *Tanakia lanceolata*.

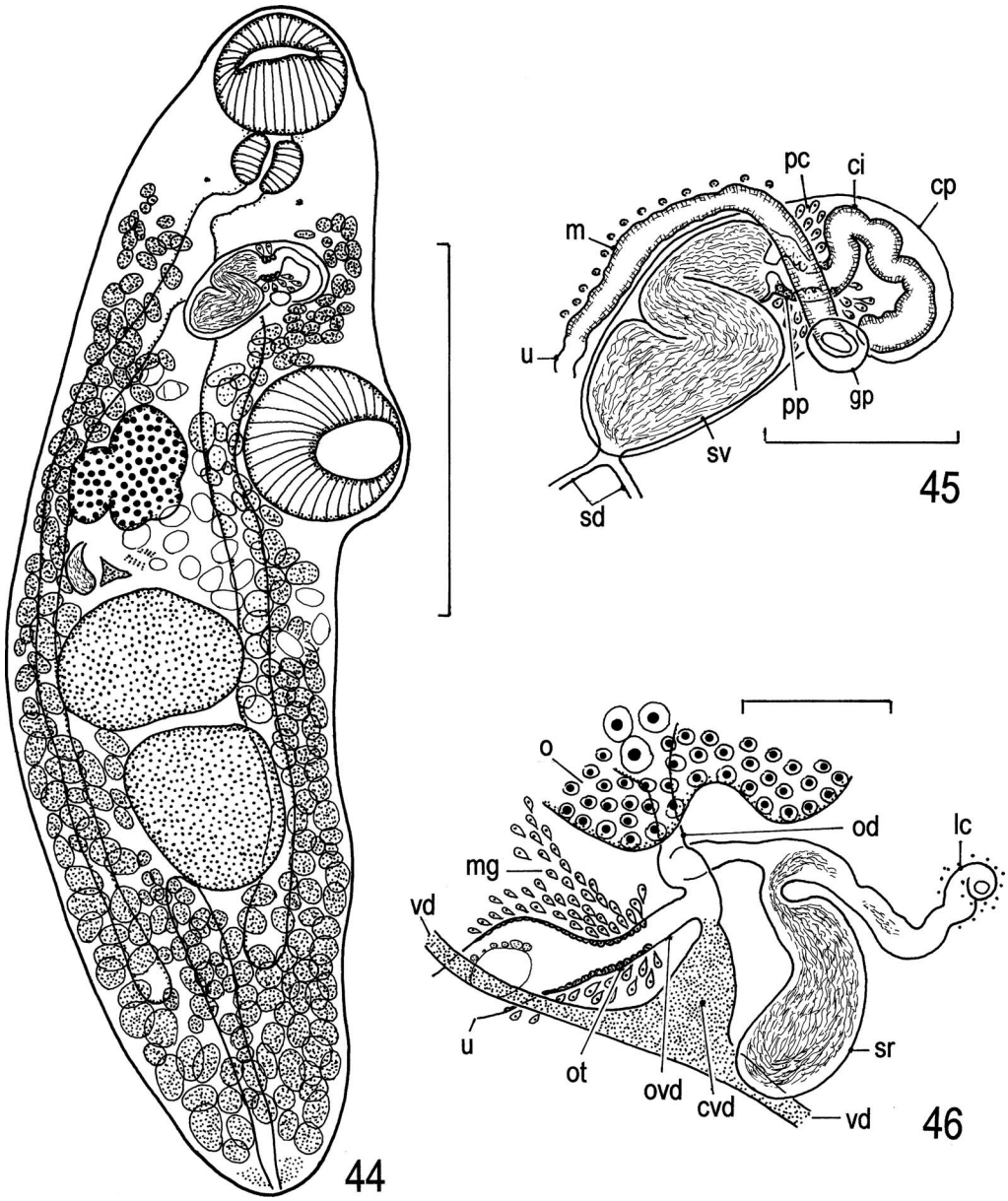
Site of infection. Intestine.

Collecting locality. Nishiyama.

Materials examined. Two mature specimens (LBM 8-26) found in the intestine of *Tanakia lanceolata* from Nishiyama on 26 April 2001.

Description. Similar to *Allocreadium gotoi* (this paper) in general morphology. Body elongate, fairly small, 3.20–3.56 by 0.88–0.94; forebody 1.17–1.20 long, occupying 33–36% of body length. Eyespot pigment solid on either side of forebody. Oral sucker globular, 0.32–0.34 by 0.36. Prepharynx very short. Pharynx broad elliptical, 0.15–0.17 by 0.19–0.20. Esophagus 0.25–0.31 long, bifurcating in front of ventral sucker. Intestines ending in post-testicular region of body. Ventral sucker globular, 0.41 by 0.43, slightly postbifurcal, located at about junction between anterior and second thirds of body; sucker width ratio 1 : 1.22. Testes large, elliptical, somewhat irregular in outline, almost contiguous, in middle third of hindbody; anterior testis 0.37–0.50 by 0.45–0.50, posterior 0.48–0.61 by 0.41–0.42. Cirrus pouch claviform, large, 0.42–0.43 by 0.15–0.17, in front of ventral sucker. Seminal vesicle large, S-shaped, occupying posterior half of cirrus pouch. Pars prostatica pyriform; prostatic cells well developed. Cirrus long. Genital atrium small. Genital pore artificially shifted to left together with ventral sucker (Fig. 45), possibly about bifurcal. Ovary weakly trilobed, 0.35–0.36 by 0.28–0.30, median, overlapping ventral sucker. Seminal receptacle 0.14–0.50 by 0.05. Laurer's canal short. Ootype and Mehlis' gland well developed. Uterus slightly folded between posterior margin of anterior testis and cirrus pouch; metraterm as long as cirrus pouch. Eggs fairly numerous, broad-ovate, bright brown, 80–89 by 57–62 μm. Vitelline follicles distributed from near posterior margin of pharynx to posterior end of body, separate anteriorly, confluent post-testicularly. Excretory vesicle reaching to posterior testis; excretory pore posteroterminal.

Discussion. These specimens resemble *Allocreadium shinanoense* Shimazu, 2003, which Shimazu (2003a) originally described from *Rhynchocypris lagowskii* (Dybowskii) (syn. *Phoxinus*



Figs. 44–46. *Allocreadium* sp. Adult specimen (LBM 8-26) found in the intestine of *Tanakia lanceolata*. 44, entire body, ventral view; 45, terminal genitalia, ventral view; 46, ovarian complex, dorsal view. Scale bars: 1 mm in Fig. 44; 0.2 mm in Fig. 45; 0.1 mm in Fig. 46.

lagowskii steindachneri Sauvage) caught in Iiyama City, Nagano Prefecture. However, they differ from the latter in that the body is smaller, 3.20–3.56 long instead of 3.74–3.80 long; the oral sucker is smaller, 0.32–0.34 by 0.36 instead of 0.38–0.41 by 0.41–0.42; the ventral sucker is smaller, 0.41 by 0.43 instead of 0.55–0.57 by 0.53–0.57; the sucker width ratio is lower, 1 : 1.22 instead of 1 : 1.28–1.35; the testes are larger, 0.37–0.61 by 0.41–0.50 instead of 0.35–0.55 by 0.26–0.44; the ovary is weakly trilobed, instead of globular, and larger, 0.35–0.36 by 0.28–0.30

instead of 0.27–0.33 by 0.33–0.39; the uterus extends posteriorly to the posterior margin of the anterior testis instead of the middle of the posterior testis; and eggs are smaller, 80–89 by 57–62 μm instead of 88–96 by 58–64 μm. Further, they are separated from *A. japonicum* (this paper) by having a more posterior ventral sucker, postbifurcal instead of bifurcal; and a more posterior genital pore, bifurcal instead of prebifurcal. The present specimens remain unidentified until additional specimens are obtained.

Life cycle. The life cycle is not known.

Family **Opecoelidae** Ozaki, 1925

Coitocaecum plagiorchis Ozaki, 1926 (Figs. 47–50)

(?) *Cercaria* No. 16 of Nakagawa, 1915: 117, fig. 16.
(?) *Cercaria distyloides* Faust, 1924: 295; Yoshida and Urabe, 2005: 241.
Coitocoecum plagiorchis Ozaki, 1926: 125–128, no figure; Yoshida and Urabe, 2005: 239, fig. 1a–b.
Coitocaecum plagiorchis: Ozaki, 1929: 77–78, 80–82, figs. 1–3; Yamaguti, 1934: 359–360, fig. 56; Yamaguti, 1939: 218–219; Yamaguti, 192: 351–352, pl. 24, fig. 1; Shimazu, 1988b: 6–7, figs. 1–4; Shimazu, 2000: 18–19, figs. 1–4.
Ozakia plagiorchis: Wiśniewski, 1934: 36–38.

Previous records. From *Gymnogobius urotaenia* (syn. *Chaenogobius annularis urotaenia* Hilgendorf) of Lake Biwa and Onoe (Yamaguti, 1939; Shimazu, 1988b, 2000), from *G. isaza* (syn. *Ch. isaza* Tanaka) of Onoe (Shimazu, 1988b, 2000), from "Small Goro" of Lake Biwa (Shimazu, 1988b, 2000), from *Pelteobagrus nudiceps* of Lake Biwa and Onoe (Yamguti, 1939; Shimazu, 1988b, 2000), and from *Cottus reinii* (syn. *Cottus ohmiensis* Watanabe) of Onoe (Shimazu, 1988b, 2000).

Hosts. *Anguilla japonica*, *Cottus reinii*, *Gymnogobius isaza*, "Small Goro" [most likely referring to *G. isaza*], *G. urotaenia*, *Odontobutis obscura*, *Pelteobagrus nudiceps*, *Rhinogobius* sp. BW, and *Tridentiger brevispinis*.

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

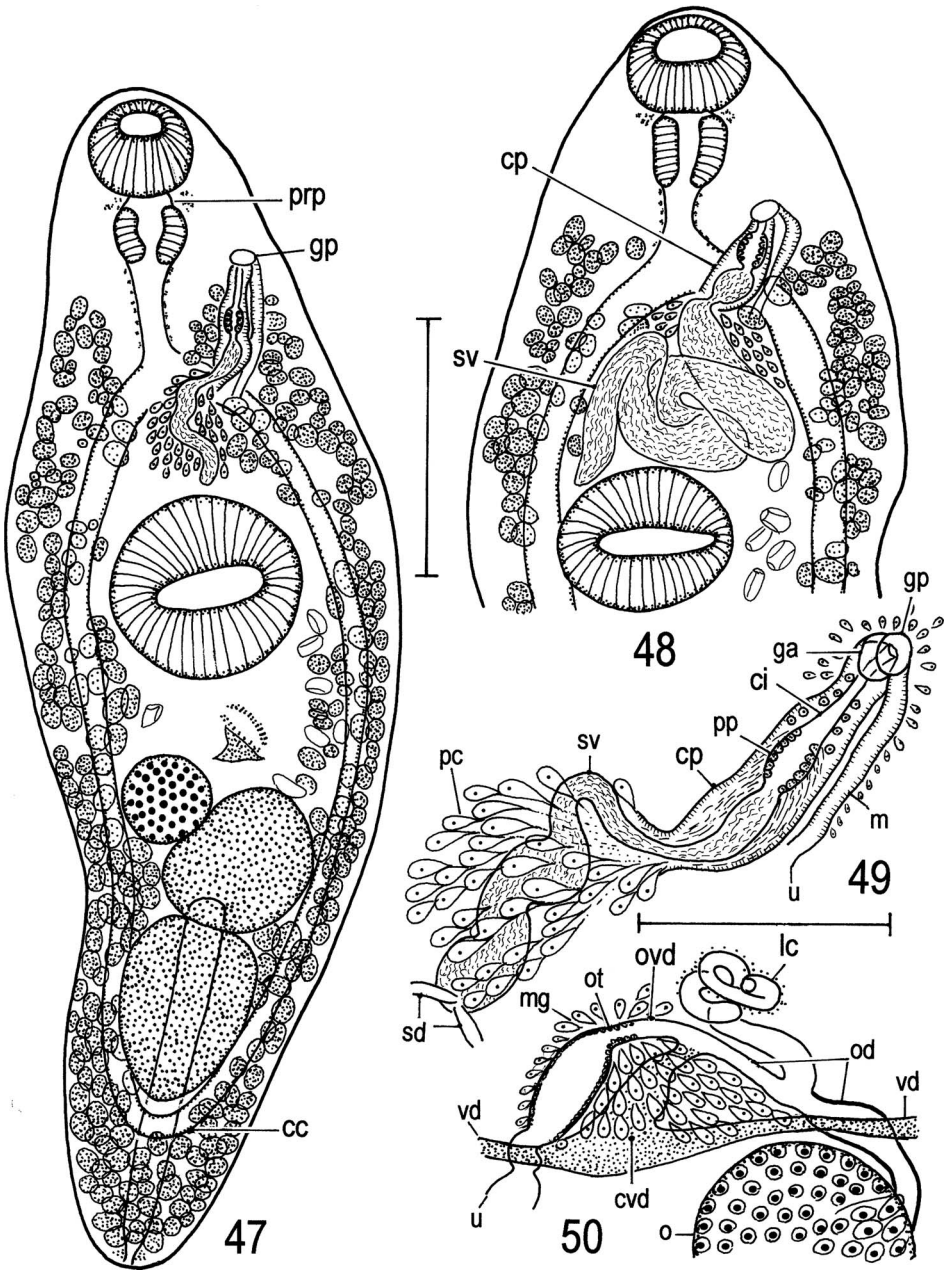
Collecting localities. Lake Biwa, Hachiyadohama, Hamabun, Imazu, Kusano River, Mano River, Momose, Onoe, Ukawa River, Uso River, and Wani.

Materials examined. (1) Specimens found in the intestine of *Gymnogobius urotaenia* (syn. *Ch. annularis urotaenia*): two mature (Yamaguti's Collection, MPM Coll. No. 22587) from Lake Biwa on 3 December 1938 (Yamaguti, 1939; Shimazu, 1988b, 2000), and two immature (NSMT-Pl 3105 and 3106) from Onoe on 4 February and 6 June 1980 (Shimazu, 1988b, 2000). (2) Three immature specimens (LBM 1-60 to -62) found in the stomach of *G. urotaenia* from Imazu on 19 May 1998. (3) Two immature specimens (NSMT-Pl 3104) found in the intestine of *G. isaza* (syn. *Ch. isaza*) from Onoe on 6 June 1980 (Shimazu, 1988b, 2000). (4) Specimens found in the intestine and rectum of *G. isaza*: two immature (LBM 1-26 from the intestine) from Hachiyadohama on 14 May 1998, 21 (LBM 1-27 and -28 from the intestine, LBM 1-29 from the rectum, and LBM 3-32 from the intestine) from Imazu on 19 May 1998 and 5 May 2000, and six immature (LBM 6-15, -16, -18 to -20, and -29 from the intestine, hot formalin-fixed, collected and identified as C. plagiorchis by Tomáš Scholz) from Momose on 1 May 2001. (5) One immature and two mature specimens (Ozaki's Collection, MPM Coll. No. 30013, labeled "Small GORO [Lake Biwa]", unidentified, unpublished) found in Small Goro from Lake Biwa (other data not given) (Shimazu, 1988b, 2000). (6) Specimens found in the intestine of *Pelteobagrus nudiceps*: two immature (Yamaguti's Collection, MPM Coll. No. 22586) from Lake Biwa on 7 December 1938

(Yamaguti, 1939; Shimazu, 1988b, 2000), one mature (NSMT-Pl 3102) from Onoe on 11 November 1980 (Shimazu, 1988b, 2000), and ten immature and two mature (NSMT-Pl 4614) from Onoe on 4 May 1992 (Shimazu, 2000). (7) One mature specimen (NSMT-Pl 5730, unidentified, collected by Nagasawa) found in the intestine of *P. nudiceps* from Onoe on 4 May 1979. (8) Specimens of *C. plagiorchis* found in the pyloric ceca and intestine of *Cottus reinii* (syn. *Co. ohmiensis*) from Onoe: one immature (NSMT-Pl 3103) on 14 February 1980 (Shimazu, 1988b, 2000), and 12 immature and two mature (NSMT-Pl 4615) on 4 May 1992 (Shimazu, 2000). (9) Specimens found in *Co. reinii*: one immature and three mature (LBM 1-69 from the intestine) from Hachiyadohama on 14 May 1998, one immature (LBM 1-71 from either stomach or intestine) from Imazu on 19 May 1998, one immature and one mature (LBM 8-46 to -47 from the intestine) from the Ukawa River on 25 April 2007, four immature and one mature (LBM 8-49 from intestine) from Wani on 25 April 2007, 36 immature and five mature (LBM 8-40 to -45 from the pyloric ceca and intestine) from Momose on 25 April 2007 and 24 November 2007, and eight immature (LBM 8-48, from the pyloric ceca and intestine) from Onoe on 27 November 2007. (10) One mature specimen (LBM 1-15) found in the "gut" [intestine (?)] of *Odontobutis obscura* from the Kusano River on 28 October 1997. (11) One immature specimen (LBM 1-6) found in the "gut" [intestine (?)] of *Rhinogobius* sp. BW from Imazu on 19 May 1998. (12) Specimens found in *Tridentiger brevispinis*: one immature (LBM 1-53 from the intestine) from Hamabun on 24 October 1997, two mature (LBM 3-38 from the "gut" [intestine (?)]) from Mano on 10 June 1999, one immature (LBM 3-37 from the intestine) from Imazu on 5 May 2000, and one immature (LBM 1340000027 from the "gut" [intestine (?)], collected and identified by Urabe) from the Mano River on 26 August 2003. (13) Nineteen immature specimens (Urabe's personal collection) found in the intestine of *Anguilla japonica* from the Uso River on 16 May 2006.

Description. 1) Yamaguti (1939) and Shimazu (1988b, 2000) described and figured the specimens then available to them, respectively.

2) Based on remaining new, mature specimens; 15 of them measured. Body elliptical to rather fusiform, slightly flat dorsoventrally, small, 1.18–2.30 by 0.48–0.88, not oculate; forebody 0.43–1.04 long, occupying 36–49% of total body length. Tegument smooth. Oral sucker round, 0.14–0.20 by 0.12–0.23, ventroterminal. Prepharynx very short, surrounded by small gland cells. Pharynx barrel-shaped, 0.07–0.13 by 0.07–0.15. Esophagus thick-walled, short, 0.06–0.20 long, surrounded by small gland cells, bifurcating at about halfway between two suckers. Intestines distally united to form cyclocoel near posterior end of body. Ventral sucker transversely elliptical, usually larger but rarely smaller than testes, 0.22–0.36 by 0.26–0.37; sucker width ratio 1 : 1.45–2.35. Testes two, globular to elliptical, entire, diagonal to nearly tandem, contiguous, usually in front of cyclocoel; anterior testis 0.13–0.28 by 0.20–0.31, posterior 0.17–0.38 by 0.19–0.34. Sperm ducts two, long; common sperm duct absent. Cirrus pouch thick-walled, muscular, 0.09–0.25 by 0.03–0.09, sinistrally submedian, in front of or overlapping shoulder of left intestine, enclosing short, tubular internal seminal vesicle, elliptical pars prostatica, a few prostatic cells, and short cirrus surrounded by small gland cells; its flap-like posterior end with structure suggestive of rupture of this part. External seminal vesicle tubular, long, undulating, rarely voluminous (Fig. 48), 0.10–0.94 by 0.05–0.12, located between intestinal bifurcation and ventral sucker. Prostatic cells present mostly around external seminal vesicle. Genital atrium small. Genital pore sinistrally submedian, at about level of posterior border of pharynx. Ovary single, globular to triangular, 0.13–0.17 by 0.10–0.19, dextrally submedian, usually anterolateral or lateral to but rarely in front of anterior (or left) testis. Ovarian complex preovarian. Laurer's canal long, convoluted to open dorsally to exterior behind ventral sucker. Ootype vesicular, large. Mehlis'



Figs. 47–50. *Coitocaecum plagiorchis*. Adult specimens. 47, specimen (LBM 8-41) found in the intestine of *Cottus reinii*, entire body, ventral view; 48, specimen (LBM 1-15) found in the intestine of *Odontobutis obscura*, forebody, showing voluminous seminal vesicle, ventral view; 49, specimen (LBM 8-41), terminal genitalia, ventral view; 50, specimen (LBM 8-41), ovarian complex, dorsal view. Scale bars: 0.5 mm in Fig. 47–48; 0.2 mm in Figs. 49–50.

gland well developed. Uterus coiled several times between anterior testis and ventral sucker, between intestines and slightly overlapping them; metraterm about half as long as cirrus pouch. Eggs fairly numerous, elliptical, brown, 53–72 by 30–43 μm (collapsed), not embryonated, with

small operculum. Vitellaria follicular, follicles extending along intestines from behind pharynx to posterior end of body, separate anteriorly, confluent posteriorly. Excretory vesicle I-shaped, extending forward to anterior testis; excretory pore posteroterminal.

Discussion. Ozaki (1926) described a new species, *Coitocoecum plagiorchis*, with no figure, based on adult specimens found in the stomach and intestine of *Odontobutis obscura* (syn. *Mogurnda obscura*) from Saijo, now Shaijo-cho, Higashihiroshima, Hiroshima Prefecture. It is believed that the holotype (No. P. 235) was lost(see Materials and Methods). The rest of Ozaki's original specimens have not yet been reexamined. When Ozaki (1929) redescribed and figured this species, he changed *Coitocoecum* Nicoll, 1915 to *Coitocaecum* Nicoll, 1915 in the generic diagnosis without mentioning the reason. We here use this subsequent spelling of the generic name, following Shimazu (2008).

Yamaguti (1939) and Shimazu (1988b, 2000) reported the adult specimens, as *Coitocaecum plagiorchis*, found in *G. isaza* (including the fish "Small Goro"), *G. urotaenia*, *P. nudiceps*, and *Co. reinii* from Lake Biwa and Onoe. All of the present new specimens are identified as *C. plagiorchis* because they are very similar in morphology to the former specimens.

Life cycle. Yoshida and Urabe (2005) experimentally studied the life cycle of *Coitocoecum plagiorchis* in Fukuoka and Oita prefectures, Kyushu, Japan. Natural first intermediate hosts were pleurocerid snails, *Semisulcospira libertina*, *S. reiniana* (Brot), and their hybrid, in which cotylomicrocercous cercariae with a two-pointed stylet developed in cylindrical daughter sporocysts. The second intermediate host (natural and experimental) was an atyid shrimp, *Neocaridina denticulata* (de Haan) (Japanese name: Minami-numaebi), in which metacercariae encysted. The intestines were not yet differentiated in cercariae, but the cyclocoel was observed in 15-day-old experimental metacercariae. Natural final hosts were *Coreoperca kawamebari* (Temminck and Schlegel) (Japanese name: Oyanirami) (Sinipercidae), *Odontobutis obscura*, *Rhinogobius flumineus*, and *Rhinogobius* sp.

Yoshida and Urabe (2005) referred to their cercaria as *Cercaria distyloides* Faust 1924 with hesitation. Their identification is somewhat questionable, because it was *Cercaria* No. 16 of Nakagawa, 1915 (with a one-pointed stylet) from Taiwan that Faust (1924) originally named *Ce. distyloides*, as has been pointed out by Shimazu (2008). Although Ito (1964) assigned several records of cotylomicrocercous cercariae with a two-pointed stylet from *S. libertina* in Japan to *Ce. distyloides*, this treatment is also considered to be problematic.

Yamaguti (1942) succeeded in experimentally infecting metacercariae obtained from the palaemonid shrimp *Palaemon paucidens* de Haan (syn. *Leander paucidens* (de Haan)) (Japanese name: Sujiebi) to *Odontobutis obscura* (syn. *Mogurnda obscura*). Komiya (1965) and Shimazu (1988a, 2000) gathered the records of metacercariae of *C. plagiorchis* from Japan and China.

Urabe (2003) found *Ce. distyloides* in *S.* (*Biwamelania*) *decipiens* from the Lake Biwa basin. Metacercariae (LBM 8-57 and -58) were found in the body muscles of *Palaemon paucidens* from North Lake on 31 October 1997.

Neoplagioporus elongatus (Goto and Ozaki, 1930) (Figs. 51–61)

Lebouria elongata Goto and Ozaki, 1930: 75, fig. 2.
Plagioporus elongata [sic; should be *elongatus*]: Price, 1934: 6.
Caudotestis orientalis Yamaguti, 1934: 288–289, fig. 19.
Caudotestis gnathopogonis Yamaguti, 1934: 290–292, fig. 20.
Plagioporus (*Caudotestis*) *elongatus*: Yamaguti, 1954 [not 1953]: 76.
Plagioporus (*Caudotestis*) *gnathopogonis*: Yamaguti, 1954 [not 1953]: 76.

Plagioporus (*Caudotestis*) *orientalis*: Yamaguti, 1954 [not 1953]: 76.
Plagioporus (*Plagioporus*) *elongatus*: Skryabin and Koval', 1958: 459, fig. 148.
Plagioporus (*Plagioporus*) *orientalis*: Skryabin and Koval', 1958: 494, 497–498, figs. 163 and 163a.
Plagioporus orientalis: Koval', 1959: 129.
Neolebouria elongatus [sic; should be *elongata*]: Gibson, 1976: 252.
Neoplagioporus elongatus: Shimazu, 1990b: 393–394, figs. 10–17.

Previous records. From *Sarcocheilichthys variegatus* of Lake Biwa, as *Lebouria elongata* (Goto and Ozaki, 1930) and as *Neoplagioporus elongatus* (Shimazu, 1990b); from *Gnathopogon elongatus elongatus* (syn. *Gnathopogon elongatus* (Temminck and Schlegel)) of Lake Biwa, as *Caudotestis gnathopogonis* (Yamaguti, 1934) and as *N. elongatus* (Shimazu, 1990b); and from *Hemibarbus barbus*, *S. variegatus microoculus*, and *Tribolodon hakonensis* of Onoe, as *N. elongatus* (Shimazu, 1990b).

Hosts. *Biwia zezera*, *Gnathopogon elongatus elongatus*, *Gymnogobius isaza*, *Hemibarbus barbus*, *H. labeo*, *Pseudogobio esocinus esocinus*, *Pungtungia herzi*, *Rhinogobius flumineus*, *Rhinogobius* sp. BW, *Sarcocheilichthys variegatus*, *S. variegatus microoculus*, *Squalidus chankaensis biwae*, *Sq. japonicus japonicus*, *Tribolodon hakonensis*, and *Tridentiger brevispinis*.

Site of infection. Intestine.

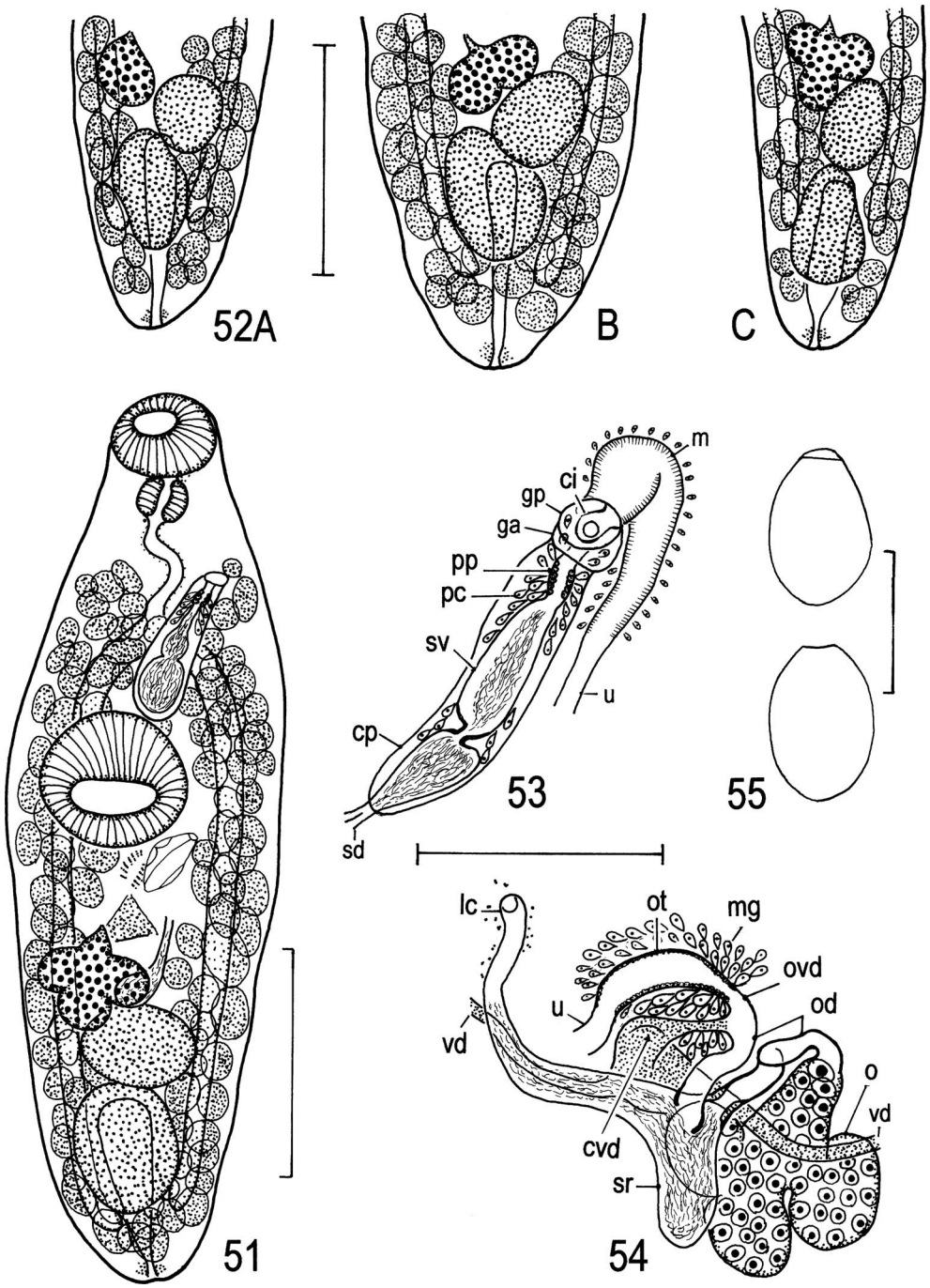
Collecting localities. Lake Biwa, Daido River, Hachiyadohama, Harie River, Imazu, Mano, Momose, Moriyama, Omatsu, Onoe, Seta River-1, and Yasu River.

Materials examined. (1) Seventy-five [not 74] specimens (Ozaki's Collection, MPM Coll. No. 30024, labeled "*Lebouria* HIGAI") found in *Sarcocheilichthys variegatus* (other data not given) (Shimazu, 1990b): 73 of *elongatus* type and two of *orientalis* type. (2) One immature and one mature specimens (Yamaguti's Collection, MPM Coll. No. 22631, labeled "*Caudotestis*", unpublished, of *orientalis* type) found in *S. variegatus* from Lake Biwa on 3 December 1938 (site of infection not given) (Shimazu, 1990b). (3) Specimens (NSMT-Pl 3628–3630) found in the intestine of *S. variegatus microoculus* from Onoe on 4 May and 3 June 1980 and 29 November 1983 (Shimazu, 1990b): 50 mature (and possibly ten immature) of *elongatus* type, and 63 mature (and possibly two immature) of *orientalis* type. (4) Specimens of *orientalis* type found in the intestine of *S. variegatus microoculus*: 17 mature (and possibly one immature) (NSMT-Pl 5731 and 5732, collected by Shimazu) from Moriyama on 1 and 2 May 1992, three mature (LBM 3-24 and -27) from Imazu on 5 May 2000, two mature (LBM 3-46) from the Harie River on 19 October 2000, and 26 mature (and possibly six immature) (LBM 8-37 to -39) from Momose on 24 November 2007. (5) One mature specimen (Yamaguti's Collection, MPM Coll. No. 22220, "Type", or the holotype, of *Caudotestis gnathopogonis*, of *orientalis* type) found in the intestine of *Gnathopogon elongatus elongatus* (syn. *G. elongatus*) from Lake Biwa on 13 March 1932 (Yamaguti, 1934; Shimazu, 1990b). (6) Thirty-three mature specimens (NSMT-Pl 3631, of *orientalis* type) of found in the intestine of *Hemibarbus barbus* from Onoe on 3 June 1980 (Shimazu, 1990b). (7) Specimens found in the intestine of *H. barbus*: one mature of *elongatus* type and some 450 mature (and possibly 33 immature) (NSMT-Pl 5733, hot formalin-fixed, collected by Shimazu) of *orientalis* type from Moriyama on 2 May 1992, 41 mature (and possibly six immature) (NSMT-Pl 3976 and 5734, collected by Shimazu) of *orientalis* type from Onoe on 4 May 1992, three mature (LBM 1-51) of *orientalis* type from Hachiyadohama on 14 May 1998, ten mature (and possibly three immature) (LBM 7-26 and -27) of *orientalis* type Momose on 1 May 2001, and 21 mature (and possibly one immature) (LBM 7-28 to -30) of *orientalis* type from Imazu on 1 May 2001. (8) Five mature specimens (LBM 5-43 to -47, hot formalin-fixed, collected and identified as *N. elongatus* by Tomáš Scholz) of *orientalis* type found in the intestine of *H.*

labeo from the Seta River-1 on 1 May 2001. (9) One mature specimen (NSMT-Pl 3632, of *orientalis* type) found in the intestine of *Tribolodon hakonensis* from Onoe on 3 June 1980 (Shimazu, 1990b). (10) Two mature specimens (LBM 1-75) of *orientalis* type found in the intestine of *Biwia zezera* from Hachiyadohama on 14 May 1998. (11) Specimens found in the intestine of *Pseudogobio esocinus esocinus*: two mature (LBM 1-30) of *elongatus* type from the Yasu River on 18 October 1997, and one mature (LBM 1-31) of *orientalis* type from Hachiyadohama on 14 May 1998. (12) Three mature specimens (LBM 3-42, -43, and -45) of *elongatus* type found in the intestine of *Pungtungia herzi* from the Yasu River on 14 October 2000. (13) One mature specimen (NSMT-Pl 5735, collected by Shimazu) of *orientalis* type found in the intestine of *Squalidus chankaensis biwae* from Omatsu on 1 May 1992. (14) Four mature specimens (and possibly 1 immature) (LBM 1-14) of *orientalis* type found in the intestine of *Sq. japonicus japonicus* from Hachiyadohama on 14 May 1998. (15) One mature specimen (NSMT-Pl 3977, collected by Shimazu) of *orientalis* type found in the intestine of *Gymnogobius isaza* from Omatsu on 30 April 1992. (16) Eleven immature specimens (LBM 3-18 and -20 to -23) possibly of *orientalis* type found in the intestine of *Rhinogobius flumineus* from the Daido River-2 on 1 May 2000. (17) Seven mature specimens (LBM 1-7 to -9) of *orientalis* type found in the "gut" of *Rhinogobius* sp. BW from Imazu on 19 May 1998. (18) Specimens of *orientalis* type found in *Tridentiger brevispinis*: one mature (NSMT-Pl 3978 from the intestine, collected by Shimazu) from Omatsu on 5 May 1992, one mature (LBM 3-38, from the "gut" [intestine (?)]) from Mano on 10 June 1999, and one mature (LBM 1340000023, collected and identified as *N. elongatus* by Urabe, from the "gut" [intestine (?)]) from Imazu on 10 July 2002.

Description. 1) For earlier descriptions and figures of *N. elongatus* (including *L. elongata*) from Lake Biwa, see Goto and Ozaki (1930), Yamaguti (1934), and Shimazu (1990b).

2) Ozaki's specimens of *elongatus* type (MPM Coll. No. 30024, 73 mature) from *S. variegatus*; ten large ones of them measured (Figs. 51–52). Body elongate-oblong, small, 0.96–1.45 by 0.29–0.61, not oculate; forebody 0.40–0.61 long, occupying 40–45% of total body length. Tegument smooth. Oral sucker subterminal, 0.10–0.13 by 0.12–0.16. Prepharynx very short, surrounded by small gland cells. Pharynx barrel-shaped, 0.05–0.06 by 0.06–0.08. Esophagus fairly long, undulating, 0.09–0.14 long, surrounded by small gland cells, bifurcating midway between pharynx and ventral sucker. Intestines distally terminating blindly in testicular zone (in 70 specimens, Figs. 52A and C, eggs 79–113 by 36–63 μm) or in post-testicular region (in three specimens, Figs. 51 and 52B, ovary two- or three-lobed, eggs 92–113 by 39–63 μm). Ventral sucker round to transversely elliptical, 0.16–0.22 by 0.19–0.21, slightly pre-equatorial; sucker width ratio 1 : 1.34–1.55. Testes two, globular to elliptical, entire, slightly diagonal, contiguous or slightly separate, in posterior half of hindbody; anterior testis 0.09–0.14 by 0.09–0.16, posterior 0.13–0.19 by 0.10–0.13. Sperm ducts two, long; common sperm duct absent. Cirrus pouch claviform, fairly thick-walled, may be muscular, 0.16–0.25 by 0.05–0.06, lateral or anterolateral to ventral sucker on left side of body, sometimes slightly overlapping ventral sucker. Seminal vesicle internal, divided distinctly into two portions; posterior portion elliptical, thin-walled, larger than anterior; anterior club-shaped, long, thick-walled. Pars prostatica small, globular; prostatic cells well developed. Cirrus short, unarmed, surrounded by small gland cells. Genital atrium small. Genital pore sinistrally submedian, at about middle level of esophagus. Ovary single, globular, two-lobed, or three-lobed (just like four-lobed, Figs. 51 and 52C), 0.09–0.12 by 0.12–0.16, dextrally submedian, usually between intestines or slightly overlapping right intestine, anterolateral to anterior testis. Ovarian complex preovarian. Oviduct connected with seminal receptacle on its way to ovovitelline duct, with sphincter at its pore opening into seminal vesicle. Seminal re-



Figs. 51–55. *Neoplagioporus elongatus*. Adult specimens of *elongatus* type. 51, specimen (MPM Coll. No. 30024) found in *Sarcocheilichthys variegatus*, entire body, ventral view; 52A–C, specimens (MPM Coll. No. 30024), posterior part of body, showing posterior extent of intestines, shape and position of ovary, shape and position of testes, posterior extent of vitelline follicles, and anterior extent of excretory vesicle, ventral view; 53, specimen (NSMT-Pl 3629) found in intestine of *S. v. microoculus*, terminal genitalia, ventral view; 54, specimen (NSMT-Pl 3629), ovarian complex, dorsal view; 55, specimen (NSMT-Pl 3629), uterine eggs. Scale bars: 0.3 mm in Figs. 51–52; 0.2 mm in Figs. 53–54; 0.1 mm in Fig. 55.

ceptacle canalicular, club-shaped, 0.16–0.19 by 0.05–0.07, lying obliquely in front of anterior testis. Laurer's canal fairly long, dorsally opening to exterior near left intestine. Ootype vesicular, large; Mehlis' gland well developed. Uterus coiled a few times between anterior testis and ventral sucker, between intestines; metraterm about half as long as cirrus pouch. Eggs small in number, broad elliptical, bright brown, 79–113 by 36–63 μm (collapsed), not embryonated; operculum small, domed or collapsed. Vitellaria follicular, follicles rather large, distributed from middle level of esophagus to near posterior end of body (Figs. 51 and 52A–C), confluent anteriorly and posteriorly, separate midway. Excretory vesicle I-shaped, anteriorly ending dorsally to posterior testis or rarely reaching barely to anterior testis; excretory pore posteroterminal.

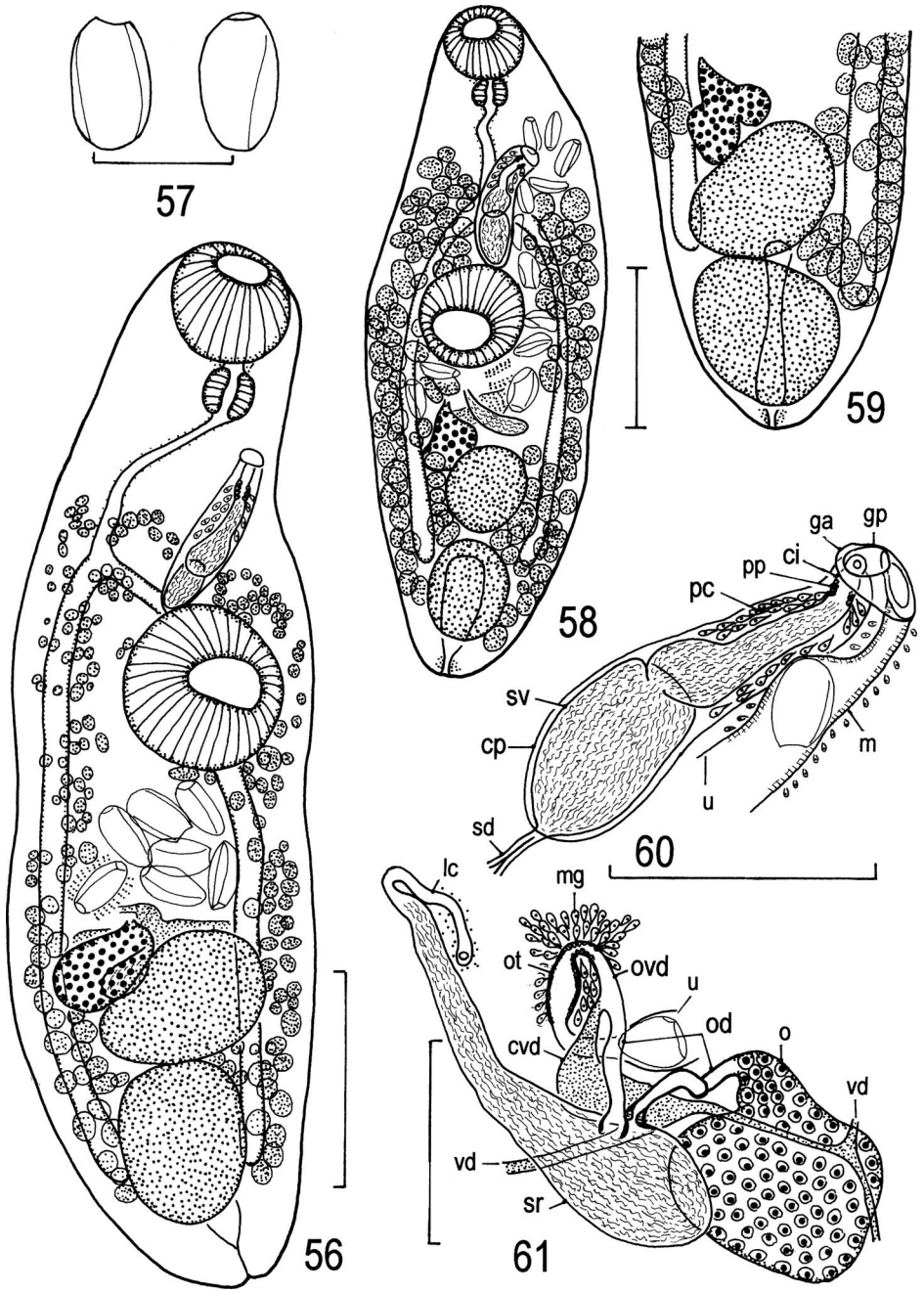
3) Remaining specimens of *elongatus* type; ten large, mature ones of Shimazu's (1990b) specimens (NSMT-Pl 3629, 50 mature) from *S. variegatus microoculus* measured (Figs. 53–55). Body 1.41–1.71 by 0.46–0.52; forebody 0.59–0.72 long, occupying 41–45% of total body length. Oral sucker 0.12–0.14 by 0.15–0.16. Pharynx 0.06–0.08 in diameter. Esophagus 0.12–0.20 long. Intestines terminating in testicular zone. Ventral sucker 0.22–0.26 by 0.22–0.24; sucker width ratio 1 : 1.37–1.58. Testes contiguous; anterior testis 0.18–0.21 by 0.12–0.19, posterior 0.20–0.27 by 0.14–0.19. Cirrus pouch 0.22–0.31 by 0.04–0.07. Ovary 0.13–0.19 by 0.16–0.22. Seminal receptacle 0.17–0.28 by 0.05–0.06. Eggs 88–94 by 43–64 μm. Vitelline follicles extending posteriorly into post-testicular region of body but not reaching to posterior end of body. Excretory vesicle extending to anterior testis.

Among the hot formalin-fixed specimens (NSMT-Pl 5733) from *H. barbus* was found a mature one of *elongatus* type, in which both the intestines and vitelline follicles extended into the post-testicular region and eggs were 76–79 by 43–46 μm.

4) The holotype of *Caudotestis gnathopogonis* (MPM Coll. No. 22220, one mature), of *orientalis* type, from *G. e. elongatus* (Figs. 56–57). Body 1.42 by 0.40; forebody 0.64, occupying 45% of total body length. Oral sucker 0.16 by 0.17. Pharynx 0.07 by 0.06. Intestines ending at about middle level of posterior testis. Ventral sucker 0.22 in diameter; sucker width ratio 1 : 1.29. Testes 0.17–0.22 by 0.21, posterior testis slightly anterior to posterior end of body. Cirrus pouch 0.23 by 0.06. Ovary elliptical 0.17 by 0.11. Seminal receptacle 0.13–0.04. Eggs seven, 88–98 by 40–54 μm; operculum domed or collapsed. Vitelline follicles distributed posteriorly nearly to posterior border of posterior testis. Excretory vesicle not clearly observed.

5) Ozaki's specimens of *orientalis* type (MPM Coll. No. 30024, two mature) from *S. variegatus* (Fig. 58). Body 1.33–1.63 by 0.45–0.58; forebody 0.62–0.69, occupying 42–47% of total body length. Oral sucker 0.14–0.16 by 0.15–0.17. Pharynx 0.06–0.07 by 0.06–0.08. Intestines extending to posterior testis. Ventral sucker 0.20–0.24 by 0.20–0.27; sucker width ratio 1 : 1.33–1.58. Testes 0.18–0.26 by 0.21–0.26. Cirrus pouch 0.23–0.28 by 0.08–0.09. Ovary two- or three-lobed, elliptical 0.13–0.15 by 0.12-0.19. Seminal receptacle 0.14–0.19 by 0.03–0.06. Eggs 71–87 by 36–54 μm; operculum domed or collapsed. Vitelline follicles distributed posteriorly to posterior border of posterior testis. Excretory vesicle ending dorsally to posterior testis.

6) Remaining specimens of *orientalis* type; ten large, mature ones of Shimazu's (1990b) specimens (NSMT-Pl 3629, 73 mature) from *S. variegatus microoculus* measured (Figs. 59–61). Body 1.38–2.80 by 0.46–0.77; forebody 0.56–1.07 long, occupying 33–47% of total body length. Oral sucker 0.12–0.20 by 0.15–0.22. Pharynx 0.05–0.09 by 0.07–0.08. Esophagus 0.16–0.28 long. Intestines terminating in testicular zone. Ventral sucker 0.22–0.31 by 0.21–0.31; sucker width ratio 1 : 1.27–1.46. Testes entire, globular to elliptical, usually contiguous but rarely separated by vitelline follicles, posterior testis sometimes located close to posterior end of body; anterior testis 0.25–0.42 by 0.19–0.34, posterior 0.22–0.53 by 0.19–0.19. Cirrus pouch 0.22–0.31 by



Figs. 56–61. *Neoplagioporus elongatus* (continued). Specimens of *orientalis* type. 56, holotype (MPM Coll. No. 22220) of *Caudotestis gnathopogonis* found in the intestine of *Gnathopogon elongatus elongatus*, entire body, ventral view; 57, holotype, uterine eggs; 58, specimen (MPM Coll. No. 30024) found in *Sarcocheilichthys variegatus*, entire body, ventral view; 59, specimen (NSMT-Pl 3629) found in the intestine of *Sarcocheilichthys variegatus microoculus*, posterior part of body, showing posterior extent of intestines, shape and position of ovary, shape and position of testes, posterior extent of vitelline follicles, and anterior extent of excretory vesicle, ventral view; 60, specimen (NSMT-Pl 3629), terminal genitalia, ventral view; 61, specimen (NSMT-Pl 3629), ovarian complex, dorsal view. Scale bars: 0.3 mm in Figs. 56 and 58–59; 0.2 mm in Figs. 60–61; 0.1 mm in Fig. 57.

0.04–0.07. Ovary globular, two or three-lobed, 0.11–0.25 by 0.12–0.25. Seminal receptacle 0.22–0.47 by 0.05–0.12. Eggs 67–86 by 37–51 μm; operculum usually domed but rarely collapsed. Vitelline follicles distributed posteriorly into testicular zone but not into post-testicular region of body. Excretory vesicle extending forward barely to anterior testis.

Posterior testis sometimes located close to posterior extremity of body in flattened specimens; but slightly apart from posterior extremity, leaving small post-testicular region behind it in hot formalin-fixed specimens. Uterine eggs 72–92 by 45–51 μm in specimens (NSMT-Pl 5733) from *H. barbus*.

Discussion. Goto and Ozaki (1930) described a new species, *Lebouria elongata*, from adult specimens found in the intestine of *Sarcocheilichthys variegatus* (Japanese name: Higai) from Lake Biwa. They did not designate the holotype for this species. *Lebouria elongata* is the only species that they reported as an adult digenean species from *S. variegatus* of Lake Biwa. Moreover, Ozaki himself did not report any species of *Lebouria* from *S. variegatus* (Shimazu, 1995b). Ozaki's specimens labeled "*Lebouria* HIGAI" are most likely part of Goto and Ozaki's original material (Shimazu, 1990b), namely syntypes; but there is no definite evidence to support this. We here tentatively include them as adult specimens from Lake Biwa. Shimazu (1990b) described and figured them under the species name *Neoplagioporus elongatus* (Goto and Ozaki, 1930).

In Goto and Ozaki's time, the fish Higai in Lake Biwa was recognized as a single species, *S. variegatus*; but it has since been divided into two species, *S. variegatus microoculus* and *S. biwaensis*. It cannot be determined at present which of them is the type host of *L. elongata*.

Yamaguti (1934, pp. 288–290) described a new species, *Caudotestis orientalis*, from *S. variegatus* of Lake Ogura in Kyoto Prefecture and *Pseudogobio esocinus esocinus* (syn. *P. esocinus* Temminck and Schlegel) of the Yodo River (locality not specified) (see also Shimazu, 1990b). Yamaguti (1934, pp. 290–292) added another new species, *Caudotestis gnathopogonis*, on the basis of two mature specimens found in *Gnathopogon elongatus elongatus* (syn. *G. elongatus*) from Lake Biwa. Yamaguti's Collection includes only one specimen (holotype, MPM Coll. No. 22220) of *C. gnathopogonis* at present. Yamaguti (1934) separated *C. gnathopogonis* from *C. orientalis* by a collapsed operculum of the eggshell in *C. gnathopogonis*. However, both collapsed and domed opercula exist in the holotype (Figs. 56–57) and in the other specimens here examined (Figs. 55 and 60). The domed condition is considered normal; and the collapsed condition, an artifact. We agree with Skryabin and Koval' (1958) and Shimazu (1990b) that *C. gnathopogonis* is a synonym of *C. orientalis*.

Yamaguti (1934) merely stated that *C. orientalis* differed distinctly from *Lebouria elongata* in the posterior extent of the intestines and vitelline follicles. From Goto and Ozaki (1930) and Yamaguti (1934), this seems to mean that the intestines and vitelline follicles end posteriorly in the testicular zone of the body in *C. orientalis* but at or near the posterior end of the body in *Lebouria elongata*. With regard to the posterior extent of the vitelline follicles, we consider that this is correct. However, the intestines end in the testicular zone or in the post-testicular region even in Ozaki's specimens (Figs. 51–52). Examining the specimens available to him at that time, Shimazu (1990b) concluded that *C. orientalis* is a junior synonym of *L. elongata*. He placed this species in his new genus, *Neoplagioporus*, as *N. elongatus* (Goto and Ozaki, 1930).

Nevertheless, the present specimens can be tentatively classified into two types, as follows. (1) Specimens of *elongatus* type: vitelline follicles extending posteriorly into post-testicular region of body, and eggs 88–112 by 43–67 μm. (2) Specimens of *orientalis* type: vitelline follicles ending posteriorly in testicular zone of body, and eggs 67–98 by 34–54 μm. These two types are similar in other morphological features: posterior extent of intestines, shape and position of

testes, shape and position of ovary, anterior extent of excretory vesicle, and others. Immature specimens cannot be classified because of lack of sufficiently differentiated vitelline follicles and uterine eggs.

In *Lebouria elongata*, Goto and Ozaki (1930, fig. 2) described the intestines as "ending near the posterior end of the body", the ovary as "with 4–6 peripheral lobes", eggs as "0.09–0.098 × 0.057–0.06 mm", and the vitelline follicles as "extending from . . . to the posterior end of the body". The present Ozaki's 75 mature specimens included (1) three specimens of *elongatus* type, in which both the intestines and vitelline follicles extended into the post-testicular region; (2) 70 of *elongatus* type, in which the intestines ended in the testicular zone, but the vitelline follicles extended into the post-testicular region; and (3) two of *orientalis* type, in which both the intestines and vitelline follicles ended in the testicular zone. The ovary was globular, two-lobed, or three-lobed (just like four-lobed). Eggs measured 71–113 by 36–63 μm (collapsed). If Ozaki's specimens are really part of Goto and Ozaki's original specimens of *L. elongata*, Goto and Ozaki seem to have used only a few, morphologically exceptional specimens with the above-mentioned characteristics for their description and to have overlooked the two specimens of the *orientalis* type.

In flattened specimens of the *orientalis* type, the posterior testis is sometimes close to the posterior extremity of the body (Fig. 59); but, in hot formalin-fixed specimens, it is slightly apart from the posterior extremity. It seems likely that flattening before fixation in the former specimens caused the posterior testis to shift a little posteriorly. Although it is possible that the above-mentioned differences between the two types are intraspecific variations (Shimazu, 1990b), further critical studies are desirable to clarify whether they are significant enough to warrant the recognition of two separate species.

Neoplagioporus elongatus is readily distinguished from the next two species, *N. zacconis* (Yamaguti, 1934) Shimazu, 1990 and *Neoplagioporus* sp. by that the body shape is elongate-oblong instead of broad-ovate.

Life cycle. The life cycle is not known.

Neoplagioporus zacconis (Yamaguti, 1934) (Figs. 62–64)

Caudotestis zacconis Yamaguti, 1934: 292–293, fig. 21; Yamaguti, 1938: 20, plate-fig. 1; Yamaguti, 1942: 332–333.
Plagioporus (*Caudotestis*) *zacconis*: Yamaguti, 1954 [not 1953]: 76.
Plagioporus (*Plagioporus*) *zacconis*: Skryabin and Koval', 1958: 533
Neoplagioporus zacconis: Shimazu, 1990b: 387–388, figs. 1–5; Urabe and Shimazu, 2005: 7–8, figs. 11–14; Shimazu, 2008: 56, fig. 11.

Previous record. None.

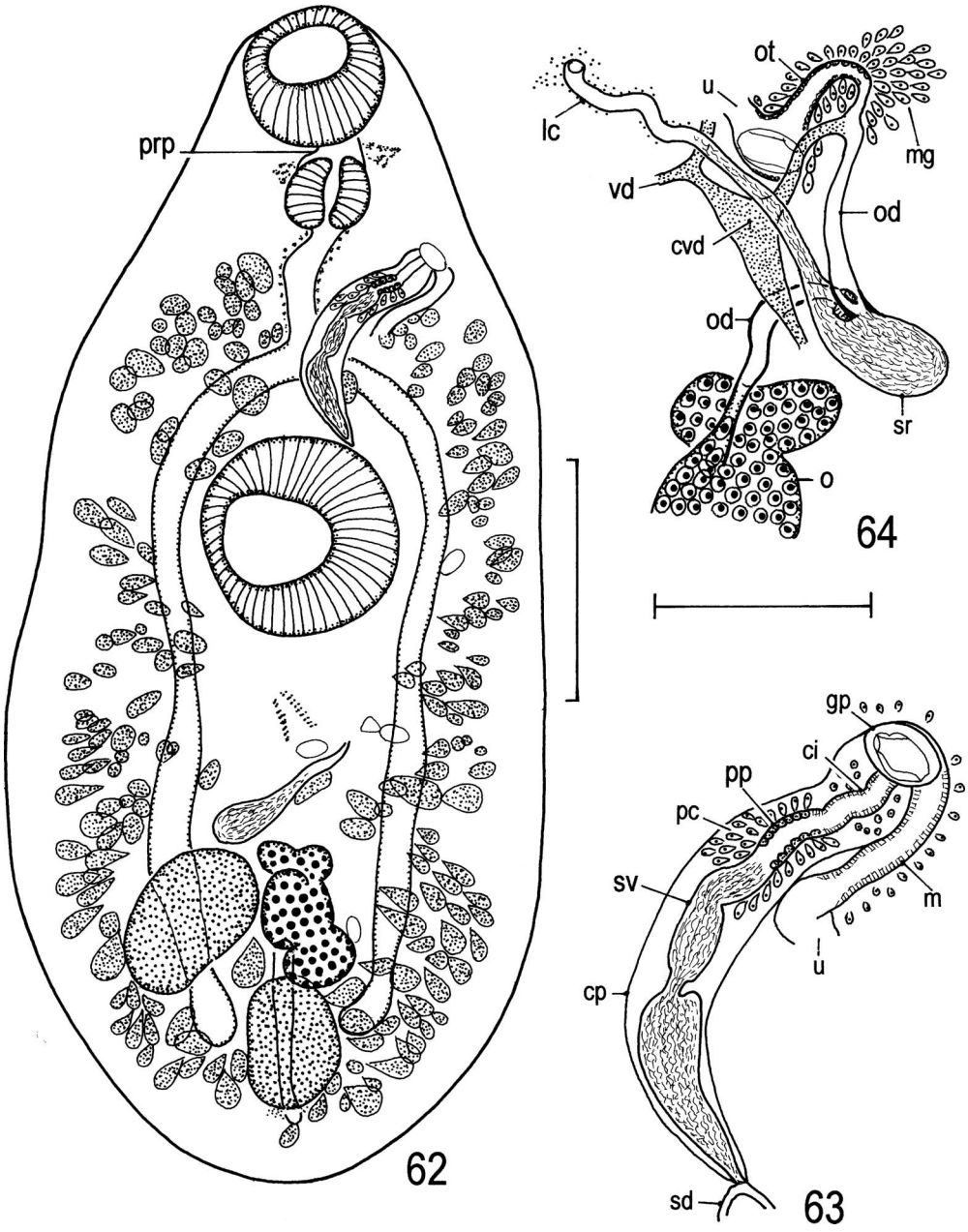
Host. *Zacco platypus*.

Site of infection. Intestine.

Collecting locality. Yasu River.

Materials examined. (1) Two immature specimens (LBM 1-54) found in the intestine of *Zacco platypus* from the Yasu River on 18 October 1997. (2) Twelve immature and one mature specimens (LBM 7-33) found in the rectum (?) of *Z. platypus* from Uji Power Station pond located on the north bank of the Uji River about 600 m upstream from the Ujibashi bridge at Yamada, Uji City, Kyoto Prefecture, on 2 February 2001.

Description. Since the two specimens from the Yasu River were immature, one mature specimen from Uji Power Station pond is described and figured herein for the convenience of



Figs. 62–64. *Neoplagioporus zacconis.* Adult specimen (LBM 7-33) found in intestine of *Zacco platypus*. 65, entire body, ventral view; 66, terminal genitalia, ventral view; 67, ovarian complex, dorsal view. Scale bars: 0.5 mm in Fig. 65; 0.2 mm in Figs. 66–67.

presenting the adult morphology. Similar to *Neoplagioporus elongatus* (this paper) in general morphology. Body broad-ovate, small, 2.53 by 1.12; forebody 1.12 long, occupying 44% of total body length. Oral sucker subterminal, 0.28 by 0.30. Prepharynx very short. Pharynx barrel-shaped, 0.16 by 0.17. Esophagus curved, 0.27 long, bifurcating about midway between pharynx and ventral sucker. Intestines terminating at middle level of posterior testis (some distance in

front of posterior end of body). Ventral sucker round, large, 0.44 by 0.42, slightly pre-equatorial; sucker width ratio 1 : 1.40. Testes transversely elliptical, oblique, separated by vitelline follicles, near posterior end of body; anterior (or right) testis 0.34 by 0.23, posterior 0.29 by 0.20. Sperm ducts long; common sperm duct absent. Cirrus pouch claviform, fairly thick-walled, may be muscular, 0.42 by 0.09, anterior to ventral sucker. Seminal vesicle distinctly divided into two portions; posterior portion elliptical; anterior club-shaped, long. Pars prostatica small, globular; prostatic cells well developed. Cirrus short. Genital atrium small. Genital pore near pharyngeal level. Ovary deeply three-lobed, 0.20 by 0.34, almost median, immediately medial (or sinistral) to anterior testis. Seminal receptacle 0.31 by 0.08. Laurer's canal passing almost transversely. Ootype and Mehlis' gland well developed. Uterus coiled a few times in field between ovary, ventral sucker, and intestines, slightly overlapping left intestine; metraterm about half as long as cirrus pouch. Eggs small in number, light brown, 61–66 by 34–40 μm (collapsed). Vitelline follicles distributed from middle level of esophagus to posterior end of body, encircling intestines, leaving free space in peripheral, lateral, and posterior margins on either side of body, anteriorly separate, posteriorly confluent. Excretory vesicle extending forward to middle level of anterior testis; excretory pore dorsal, near posterior end of body.

In immature specimens (0.56–1.06 long), ovary globular, transversely elongated, slightly two or three-lobed; and located median or submedian on right side of anterior testis.

Discussion. Yamaguti (1934) originally described *Caudotestis zacconis* as a new species based on adult specimens found in the intestine of *Zacco platypus* from the Asago River in Hyogo Prefecture. Shimazu (1990b) proposed a new genus, *Neoplagioporus*, with *C. zacconis* as the type species.

In the present mature specimen (Fig. 62), the ovary was located unusually on the left side of the anterior testis. The ovary is either median and pretesticular or submedian. When submedian, it is usually located on the right side of the anterior testis (Yamaguti, 1934, 1938, 1942; Shimazu, 1990b), as is seen in the present immature specimens.

Neoplagioporus zacconis is separated from the next species *Neoplagioporus* sp. (this paper) mainly by lacking the vitelline follicles in the peripheral, lateral, and posterior spaces. Shimazu and Urabe (2005) have found this species in *Z. platypus* from the Uji River at Uji City.

Life cycle. The life cycle is not known.

Neoplagioporus sp. (Figs. 65–67)

Previous record. None.

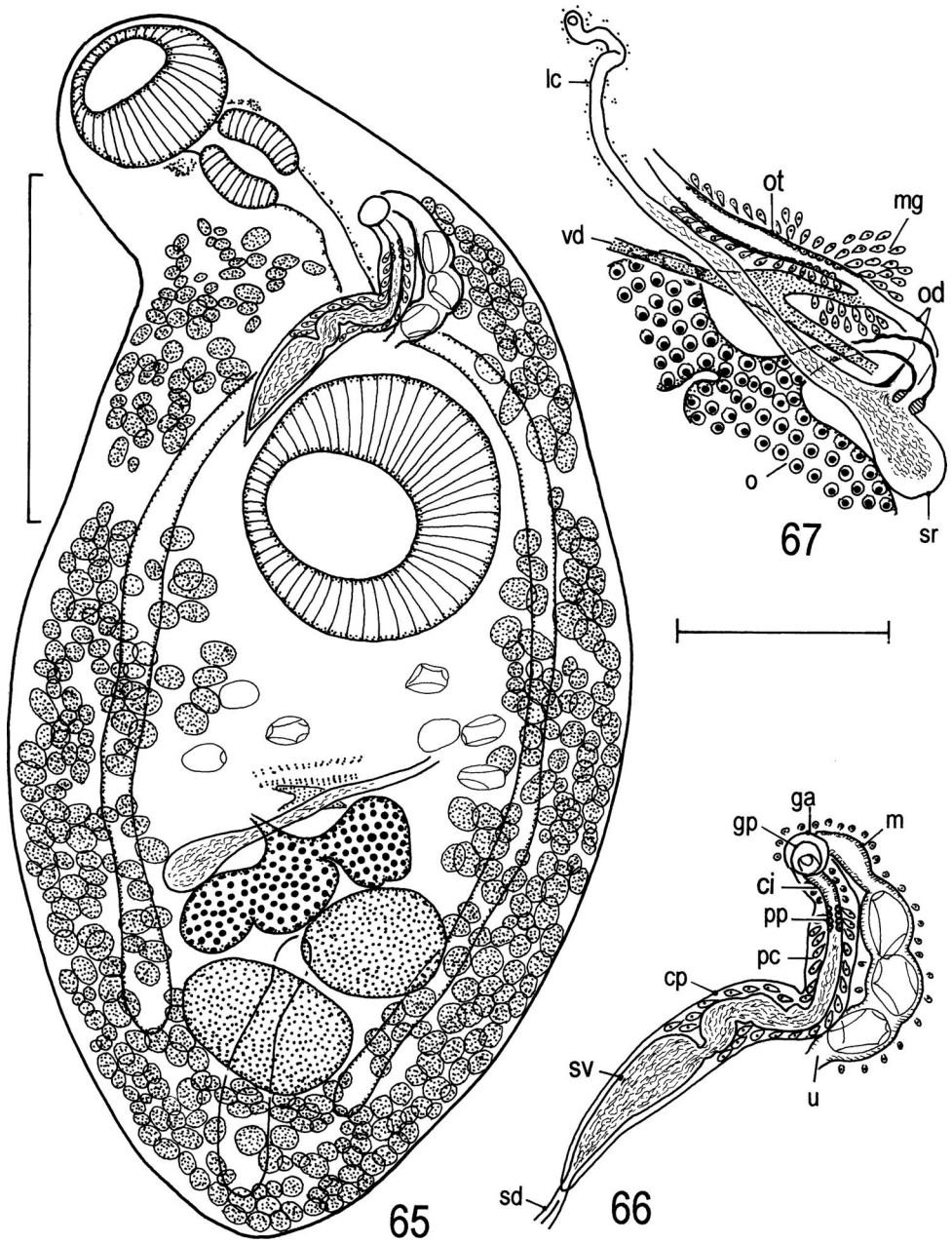
Host. *Odontobutis obscura*.

Site of infection. Rectum.

Collecting locality. Mano-ono

Material examined. One mature specimen (LBM 3-28) found in the rectum of *Odontobutis obscura* from Mano-ono on 3 May 2000.

Description. Similar to *Neoplagioporus elongatus* (this paper) in general morphology. Body broad-ovate, small, 1.84 by 0.88; forebody 0.80 long, occupying 43% of body length. Oral sucker subterminal, 0.20 by 0.22. Prepharynx very short. Pharynx barrel-shaped, 0.16 by 0.12. Esophagus 0.14 long, bifurcating in front of ventral sucker; intestines distally terminating at level of posterior border of posterior testis (or some distance in front of posterior extremity of body). Ventral sucker round, large, 0.39 by 0.37, slightly pre-equatorial; sucker width ratio 1 : 1.68. Testes transversely elliptical, diagonal, almost contiguous, in third fourth of hindbody; anterior



Figs. 65–67. *Neoplagioporus* sp. Adult specimen (LBM 3-28) found in rectum of *Odontobutis obscura*. 62, entire body, ventral view; 63, terminal genitalia, ventral view; 64, ovarian complex, dorsal view. Scale bars: 0.5 mm in Fig. 62; 0.2 mm in Figs. 63–64.

(or left) testis 0.16 by 0.20, posterior 0.17 by 0.27. Sperm ducts long; common sperm duct absent. Cirrus pouch claviform, fairly thick-walled, muscular, 0.41 by 0.06, anterior to ventral sucker. Seminal vesicle bipartite; posterior portion elliptical; anterior club-shaped, long. Pars prostatica small, globular; prostatic cells well developed. Cirrus short. Genital atrium small. Genital pore at middle level of esophagus. Ovary deeply three-lobed, 0.17 by 0.38, almost median, immediate-

ly in front of anterior testis. Seminal receptacle 0.44 by 0.06. Laurer's canal passing forward. Ootype and Mehlis' gland well developed. Uterus coiled a few times in field encircled ovary, ventral sucker, and intestines; metraterm about half as long as cirrus pouch. Eggs small in number, broad elliptical to broad-ovate, brown, 58–69 by 38–45 μm (collapsed). Vitelline follicles distributed from pharynx to posterior end of body, encircling intestines, filling up lateral and posterior fields of body, anteriorly slightly separate, posteriorly confluent. Excretory vesicle extending forward to middle of anterior testis; excretory pore almost dorsal, near posterior end of body.

Discussion. This specimen resembles the foregoing species *N. zacconis* in having a broad-ovate body but differs from the latter in having the vitelline follicles filling up even the peripheral lateral and posterior spaces instead of being absent from these spaces. It remains unidentified.

Life cycle. The life cycle is not known.

Urorchis acheilognathi Yamaguti, 1934 (Figs. 68–73)

Urorchis acheilognathi Yamaguti, 1934: 415–417, figs. 81–82; Yamaguti, 1942: 359; Shimazu, 1990a: 208–209, figs. 9–15.

Previous record. From *Gnathopogon caerulescens* of Lake Biwa (Shimazu, 1990a).

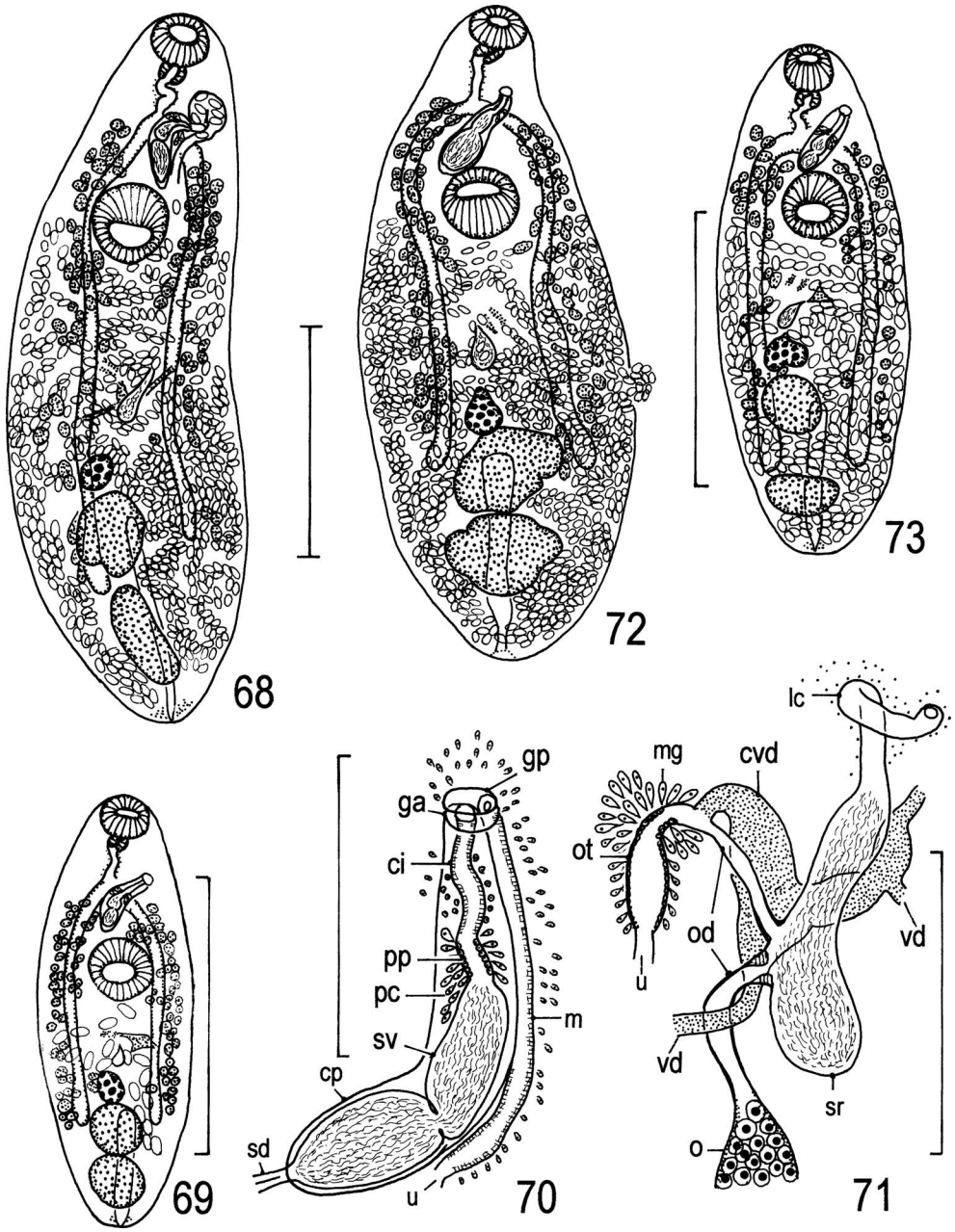
Hosts. *Acheilognathus rhombeus*, *Gnathopogon caerulescens*, and *Tanakia lanceolata*.

Site of infection. Intestine.

Collecting localities. Lake Biwa, Kame-ga-ike Pond, Miyake, Nishiyama, and Tai.

Materials examined. (1) One mature specimen (Yamaguti's Collection, MPM Coll. No. 22014, labeled "*Urorchis goro*", unpublished) found in the intestine of *Gnathopogon caerulescens* from Lake Biwa on 26 May 1936 (Shimazu, 1990a). (2) Specimens found in the intestine of *Tanakia lanceolata*: two mature (LBM 3-49 and -50) from Miyake on 27 October 2000, and four immature and nine mature (LBM 7-31 and 8-26, -52, and -53) from Nishiyama on 26 April 2001 and 27 November 2007. (3) Two mature specimens (LBM 1-38) found in the intestine of *Acheilognathus rhombeus* from Kame-ga-ike Pond on 17 May 1998.

Description. 1) Based on 11 mature specimens from *T. lanceolata*; ten of them measured (Figs. 68–71). Body elongate-oval, slightly flattened dorsoventrally, small, 2.03–3.36 by 0.72–1.12, not oculate; forebody 0.75–1.12 long, occupying 28–40% of total body length. Tegument smooth. Oral sucker spherical, 0.16–0.25 by 0.18–0.26, subterminal. Prepharynx very short, surrounded by small gland cells. Pharynx barrel-shaped, 0.08–0.09 by 0.06–0.11. Esophagus straight or curved, 0.16–0.33 long, surrounded by small gland cells, bifurcating about midway between two suckers. Intestines long, ending blindly in testicular zone of body. Ventral sucker subglobular, 0.24–0.34 by 0.25–0.33, located at about junction between anterior and middle thirds of body; sucker width ratio 1 : 1.20–1.42. Testes two, irregular in outline, median, tandem, contiguous, in posterior third of hindbody (or considerably anterior to posterior end of body) in fully matured specimens (Fig. 68); anterior testis 0.31–0.42 by 0.17–0.34, posterior 0.22–0.47 by 0.17–0.34. Sperm ducts two, long; common sperm duct absent. Cirrus pouch clavate, curved, thin-walled, 0.25–0.56 by 0.08–0.09, in front of ventral sucker or slightly overlapping it posteriorly. Seminal vesicle internal, distinctly bipartite. Pars prostatica elliptical, small; prostatic cells well developed. Cirrus fairly long, surrounded by small gland cells, sometimes everted slightly. Genital atrium small, shallow, surrounded by small gland cells. Genital pore sinistrally submedian, slightly anterior to bifurcal level. Ovary single, globular to ovate, 0.12–0.25 by 0.12–0.20, almost median, immediately pretesticular. Ovarian complex preovarian. Oviduct connected with seminal receptacle on its way to ovovitelline duct, with sphincter at its pore opening into seminal



Figs. 68–73. *Urorchis acheilognathi*. Adult specimens. 68, fully matured specimen (LBM 8-52) found in intestine of *Tanakia lanceolata*, entire body, ventral view; 69, weakly matured specimen (LBM 8-53) found in intestine of *T. lanceolata*, entire body, ventral view; 70, specimen (LBM 7-31) found in intestine of *T. lanceolata*, terminal genitalia, ventral view; 71, specimen (LBM 8-52), ovarian complex, dorsal view; 72, fully matured specimen (LBM 1-38) found in intestine of *Acheilognathus rhombeus*, entire body, ventral view; 73, fully mature specimen (MPM Coll. No. 22014) found in intestine of *Gnathopogon caerulescens*, entire body, ventral view. Scale bars: 1 mm in Figs. 68–69 and 72–73; 0.3 mm in Fig. 71; 0.2 mm in Fig. 70.

receptacle. Seminal receptacle canalicular, clavate, long, 0.11–0.20 by 0.08–0.11. Laurer's canal fairly long, running forward, curved or coiled to open dorsally to exterior. Ootype vesicular, large. Mehlis' gland well developed. Uterus occupying all available space of hindbody in fully mature specimens, one or two uterine loops descending into post-testicular region of body to elongate this region posteriorly on either side of body; metraterm well developed, about two-thirds as long as cirrus pouch, surrounded by small gland cells. Eggs numerous, elliptical, light brown, 64–80 by 32–43 μm (collapsed), thin-shelled, with small operculum, fully embryonated. Vitellaria follicular, follicles sparse, distributed along intestines between bifurcal level and intestinal ends, separate. Excretory vesicle I-shaped, extending forward to near anterior border of anterior testis; excretory pore posterodorsal.

In immature and barely mature specimens, testes globular to subglobular, large, and close to posterior end of body (Fig. 69).

2) Based on three mature specimens from *G. caerulescens* and *A. rhombeus* (Figs. 72–73). Body 1.84–2.88 by 0.69–1.17; forebody 0.59–0.88 long, occupying 28–32% of total body length. Oral sucker 0.13–0.20 by 0.17–0.24. Pharynx 0.06–0.11 in diameter. Esophagus 0.08–0.19 long. Ventral sucker 0.25–0.31 by 0.23–0.33; sucker width ratio 1 : 1.33–1.37. Testes two, contiguous or separated by descending inner uterine loops; anterior testis 0.23–0.37 by 0.19–0.48, posterior 0.16–0.34 by 0.26–0.50. Cirrus pouch 0.26–0.47 by 0.07–0.15. Ovary 0.13–0.20 by 0.12–0.16. Seminal receptacle 0.12–0.19 by 0.08–0.12. Eggs 61–73 by 35–45 μm (collapsed).

Discussion. *Urorchis acheilognathi* was described as a new species by Yamaguti (1934) from adult specimens found in the intestine of *Tanakia lanceolata* (syn. *Acheilognathus intermedia* (Temminck and Schlegel)) from Lake Ogura, Kyoto Prefecture, and *A. cyanostigma* Jordan and Fowler (Japanese name: Ichimonji-tanago) from Lake Kobata [not Kohata] in Uji City, Kyoto Prefecture (Shimazu, 1990a). Shimazu (1990a) redescribed this species from the type series, Yamaguti's specimen (MPM Coll. No. 22014) from *G. caerulescens* of Lake Biwa, and others. The present new specimens from *A. rhombeus* and *T. lanceolata* agree well with *U. acheilognathi* as originally described by Yamaguti (1934) and redescribed by Shimazu (1990a).

Yamaguti (1934) merely stated that *U. acheilognathi* differed from *U. goro* Ozaki, 1927 (see the next species) distinctly in the characters of the eggs. This may refer to the fact that the elliptical eggs are 84–90 by 51–54 μm in *U. acheilognathi* (Yamaguti, 1934) but 63–72 by 38–42 μm with a small knoblike projection at the antiopecular pole in *U. goro* (Ozaki, 1927). Shimazu (1990a) showed that *U. acheilognathi* is separated from *U. goro* not by egg size but instead by other morphological features: a broader body, longer intestines entering the testicular zone of the body, a lower sucker width ratio, smaller testes sometimes separated by the uterus, a longer cirrus, more sparsely distributed vitelline follicles, and a longer excretory vesicle reaching to the anterior border of the anterior testis.

Yamaguti's Collection also includes an adult specimen (MPM Coll. No. 22626) found in the intestine of *G. caerulescens* from Lake Biwa. Shimazu (1990a) regarded it as *U. acheilognathi*, but it will be dealt with as *Urorchis* sp. below.

Acheilognathus rhombeus is a new host record for the species.

Life cycle. The life cycle is not known.

Urorchis goro Ozaki, 1927 (Figs. 74–77)

Urorchis goro Ozaki, 1927: 160–163, figs. 5–7; Shimazu, 1990a: 205–207, figs. 1–8; Shimazu, 2005: 141, fig. 5.

Previous record. None.

Hosts. *Cottus reinii*, *Gymnogobius urotaenia*, *Rhinogobius flumineus*, *Rhinogobius* sp. OR, and *Tridentiger brevispinis*.

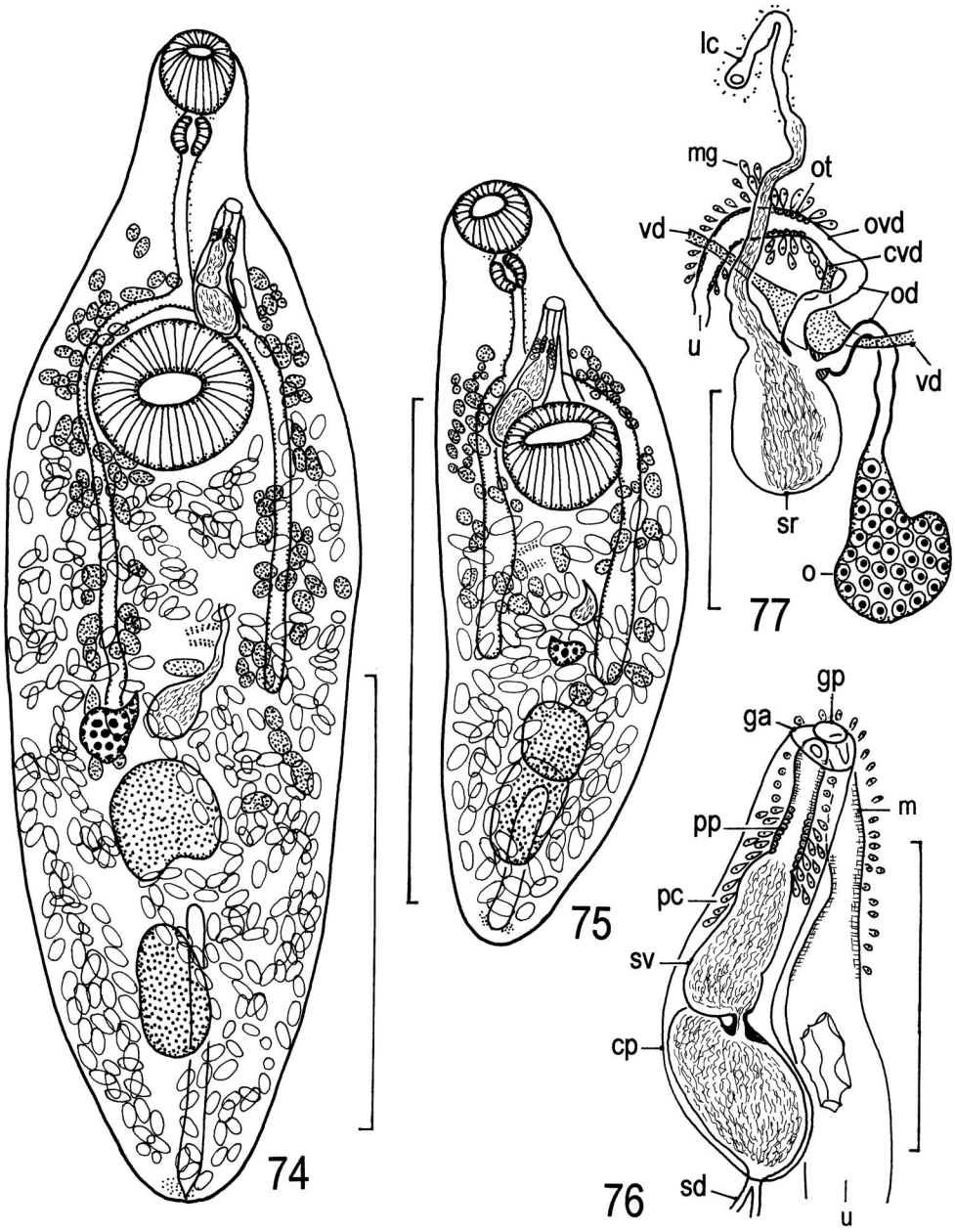
Site of infection. Primarily intestine, and also stomach and rectum (accidental (?)).

Collecting localities. Daido River-2, Harie River, Imazu, Kame-ga-ike Pond, and Yasu River.

Materials examined. (1) Specimens found in *Rhinogobius* sp. OR: one mature (LBM 1-4 from intestine) from the Yasu River on 18 October 1997, and three mature (LBM 3-53 from rectum) from the Harie River on 19 October 2000. (2) Specimens found in *Gymnogobius urotaenia*: one mature (LBM 1-66 from stomach) from Kame-ga-ike Pond on 17 May 1998, and two immature (LBM 3-56 from "gut" [intestine (?)]) from the Harie River on 19 October 2000. (3) One immature and one mature specimens (LBM 3-17 and -19) found in the intestine of *Rhinogobius flumineus* from the Daido River-2 on 1 May 2000. (4) Specimens found in *Tridentiger brevispinis* from Imazu: one mature (LBM 3-37 from intestine) on 5 May 2000, one mature (LBM 1340000024, collected and misidentified as *Genarchopsis goppo* by Urabe, site of infection not given [intestine (?)]), and one mature (LBM 1340000025, collected and identified as *U. goro* by Urabe, site of infection not given [intestine (?)]) on 1 August 2002. (5) Seven mature specimens (LBM 3-39) found in the intestine of *Cottus reinii* from Imazu on 5 May 2000.

Description. Based on 15 mature specimens; ten of them measured. Similar to *Urorchis acheilognathi* (this paper) in general morphology. Body elongate-oval, small, 1.60–2.60 by 0.54–0.80; forebody 0.56–0.88 long, occupying 30–38% of total body length. Oral sucker round, 0.15–0.22 by 0.16–0.23, subterminal. Prepharynx very short. Pharynx barrel-shaped, 0.07–0.11 by 0.08–0.12. Esophagus straight or winding, 0.19–0.30 long, bifurcating in front of ventral sucker. Intestines short, usually ending pretesticularly but rarely extending slightly into testicular zone of body. Ventral sucker subglobular, 0.23–0.39 by 0.26–0.39, located slightly behind junction between anterior and middle thirds of body; sucker width ratio 1 : 1.40–2.11. Testes globular to elliptical, usually contiguous but rarely separated slightly by uterus, located at about junction between middle and posterior thirds of hindbody (or some distance from posterior extremity of body) in fully mature specimens but near posterior extremity in immature and barely mature specimens; anterior testis 0.12–0.31 by 0.19–0.31, posterior 0.17–0.37 by 0.09–0.33. Cirrus pouch clavate, curved, 0.30–0.39 by 0.06–0.11, slightly overlapping ventral sucker posteriorly. Seminal vesicle bipartite. Pars prostatica elliptical; prostatic cells well developed. Cirrus short. Genital atrium small. Genital pore at about middle level of esophagus. Ovary globular, oval, two or three-lobed, 0.07–0.19 by 0.11–0.19. Seminal receptacle retort-shaped, 0.15–0.28 by 0.06–0.09. Laurer's canal fairly long. Ootype and Mehlis' gland well developed. Uterus occupying all available space of hindbody in fully mature specimens; metraterm about half as long as cirrus pouch. Eggs numerous, elliptical, light brown, 61–80 by 33–43 μm (collapsed), fully embryonated. Vitelline follicles sparse, distributed along intestines between middle level of esophagus and slightly behind intestinal ends, separate. Excretory vesicle ending at about anterior border of posterior testis; excretory pore posterodorsal.

Discussion. *Urorchis goro* was described by Ozaki (1927) as a new genus and species based on adult specimens found in the intestine of *Tridentiger obscurus* (Temminck and Schlegel) (Japanese name: Chichibu) caught in Lake Kasumigaura in Ibaraki Prefecture and in a swamp near Sendai, Miyagi Prefecture, both in August, 1925. Probably, the holotype (No. P. 260) was lost, as in the case of *Allocreadium hasu*. Ozaki did not indicate which locality the holotype was from, and thus the type locality is ambiguous. The host fish at least from Lake Kasumigaura should have been *T. brevispinis* (see Shimazu, 1995a). The present specimens are identified as *U.*



Figs. 74–77. *Urorchis goro.* Adult specimens. 74, specimen (LBM 1340000025) found in *Tridentiger brevispinis*, entire body, ventral view; 75, specimen (LBM 3-53) found in rectum of *Rhinogobius* sp. OR, entire body, ventral view; 76, specimen (LBM 1340000025), terminal genitalia, ventral view; 77, specimen (LBM 1340000025), ovarian complex, dorsal view. Scale bars: 1 mm in Figs. 74–75; 0.2 mm in Figs. 76–77.

goro according to Ozaki's (1927) original description and Shimazu's (1990a) redescription for this species.

Life cycle. The life cycle is not known.

Urorchis sp. of Shimazu, 1990 (Figs. 78–80)

Urorchis sp. of Shimazu, 1990a: 211, fig. 17.

Previous record. From *Odontobutis obscura* of Lake Biwa (Shimazu, 1990a).

Hosts. *Gnathopogon caerulescens*, *Odontobutis obscura*, and *Tanakia limbata*.

Site of infection. Intestine.

Collecting locality. Lake Biwa.

Materials examined. (1) One mature specimen (Ozaki's Collection, MPM Coll. No. 30023, labeled "[Goppo] [Lake Biwa]", unidentified, unpublished) found in *Odontobutis obscura* from Lake Biwa (other data not given) (Shimazu, 1990a). (2) One mature specimen (Yamaguti's Collection, MPM Coll. No. 22626, labeled "*Urorchis*", unpublished) found in the intestine of *G. caerulescens* from Lake Biwa on 9 July 1927 (Shimazu, 1990a). (3) One mature specimen (LBM 1-37) found in the intestine of *Tanakia limbata* from Tai on 25 October 1997.

Description. Measurements of the specimens from *O. obscura*, *G. caerulescens*, and *A. rhombeus* given in this order. Similar to *Urorchis acheilognathi* (this paper) in general morphology. Body 2.40 by 0.61, 1.76 by 0.64, 1.19 by 0.45; forebody 0.80, 0.46, 0.50 long, occupying 33, 26, 42% of total body length. Oral sucker 0.21 in diameter, 0.13 by 0.15, 0.14 by 0.16. Pharynx 0.10 by 0.09, 0.06 by 0.09, 0.06 by 0.05. Intestines long, extending into post-testicular region of body. Ventral sucker 0.30 by 0.31, 0.25 in diameter, 0.22 by 0.23; sucker width ratio 1 : 1.47, 1.66, 1.43. Testes globular, elliptical, or irregular in outline, 0.17–0.19 by 0.11–0.13, 0.16–0.19 by 0.12, 0.12–0.13 by 0.09–0.11, tandem or diagonal, separate, contiguous, or separated by uterus. Cirrus pouch 0.37 by 0.02, 0.30 by 0.07, 0.17 by 0.06. Cirrus fairly long. Ovary ovate or bilobed, 0.16 in diameter, 0.11 by 0.07, 0.08 in diameter. Uterus occupying all available space of hindbody. Eggs numerous, elliptical, light brown, 72–80 by 32–35, 57–72 by 22–37, 61–83 by 37–51 μm (collapsed). Vitelline follicles scattered, extending along intestines. Excretory vesicle extending to near anterior border of anterior testis; excretory pore posteroterminal.

Discussion. These specimens differ from *U. acheilognathi*, *U. goro*, and *U. imba* Ishii, 1935 in that the intestines are longer, extending into the post-testicular region of the body (Shimazu, 1990a). Shimazu (1990a) misidentified Yamaguti's specimen (MPM Coll. No. 22626, Fig. 79) as *U. acheilognathi*. The present three specimens seem to be different from one another in egg size (Figs. 78–80). They remain unidentified until additional specimens are obtained.

Life cycle. The life cycle is not known.

Family **Orientocreadiidae** Yamaguti, 1958

Orientocreadium pseudobagri Yamaguti, 1934 (Figs. 81–85)

Orientocreadium pseudobagri Yamaguti, 1934: 334–335, fig. 39; Bykhovskaya-Pavlovskaya and Kulakova, 1987: 143, fig. 172; Shimazu, 1990c: 936–937, figs. 4–6.

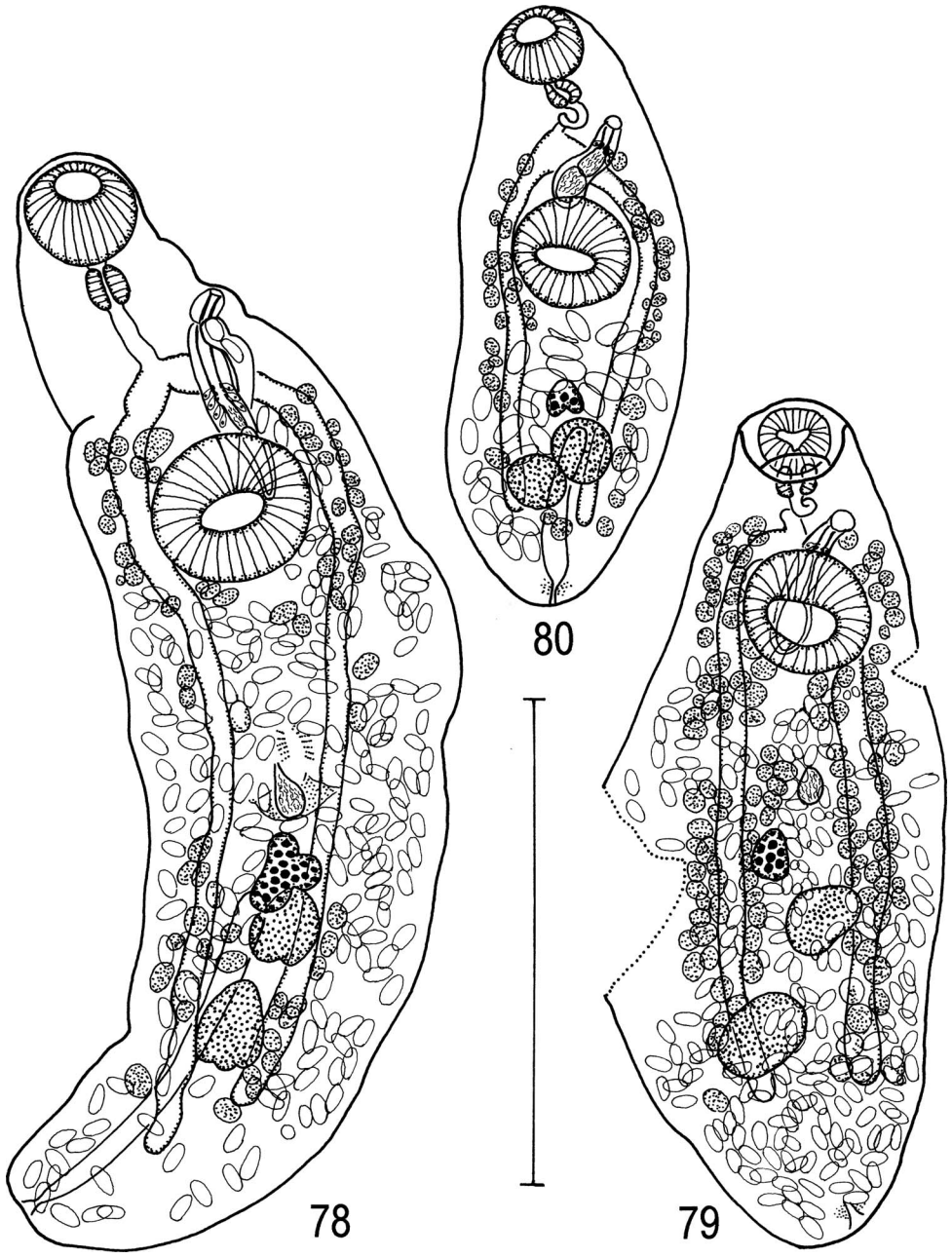
Macroderoides asiaticus Belous in Skryabin and Antipin, 1958: 519–520, fig. 149.

Previous records. From *Pelteobagrus nudiceps* [not *Pseudobagrus aurantiacus* (Temminck and Schlegel)] of Lake Biwa (Yamaguti, 1934; Shimazu, 1990c) and Onoe (Shimazu, 1990c), and *Silurus lithophilus* of Onoe (Shimazu, 1990c).

Hosts. *Pelteobagrus nudiceps* and *Silurus lithophilus*.

Site of infection. Intestine.

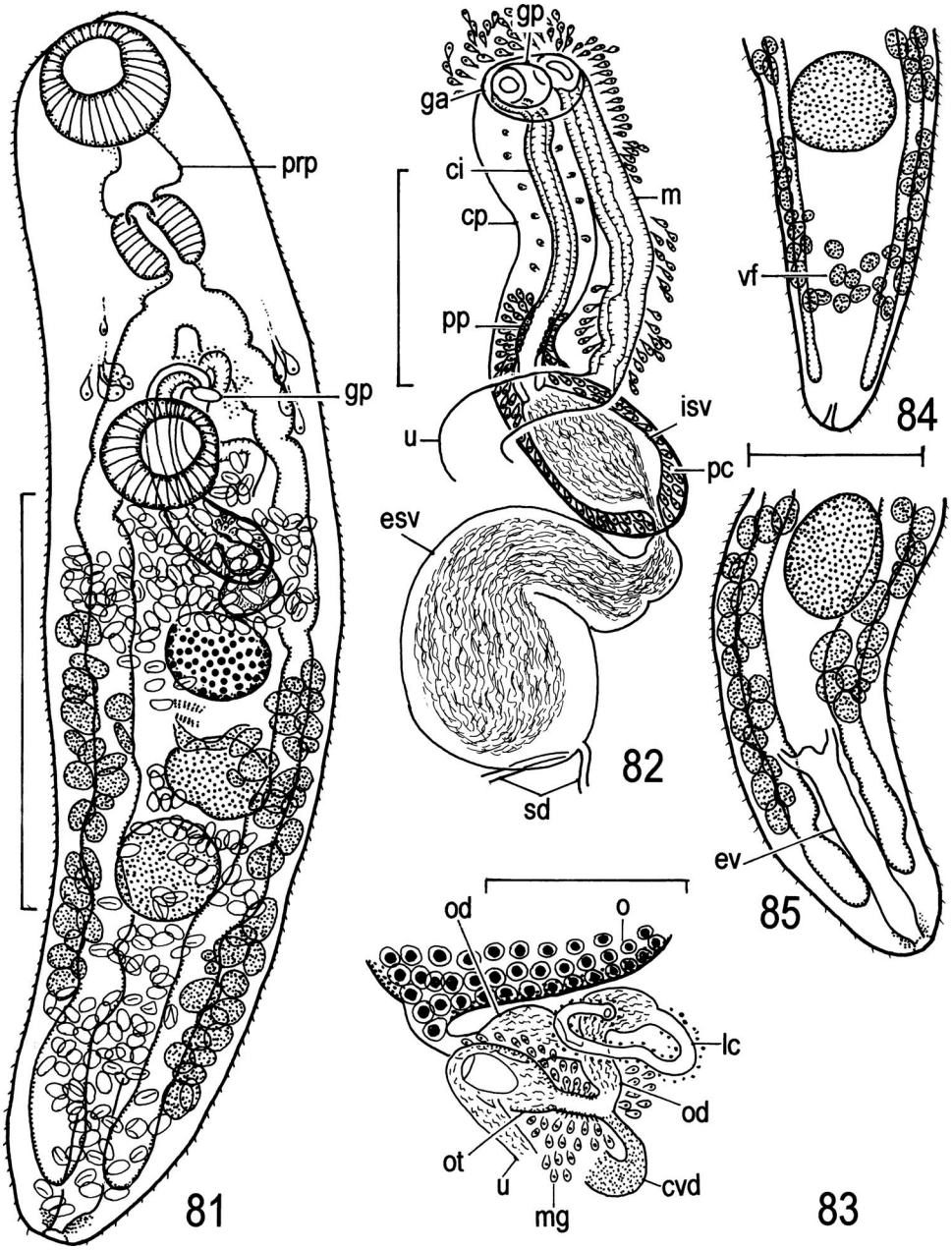
Collecting localities. Lake Biwa and Onoe.



Figs. 78–80. *Urorchis* sp. Adult specimens. 78, specimen (MPM Coll. No. 30023) found in *Odontobutis obscura*, entire body, ventral view; 79, specimen (MPM Coll. No. 22626) found in intestine of *Gnathopogon caerulescens*, entire body, ventral view; 80, specimen (LBM 1-37) found in intestine of *Tanakia limbata*, entire body, ventral view. Scale bar: 1 mm in Figs. 78–80.

*Materials examined. (*1) Four mature specimens (Yamaguti's Collection, MPM Coll. No. 22290, type series, holotype and three paratypes) of found in the small intestine [sic] of *Pelteobagrus nudiceps* [not *Pseudobagrus aurantiacus*] from Lake Biwa on 15 July 1927 (Yamaguti, 1934; Shimazu, 1990c). (2) Five mature specimens (NSMT-Pl 3633 and 3634) found in the intes-

tine of *P. nudiceps* from Onoe on 4 May 1979 and 3 June 1980 (Shimazu, 1990c). (3) One mature specimen (NSMT-Pl 5560, collected by Shimazu) found in the intestine of *P. nudiceps* from Onoe on 4 May 1992. (4) One mature specimen (NSMT-Pl 3635) of *O. pseudobagri* found in the intes-



Figs. 81–85. *Orientocreadium pseudobagri*. Adult specimens found in intestine of *Pelteobagrus nudiceps*. 81, holotype (MPM Coll. No. 22290), entire body, ventral view; 82, specimen (NSMT-Pl 5560), terminal genitalia, ventral view; 83, specimen (NSMT-Pl 3633), ovarian complex, dorsal view; 84, specimen (NSMT-Pl 3633), post-testicular part of body, showing vitelline follicles being confluent posteriorly, uterine eggs omitted, ventral view; 85, specimen (NSMT-Pl 5560), post-testicular part of body, showing excretory vesicle, dorsal view. Scale bars: 0.5 mm in Figs. 81 and 84–85; 0.2 mm in Fig. 82; 0.1 mm in Fig. 83.

tine of *Silurus lithophilus* from Onoe on 3 June 1980 (Shimazu, 1990c).

Description. 1) Based on the type series (Fig. 81). The holotype and one paratype were measured. The two remaining paratypes lacked the anterior and posterior part of the body, respectively. Body elongate, flattened dorsoventrally, small, 1.19–1.47 by 0.23–0.34, broadest at about ovarian level, not oculate; forebody 0.44–0.53 long, occupying 36–37% of total body length. Tegumental spines densely located, becoming sparser posteriorly. Large gland cells present lateral to anterior part of intestine on either side of forebody. Oral sucker subglobular, 0.10–0.13 by 0.10–0.15, subterminal. Prepharynx thick, 0.08–0.11 long. Pharynx globular, 0.06–0.10 in diameter, with four (one ventral, one dorsal, and two lateral) anterior muscular protuberances. Esophagus short, 0.06–0.14 long, bifurcating some distance in front of ventral sucker (or at about junction of middle and posterior thirds of forebody). Intestines slightly sinuous, reaching posteriorly to near posterior end of body. Ventral sucker subglobular, smaller than oral sucker in two specimens but larger in one specimen, 0.10–0.14 by 0.10–0.13, slightly posterior to junction between anterior and middle thirds of body; sucker width ratio 1 : 0.86–1.15. Testes two, subglobular, 0.07–0.09 by 0.11–0.12, tandem or slightly diagonal, usually separated by uterus, between intestines, in middle third of hindbody; anterior testis 0.06–0.09 by 0.07–0.12, posterior 0.07–0.12 by 0.07–0.11. Sperm ducts two, long; common sperm duct absent. External seminal vesicle voluminous, usually bent once, 0.08 by 0.05–0.06, usually reaching ovary. Cirrus pouch clavate, curved, fairly thick-walled, muscular, 0.22–0.28 by 0.05–0.07, between intestines, extending backward farther beyond ventral sucker; circular and longitudinal muscle fibers well developed in its posterior part. Internal seminal vesicle oval, small, 0.04–0.05 by 0.02–0.04. Pars prostatica oblong, with well-developed sphincter at its posterior end; prostatic cells numerous, small, densely surrounding pars prostatica and internal seminal vesicle. Cirrus long, slender, about two-thirds as long as cirrus pouch, internally spinose, eversible. Genital atrium fairly wide, shallow, surrounded by small gland cells. Genital pore median or only slightly shifting to left, between ventral sucker and intestinal bifurcation. Ovary single, spherical, 0.07–0.12 in diameter, almost median, pretesticular, some distance behind ventral sucker. Ovarian complex between ovary and anterior testis, not clearly observed. Uterus first descending from ootype to near posterior end of body and then ascending to ovary along median line of body, and then transversely folded tightly between ovary and metraterm (or ventral sucker), overlapping intestines; uterine seminal vesicle well developed; metraterm shorter than cirrus pouch, internally spinose, surrounded by gland cells. Eggs numerous, elongate-elliptical, bright brown, 29–32 by 14–19 μm (collapsed), operculate, weakly embryonated. Vitellaria follicular, follicles various in shape and size, lateral and ventral to intestines, extending from ovarian level to some distance in front of intestinal ends, separate. Excretory vesicle obscured by uterine eggs; excretory pore postero-dorsal to -terminal.

2) Based on the remaining specimens (Figs. 82–85). Body 1.10–3.63 by 0.23–0.66; forebody 0.43–1.13 long, occupying 28–39% of total body length. Oral sucker 0.09–0.22 by 0.10–0.23. Prepharynx 0.05–0.25 long. Pharynx 0.08–0.14 by 0.05–0.14. Esophagus 0.04–0.16 long. Ventral sucker smaller than oral sucker, 0.09–0.19 by 0.11–0.21; sucker width ratio 1 : 0.82–0.93. Testes 0.06–0.37 by 0.07–0.30. External seminal vesicle retort-shaped, 0.11–0.33 by 0.06–0.16, usually curved (Fig. 82). Cirrus pouch 0.16–0.40 by 0.04–0.12. Internal seminal vesicle 0.05–0.14 by 0.03–0.08. Ovary 0.08–0.22 by 0.09–0.22. Oviduct dilated in proximal and distally portions to contain sperm (Fig. 83). Laurer's canal fairly long, running forward or coiled, dilated in proximal portion to contain sperm (Fig. 83). Seminal receptacle absent. Ootype large, may be vesicular; Mehlis' gland well developed (Fig. 83). Eggs 30–44 by 18–22 μm (collapsed), not fully embryonated. Vitelline follicles separate anteriorly, usually separate but rarely confluent posteriorly,

rarely interrupted at testicular level (Fig. 84). Excretory vesicle I-shaped, ending anteriorly midway in post-testicular region of body (Fig. 85).

Discussion. Yamaguti (1934) described a new species, *Orientocreadium pseudobagri*, based on the type series found in *Pelteobagrus nudiceps* [not *Pseudobagrus aurantiacus*] from Lake Biwa (see also Shimazu, 1990c). Shimazu (1990c) redescribed this species from the type series and his own specimens.

Shimazu (1990c, figs. 5–6) described the external seminal vesicle as saccular and both the oviduct (after giving off Laurer's canal) and the proximal part of Laurer's canal as storing sperm. These descriptions were somewhat incorrect. The external seminal vesicle is clavate, voluminous, and usually bent once (Fig. 82). The oviduct is dilated in the proximal and distal portions to contain sperm, and Laurer's canal is dilated in the proximal portion to contain sperm (Fig. 83). Yamaguti (1934) and Shimazu (1990c) were wrong in stating that the excretory vesicle reaches to the posterior testis. The excretory vesicle is distinctly I-shaped and actually ends anteriorly midway in the post-testicular region of the body (Fig. 85).

Life cycle. The life cycle is not known in Japan. In Primorye, Russia, a first intermediate host (experimental and natural) was a pulmonate snail, *Lymnaea peregra amurensis*, in which xiphidiocercariae with a Y-shaped [sic] excretory vesicle were produced in daughter sporocysts. Second intermediate hosts (experimental and natural) were fishes and mollusks of several species, in which metacercariae encysted. Final hosts (natural) were *Perccottus glennii* Dybowski (Odontobutidae) in the Lake Khanka region (Besprozvannykh, 1984; Ermolenko and Besprozvannykh, 1987), and *Pseudobagrus fulvidraco* (Richardson) (Bagridae) in the Amur River basin (Bykhovskaya-Pavlovskaya and Kulakova, 1987).

Family **Gorgoderidae** Looss, 1899

Phyllodistomum carassii Long and Wai, 1958 (Figs. 86–88)

Phyllodistomum (*Catoptroides*) *carassii* Long and Wai, 1958: 356–357, 367–368, fig. 8.
Phyllodistomum carassii: Yamaguti, 1971: 88.

Previous record. None.

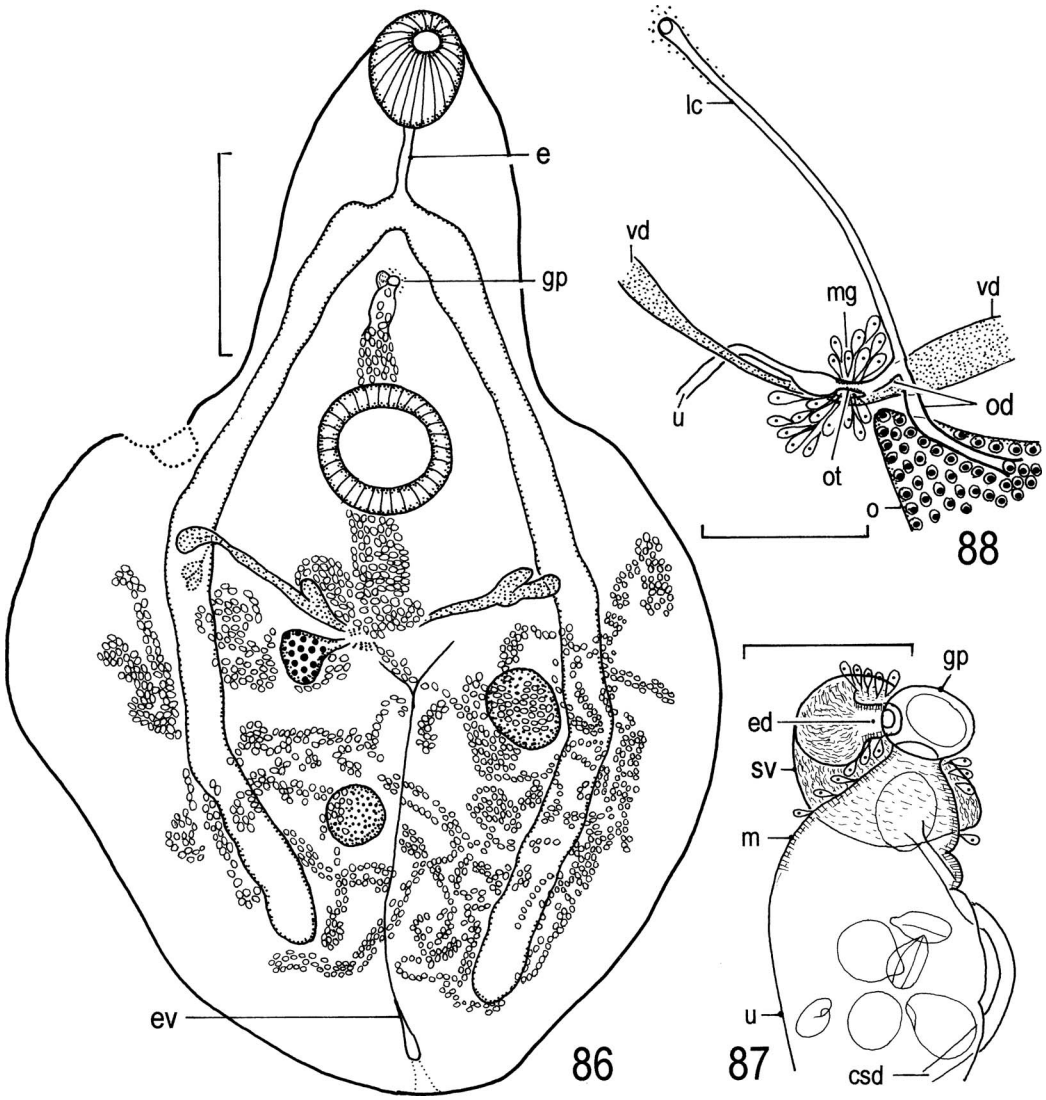
Host. Carassius auratus grandoculis.

Site of infection. Ureters.

Collecting locality. Onoe.

Materials examined. Two mature specimens (NSMT-Pl 5715, collected by Shimazu) found in the ureters of *Carassius auratus grandoculis* from Onoe on 3 June 1980.

Description. One of the two specimens was slightly damaged. The other had been artificially cut transversely into two pieces representing the anterior and posterior parts of the body. Body banjo-shaped (narrower forebody and broader, foliate hindbody), dorsoventrally flat, translucent, 3.92–5.37 by 2.96–3.42, not oculate; forebody 2.08–2.21 long, occupying 41–53% of total body length. Tegument smooth. Oral sucker slightly elongated longitudinally, 0.56 by 0.45–0.48, subterminal. Pharynx absent. Esophagus thick-walled, 0.35–0.53 long, bifurcating about halfway between two suckers, surrounded by small gland cells. Intestines not undulating, not diverticulated, posteriorly ending blindly some distance in front of posterior extremity of body. Ventral sucker round, larger than oral sucker, 0.61–0.62 by 0.53–0.64, median, about equatorial; sucker width ratio 1 : 1.10–1.42. Testes two, seemingly atrophied, elliptical, oblique, separate, submedian, medial to intestines, in middle third of hindbody; anterior testis 0.35 by 0.27, posterior 0.19–0.29 by



Figs. 86–88. *Phyllodistomum carassii.* Adult specimen (NSMT-Pl 5715) found in ureter of *Carassius auratus grandoculis*. 86, entire body, ventral view; 87; terminal genitalia, ventral view; 88, ovarian complex, dorsal view. Scale bars: 1 mm in Fig. 86; 0.2 mm in Fig. 88; 0.1 mm in Fig. 87.

0.10–0.24. Sperm ducts two, long; common sperm duct long, median, in front of ventral sucker. Cirrus pouch absent. Seminal vesicle pyriform, 0.12–0.14 by 0.07–0.08, median, dorsal to metraterm. Pars prostatica and prostatic cells absent. Ejaculatory duct short, 0.02–0.03 long, distally surrounded by small gland cells, opening into small genital atrium anteriorly to metraterm. Genital pore median, slightly postbifurcal. Ovary single, oval, 0.24 by 0.19 (damaged in one specimen), dextrally submedian, between intestines, on opposite side of anterior testis, slightly pretesticular. Ovarian complex preovarian. Seminal receptacle absent. Laurer's canal long, opening dorsally to exterior between ventral sucker and left vitellarium. Ootype not vesicular, median, between two vitellaria. Mehlis' gland large. Uterus much folded in all available space in postvitelline field of hindbody except in lateral and posterior marginal fields of body; metraterm

0.10–0.16 long, proximally wide, distally thin, surrounded by small gland cells; uterine seminal receptacle not seen. Uterine eggs numerous, elliptical, thin-shelled, light brown, not operculate, fully embryonated; eggs formed with no ovum 17–19 by 13 μm, unsegmented eggs 25–27 by 19–21 μm, large embryonated eggs 33–38 by 24–29 μm; miracidia seen in uterus, 48–64 by 32–41 μm, each enclosed tightly by thin, torn eggshell. Vitellaria two, transversely elongated, each with at least two long transverse branches, 0.48–0.75 by 0.05–0.12, symmetrical, submedian, between intestines and slightly overlapping them, separate, posterolateral to ventral sucker. Excretory vesicle I-shaped, extending anteriorly to ovarian level; excretory pore posterodorsal.

Discussion. Long and Wai (1958) originally described a new species, *Phyllodistomum* (*Catoptroides*) *carassii*, from adult specimens found in the urinary bladder and ureters of *Carassius auratus* (Linnaeus) from Lake Tai in Zhejiang Province and Shanghai, China. The present specimens morphologically agree well with their original description except for larger embryonated eggs, 33–38 by 24–29 μm instead of 25–26 by 17–20 μm (Long and Wai, 1958). In two other Chinese papers, the egg size is given as 15–25 by 11–17 μm (Institute of Hydrobiology, Hubei Province, China (chief ed.), 1973) and 17–26 by 10–16 μm (Sun and Jiang, 1991). None of the specimens reported from China was made available to us for reexamination. Judging from close similarity in morphology, we identify the present specimens as *P.* (*C.*) *carassii*. We here use the species name *P. carassii*, following Yamaguti (1971) and Campbell (2008). This is the first published record of this species from Japan.

Embryonated eggs increase in size as the embryos develop, as is seen also in other species of *Phyllodistomum* Braun, 1899 (see Tang, 1985; this paper). In the uterus of the present balsam-mounted specimens, hatched miracidia were seen; and each of them was found enclosed tightly by a thin, torn eggshell. The thin, anoperculate eggshells of fully embryonated eggs containing a fully formed miracidium must have been torn during the procedure of preparation. Although the size of these fully embryonated eggs is only slightly larger than that of the fully formed miracidia in them, as is seen in the other species (this paper), the size of fully formed miracidia in the uterus may be nearly equal to that of fully embryonated eggs. It would be better to measure at least the fully embryonated eggs in life.

Life cycle. The life cycle is not known.

Phyllodistomum mogurndae Yamaguti, 1934 (Figs. 89–90)

Phyllodistomum mogurndae Yamaguti, 1934: 425–427, figs. 87–88; Shimazu, 2007: 13, figs. 20–22.

Previous record. From *Pelteobagrus nudiceps* of Lake Biwa (Shimazu, 2007).

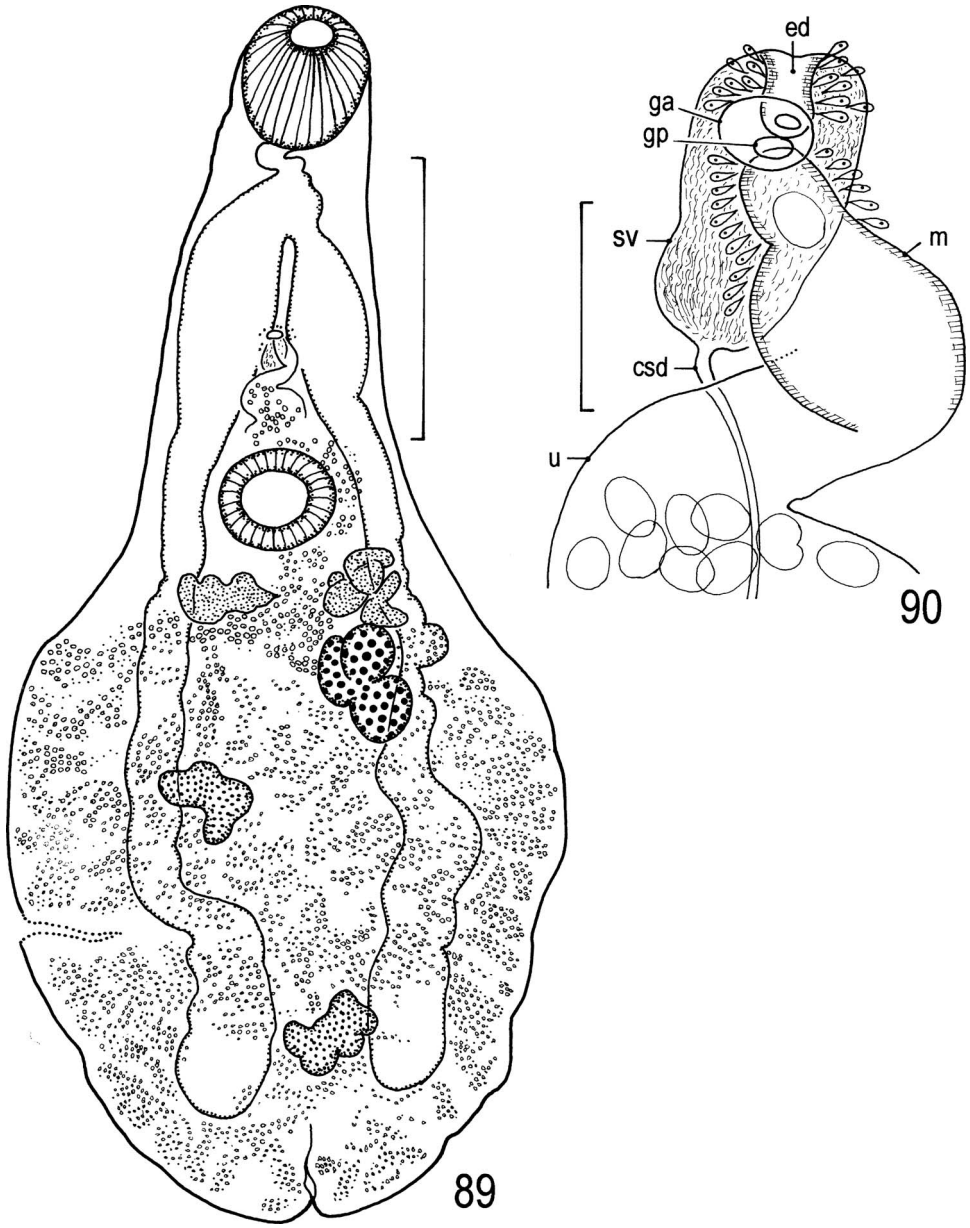
Host. *Pelteobagrus nudiceps*.

Site of infection. Urinary bladder.

Collecting locality. Lake Biwa.

Materials examined. One mature specimen (Yamaguti's Collection, MPM Coll. No. 22542, labeled "*Phyllod. mogurndae*?", unpublished) found in the urinary bladder of *Pelteobagrus nudiceps* from Lake Biwa on 7 December 1938 (Shimazu, 2007).

Description. Similar to *Phyllodistomum carassii* (this paper) in general morphology. Body banjo-shaped, 4.16 by 1.92; forebody 1.76 long, occupying 42% of total body length. Oral sucker elliptical, longer than wide, 0.50 by 0.41, subterminal. Esophagus bifurcating at about border between anterior and second thirds of forebody. Intestines slightly undulating, weakly diverticulated, ending near posterior extremity of body. Ventral sucker subglobular, 0.42 by 0.38, pre-equatorial; sucker width ratio 1 : 0.93. Testes indented irregularly, medial to intestines or slightly over-



Figs. 89–90. *Phyllodistomum mogurndae*. Adult specimen (MPM Coll. No. 22542) found in urinary bladder of *Pelteobagrus nudiceps*. 89; entire body, ventral view; 90, terminal genitalia, ventral view. Scale bars: 1 mm in Fig. 89; 0.1 mm in Fig. 90.

lapping them, in posterior half of hindbody, posterior testis slightly anterior to intestinal ends; anterior testis 0.37 by 0.51, posterior 0.28 by 0.51. Sperm ducts not clearly observed; common sperm duct in front of ventral sucker. Seminal vesicle elliptical, 0.14 by 0.06. Ejaculatory duct short, 0.06 long. Genital pore midway between intestinal bifurcation and ventral sucker. Ovary slightly three-lobed, 0.39 by 0.31, sinistrally submedian, slightly overlapping left intestine, pretesticular, on opposite side of anterior testis. Ovarian complex obscured by uterine eggs.

Uterus much folded in all available space in postvitelline field of hindbody; metraterm well developed, anterior to ventral sucker; uterine seminal receptacle not seen. Uterine eggs numerous, elliptical, light brown; eggs formed with no ovum 16–19 by 13–14 μm, unsegmented eggs 21–24 by 16–17 μm, large embryonated eggs 27–32 by 22–24 μm; a few miracidia seen in uterus, 32 by 27 μm, each enclosed tightly by thin torn eggshell. Vitellaria irregularly indented or lobed, 0.28 by 0.15–0.31, between intestines or slightly overlapping them. Excretory vesicle not clearly observed; excretory pore posterodorsal.

Discussion. *Phyllodistomum mogurndae* was described as a new species by Yamaguti (1934) based on adult specimens (MPM Coll. No. 22539, holotype and three paratypes, mature) found in the urinary bladder of *Odontobutis obscura* (syn. *Mogurnda obscura*) from Lake Ogura in Kyoto Prefecture. Shimazu (2007) identified the present specimen as *P. mogurndae*.

The present specimen had large embryonated eggs (29–32 by 22–24 μm) and a few miracidia (32 by 27 μm) in the uterus. Yamaguti (1934) gave the egg size as 42–48 by 30–37 μm in life. Two of the three paratypes are labeled "Egg embryonated (0.045–0.048) × (0.036–0.037)". On our reexamination of the type series, eggs formed with no ovum were 16–17 by 11–13 μm; unsegmented eggs, 21–24 by 14–16 μm; large embryonated eggs, 25–32 by 19–24 μm; and miracidia in the uterus, 33–48 by 25–32 μm. Yamaguti (1934) must have measured live, fully embryonated eggs.

Shimazu (2007) reported adult specimens from *Gymnogobius urotaenia* and *Rhinogobius* sp. [*Rhinogobius* sp. OR] from Lake Suwa at Suwa City, Nagano Prefecture. In his description, "weakly-" and "fully-embryonated eggs" should be read "large embryonated" and "miracidia in uterus", respectively.

Phyllodistomum mogurndae is morphologically different from *P. carassii* (this paper) in that the oral sucker is larger than the ventral sucker, with the sucker width ratio of 1 : 0.93 instead of 1 : 1.10–1.42; the ovary is three-lobed instead of oval; fully embryonated eggs (or miracidia) are smaller, 33–48 by 25–32 μm instead of 48–64 by 32–41 μm; and the vitellaria are lobed instead of branched.

Life cycle. The life cycle is not known.

Phyllodistomum parasiluri Yamaguti, 1934 (Figs. 91–94)

Phyllodistomum parasiluri Yamaguti, 1934: 423–425, fig. 86; Shimazu, 2007: 15–16, figs. 23–26.

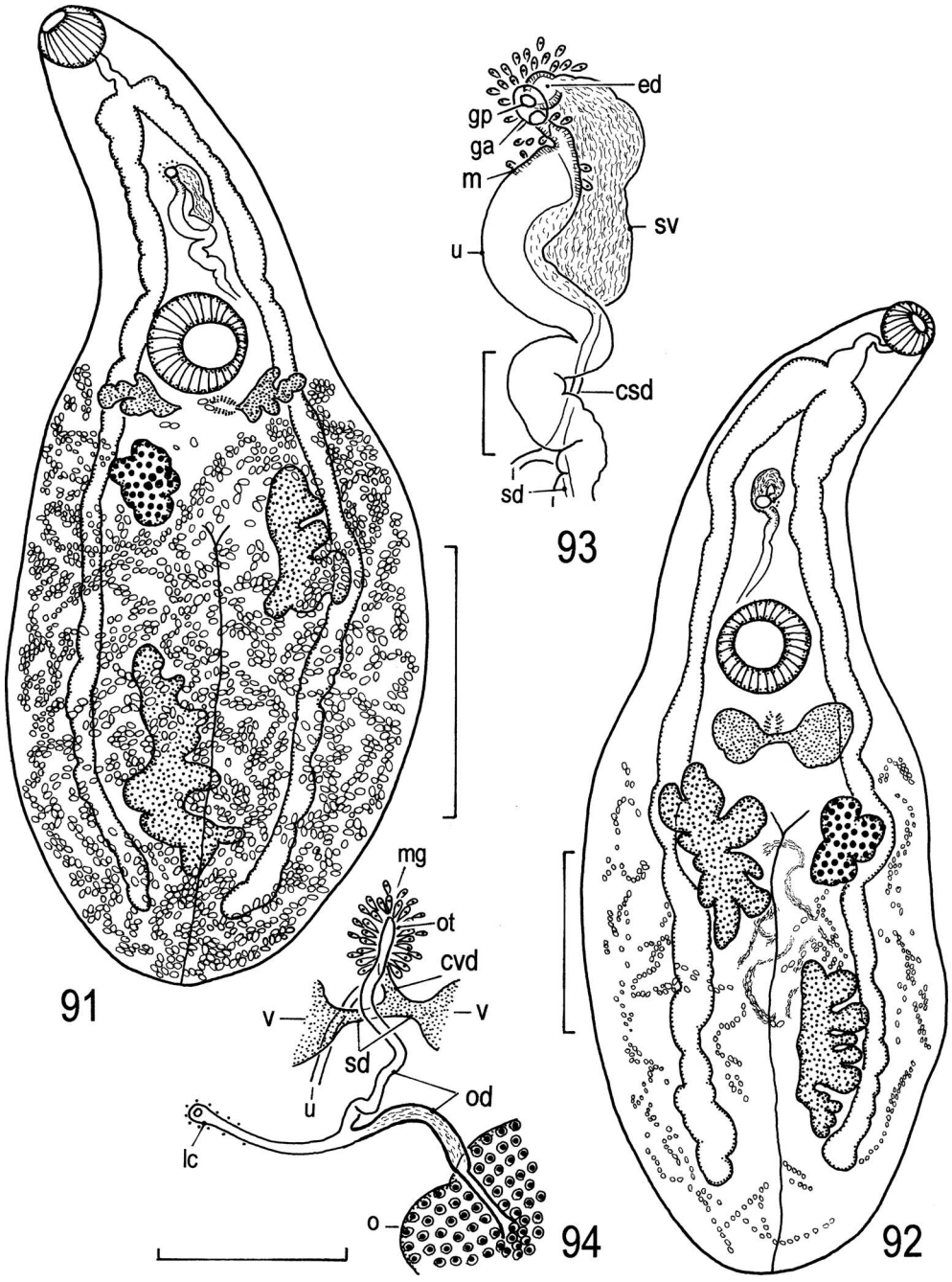
Previous record. From *Silurus asotus* of Lake Biwa (Shimazu, 2007).

Hosts. *Pelteobagrus nudiceps*, *Silurus asotus*, and *S. lithophilus.*

Sites of infection. Urinary bladder and ureters.

Collecting localities. Lake Biwa, Minamifunaki, Momose, and Onoe.

Materials examined. (1) One immature specimen (Yamaguti's Collection, MPM Coll. No. 22538, unidentified, unpublished) found in the urinary bladder of *Silurus asotus* from Lake Biwa on 1 November 1931 (Shimazu, 2007). (2) Specimens found in the urinary bladder of *S. asotus*: four mature (NSMT-Pl 5716, collected by Shimazu) from Onoe on 4 May 1992, eight mature (LBM 8-27 to -29 and -31) from Momose on 19 April 2007 and 24 November 2007, and two mature (LBM 8-30) from Minamifunaki on 24 April 2007. (3) Specimens found in the urinary bladder and ureters of *S. lithophilus* from Onoe: one immature and ten mature (NSMT-Pl 5717, collected and identified as *P. parasiluri* by Nagasawa) on 4 May 1979, and two mature (NSMT-Pl 5718, collected by Shimazu) on 3 June 1980. (4) Three mature specimens (NSMT-Pl 5719, collected and identified as *P. parasiluri* by Nagasawa) found in the urinary bladder of *Pe. nudiceps*



Figs. 91–94. *Phyllodistomum parasiluri.* Adult specimens. 91, specimen (NSMT-Pl 5718) found in urinary bladder of *Silurus lithophilus*, entire body, ventral view; 92, specimen (LBM 8-30) found in urinary bladder of *S. asotus*, entire body, ventral view; 93, specimen (NSMT-Pl 5718), terminal genitalia, ventral view; 94, specimen (NSMT-Pl 5718), ovarian complex, dorsal view. Scale bars: 1 mm in Figs. 91–92; 0.4 mm in Figs. 93–94.

from Onoe on 4 May 1979.

Description. Based on seven well-prepared, mature specimens. Similar to *Phyllodistomum carassii* (this paper) in general morphology. Body lanceolate-oblong or oval, 3.36–6.72 by 1.89–2.08; forebody 1.20–2.88 long, occupying 36–44% of total body length. Oral sucker subglobular, 0.20–0.34 by 0.22–0.31, subterminal. Esophagus 0.15–0.50 long, bifurcating at about border between anterior and second thirds of forebody; intestines undulating, ending near posterior extremity of body, with weak diverticula. Ventral sucker subglobular, 0.37–0.59 by 0.35–0.63, located at about border between anterior and middle thirds of body; sucker width ratio 1 : 1.37–1.85. Testes large, deeply lobed irregularly, oblique, separate, medial to and slightly overlapping intestines, degenerated in old adult specimens (Fig. 91); anterior testis slightly posterior to or level with ovary, 0.44–1.10 by 0.22–0.65; posterior slightly in front of intestinal ends, 0.54–1.63 by 0.31–0.75. Sperm ducts long; common sperm duct short, in front of ventral sucker. Seminal vesicle pyriform, 0.22–0.41 by 0.35–0.63. Ejaculatory duct short, usually dilated like pars prostatica, opening into genital atrium anteriorly to metraterm. Genital pore small, midway between intestinal bifurcation and ventral sucker. Ovary three- to four-lobed or irregularly indented, 0.28–0.59 by 0.25–0.46, dextrally submedian, slightly overlapping intestine, in front of or level with anterior testis, on opposite side of anterior testis, sometimes degenerated in old adult specimens. Ovarian complex preovarian. Oviduct long, dilated to include sperm before giving off Laurer's canal. Laurer's canal opening dorsally to vitellarium located opposite to ovary. Ootype in front of vitelline ducts; Mehlis' gland large, well developed. Uterus much folded in all available space of postvitelline field of hindbody; metraterm well developed, in front of ventral sucker; uterine seminal receptacle present. Uterine eggs numerous, elliptical, light brown, fully embryonated; eggs formed with no ovum 19–25 by 14–17 μm, unsegmented eggs 27–33 by 17–21 μm, large embryonated eggs 29–40 by 19–29 μm; miracidia in uterus 37–51 by 33–40 μm, each enclosed tightly by thin torn eggshell. Vitellaria elongate, entire or irregularly indented, 0.15–0.31 by 0.06–0.12, symmetrical, separate, between intestines or slightly overlapping them, posterolateral to ventral sucker. Excretory vesicle extending anteriorly to ovarian level; excretory pore posteroterminal.

Discussion. Yamaguti (1934) described a new species, *Phyllodistomum parasiluri*, based on adult specimens (holotype and four paratypes, mature) found in the urinary bladder of *Silurus asotus* (syn. *Parasilurus asotus*) from Lake Ogura in Kyoto Prefecture. Shimazu (2007) redescribed this species from adult specimens found in *S. asotus* from Lake Kizaki in Oomachi City and Lake Suwa at Suwa City, Nagano Prefecture. The present specimens agree well with Yamaguti's (1934) description and Shimazu's (2007) redescription.

Old individuals among the present adult specimens had degenerate testes. As adult worms grow older, the gonads degenerate, especially the testes first (Shimazu, 2007). In Shimazu's (2007) redescription, "weakly-" and "fully-embryonated eggs" should be read as "large embryonated eggs" and "miracidia in uterus", respectively.

This species morphologically differs from *P. carassii* (this paper) in that the body is lanceolate-oblong instead of banjo-shaped; the sucker width ratio is higher, 1 : 1.37–1.85 instead of 1 : 1.10–1.42; the testes are larger, 0.44–1.63 by 0.22–0.75 instead of 0.19–0.35 by 0.10–0.27, and much lobed instead of elliptical; the ovary is lobed instead of oval; fully embryonated eggs (or miracidia) are smaller, 37–51 by 33–40 μm instead of 48–64 by 32–41 μm; and the vitellaria are lobed instead of branched. Furthermore, the species is morphologically different from *P. mogurndae* (Yamaguti, 1934; Shimazu, 2007; this paper) in having a lanceolate-oblong (instead of banjo-shaped) body; a higher sucker width ratio, 1 : 1.58–1.97 instead of 1 : 0.93–1.12; and larger

(0.25–1.63 by 0.13–0.75 instead 0.22–0.63 by 0.16–0.51), deeply lobed (instead of weakly indented) testes.

Life cycle. The life cycle is not known.

Pseudophyllodistomum macrobrachicola (Yamaguti, 1934) (Figs. 95–99)

Phyllodistomum macrobrachicola Yamaguti, 1934: 430–431, fig. 90.
Pseudophyllodistomum macrobrachicola: Cribb, 1987: 1131.
Phyllodistomum anguilae: Shimazu, 2005, not Long and Wai, 1958: 142–143, figs. 7–9; Shimazu, 2007: 11–12, figs. 16–19; Shimazu, 2008: 49, fig. 6.

Previous record. None.

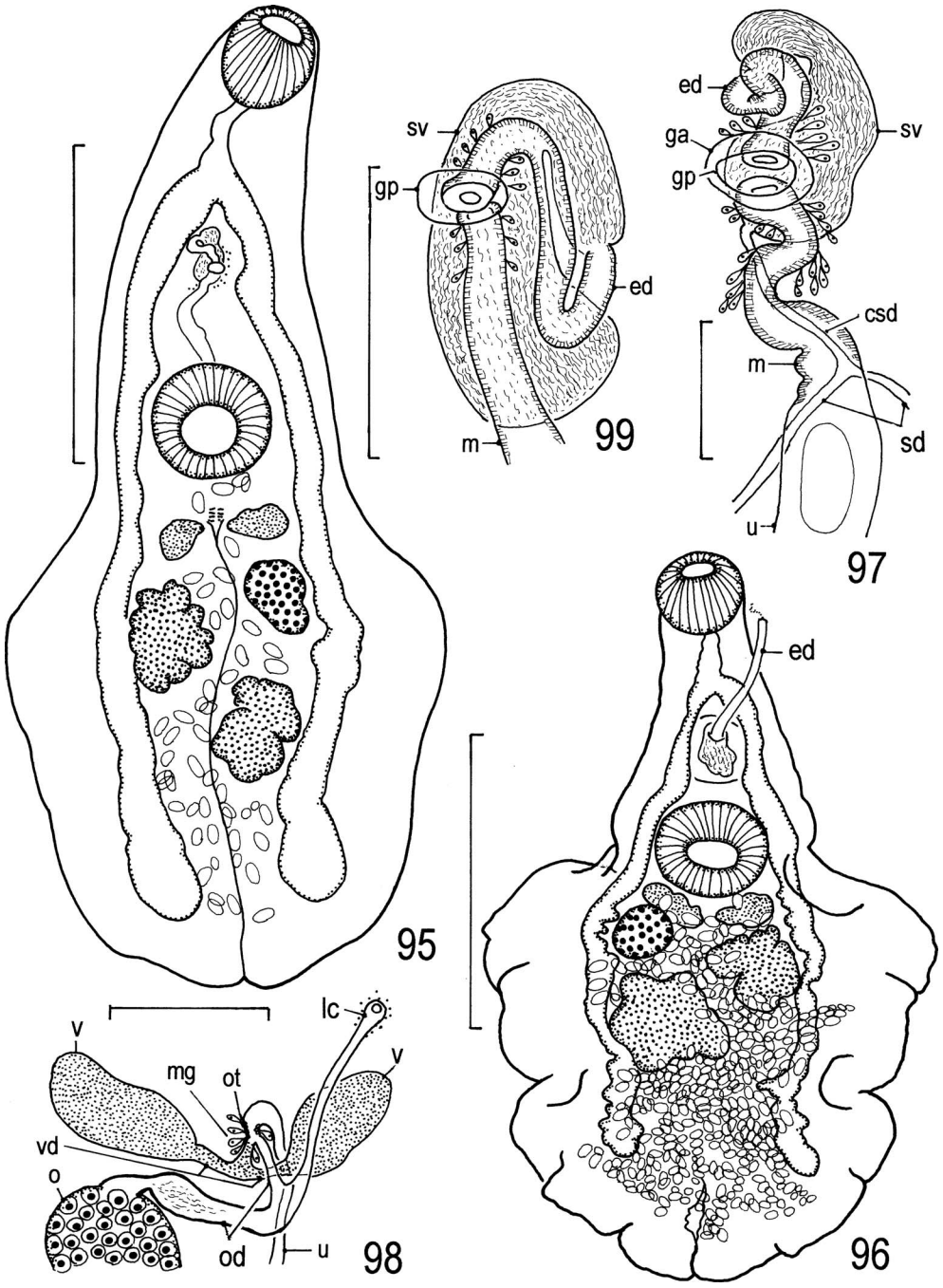
Hosts. *Anguilla japonica*, *Cottus reinii*, "Kajika" [most likely referring to *C. reinii*], *Gymnogobius urotaenia*, *Odontobutis obscura*, *Pelteobagrus nudiceps*, and *Silurus asotus*.

Site of infection. Urinary bladder.

Collecting localities. Lake Biwa, Imazu, Kaizu, Momose, and Onoe.

Materials examined. (1) Specimens found in the urinary bladder of *Anguilla japonica*: one immature and four mature (LBM 8-19) from Imazu on 19 May 1998, and six mature (LBM 8-20) from Momose on 1 May 2001. (2) Six mature specimens (Ozaki's Collection, MPM Coll. No. 30213, labeled "[Donko] [Lake Biwa]", unidentified, unpublished) found in *Odontobutis obscura* from Lake Biwa (other data not given). (3) One immature and one mature specimens (NSMT-Pl 5722, collected by Shimazu) found in the urinary bladder of *Gymnogobius urotaenia* from Onoe on 3 June 1980. (4) One mature specimen (LBM 8-29) found in the urinary bladder of *Silurus asotus* from Momose on 24 April 2007. (5) Specimens found in the urinary bladder of *Pelteobagrus nudiceps* from Onoe: two immature (NSMT-Pl 5723, collected and identified as "*Phyllodistomum* (immature)" by Nagasawa) on 5 May 1979, and one immature (NSMT-Pl 5724, collected by Shimazu) on 3 June 1980. (6) Specimens found in the urinary bladder of *Cottus reinii*: 39 immature (NSMT-Pl 5725–5727, collected by Shimazu) from Onoe on 3 June 1980 and 4 and 6 May 1992, and one immature (LBM 8-22) from Momose on 24 November 2007. (7) One mature specimen (Yamaguti's Collection, MPM Coll. No. 22549, labeled "[Kajika] [Kaizu]", unidentified, unpublished) found in the urinary bladder of "Kajika" from Kaizu on 26 March 1928.

Description. Based on 18 mature specimens. Similar to *Phyllodistomum carassii* (this paper) in general morphology. Body narrow-ovate to banjo-shaped, 1.87–3.84 by 0.91–1.92, rarely depressed ventrally in region of seminal vesicle; forebody 0.85–1.49 long, occupying 36–46% of total body length. Oral sucker subglobular, 0.22–0.31 by 0.20–0.29, subterminal. Esophagus slightly undulating, 0.17–0.31 long, bifurcating at about junction between anterior and second thirds of forebody; intestines slightly undulating, ending near posterior extremity of body, with weak diverticula. Ventral sucker subglobular, 0.27–0.37 by 0.28–0.39, slightly preequatorial; sucker width ratio 1 : 1.17–1.40. Testes indented irregularly, usually oblique but rarely almost symmetrical, slightly separate, medial to intestines, far anterior to intestinal ends, in middle third of hindbody; anterior testis 0.19–0.44 by 0.15–0.37, posterior 0.15–0.50 by 0.18–0.42. Sperm ducts long; common sperm duct long, in front of ventral sucker. Seminal vesicle pyriform or retort-shaped, 0.10–0.22 by 0.05–0.12. Ejaculatory duct long, convoluted, opening into genital atrium anteriorly to metraterm, rarely everted (0.44 long) through genital pore (Fig. 96). Genital atrium large, shallow. Genital pore large, midway between intestinal bifurcation and ventral sucker, with radial muscle fibers (not illustrated). Ovary almost globular, 0.15–0.25 by 0.11–0.17, dextrally or sinistrally submedian, slightly pretesticular, on opposite side of anterior testis. Ovari-



Figs. 95–99. *PseudoPhyllodistomum macrobrachicola.* Adult specimens. 95, specimen (LBM 8-19) found in urinary bladder of *Anguilla japonica*, entire body, ventral view; 96, specimen (MPM Coll. No. 30213) found in *Odontobutis obscura*, entire body, ventral view; 97, specimen (LBM 8-19), terminal genitalia, ventral view; 98, specimen (LBM 8-19), ovarian complex, dorsal view; 99, holotype (MPM Coll. No. 22543) of *Phyllodistomum macrobrachicola*, terminal genitalia, ventral view. Scale bars: 1 mm in Figs. 95–96; 0.2 mm in Fig. 98; 0.1 mm in Figs. 97 and 99.

an complex anteromedial to ovary. Oviduct dilated to include sperm. Laurer's canal long, opening anteriorly to vitellarium located on opposite side of ovary. Ootype small, median, slightly anterior to vitelline ducts. Mehlis' gland weakly developed. Uterus much folded in hindbody, between and posterior to intestines, rarely overlapping intestines and slightly extending into lateral fields of body; metraterm well developed, anterior to ventral sucker; uterine seminal receptacle sometimes seen. Eggs numerous, elongate-elliptical, slightly curved, brown, embryonated; eggs formed with no ovum 35–50 by 21–24 μm, unsegmented eggs 50–73 by 27–35 μm, large, apparently fully embryonated eggs 64–88 by 32–43 μm; no miracidium seen in uterus. Vitellaria elliptical, weakly indented, 0.08–0.22 by 0.07–0.12, posterolateral to ventral sucker, separate, between intestines. Excretory vesicle extending anteriorly to ovarian level; excretory pore posteroterminal.

Some of the adult specimens from *A. japonica*, *O. obscura*, and *S. asotus* were apparently fully mature with numerous uterine eggs, but those from *G. urotaenia* and the fish Kajika contained a few uterine eggs.

Discussion. Yamaguti (1934) found metacercariae encysted [sic; should be encapsulated] in the ovary of the palaemonid shrimp *Macrobrachium nipponense* (de Haan) (Japanese name: Tenaga-ebi) from Lake Kasumigaura in Ibaraki Prefecture and from the Yodo River (locality not specified). He fed them to *Odontobutis obscura* (syn. *Mogurnda obscura*) from [Lake Ogura in Kyoto Prefecture] and to *Silurus asotus* (syn. *Parasilurus asotus*) from [Lake Biwa] and subsequently recovered an adult from the urinary bladder of *O. obscura* 78 days after feeding. Yamaguti (1934) described a new species, *Phyllodistomum macrobrachicola*, from this experimental adult (MPM Coll. No. 22543, holotype).

In addition, Yamaguti's Collection includes a mature specimen (MPM Coll. No. 22265, unidentified, unpublished) recovered from the urinary bladder of *O. obscura* (origin not given) on day 20 after feeding of metacercariae (origin not given) on 20 July 1940. This specimen also is identified as *P. macrobrachicola*. The specimen was mature and oviferous in spite of the fact that it was obtained as early as 20 days after feeding. It seems likely from the results of Yamguti's (1934) feeding experiments that the specimen was the product not of experimental infection but of natural infection.

Yamaguti (1934) did not fully describe the male terminal genitalia in the holotype. We reexamined the holotype in balsam. The neck of the retort-shaped seminal vesicle curved backward to connect to the long ejaculatory duct, which turned forward and then backward to open into the genital atrium (Fig. 99). Furthermore, uterine eggs were unsegmented: eggs formed with no ovum were 37–40 by 16–24 μm; and unsegmented eggs, 56–64 by 29–35 μm, instead of 60–73 by 30–33 μm in life (Yamaguti, 1934).

The present specimens, especially barely mature ones (Fig. 95) of them, are morphologically identical with the holotype. Consequently, we identify them as *P. macrobrachicola*. Cribb (1987) transferred this species to his new genus, *Pseudophyllodistomum*, as *Ps. macrobrachicola* (Yamaguti, 1934) comb. nov.

Shimazu (2005, 2007, 2008) described, as *P. anguilae* Long and Wai, 1958, adult specimens found in the urinary bladder of *A. japonica* from Aomori, Nagano, and Tokushima prefectures. After reexamining his specimens (NSMT-Pl 5247, 5322–5325, and 5526), we regard them also as *Ps. macrobrachicola*. In his specimens, eggs formed with no ovum were 32–37 by 17–22 μm; unsegmented eggs, 48–64 by 32–37 μm; fully embryonated eggs (intact) ("weakly-embryonated eggs" in Shimazu (2007)), 72–83 by 40–56 μm; and miracidia ("large embryonated eggs" in Shimazu (2007)) in the uterus, 88–96 by 72–93 μm. In this connection, the following immature

specimens also should be assigned to *Ps. macrobrachicola*: two specimens (Yamaguti's Collection, MPM Coll. No. 22261, unpublished) found in the intestine of *A. japonica* from Tsuchiura, Ibaraki Prefecture, on 16 April 1929 (see Shimazu, 2005); and one specimen (Yamaguti's Collection, MPM Coll. No. 22264, labeled "*Phyllodistomum* immature", unpublished) found in the urinary bladder of *G. urotaenia* from Tsuchiura on 4 April 1940.

One of the morphological diagnostic characteristics in *Pseudophyllodistomum* is a long, convoluted, eversible ejaculatory duct (Cribb, 1978), as is seen in *Ps. macrobrachicola* (Figs. 96–97). *Phyllodistomum anguilae* was originally described, as *P.* (*Catoptroides*) *anguilae* [sic], by Long and Wai (1958) from adult specimens found in the urinary bladder of *A. japonica* and *Siniperca chuatsi* (Basilewsky) (Percichthyidae) caught in Lake Tai, Zhejiang, China. In morphology, this species closely resembles *Ps. macrobrachicola*. However, the male terminal genitalia in it have not yet been fully described. The species would be considered a junior synonym of *Ps. macrobrachicola*, if it proves to have a long ejaculatory duct.

Life cycle. The first intermediate host has not been determined as yet. A cercaria, "Apharyngeal stylet cercaria", of *Phyllodistomum* sp. with three pairs of the penetration glands, a long tail about 10 times as long as the body proper, and a flame-cell formula of 2[(3+3+3)+(3+3+3)]=36 was found in the corbiculid bivalve *Corbicula sandai* Reinhardt (Japanese name: Seta-shijimi) in Lake Biwa (Yamaguti, [1954]). Yamaguti's Collection includes sporocysts containing developing cercariae (MPM Coll. No. 22269, labeled "*Phyllodistomum* cerc.") obtained from *C. sandai* on 18 October 1931. These specimens are probably part of Yamaguti's [1954] material. Possibly, the cercaria belongs to *Ps. macrobrachicola*, because it is similar to cercariae of *Pseudophyllodistomum* known from corbiculid bivalves: the cercaria of *Ps. johnstoni* Cribb, 1987 (the type species of the genus) from *Corbiculina* sp. in Australia (Cribb, 1987); and the cercaria of *Ps. mingensis* (Tang, 1985) Cibb, 1987 (syn. *P. mingensis* Tang, 1985) from *Corbicula fluminea* Müller in China (Tang, 1985). A morphologically similar, long-tailed cercaria, *Cercaria longicrura* Faust, 1924, is known to develop in another bivalve, *Corbicula leana* Prime (Japanese name: Ma-shijimi), from Okayama (Osafune, 1898; Faust, 1924). Because Osafune (1898, fig. IIb) described and figured this cercaria as having a pharynx but as lacking a stylet, the cercaria needs to be reexamined (Cribb, 1987).

Natural second intermediate hosts in Japan are freshwater shrimps, *Macrobrachium nipponense*, *Palaemon paucidens* (syn. *Leander paucidens*) (Palaemonidae), and *Neocaridina denticulata* (de Haan) (Japanese name: Minami-numa-ebi) (Atyidae), in which metacercariae are found either free or encapsulated by host tissue (Yamaguti, 1934; Shibue, 1954; Komiya, 1965; Shimazu, 1999, 2003b). In Lake Biwa, metacercariae have been found in *M. nipponense* (Yamaguti, 1934). Yamaguti's Collection includes many whole-mounted metacercariae found in *M. nipponense* from Lake Biwa (MPM Coll. No. 22547, unidentified, unpublished, on 25 October 1931; and MPM Coll. No. 22023, labeled "*Phyllodistomum macrobrachicola*" (other data not given)). In addition, metacercariae (NSMT-Pl 5729, collected by Shimazu, on 30 April and 4 May 1992; and LBM 8-56, on 31 October 1997) were found in *Pa. paucidens*. The ejaculatory duct is long even in the above-mentioned metacercarial worms.

Natural final hosts are at least *A. japonica*, *O. obscura*, and *S. asotus* in Japan, because parasite specimens found in the urinary bladder of these fishes were fully mature (Shimazu, 2005, 2007, 2008; this paper). Since those found in the urinary bladder of *Pe. nudiceps*, *C. reinii* (including the fish Kajika), and *G. urotaenia* were immature or barely mature (Shimazu, 2005, 2007, 2008; this paper), these fishes may be unsuitable as a final host. Natural final hosts in the Amur basin, Russia, are *S. asotus* and *S. soldatovi* Nikolskii and Soin (Akhmerov, 1961).

Small immature worms were found by Nagasawa in the intestine of fishes: two (NSMT-Pl 5728) from *Hemibarbus barbus* of Onoe on 3 May 1979; one (NSMT-Pl 5720, labeled "*Phyllodistomum* (immature)") from *O. obscura* of Onoe on 4 May 1979; and one (NSMT-Pl 5721, labeled "*Phyllodistomum* (immature)") from *G. urotaenia* of Onoe on 3 May 1979. These fishes may have ingested either shrimps harboring metacercariae or fish harboring immature worms or both.

Family **Lissorchiidae** Magath, 1917

Asymphylodora innominata (Faust, 1924) comb. nov. (Figs. 100–103)

Cercaria H of Kobayashi, 1918: 70–73, 1 pl., fig. 16. Syn. nov.

(?) *Cercariaeum* A of Kobayashi, 1922: 266–267.

Cercariaeum innominatum Faust, 1924: 295. Syn. nov.

Asymphylodora macrostoma Ozaki, 1925: 104–106, fig. 4; Yamaguti, 1934: 393; Shimazu, 1992: 8–10, figs. 6–11; Shimazu and Urabe, 2005: 11–12, figs. 18–20; Shimazu, 2007: 18 ; Shimazu, 2008: 56–57, fig. 12. Syn. nov.

Parasymphylodora macrostoma: Szidat, 1943: 44. Syn. nov.

Cercaria innominatum [sic; should be *innominata*]: Ito, Mochizuki and Noguchi, 1959: 918; Ito, 1960: 67–68, fig. 13; Shimazu, 2007: 18, figs. 27–29. Syn. nov.

Orientotrema macrostoma: Tang, 1962: 169. Syn. nov.

Asymphylodora (*Asymphylodora*) *macrostoma*: Yamaguti, 1971: 97. Syn. nov.

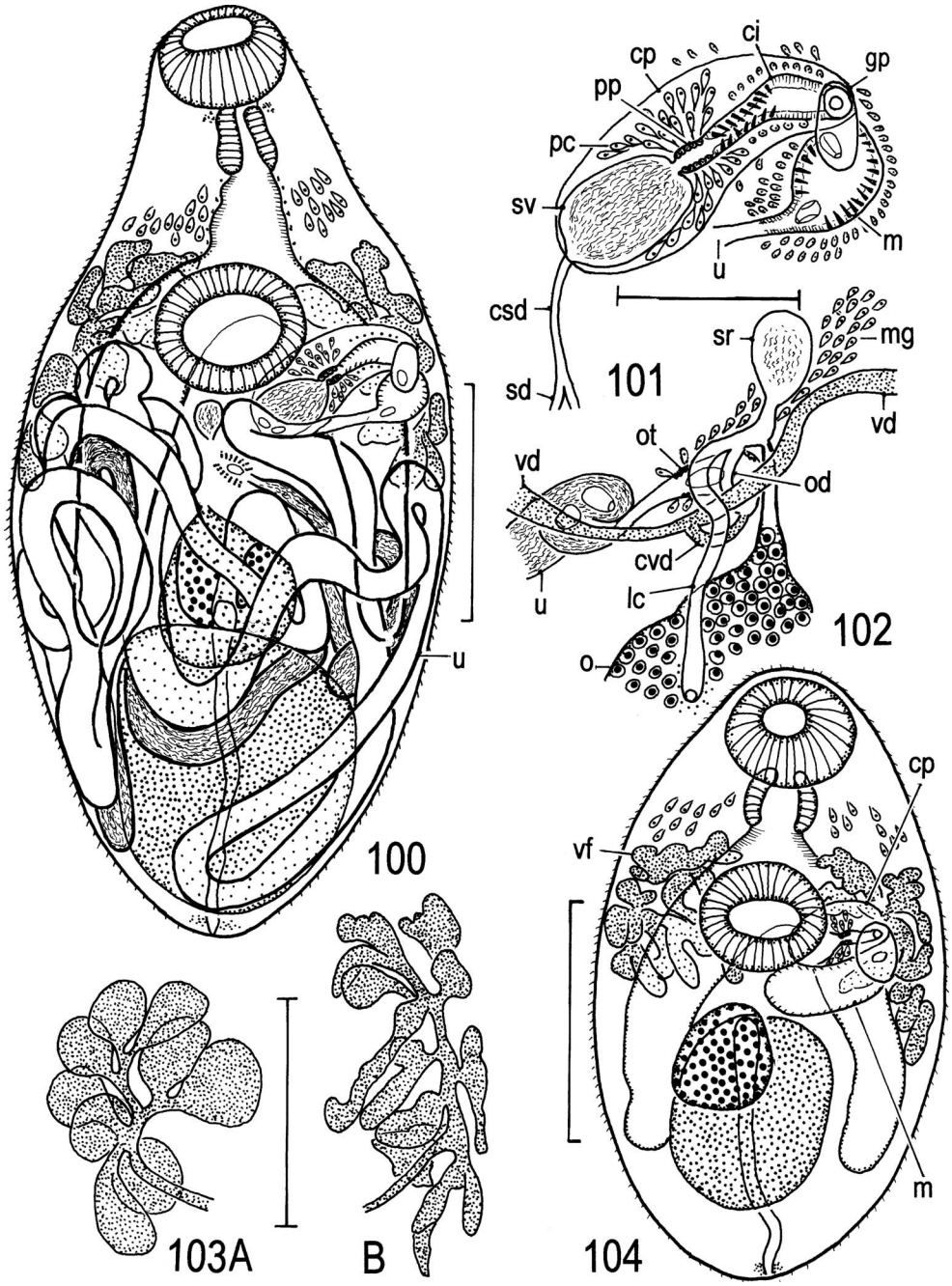
Previous records. From *Opsariichthys uncirostris uncirostris* (syn. *O. uncirostris*) of Moriyama, Omatsu, and Onoe, as *Asymphylodora macrostoma* (Yamaguti, 1934; Shimazu, 1992); from *Tribolodon hakonensis* of Omatsu and Onoe, as *A. macrostoma* (Shimazu, 1992); from *Hemibarbus barbus* of Onoe, as *A. macrostoma* (Shimazu, 1992); from "Ukikamatsuka?" of Lake Biwa, as *A. macrostoma* (Shimazu, 1992); and from *Gymnogobius isaza* (syn. *Chaenogobius isaza*) of Omatsu, as *A. macrostoma* (Shimazu, 1992).

Hosts. *Gymnogobius isaza*, *Hemibarbus barbus*, *Opsariichthys uncirostris uncirostris*, *Tribolodon hakonensis*, and "Ukikamatsuka?" [most likely referring to *H. longirostris* (Regan) (Japanese name: Zunaga-nigoi) (Cyprinidae)].

Site of infection. Intestine, and also "gut".

Collecting localities. Lake Biwa, Moriyama, Omatsu, and Onoe.

Materials examined. (1) Specimens of *Asymphylodora macrostoma* found in the intestine of *Opsariichthys uncirostris uncirostris*: three mature (Yamaguti's Collection, MPM Coll. No. 22746) from Omatsu on 17 July 1927 (Yamaguti, 1934; Shimazu, 1992); and [six immature and 113 mature] (NSMT-Pl 3684–3686) from Onoe on 5 May 1979 and 3 June and 11 November 1980 (Shimazu, 1992), [seven mature] (NSMT-Pl 3700) from Omatsu on 30 April 1992 (Shimazu, 1992), and [nine mature] (NSMT-Pl 3973) from Moriyama on 2 May 1992 (Shimazu, 1992). (2) Specimens found in the intestine of *O. u. uncirostris*: some 50 mature (LBM 1-17 to -20) from the Tenjin River on 21 May 1998 and six mature (LBM 5-8 to -10, hot formalin-fixed, collected and identified as *A. macrostoma* by Tomáš Scholz) from Momose on 1 May 2001. (3) Specimens of *A. macrostoma* found in the intestine of *Tribolodon hakonensis*: [two mature] (NSMT-Pl 3690) from Onoe on 4 February 1980 and [eight mature] (NSMT-Pl 3974) from Omatsu on 30 April 1992 (Shimazu, 1992). (4) Six mature specimens (NSMT-Pl 3632, collected by Shimazu) found in the intestine of *T. hakonensis* from Onoe on 3 June 1980. (5) One immature specimen (NSMT-Pl 3976) of *A. macrostoma* found in the intestine of *Hemibarbus barbus* from Onoe on 4 May 1992 (Shimazu, 1992). (6) One immature specimen (Yamaguti's Collection, MPM Coll. No. 22747, labeled "*Asymphylodora* [Ukikamatsuka?]", unpublished) of *A. macro-*



Figs. 100–103. *Asymphylodora innominata* (Faust, 1924) comb. nov., adult specimens (NSMT-Pl 3685) found in intestine of *Osparüichthys uncirostris uncirostris* (Figs. 100–103) and *Asymphylodora* sp., immature specimen (NSMT-Pl 3978) found in intestine of *Tridentiger brevispinis* (Fig. 104). 100, entire body, uterine eggs omitted, ventral view; 101, terminal genitalia, ventral view; 102, ovarian complex, dorsal view; 103, showing cluster of vitelline follicles in young adult specimen (A) and in old adult specimen (B), ventral view.

Fig. 104. *Asymphyodora* sp., immature specimen (NSMT-Pl 3978) found in intestine of *Tridentiger brevispinis*, entire body, ventral view. Scale bars: 0.3 mm in Figs. 100 and 103–104; 0.1 mm in Figs. 101–102.

stoma found in the intestine of "Ukikamatsuka?" from Lake Biwa on 4 December 1938 (Shimazu, 1992). (7) One immature specimen (NSMT-Pl 3977) of *A. macrostoma* found in the intestine of *Gymnogobius isaza* (syn. *Chaenogobius isaza*) from Omatsu on 30 April 1992 (Shimazu, 1992).

Description. 1) For earlier descriptions and figures for *A. macrostoma* from Lake Biwa, see Yamaguti (1934) and Shimazu (1992).

2) Based on the remaining new specimens from *O. u. uncirostris* and *T. hakonensis*; ten large, mature ones of them measured. Body ovate or fusiform, anteriorly tapering, 0.85–1.52 by 0.47–0.72, not oculate; forebody 0.31–0.63 long, occupying 31–39% of total body length. Tegument spinose. Gland cells seen in parenchyma of forebody. Oral sucker subglobular, large, 0.11–0.14 by 0.15–0.19, subterminal. Prepharynx very short, with mass of small gland cells on either side. Pharynx pyriform to oblong, 0.07–0.12 by 0.08–0.11. Esophagus thick, muscular, short, 0.07–0.12 long, bifurcating dorsally to anterior part of ventral sucker or rarely in front of it, surrounded by small gland cells. Intestines thick, short, ending blindly at level of posterior border of ovary in hindbody. Ventral sucker subglobular, 0.10–0.18 by 0.13–0.20, located at about junction between anterior and middle thirds of body; sucker width ratio 1 : 0.80–1.18. Testis single, longitudinally oblong, large, 0.28–0.59 by 0.22–0.37, close to posterior end of body. Sperm ducts two, short; common sperm duct fairly long. Cirrus pouch club-shaped, slightly curved, fairly thick-walled, muscular, 0.19–0.31 by 0.07–0.12, posterolateral to ventral sucker (sometimes in front of ventral sucker in flattened specimens), lying obliquely across left intestine, not reaching to median line of body. Seminal vesicle spherical to elliptical, fairly thick-walled, 0.09–0.13 by 0.07–0.09. Pars prostatica elliptical, small; prostatic cells well developed. Cirrus (or ejaculatory duct) club-shaped, its posterior two-thirds lined by spines measuring about 11 μm long, sometimes slightly everted. Genital atrium shallow. Genital pore sinistrally submarginal or marginal at level of ventral sucker. Ovary single, oval, 0.14–0.29 by 0.12–0.21, immediately anterior to testis or slightly overlapping it. Ovarian complex between ventral sucker and ovary. Laurer's canal fairly long. Seminal receptacle small, 0.02–0.07 in diameter, empty (or functionless) or containing a small number of sperm. Ootype vesicular, large; Mehlis' gland well developed. Uterus much coiled basically on either side of ovary and testis in hindbody, sometimes extending forward even to pharyngeal level in median field; uterine seminal receptacle well developed in proximal coils; metraterm thick-walled, dilated in middle to form subglobular chamber (0.09–0.12 by 0.06–0.08) armed with spines measuring about 11 μm long, sometimes slightly everted. Eggs numerous, ovate, yellow to bright brown, 21–26 by 13–14 μm, with domed operculum at attenuated pole, fully embryonated. Vitellaria follicular, follicles large, entire in young adult specimens (Fig. 103A) but lobed or irregular in outline in old adult specimens (Fig. 103B), possibly nine forming bunch on either side of body, lateral, lying longitudinally along anterior two-thirds of intestines (or at level of ventral sucker). Excretory vesicle I-shaped, extending forward to middle of ovary; excretory pore posteroterminal.

Discussion. *Asymphylodora macrostoma* was described as a new species by Ozaki (1925) on the basis of adult specimens found in the cloaca [presumably the lowermost part of the rectum] of *Odontobutis obscura* (syn. *Mogurnda obscura*) caught in a brook in the vicinity of Saijo, now Saijo-cho, Higashihiroshima City, Hiroshima Prefecture. Ozaki's original specimens have not yet been reexamined.

Shimazu (2007) experimentally demonstrated that cercariae of *Cercariaeum innominatum* Faust, 1924 developed into adults of *Asymphylodora macrostoma* Ozaki, 1925. Because the specific name *innominatum* has priority over the specific name *macrostoma* (ICZN, Article 23.3.2.2), we propose a new combination, *Asymphylodora innominata* (Faust, 1924) comb. nov.,

for *A. macrostoma*.

Shimazu (1992) redescribed *A. macrostoma* (now *A. innominata*) from Ozaki's and Yamaguti's specimens and his own specimens including those from Lake Biwa. The ootype (Shimazu, 1992, fig. 11) should have been vesicular and large. The present new specimens from *O. u. uncirostris* and *T. hakonensis* are readily identified as *A. innominata*.

Ozaki (1925, fig. 4) originally described the clavate cirrus pouch was slightly larger than the elongated, spinose chamber (vagina of Ozaki) of the metraterm. However, the cirrus pouch is actually much larger than the globular, spinose chamber (Shimazu, 1992; this paper).

Life cycle. Shimazu (2007) revealed the life cycle of *A. macrostoma* (now *A. innominata*) in the field and laboratory. Natural first intermediate hosts were pleurocerid snails, *Semisulcospira* spp., in which cercariaea of *Cercariaeum innominatum* (syn. *Cercaria innominata*) developed in [daughter (?)] rediae (see also Ito, 1960, 1964). Natural and experimental second intermediate hosts were small fish, in the gills and buccal cavity of which metacercariae encysted (see also Komiya, 1965). *Tribolodon hakonensis* was used as both an experimental and a natural final host. Shimazu (1992) listed the other natural final hosts known at that time.

In Lake Biwa, Urabe (2003) found *Cercaria innominata* in *S.* (*Biwamelania*) *habei*, *S.* (*B.*) *niponica*, *S.* (*B.*) *nakasekoae*, and *S.* (*S.*) *libertina*. Encysted metacercariae were found in small fish, such as *Acheilognathus rhombeus*, *Pseudogobio esocinus esocinus*, etc. (our unpublished data). An immature specimen (NSMT-Pl 3977) was found in the intestine of *G. isaza* (Shimazu, 1992; this paper). Since metacercariae encyst in fishes, the infection route of this worm to this small, non-piscivorous fish is puzzling.

Asymphylodora japonica Yamaguti, 1938 (Figs. 105–107)

Asymphylodora japonica Yamaguti, 1938: 87–88, fig. 47; Yamaguti, 1942: 371; Shimazu, 1992: 3, 5, figs. 1–3.
Asymphylodora tincae: Nagano, 1930, not (Modeer, 1790) Looss, 1899: 24.
Orientotrema japonica [sic; should be *japonicum*]: Tang, 1962: 169.
Asymphylodora (*Asymphylodora*) *japonica*: Yamaguti, 1971: 97.
Parasymphilodora japonica [sic; misspelling of *Parasymphylodora*]: Besprozvannykh, 2005: 138, 141, fig. 2A.

Previous record. From *Cyprinus carpio* of Lake Biwa (Yamaguti, 1938; Shimazu, 1992).

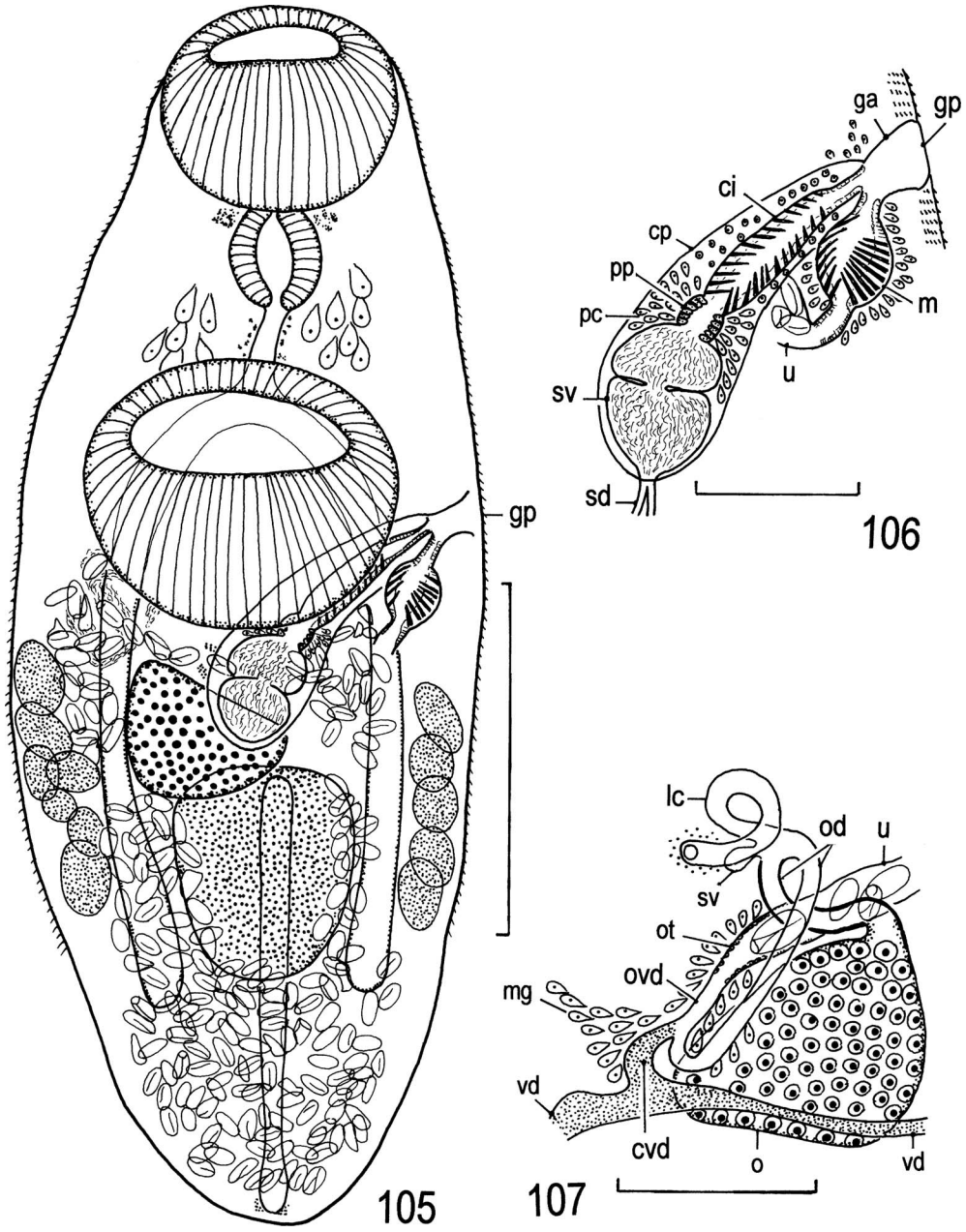
Host. *Cyprinus carpio*.

Site of infection. Intestine.

Collecting locality. Lake Biwa.

Materials examined. Some 50 mature specimens (Yamaguti's Collection, MPM Coll. No. 22272, paratypes) of *Asymphylodora japonica* found in the intestine of *Cyprinus carpio* from Lake Biwa on 1 June 1936 (Yamaguti, 1938; Shimazu, 1992).

Description. Ten large, mature specimens measured. Similar to *Asymphylodora innominata* (this paper) in general morphology. Body elongate-oblong, 0.83–1.05 by 0.36–0.46; forebody 0.34–0.41, occupying 36–40% of total body length. Oral sucker subglobular, 0.15–0.18 by 0.17–0.19, subterminal. Prepharynx very short. Pharynx pyriform or elliptical, 0.08–0.09 by 0.07. Esophagus short, 0.04–0.07 long, bifurcating dorsally to anterior half of ventral sucker. Intestines short, posteriorly terminating at about junction between middle and posterior thirds of hindbody (or at level of posterior border of testis). Ventral sucker subglobular, large, 0.17–0.22 by 0.23–0.25, slightly pre-equatorial; sucker width ratio 1 : 1.22–1.45. Testis longitudinally elongated, 0.13–0.20 by 0.09–0.16, in middle third of hindbody. Sperm ducts short; common sperm duct absent. Cirrus pouch 0.23–0.27 by 0.07–0.08, reaching posteriorly to median line of body.



Figs. 105–107. *Asymphylodora japonica.* Adult specimens, paratypes (MPM Coll. No. 22272) found in intestine of *Cyprinus carpio*. 105, entire body, ventral view; 106, terminal genitalia, ventral view; 107, ovarian complex, dorsal view. Scale bars: 0.3 mm in Fig. 105; 0.1 mm in Figs. 106–107.

Seminal vesicle distinctly bipartite, 0.06–0.09 by 0.06–0.10. Pars prostatica globular, small; prostatic cells well developed. Cirrus clavate, straight, its posterior four-fifths lined by spines measuring about 20 μm long. Genital atrium fairly deep. Genital pore on left lateral margin of body at about middle level of ventral sucker. Ovary subglobular to pyriform, sometimes irregular in outline, 0.10–0.14 by 0.11–0.16, dextrally submedian, immediately pretesticular. Laurer's canal fair-

ly long. Seminal receptacle very small, empty (or functionless). Ootype and Mehlis' gland well developed. Uterus much coiled in all available space in hindbody, proximal coils extending anteriorly sometimes to anterior border of ventral sucker, proximally acting as uterine seminal receptacle; metraterm short, dilated in middle to form globular chamber (0.04–0.05 in diameter) armed with spines measuring about 29 μm long, surrounded by gland cells. Eggs numerous, narrow ovate, yellow, 32–38 by 16–19 μm, operculate, fully embryonated. Vitelline follicles rather large, several in number (more than seven?), distributed in lateral field of middle third of hindbody on either side of body. Excretory vesicle reaching forward to anterior border of testis; excretory pore posteroterminal.

Discussion. *Asymphylodora japonica* was originally described as a new species by Yamaguti (1938) based on adult specimens found in the intestine of *Cyprinus carpio* (type host) caught in Fukuda Village, now in Okayama City, Okayama Prefecture (type locality), and in Lake Biwa (see also Shimazu, 1992). The present specimens are part of the paratypes of this species. Shimazu (1992) redescribed the species. Since Yamaguti (1938), no additional specimen of the species has been obtained from Lake Biwa. Kobayashi (1918) had stated that a digenean similar to *A. perlata* (Nordmann, 1832) Looss, 1899 (syn. *A. tincae* (Modeer, 1790) Looss, 1899) was found in great numbers in the intestine of *C. carpio* from Lake Biwa in November, 1911. He must have encountered *A. japonica* then, because, among the Japanese lissorchiids, *A. japonica* is the only species that parasitizes *C. carpio* (Shimazu, 1992, 1999, 2003b; this paper).

Yamaguti (1938) did not make a morphological comparison between *A. japonica* and *A. macrostoma* (now *A. innominata*). *A. japonica* is distinguished from *A. innominata* by the longer intestines ending at the level of the posterior border of the testis instead of the ovary, higher sucker width ratio (1 : 1.22–1.45 instead of 1 : 0.80–1.18), bipartite instead of oval seminal vesicle, larger eggs (32–38 by 16–19 μm instead of 21–26 by 13–14 μm), and posterior extent of the vitelline follicles reaching posteriorly to the ventral sucker instead of ending laterally to it (Shimazu, 1992; this paper).

In China, Tang (1962) and Wang and Pan (1984) reported adults, metacercariae, and cercariae of *A. japonica*; but their specimens are morphologically different from those of *A. japonica* in Japan (Shimazu, 1992).

Life cycle. Bithyniid snails are natural first and second intermediate hosts for *A. japonica* in Japan. Cercariaea (or tailless cercariae) are produced in daughter rediae. Some workers have misidentified the cercariaea as *A. tincae* (see Shimazu, 1992). Yamaguti (1938) obtained cercariaea and metacercariae (MPM Coll. No. 22281 and 22744) from *Parafossarulus manchouricus* (Bourguignat)) (syn. *Bulimus striatulus japonicus* (Pilsbry)) (Japanese name: Mame-tanishi) collected in Kojo Village, now in Okayama City. It is uncertain what organs of the snail he found cercariaea and metacercariae in. On his two slides were mounted daughter (?) rediae, cercariaea, and metacercariae; and some rediae contained an encysted metacercaria (Shimazu, 1992). It is considered that cercariaea do not encyst while still in the host snail and even while still in daugther rediae; but, once emerging from the host snail, they invade nearby snails again to encyst in some organs, even in rediae, in them, as seen in Primorye, Russia (Besprozvannykh, 2005), and in China (Institute of Hydrobiology, Hubei Province, China (chief ed.), 1973). It is probable that the final host (*C. carpio*) acquires infection with worms by eating host snails harboring encysted metacercariae (Shimazu, 1999). The digenean that was identified as *A. japonica* (syn. *Orientotrema japonicum*) in China (e.g., Tang, 1962; Institute of Hydrobiology, Hubei Province, China (chief ed.), 1973; Wang, 1991b) differs from *A. japonica* in Japan in having a non-bipartite, oblong seminal vesicle (see also Shimazu, 1992).

In Primorye, Russia, natural first intermediate hosts were *P. manchouricus* and *P. spiridonovi*; natural second intermediate hosts were snails of the genus *Boreoelona*; and natural final hosts were *C. carpio haematopterus* and *Carassius auratus gibelio* (Besprozvannykh, 2005).

Asymphylodora sp. (Fig. 104)

Asymphylodora macrostoma: Shimazu, 1992, not Ozaki, 1925: 8.

Previous record. From *Tridentiger brevispinis* of Omatsu, as *Asymphylodora macrostoma* (Shimazu, 1992).

Host. Tridentiger brevispinis.

Site of infection. Intestine.

Collecting locality. Omatsu.

Materials examined. One immature specimen (NSMT-Pl 3978) of *Asymphylodora macrostoma* found in the intestine of *Tridentiger brevispinis* from Omatsu on 5 May 1992 (Shimazu, 1992).

Description. Similar to *Asymphylodora innominata* (this paper) in general morphology. Body elliptical, 0.76 by 0.42; forebody 0.31 long, occupying 41% of total body length. Oral sucker 0.14 by 0.16. Pharynx 0.07 by 0.09. Esophagus short, 0.06 long, bifurcating dorsally to anterior half of ventral sucker. Intestines thick, ending at junction between middle and posterior thirds of hindbody (farther beyond posterior border of ovary). Ventral sucker 0.14 by 0.16, located at about junction between anterior and middle thirds of body; sucker width ratio 1 : 1.00. Testis oblong, large, 0.26 by 0.19, located some distance in front of posterior end of body. Cirrus pouch clavate, 0.12 by 0.06, lateral to ventral sucker, lying across left intestine, not reaching median line of body. Seminal vesicle spherical, 0.05 by 0.04. Pars prostatica small; prostatic cells well developed. Cirrus 0.05 by 0.01, lined heavily with spines measuring about 8 μm long. Genital atrium large. Genital pore small, sinistrally submedian at level of ventral sucker. Ovary oval, 0.14 by 0.11, dextrally submedian, ventral to anterior part of testis. Ovarian complex not clearly observed. Metraterm (or spinose chamber) elongate, large, 0.19 by 0.07, heavily armed with many, small spines measuring about 5 μm long. Vitelline follicles in irregular and complicated shape at level of ventral sucker on either side of body, between lateral margin of body and ventral sucker, overlapping ventral sucker. Excretory vesicle extending forward to anterior border of testis; excretory pore posteroterminal.

Discussion. Shimazu (1992) misidentified this specimen as *A. macrostoma* (now *A. innominata*). It is distinct from *A. innominata* (this paper) in that the clavate cirrus pouch is smaller than the elongate chamber of the metraterm, the spines of the chamber are greater in number and much smaller, and the vitelline follicles are in an irregular, much more complicated shape in spite of the fact that it is still immature. It may represent an undescribed species of *Asymphylodora* Looss, 1899, but it remains unidentified until additional adult specimens are obtained.

Life cycle. The life cycle is not known.

Asymphylotrema hamajimai (Fujino and Kifune, 1991) (Figs. 108–110)

(?) *Cercaria monostyloides* Ito, 1960: 68–69, fig. 15.

Anapalaeorchis hamajimai Fujino and Kifune, 1991: 35–36, figs. 1–8; Shimazu, 1992: 12, 14, figs. 12–16.

Asymphylotrema hamajimai: Bray, 2008: 178.

Previous record. None.

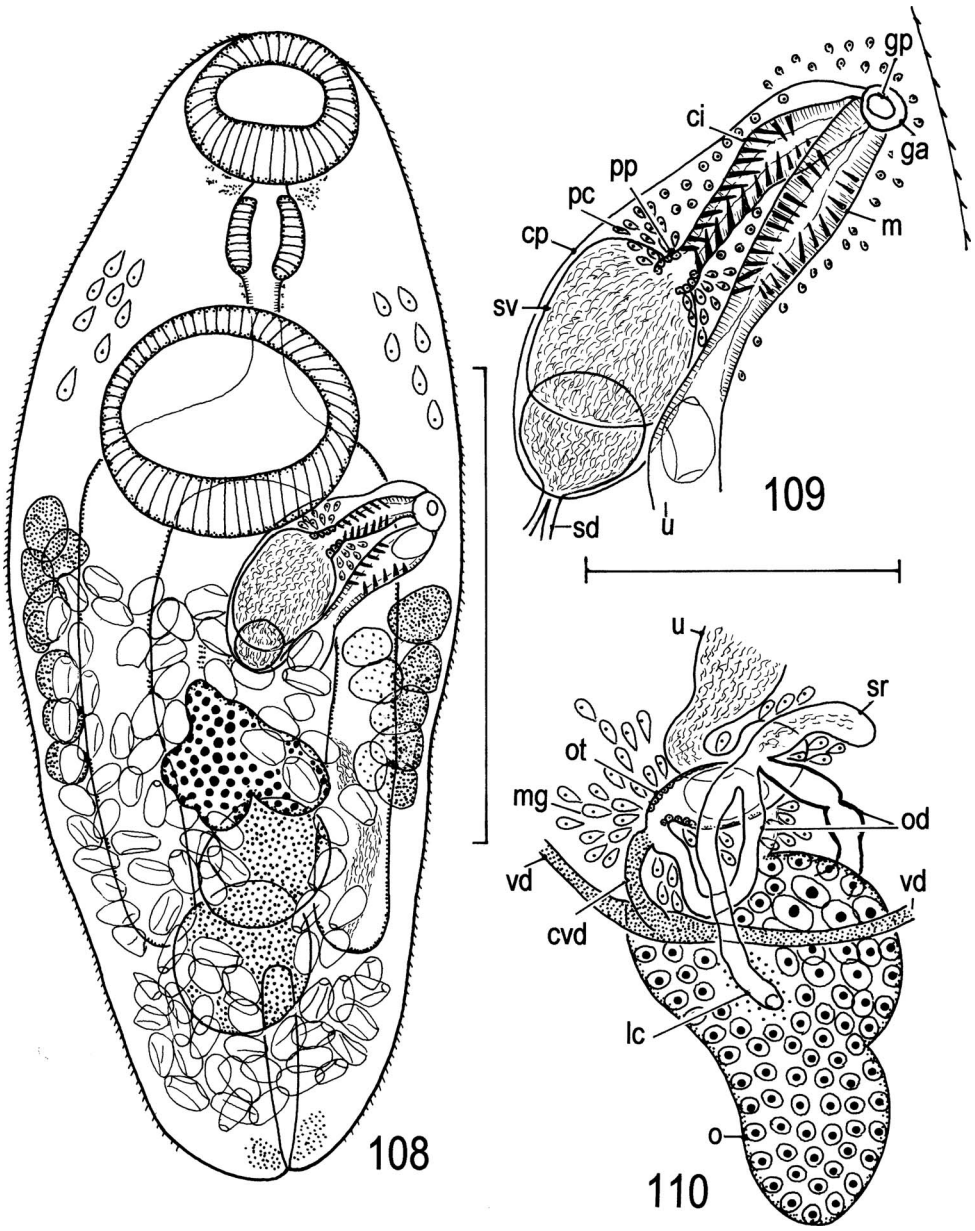
Host. *Cobitis biwae.*

Site of infection. Intestine.

Collecting locality. Hamabun.

Materials examined. Seven mature specimens (LBM 1-55 and 3-40) found in the intestine of *Cobitis biwae* from Hamabun on 24 October 1997 and 1 November 2000.

Description. Of the seven specimens, one lacked the anterior part of the body, one lacked



Figs. 108–110. *Asymphylotrema hamajimai*. Adult specimens found in intestine of *Cobitis biwae.* 108, specimen (LBM 1-55), entire body, ventral view; 109, specimen (LBM 1-55), terminal genitalia, ventral view; 110, specimen (LBM 3-40), ovarian complex, dorsal view. Scale bars: 0.3 mm in Fig. 108; 0.1 mm in Figs. 109–110.

the posterior part of the body, and two had the anterior part of the body folded. The three remaining, better-prepared specimens were measured. Body elongate, dorsoventrally flattened, 0.60–0.72 by 0.25–0.27, not oculate; forebody 0.22–0.28, occupying 34–39% of total body length. Tegument spinose. Gland cells seen in parenchyma of forebody. Oral sucker subglobular, 0.09 by 0.10–0.12, subterminal. Prepharynx very short, with mass of gland cells on either side. Pharynx pyriform, 0.05 by 0.04–0.05. Esophagus short, 0.06–0.08 long, surrounded by small gland cells, bifurcating dorsally to ventral sucker. Intestines thick, fairly long, posteriorly terminating blindly at about junction between middle and posterior thirds of hindbody (about midway in testicular zone of body). Ventral sucker subglobular, large, 0.13–0.15 by 0.15–0.16, median, at about junction between anterior and middle thirds of body; sucker width ratio 1 : 1.38–1.55. Testes two, globular to longitudinally elongate, median, tandem or slightly diagonal, contiguous or slightly overlapping each other, at about junction between middle and posterior thirds of hindbody: anterior testis 0.06–0.09 by 0.07–0.08, posterior 0.07–0.11 by 0.08. Sperm ducts short; common sperm duct not seen. Cirrus pouch clavate, slightly curved, thin-walled, 0.16 by 0.05–0.06, lying obliquely across left intestine, posterolateral to ventral sucker, reaching to median line of body. Seminal vesicle internal, thin-walled, 0.06–0.09 by 0.04–0.06, occupying posterior half of cirrus pouch, distinctly bipartite, anterior portion much larger than posterior. Pars prostatica globular, small; prostatic cells well developed. Cirrus club-shaped, straight, its posterior two-thirds lined by spines about 13 μm long. Genital atrium fairly deep. Genital pore sinistrally submarginal, slightly anterior to level of posterior border of ventral sucker. Ovary single, weakly three-lobed, 0.06–0.12 by 0.07–0.10, median, pretesticular. Ovarian complex anterodorsal to ovary. Laurer's canal fairly long, sometimes including sperm. Seminal receptacle very small, 0.03 long, empty (or functionless) or including a small number of sperm. Ootype vesicular, large. Mehlis' gland well developed. Uterus fairly much coiled in all available space in hindbody, acting as uterine seminal receptacle; metraterm claviform, short, about half as long as cirrus pouch, 0.07–0.08 long, armed with spines measuring about 10 μm long, surrounded by gland cells. Eggs numerous, ovate, yellow, 30–34 by 19–21 μm, with domed operculum at attenuated pole, fully embryonated. Vitellaria follicular, follicles large, about eight making longitudinal cluster lying along intestine in lateral field between ventral sucker and anterior testis on either side of body. Excretory vesicle I-shaped, reaching forward to middle of posterior testis; excretory pore posterotermi-nal.

Discussion. *Anapalaeorchis hamajimai* was established as a new genus and species by Fujino and Kifune (1991) based on adult specimens found in the intestine of *Cobitis biwae* (type host) collected in the Toki River (type locality) in Tokigawa Town, Saitama Prefecture. Bray (2008) synonymized *Anapalaeorchis* with *Asymphylotrema* Dvoryadkin and Besprozvannykh, 1985, which had been predicted by Shimazu (1992). The latter genus was erected by Dvoryadkin and Besprozvannykh (1985) with *Asymphylodora macracetabulum* Belous, 1953 as the type species that was described from *Misgurnus anguillicaudatus* taken in the Lake Khanka system in Primorye, Russia. Accordingly, the species name of the present digenean has become *Asymphylotrema hamajimai* (Fujino and Kifune, 1991) Bray, 2008.

Shimazu (1992) redescribed *A. hamajimai* (now *As. hamajimai*) from specimens made available to him at that time. The present specimens agree well with *A. hamajimai* as originally described by Fujino and Kifune (1991) and redescribed by Shimazu (1992) except for the anterior extent of the excretory vesicle. Fujino and Kifune (1991) failed to observe the excretory vesicle in the type series. Shimazu (1992, fig. 12) erroneously described the excretory vesicle as extending forward to the middle of the anterior testis in the holotype. The excretory vesicle is actually

shorter, ending at the middle of the posterior testis in the holotype, as seen in the specimen figured by Shimazu (1992, fig. 15) and the present specimens (Fig. 108).

Asymphylotrema hamajimai morphologically differs from *As. macracetabulum* as redescribed by Dvoryadkin and Besprozvannykh (1985) in having shorter intestines ending posteriorly about midway in the testicular zone of the body, instead of at the level of the posterior border of the posterior testis; a lower sucker width ratio, 1 : 1.38–1.55 instead of 1 : 1.7 (our calculation); a larger cirrus pouch reaching to the median line of the body, instead of not; a seminal vesicle occupying the posterior half, instead of the posterior two thirds, of the cirrus pouch; and smaller eggs, 30–34 by 19–21 μm instead of 33–44 by 11–22 μm. Furthermore, *As. hamajimai* has not be recorded from *M. anguillicaudatus* in Japan (Shimazu, 1992, 1999, 2003b, 2007).

Life cycle. Shimazu (2007) regarded *Cercaria monostyloides* Ito, 1960 as belonging to *A. hamajimai* (now *As. hamajimai*) from circumstantial evidence (see also Shimazu, 1992, 1999, 2003b). This awaits experimental confirmation.

Cercariaea (or tailless cercariae) of *Ce. monostyloides* develop in daughter rediae in pleurocerid snails, *Semisulcospira* spp. (Ito, 1960; Urabe, 2003; Shimazu, 2007). Urabe (2003) obtained *Ce. monostyloides* from *S.* (*S.*) *libertina* of the Lake Biwa basin. A second intermediate host is not known. A final host is *C. biwae* (Fujino and Kifune, 1991; Shimazu, 1992, 2007; this paper).

Palaeorchis diplorchis (Yamaguti, 1936) (Figs. 111–115)

Asymphylodora diplorchis Yamaguti, 1936b: 4–5, fig. 8.
Steganoderma kamatukae Takeuti, 1936: 582–583, fig. 1; Yamaguti, 1954: 51.
Palaeorchis diplorchis: Szidat, 1943: 48; Shimazu, 1992: 15, 17, figs. 17–22; Shimazu and Urabe, 2005: 12–13, figs. 21–23.

Previous records. From *Pseudogobio esocinus esocinus* (syn. *Ps. esocinus* (Temminck and Schlegel)) of Lake Biwa, as *Steganoderma kamatukae* (Takeuti, 1936); and of Omatsu and Onoe, as *Palaeorchis diplorchis* (Shimazu, 1992).

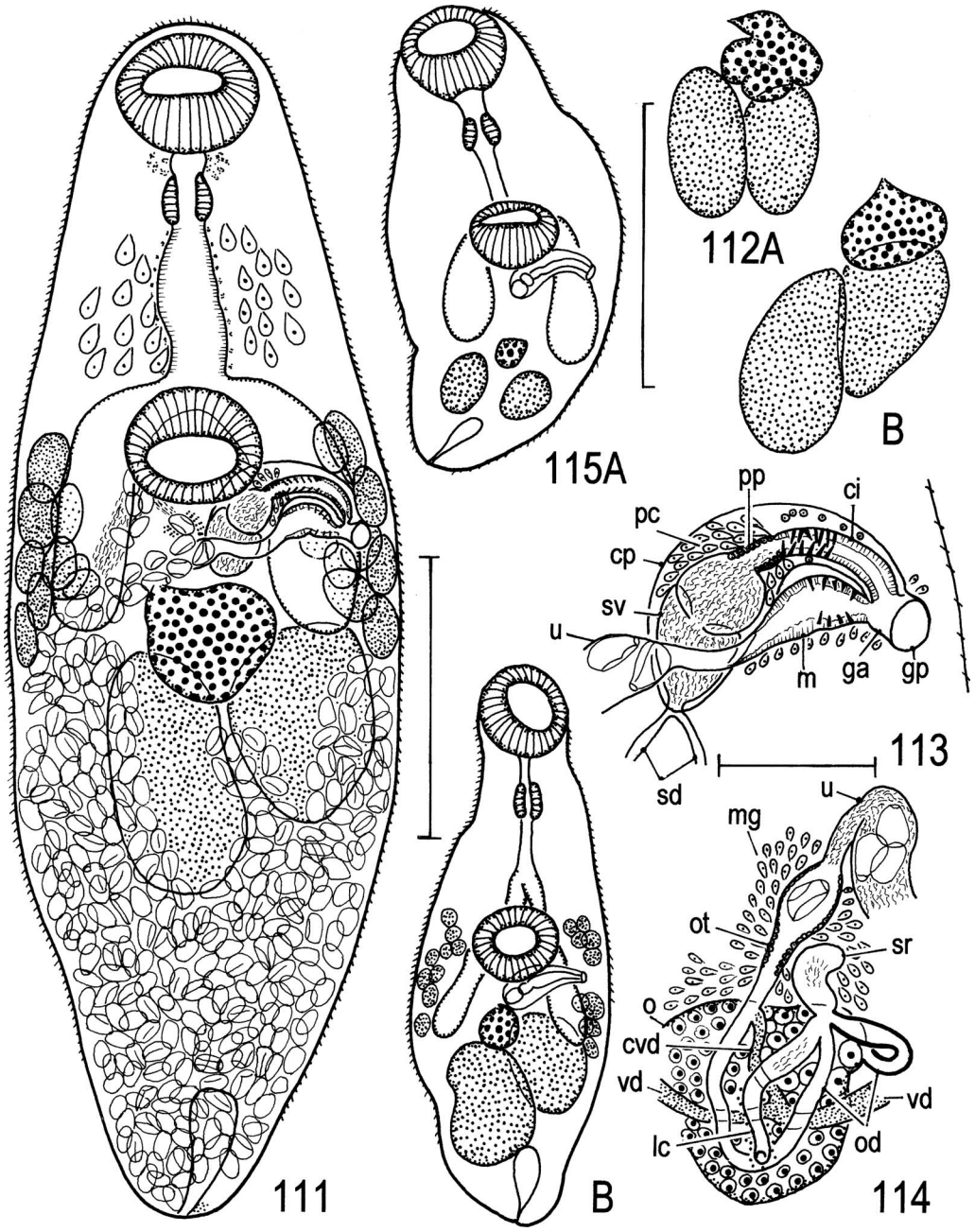
Hosts. *Anguilla japonica*, *Biwia zezera*, *Hemibarbus barbus*, and *Pseudogobio esocinus esocinus*.

Site of infection. Primarily intestine, and also stomach (accidental (?)).

Collecting localities. Lake Biwa, Moriyama, Omastu, and Onoe.

Materials examined. (1) Specimens of *Palaeorchis diplorchis* found in the intestine of *Pseudogobio esocinus esocinus* (syn. *Ps. esocinus*): [one immature and 25 mature] (NSMT-Pl 3695 and 3981) from Onoe on [4 February 1980 and 4 May 1992], [46 mature] (NSMT-Pl 3980) from [Moriyama] on [2 May 1992], and [21 mature] (NSMT-Pl 3979 and 3982–3983) from Omatsu on [1, 5, and 6 May 1992] (Shimazu, 1992). (2) Specimens found in the intestine of *Ps. e. esocinus*: three mature (LBM 1-35, from intestine) from Imazu on 19 May 1998, 5 mature (LBM 6-21 to -25, hot formalin-fixed, collected and identified as *P. diplorchis* by Tomáš Scholz), and three immature (LBM 8-50) from Momose on 24 November 2007. (3) One mature specimen (NSMT-Pl 4013, collected by Shimazu) found in the stomach of *Anguilla japonica* from Omatsu on 4 May 1992. (4) Two mature specimens (NSMT-Pl 5733, collected by Shimazu) found in the intestine of *Hemibarbus barbus* from Moriyama on 2 May 1992. (5) One immature specimen (NSMT-Pl 5736, collected by Shimazu) found in the intestine of *Biwia zezera* from Onoe on 4 May 1992.

Description. Ten large, mature specimens from *Ps. e. esocinus* measured. Body elongate-



Figs. 111–115. *Palaeorchis diplorchis.* Immature and mature specimens. 111, mature specimen (NSMT-Pl 3980) found in intestine of *Pseudogobio esocinus esocinus*, entire body, ventral view; 112, mature specimens (NSMT-Pl 3980), showing relative position of two testes (A, symmetrical; B, slightly diagonal) and shape of ovary (A, weakly tri-lobed; B, almost globular), ventral view; 113, mature specimen (NSMT-Pl 3980), terminal genitalia, ventral view; 114, mature specimen (NSMT-Pl 3980), ovarian complex, dorsal view; 115, immature specimens, A (LBM 8-50) found in intestine of *Ps. e. esocinus*, showing symmetrical testes; B (NSMT-Pl 5736) found in intestine of *Biwia zezera*, showing diagonal testes, both ventral view. Scale bars: 0.3 mm in Figs. 111–112 and 115A–B; 0.1 mm in Figs. 113–114.

fusiform, slightly flat dorsoventrally, 0.96–1.31 by 0.32–0.43, not oculate; forebody 0.30–0.46, occupying 30–37% of total body length. Tegument covered with fairly large spines. Gland cells seen in parenchyma of forebody. Oral sucker subglobular, 0.10–0.12 by 0.12–0.15, subterminal. Prepharynx short, with mass of gland cells on either side. Pharynx pyriform, 0.03–0.05 by 0.04–0.05. Esophagus long, 0.09–0.17 long, surrounded by small gland cells, bifurcating dorsally to ventral sucker. Intestines short, pre-equatorial, pretesticular. Ventral sucker subglobular, slightly smaller than oral sucker, 0.10–0.13 by 0.11–0.14, median, at about junction between anterior and middle thirds of body; sucker width ratio 1 : 0.89–0.98. Testes two, longitudinally elongate, symmetrical or slightly diagonal, contiguous or separated by uterus, submedian on either side of body (Figs. 111–112): right testis 0.19–0.30 by 0.09–0.14, left 0.14–0.27 by 0.10–0.16. Sperm ducts two; common sperm duct absent. Cirrus pouch club-shaped, curved, fairly thick-walled, muscular, 0.13–0.22 by 0.06–0.07, lying oblique across left intestine, reaching posteriorly to median line of body. Seminal vesicle internal, distinctly bipartite, thin-walled, 0.08–0.14 by 0.05–0.06. Pars prostatica globular, small; prostatic cells well developed. Cirrus clavate, straight, its proximal half lined by spines measuring about 24 μm long, rarely slightly everted. Genital atrium fairly deep. Genital pore sinistrally marginal or submarginal, slightly behind level of posterior border of ventral sucker. Ovary single, irregular in shape (subglobular, triangular, weakly two-lobed, or weakly three-lobed), 0.11–0.16 by 0.12–0.15, median or dextrally submedian, immediately pretesticular (Figs. 111–112). Ovarian complex dorsal or anterodorsal to ovary. Laurer's canal fairly long. Seminal receptacle very small, 0.05–0.06 by 0.01, empty (or functionless) or containing a small number of sperm. Ootype vesicular, large, preovarian. Mehlis' gland well developed. Uterus much coiled in all available space in hindbody, proximal coils extending anteriorly to middle level of ventral sucker and acting as uterine seminal receptacle; metraterm fairly long, 0.06–0.08 long, surrounded by gland cells, its distal fourth–fifths dilated to form oblong chamber; distal half of chamber armed with spines measuring about 16 μm long. Eggs numerous, oviform, brown, 35–41 by 21–24 μm, with small domed operculum at attenuated pole, fully embryonated. Vitellaria follicular, follicles large, about nine making longitudinal cluster distributed in lateral field along intestine from intestinal shoulder to slightly beyond intestinal end on either side of body. Excretory vesicle I-shaped, short, not reaching forward to testes in fully matured specimens; excretory pore posteroterminal.

In immature specimens (Fig. 115A–B), testes symmetrical (Fig. 115A) or diagonal (Fig. 115B), and excretory vesicle reaching to testes.

Discussion. Yamaguti (10 September 1936) described a new species, *Asymphylodora diplorchis*, based on adult specimens found in the intestine of *Ps. e. esocinus* (syn. *Ps. esocinus*) of Lake Suwa, Nagano Prefecture. Takeuti (15 October 1936) proposed a new genus and species, *Steganoderma kamatukae*, based on adult specimens found in the intestine of *Ps. esocinus* of Lake Biwa. Szidat (1943) established a new genus, *Palaeorchis*, with *A. diplorchis* as the type species; but he was unaware of *S. kamatukae* at that time. Yamaguti (1954) (not 1953) listed *S. kamatukae* as a junior synonym of *P. diplorchis*. Shimazu (1992) agreed to this treatment. Takeuti's original material has not yet been reexamined; but it must have been lost (see Materials and Methods).

Shimazu (1992) redescribed adults of *P. diplorchis* from the material made available to him at that time. The present new specimens also are identified as *P. diplorchis*. In them, the ovary varies more widely in shape from subglobular, triangular, weakly two-lobed, or weakly three-lobed than was described by Yamaguti (1936b), Takeuti (1936), and Shimazu (1992) (subglobular to triangular).

Life cycle. The life cycle is not known.

Family **Heterophyidae** Leiper, 1909

Pseudexorchis major (Hasegawa, 1935) (Figs. 116–118)

Exorchis major Hasegawa, 1935a: 1193–1197, 1 pl., figs. 1–2; Hasegawa, 1935b: 1546, 1 pl.
Pseudexorchis major: Yamaguti, 1938: 68; Shimazu, 2007: 24–25, figs. 31–34; Shimazu, 2008, 57, fig. 13.

Previous record. None.

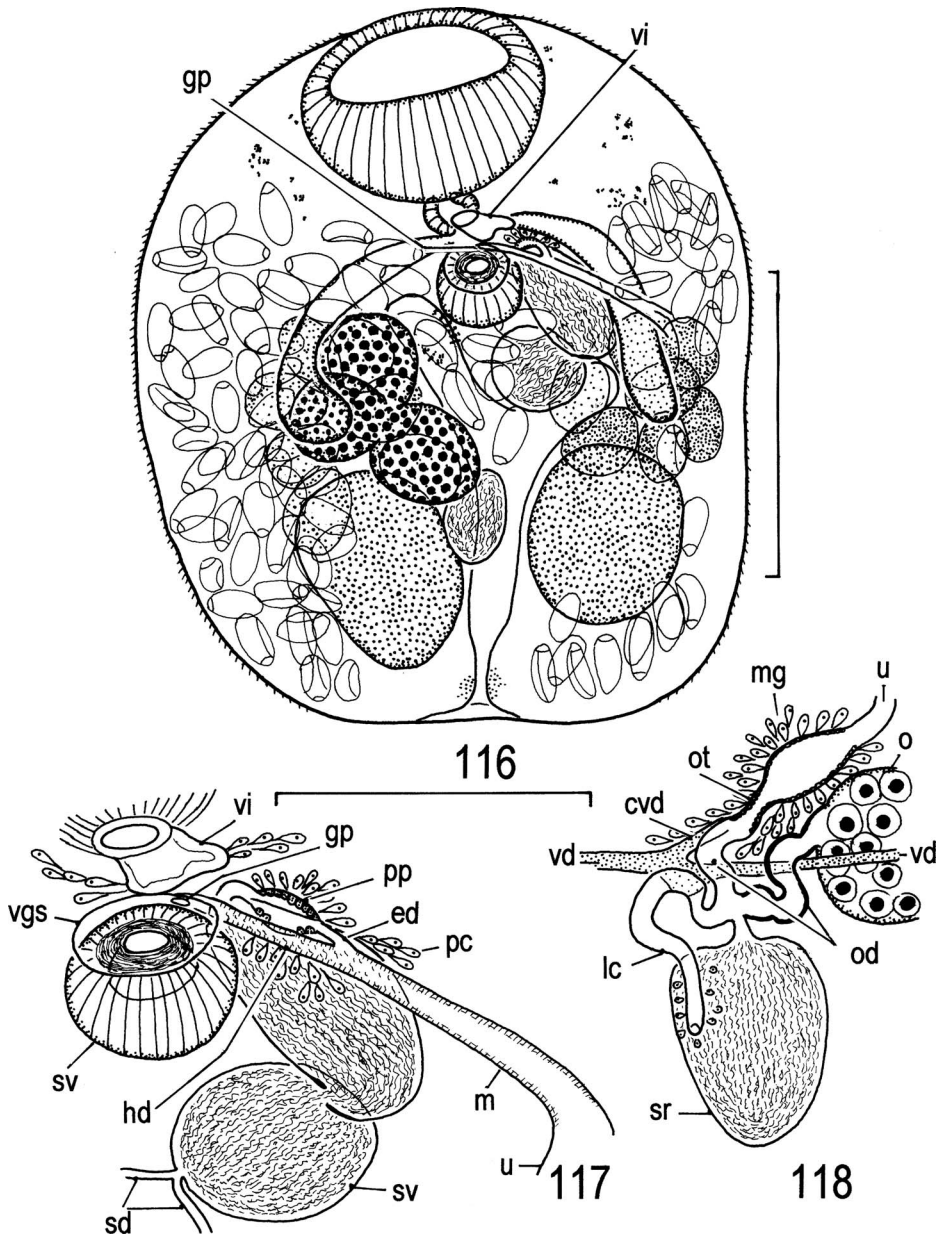
Hosts. *Silurus asotus* and *S. biwaensis*.

Site of infection. Intestine.

Collecting localities. Imazu, Momose, Onoe, and Shina.

Materials examined. (1) Specimens found in the intestine of *Silurus asotus*: 12 mature (NSMT-Pl 5737, unidentified, collected by Nagasawa) from Shina on 11 November 1980, one mature (LBM 1-50) from Imazu on 19 May 1998, and one mature (LBM 8-51) from Momose on 24 November 2007. (2) Eighteen mature specimens (NSMT-Pl 5738, collected by Shimazu) found in the intestine of *S. biwaensis* from Onoe on 4 May 1992.

Description. Ten fully mature specimens measured. Body spherical, oval, or elliptical, anteriorly rounded, posteriorly rotundate, truncate, or cordate, 0.38–0.63 by 0.31–0.48; forebody 0.15–0.25 long, occupying 35–40% of total body length. Tegumental spines scale-like, rotundate, and dense in anterior part of body, posteriorly becoming sparse, acute spines, not seen on posteriormost part of body. Eyespot pigment solid or dispersed mainly in forebody. Ventral invagination invaginated, 0.02–0.05 by 0.02–0.03, median, between two suckers. Oral sucker round or transversely elliptical, large, 0.09–0.16 by 0.13–0.18, anteroventral. Prepharynx very short. Pharynx round or oval, 0.03–0.05 by 0.02–0.03. Esophagus very short, bifurcating between pharynx and ventral sucker. Intestines short, posteriorly terminating blindly at about equatorial level of hindbody. Ventral sucker median, round, small, 0.05–0.06 in diameter, slightly posterior to junction between anterior and middle thirds of body; aperture located on anteroventral margin of ventral sucker, with thick-walled periphery (sphincter (?)); sucker width ratio 1 : 0.35–0.43. Ventrogenital sac present, small, shallow, median, enclosing anteroventral half of ventral sucker. Testes two, globular to elliptical, 0.08–0.19 by 0.05–0.12, usually symmetrical but rarely pushed slightly more posteriorly by ovary on ovarian side of body, submedian, separate, behind intestines. Sperm ducts two, long; common sperm duct absent. Seminal vesicle voluminous, bipartite, 0.11–0.24 by 0.05–0.12, curved, lateral to ventral sucker. Cirrus pouch absent. Pars prostatica elliptical, near anterior end of seminal vesicle, surrounded by prostatic cells. Ejaculatory duct short, running toward lateral margin of body, uniting with metraterm usually ventrally to anterior chamber of seminal vesicle to form fairly long hermaphroditic duct opening into ventrogenital sac. Genital pore median, on anterior wall of ventrogenital sac. Ovary single, three-lobed, 0.09–0.13 by 0.08–0.11, submedian, posterolateral to ventral sucker on opposite side of seminal vesicle. Ovarian complex posterolateral to ventral sucker, on ovarian side of body. Seminal receptacle globular to elliptical, 0.06–0.09 by 0.05–0.06, posteromedial to ovary. Laurer's canal almost median, short, running backward. Ootype vesicular, large, between ventral sucker and ovary, surrounded by well developed Mehlis' gland. Uterus folded in all available space of body in large, fully mature, adult specimens. Metraterm transversely running in front of vitelline follicles on opposite side of ovary. Eggs numerous, narrow-ovate, slightly asymmetrical, dark brown, 34–40 by 18–24 μm, with large domed operculum, fully embryonated; surface markings seen on eggshell.



Figs. 116–118. *Pseudexorchis major*. Adult specimen (NSMT-Pl 5738) found in intestine of *Silurus biwaensis*. 116, entire body, ventral view; 117, ventral invagination and terminal genitalia, ventral view; 118, ovarian complex, dorsal view. Scale bars: 0.2 mm in Fig. 116; 0.1 mm in Figs. 117–118.

Vitellaria follicular, follicles large, in dorsal parenchyma, seven making compact, submedian cluster at ovarian level on either side of body. Excretory vesicle Y-shaped, with short arms anteriorly ending between ovary and ventral sucker (or behind intestinal shoulders); excretory pore postero-ventral or -dorsal.

Discussion. Hasegawa (1935a) described a new species, *Exorchis major*, on the basis of adult specimens found in the intestine of *Silurus asotus* (syn. *Parasilurus asotus*). He did not

clearly show the locality, but he found this species in *S. asotus* from Senoo, now in Minami-ku, Okayama City, Okayama Prefecture, and from the Kobe Market in Hyogo Prefecture. Yamaguti (1938) established a new genus, *Pseudexorchis* to accommodate *E. major* as the type and only species. Takahashi (1929a) observed the anatomy of the ovarian complex of this species. Hasegawa (1935b) observed the surface markings on the eggshell. Shimazu (2007) redescribed adults of *P. major* from the material made available to him at that time. He showed that Hasegawa (1935a) mistook the "ventral invagination" (terminology of Shimazu, 2007) for a genital atrium. The present specimens agree well with *P. major* as redescribed by Shimazu (2007, 2008). The ootype (Shimazu, 2007, fig. 34) should have been vesicular and large.

Life cycle. The life cycle of *P. major* is well known in Japan. First intermediate hosts are pleurocerid snails, *Semisulcospira* spp., in which pleurolophocercous cercariae develop in [daughter (?)] rediae (Hasegawa, 1927; Takahashi, 1929b; Yamaguti, 1938; Ito, 1956, 1964; Shimazu, 1999, 2003b). Second intermediate hosts are freshwater fishes of various species, in which metacercariae encyst (Hasegawa, 1927, 1934, 1935a; Takahashi, 1929b; Yamaguti, 1938; Ito, 1956; Komiya, 1965; Shimazu, 1999, 2003b). Final hosts are *Silurus asotus* and *S. biwaensis* (Hasegawa, 1935a, b; Takahashi, 1929a, b; Yamaguti, 1938; Shimazu, 1999, 2003b, 2007; this paper).

In the Lake Biwa basin, Urabe (2003) obtained cercariae of *P. major* from *Semisulcospira* (*Biwamelania*) *habei*, *Se.* (*B.*) *niponica*, *Se.* (*B.*) *decipiens*, *Se.* (*B.*) *nakasekoae*, and *Se.* (*Se.*) *libertina*. Sakai (1953) recorded metacercariae from *Plecoglossus altivelis altivelis* and *Pseudorasbora parva* of Lake Biwa. Metacercariae were found in *Acheilognathus rhombeus*, *Tanakia lanceolata*, etc. (our unpublished data).

Family **Bucephalidae** Poche, 1907

Parabucephalopsis parasiluri Wang, 1985 (Figs. 119–121)

Parabucephalopsis parasiluri Wang, 1985: 76, fig. 10; Urabe *et al.*, 2007: 270, fig. 1A–C.

Previous record. From *Silurus biwaensis* of the Seta River (Urabe *et al.*, 2008).

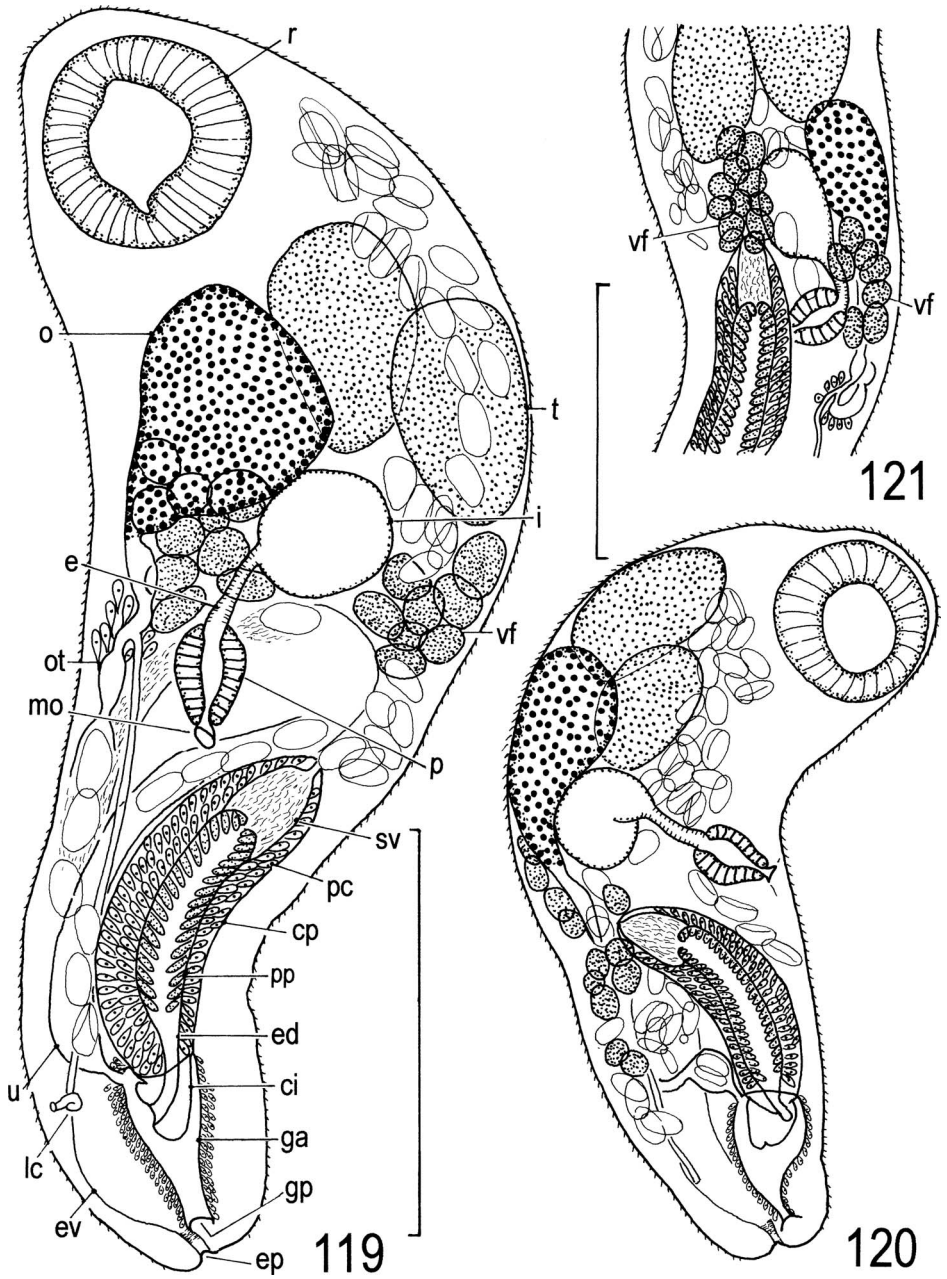
Host. *Silurus biwaensis*.

Site of infection. Rectum.

Collecting locality. Seta River-2.

Materials examined. Thirty-four immature and 12 mature specimens (NSMT-Pl 5743, collected by Urabe) found in the rectum of *Silurus biwaensis* from the Seta River-2 on 1 June 2007 (Urabe *et al.*, 2008).

Description. Based on 12 mature specimens; three of them measured. Body elongate-ovate, broader anteriorly, 0.58–0.64 by 0.17–0.22, not oculate. Tegument spinose. Oral and ventral suckers absent. Rhynchus simple, suckerlike, round, 0.10 by 0.09–0.11, almost ventral, close to anterior end of body. Mouth ventral, opening on tip of pharynx. Pharynx directed anteriorly from mouth, pyriform, 0.04–0.05 by 0.03–0.04, almost median, slightly postequatorial. Esophagus directed anteriorly, 0.04 long, surrounded by small gland cells. Intestine directed anteriorly, globular, 0.07–0.08 by 0.05–0.06, in front of pharynx. Testes two, elliptical, diagonal, slightly overlapping each other, far behind rhynchus; anterior (or right) testis 0.10–0.11 by 0.06–0.07, posterior (or left) 0.10–0.12 by 0.05–0.06. Sperm ducts two, short; common sperm duct long. Cirrus pouch tubular, slightly curved, thick-walled, muscular, 0.19–0.23 by 0.05, median or sinistrally submedian, its anterior (or proximal) end opposite pharynx. Seminal vesicle internal, elliptical,



Figs. 119–121. *Parabucephalopsis parasiluri*. Adult specimens (NSMT-Pl 5743) found in rectum of *Silurus biwaensis*. 119, entire body, ventral view; 120, entire body, ventrolateral view; 121, middle third of body, showing vitelline follicles, dorsal view. Scale bars: 0.2 mm in Figs. 119–121.

0.04–0.05 by 0.03. Pars prostatica curved, about half as long as cirrus pouch. Ejaculatory duct short. Cirrus (or genital lobe) projecting into genital atrium, 0.03 long, in form of crooked lobe. Genital atrium deep, with sphincter at aperture, surrounded by small gland cells. Genital pore almost median, near posterior end of body. Ovary single, obovate, 0.12–0.13 by 0.06–0.09, dextrally submedian, level with testes or post-testicular, anterolateral or lateral to intestine. Ovarian

complex postovarian. Oviduct forming dilatation, possibly for sperm storage, before giving off Laurer's canal. Ootype vesicular, small, dextrally lateral to submedian; Mehlis' gland weakly developed. Laurer's canal long, running backward, apparently opening dorsally near lateral margin at level of cirrus on right side of body. Seminal receptacle absent. Uterus folded between rhynchus and testes, on either side of intestine, and on right side of cirrus pouch; metraterm short, opening into lateral side of base of genital atrium, facing cirrus; sometimes uterine seminal receptacle weakly developed. Eggs fairly numerous, elliptical, sometimes curved, light brown, 27–35 by 13–16 μm (collapsed), thin-shelled, operculate, embryonated. Vitellaria follicular, follicles small, forming two compact clusters, oblique or nearly symmetrical, close to each other, posterolateral to posterior to ovary. Excretory vesicle saccular, anteriorly terminating at about anterior end of cirrus pouch; excretory pore posteroterminal.

Discussion. These specimens morphologically agree well with *Parabucephalopsis parasiluri* as redescribed by Urabe *et al.* (2007) from *Silurus biwaensis* caught in the Uji River at Uji City, Kyoto Prefecture.

Parabucephalopsis parasiluri is a parasite originally found in *Silurus asotus* from Fuzhou, Fujian Province, China (Wang, 1985). It is known to occur in central and southern parts of China (Urabe *et al.*, 2001; Urabe *et al.*, 2008). In Japan, it was recorded from the Uji River in 2000 for the first time (Urabe *et al.*, 2007).

The main stream of the Yodo River system originates in Lake Biwa (Fig. 1). It changes its name three times: upper reaches are called the Seta River, in Shiga Prefecture (Fig. 1); middle reaches, the Uji River, in Kyoto Prefecture; and lower reaches, the Yodo River in Kyoto and Osaka prefectures. The last finally empties into Osaka Bay. The Amagase Dam which crosses the Uji River was completed in 1964 (see Urabe *et al.*, 2008, fig. 1); and, consequently, this dam has completely blocked the upstream migration of fishes through the main stream from the Yodo and Uji rivers into the Seta River and Lake Biwa since then.

The present locality (Seta River-2, 35 in Fig. 1) is located about 15 km upstream through the Amagase Dam from the Uji River at Uji City. As will be shown later in "*Life cycle*", a natural first intermediate host of *P. parasiluri* in the Uji River is *Limnoperna fortunei* (Dunker) (Japanese name: Kawahibarigai) (Mytilidae, Bivalvia). After this host mytilid had been artificially and accidentally (as a contaminant) introduced from the Asian continent into Japan possibly not once but repeatedly, it very likely established itself in Lake Biwa in about 1992 and then in the Yodo River system in about 1994 (Urabe *et al.*, 2001). Probably, some mytilids infected with sporocysts and cercariae of *P. parasiluri* were introduced from the Asian continent into Japan sometime ago, so that eventually the parasite has settled itself in the Uji River (Urabe *et al.*, 2001) and then in the Seta River (Urabe *et al.*, 2008). The parasite evidently completes its life cycle in these two localities now (Urabe *et al.*, 2001; Urabe *et al.*, 2007; Urabe *et al.*, 2008). However, its introduction route into either of them is still unknown. The parasite has not as yet been recorded from Lake Biwa (this paper).

Life cycle. The life cycle of *P. parasiluri* in the Uji and Seta rivers is briefly as follows (Urabe *et al.*, 2001; Urabe *et al.*, 2007; Urabe *et al.*, 2008). A first intermediate host is *Limnoperna fortunei*, in which bucephaloid cercariae develop in [probably mother] sporocysts. Second intermediate hosts are freshwater fishes of several species, in which metacercariae encyst. A final host is *Silurus biwaensis*. Immature worms were found in *S. asotus* and *Micropterus salmoides*. The entire life cycle in China is unknown.

Other species recorded from Lake Biwa

1. **Sanguinicolidae** gen. sp. of Shimazu, 1999 (Family Aporocotylidae Odhner, 1912)

Species of the genus *Sanguinicola* Plehn, 1905 are parasitic in the blood vessels of freshwater fishes. An immature specimen presumably of this genus was found in the gill of *Acheilognathus tabira tabira* from Onoe on [3 June 1980] (Shimazu, 1999, 2003b). This specimen was lost before morphological observations for precise identification and description could be undertaken.

2. ***Allocreadium*** sp. of Kataoka and Momma, 1934 *incertae sedis*

Kataoka and Momma (1934, pp. 59–60) described this species, with no figure, from a single adult specimen found in the intestine of *Plecoglossus altivelis altivelis* (syn. *P. altivelis*) from Lake Biwa. According to their original description, the morphology of the specimen is briefly as follows:

Body ellipsoidal, somewhat elongated, 2.23 by 0.73. Tegument smooth. Oral sucker 0.16 in diameter. Prepharynx absent. Pharynx globular, 0.12 in diameter. Esophagus short, 0.093 long, bifurcating into two intestinal ceca in front of ventral sucker. Ventral sucker larger than oral sucker, 0.296 by 0.31, a little anterior to one-sixth of body length. Genital organs occupying "on the whole the entire part" behind ventral sucker. Testes two, tandem, close to each other on median line; anterior testis almost round, 0.41 by 0.44; posterior irregularly ellipsoidal, 0.59 by 0.38. Either cirrus pouch or genital pore not clearly observed. Ovary single, kidney-shaped, 0.067 by 0.14 wide, pretesticular. Seminal receptacle "elongated gourd-shaped", dorsal to ovary. Uterus not clearly observed. Egg oval, 73 by 49 μm, operculate. Vitelline follicles comparatively "gross", "not compact", posterior to ventral sucker, along both lateral margins, post-testicularly confluent. Excretory vesicle not clearly observed.

Since their brief description does not indicate the anatomy of the cirrus pouch, nor the position of the genital pore, nor the position of the ootype complex, the specimen cannot be identified even to the family level. It has not yet been reexamined. Kataoka and Momma (1934) stated that it closely resembled *Allocreadium oncorhynchi* Eguchi, 1931 [now *Dimerosaccus oncorhynchi* (Eguchi, 1931) Shimazu, 1980] (Family Opecoelidae). However, it cannot be assigned to *D. oncorhynchi* because it has a distinct, "elongated gourd-shaped" seminal receptacle (Shimazu, 1988a). The life cycle is not known. Shimazu (1999, 2003b) referred to this species as *Allocreadium* sp. 1.

3. ***Phyllodistomum folium*** (Olfers, 1816) Braun, 1899 (Family Gorgoderidae Looss, 1899)

Phyllodistomum folium is parasitic in the urinary bladder of freshwater fishes of various species in Europe (Yamaguti, 1971). Kobayashi (1915b–d) made a histological study and observed the egg formation in adults of "*P. folium*". Kobayashi (1921) suggested that the material used had been found in the urinary bladder of *Pseudobagrus aurantiacus* from Lake Biwa and Lake Kasumigaura (Ibaraki Prefecture). The bagrid fish in Lake Biwa is *Pelteobagrus nudiceps*. Because Kobayashi (1915b–d, 1921) did not describe the gross morphology of the adult, it is quite uncertain whether his identification as *P. folium* is correct.

Kurokawa (1934a, b) found metacercariae in the palaemonid prawn *Macrobrachium nipponense* from Lake Biwa near Katata. In experimental attempts to feed them to *Pseudobagrus aurantiacus* [sic], *Silurus asotus* (syn. *Parasilurus asotus*), and the newt *Cynops pyrrhogaster* (Boie) (syn. *Diemyctylus pyrrhogaster*) (Japanese name: Imori), he claimed to have recovered

adults identifiable as *P. folium* from the urinary bladder of these final hosts. According to Cribb (1987), the metacercariae figured by Kurokawa (1934b, figs. 3–5) belonged to *Pseudophyllodistomum* (see this paper), but the adults figured by Kurokawa (1934b, figs. 6–7) did not. The metacercariae certainly resemble Yamaguti's (1934) and the present metacercariae of *Ps. macrobrachicola*; but the adults resemble *P. patellae* (Sturges, 1897) Braun, 1899 (syn. *P. entercolpium* Holl, 1930) as was briefly redescribed by Yamaguti (1936a, MPM Coll. Nos. 22550–22551) from *C. pyrrhogaster* in Kyoto. It is evident that Kurokawa (1934a, b) erroneously regarded two different species as belonging to a single species, *Phyllodistomum macrobrachicola* [now *Ps. macrobrachicola*].

Kobayashi's (1915b–d) and Kurokawa's (1934a, b) specimens need reexamining, but they must have been lost. Yamaguti (1971) doubted whether the European species *P. folium* was distributed in Japan. Moreover, the present specimens from the Lake Biwa basin did not include any specimens of *P. folium*.

4. ***Exorchis oviformis*** Kobayashi, 1915 (Family Cryptogonimidae Ward, 1917)

Exorchis oviformis is an intestinal parasite of *Silurus asotus* (syn. *Parasilurus asotus*) in Japan (Kobayashi, 1915a, 1921; Shimazu, 2005). Kobayashi (1915a) said that he had found adults of this species in *S. asotus* and metacercarie in several species of fishes (or second intermediate hosts) from several places including Lake Biwa in Japan, but he (1921) excluded Lake Biwa from the locality list of the species without mentioning the reason. Sakai (1953) claimed to have found the metacercaria in fishes, *Plecoglossus altivelis altivelis* (syn. *P. altivelis*), *Pseudorasbora parva* (syn. *Ps. parva parva*), and *Biwia zezera*, from Lake Biwa.

Okabe (1936) revealed that the first intermediate host of *E. oviformis* is a stenothyrid snail (Japanese name: Mizugomatsubo). He referred to this snail as "*Stenothyra japonica* (Hirase Ms.) Kuroda" [sic] according to Tokubei Kuroda's identification; but Kuroda's description for the snail as a new species, *St. japonica* Kuroda, was officially published later in 1962 (Hosaka and Fukuda, 1996). The snail inhabits both fresh and brackish water. In fresh water, its occurrence is limited to coastal areas within 15–20 km of the coastline (Hosaka and Fukuda, 1996; Hiroshi Fukuda, personal communication). As has already been mentioned in "*Parabucephalopsis parasiluri*", the main stream of the Yodo River system is constituted of the Seta (upper reaches), Uji (middle reaches) and Yodo (lower reaches) rivers. *Stenothyra japonica* has been recorded from the Yodo River in Osaka Prefecture, but neither from the Uji and Seta rivers nor from Lake Biwa (Kihira *et al.*, 2003; Takaki Kondo, personal communication). Second intermediate hosts of *E. oviformis* are freshwater fishes and tadpoles of various species, in which metacercariae encyst (Kobayashi, 1915a, 1921; Okabe, 1936; Komiya, 1965). *Exorchis oviformis* has been recorded from the Yodo River: an adult from *S. asotus* (collecting locality not specified) (Yamaguti, 1942; Shimazu, 2005); and encysted metacercariae from freshwater fishes in Osaka Prefecture (Marugame, 1940).

Exorchis oviformis evidently occurred in the lower reaches of the Yodo River in the past at least. In Lake Biwa, its entire life cycle cannot have been completed, nor cannot have taken place the cercarial infection to fishes, for lack of the first intermediate host there. If Kobayashi (1915a) and Sakai (1953) correctly identified their specimens from Lake Biwa as *E. oviformis*, their second intermediate hosts must have migrated from the lower reaches of the Yodo River up into Lake Biwa. Kobayashi's final host *S. asotus* also either must have moved in this way or may have acquired infection by eating the infected second intermediate hosts in Lake Biwa. There were actually two possible routes leading from the Yodo River into Lake Biwa in those days: one is the

route by way of the main stream (the Uji and Seta rivers); and the other is the route by way of two artificial canals, "Biwako Sosui", the latter of which has been functioning from the Uji River to Otsu on Lake Biwa. Biwako Sosui in part flows into the Kamo River joining the Katsura River, which is finally connected to the Yodo River. However, *E. oviformis* has previously been recorded from Lake Biwa only twice (Kobayashi, 1915a; Sakai, 1953). Yamaguti (1938) stated that the metacercaria of *E. oviformis* was not detected in fishes from Lake Biwa far away from the sea. *Exorchis oviformis* was not found in *S. asotus* nor *S. biwaensis* from Lake Biwa and the Uji and Seta rivers (Shimazu, 2005; Shimazu and Urabe, 2005; Urabe, 2005–2009, unpublished data; this paper). It is still uncertain whether *E. ovoformis* really occurred in Lake Biwa in the past, because neither Kobayashi (1915a) nor Sakai (1953) gave a morphological description for his specimens from Lake Biwa. Their specimens need reexamining first of all, but they must have been lost.

Key to the families, genera, and species of the adult digeneans in this paper*

1.1. Parasitic in blood vessels; male and female genital pores separate, dorsal, near posterior end of body; tegument spinose; oral and ventral suckers absent; pharynx absent; testes single, median; ovary butterfly-shaped, post-testicular; vitellaria follicular; excretory vesicle V-shaped ····· Family Aporocotylidae. Sanguinicolidae gen. sp.

1.2. Parasitic in other organs; genital pore single, ventral, near anterior end of body, median, submedian, marginal, or near posterior end of body ····· 2.

2.1. Parasitic in connective tissue; genital pore near anterior end of body; tegument smooth; oral and ventral suckers present; pharynx present; testes two, tubular, submedian, postbifurcal; ovary single, tubular, in hindbody; cirrus pouch absent; hermaphroditic duct present; vitellaria two, tubular, lateral, in hindbody; excretory vesicle I-shaped ····· Family Didymozoidae. Genus *Philopinna*.

2.1.1. Testes pre-equatorial ····· *Philopinna higai*.

2.1.2. Testes extending to near posterior end of body ···· *Philopinna kawamutsu* sp. nov.

2.2. Parasitic in air bladder; genital pore median, postbifurcal; tegument smooth; oral and ventral suckers present; pharynx present; testes two, entire, symmetrical, behind ventral sucker; ovary single, tubular, post-testicular; sinus sac and sinus organ present; hermaphroditic duct present; vitellaria dendritic, postovarian; excretory vesicle Y-shaped, with separate arms ····· Family Isoparorchiidae. Genus *Isoparorchis*. *Isoparorchis hypselobagri*.

2.3. Parasitic in urinary organs; genital pore median, postbifurcal; tegument smooth; oral and ventral suckers present; pharynx absent; testes two, diagonal, postovarian; ovary single, submedian, behind vitellaria; vitellaria two compact masses, symmetrical, behind ventral sucker; excretory vesicle I-shaped ····· Family Gorgoderidae.

2.3.1. Uterus inter- and post-cecal in hindbody; ejaculatory duct long ····· Genus *Pseudophyllodistomum.* *Pseudophyllodistomum macrobrachicola*.

2.3.2. Uterus in all available space in hindbody; ejaculatory duct short ····· Genus *Phyllodistomum*.

2.3.2.1. Testes globular; vitellaria branched ····· *Phyllodistomum carassii*.

2.3.2.2. Testes irregular; vitellaria lobed ····· *Phyllodistomum mogurndae*.
2.3.2.3. Testes deeply lobed; vitellaria globular ····· *Phyllodistomum parasiluri*.
2.4. Parasitic in alimental canal or gall bladder ····· 3.
3.1. Oral and ventral suckers present; pharynx present; mouth near anterior end of body; genital pore median, submedian, or marginal; tegument smooth or spinose ····· 4.
3.2. Oral and ventral suckers absent; pharynx present; mouth ventral; genital pore near posterior end of body; tegument spinose; testes two, preovarian; ovary single, submedian; vitellaria follicular, postovarian; excretory vesicle saccular ····· Family Bucephalidae.
Genus *Parabucephalopsis*.
Parabucephalopsis parasiluri.
4.1. Tegument smooth ····· 5.
4.2. Tegument spinose ····· 6.
5.1. Cirrus pouch present, enclosing internal seminal vesicle, prostatic complex, and ejaculatory duct; external seminal vesicle present or absent; prostatic sac absent; sinus sac and sinus organ absent; genital pore median or submedian ····· 7.
5.2. Prostatic sac present, enclosing seminal vesicle and prostatic complex; cirrus pouch absent; sinus sac absent; sinus organ present; genital pore median, in forebody; testes two, tandem or diagonal, median, postovarian; ovary single, median or submedian, in hindbody; vitellaria follicular, lateral; excretory vesicle Y-shaped, with separate arms ····· Family Azygiidae.
Genus *Azygia*.
Azygia gotoi.
5.3. Sinus sac present, enclosing seminal vesicle, prostatic complex, ejaculatory duct, and distalmost part of metraterm; sinus organ present; cirrus pouch absent; prostatic sac absent; genital pore median, ventral to esophagus; cyclocoel present; testes two, symmetrical, in hindbody; ovary single, submedian, post-testicular; vitellaria two compact masses, postovarian; excretory vesicle Y-shaped, with united arms ····· Family Derogenidae.
Genus *Genarchopsis*.
5.3.1. Ventral sucker much larger than oral sucker ····· *Genarchopsis goppo*.
5.3.2. Ventral sucker nearly equal to oral sucker in size ····· *Genarchopsis yaritanago* sp. nov.
6.1. Genital pore median, in front of ventral sucker; cirrus pouch present; hermaphroditic duct absent; ventral invagination absent; ventrogenital sac absent; testes two, tandem or diagonal, postovarian; external seminal vesicle present; ovary single, median or submedian, in hindbody; vitellaria follicular, lateral; excretory vesicle I-shaped ····· Family Orientocreadiidae.
Orientocreadium pseudobagri.
6.2. Genital pore median, in forebody; cirrus pouch absent; hermaphroditic duct present; ventral invagination present between two suckers; ventrogenital sac present, enclosing ventral sucker; testes two, symmetrical, submedian, postovarian; ovary single, submedian, in hindbody; vitellaria follicular, symmetrical, submedian, level with ovary; excretory vesicle Y-shaped ····· Family Heterophyidae.
Genus *Pseudexorchis.*
Pseudexorchis major.
6.3. Genital pore lateral or marginal, level with ventral sucker; testes single or two, postovari-

an; cirrus pouch present; external seminal vesicle absent; ovary single, median, in hindbody; vitellaria follicular, lateral to intestines; excretory vesicle I-shaped ····· Family Lissorchiidae.

6.3.1. Testis single ····· Genus *Asymphylodora*.

6.3.1.1. Seminal vesicle bipartite ····· *Asymphylodora japonica*.

6.3.1.2. Seminal vesicle oval; cirrus pouch larger than metraterm ····· *Asymphylodora innominata* comb. nov.

6.3.1.3. Seminal vesicle oval; cirrus pouch smaller than metraterm ····· *Asymphylodora* sp.

6.3.2. Testes two, almost tandem ····· Genus *Asymphylotrema*. *Asymphylotrema hamajimai*.

6.3.3. Testes two, almost symmetrical ····· Genus *Palaeorchis*. *Palaeorchis diplorchis*.

7.1. Genital pore median, in forebody; testes two, tandem or diagonal, postovarian; external seminal vesicle absent; ovary single, submedian, in hindbody; vitellaria follicular, lateral; excretory vesicle I-shaped ····· Family Allocreadiidae. Genus *Allocreadium*.

7.1.1. Genital pore postbifurcal; testes entire; excretory vesicle not reaching to posterior testis ····· *Allocreadium gotoi*.

7.1.2. Genital pore almost bifurcal; testes entire; excretory vesicle reaching to posterior testis ····· *Allocreadium* sp.

7.1.3. Genital pore slightly prebifurcal; testes deeply indented; excretory vesicle not reaching to posterior testis ····· *Allocreadium hasu*.

7.1.4. Genital pore near pharynx; testes slightly indented; excretory vesicle not reaching to posterior testis ····· *Allocreadium japonicum*.

7.2. Genital pore submedian, in forebody; testes two, tandem or diagonal, postovarian; cirrus pouch entire or bipartite, posterior portion of bipartite pouch absent; ovary single, submedian, in hindbody; vitellaria follicular, lateral; excretory vesicle I-shaped ····· Family Opecoelidae.

7.2.1. Cirrus pouch entire; cyclocoel absent ····· 8.

7.2.2. Cirrus pouch bipartite; cyclocoel present ····· Genus *Coitocaecum*. *Coitocaecum plagiorchis*.

8.1. Uterus pretesticular ····· Genus *Neoplagioporus*.

8.1.1. Body elongate ····· *Neoplagioporus elongatus*.

8.1.2. Body broad-oval; vitelline follicles present in lateral marginal fields of body ····· *Neoplagioporus* sp.

8.1.3. Body broad-oval; vitelline follicles absent in lateral marginal fields of body ····· *Neoplagioporus zacconis*.

8.2. Uterus extending into post-testicular regions of body ····· Genus *Urorchis*.

8.2.1. Intestines pretesticular ····· *Urorchis goro*.

8.2.2. Intestines ending in testicular region of body ····· *Urorchis acheilognathi*.

8.2.3. Intestines entering post-testicular region of body ····· *Urorchis* sp.

* This key excludes three questionable species, *Allocreadium* sp. of Kataoka and Momma, *Phyllodistomum folium*, and *Exorchis oviformis*.

Abbreviations used in the figures

cc, cyclocoel; ci, cirrus; cp, cirrus pouch; csd, common sperm duct; cvd, common vitelline duct; dm, Drüsenmargen; e, esophagus; ed, ejaculatory duct; egg, egg: ep, excretory pore; esp, esophageal pouch; esv, external seminal vesicle; ev, excretory vesicle; eyp, eyespot pigment; ga, genital atrium; gp, genital pore; hd, hermaphroditic duct; i, intestine; isv, internal seminal vesicle; lc, Laurer's canal; m, metraterm; mg, Mehlis' gland; mo, mouth; o, ovary; od, oviduct; op, ootype pouch; os, oral sucker; ot, ootype; ovd, ovovitelline duct; p, pharynx; pc, prostatic cells; pp, pars prostatica; prp, prepharynx; ps, prostatic sac; r, rhynchus; sd, sperm duct; so, sinus organ; sr, seminal receptacle; ss, sinus sac; sv, seminal vesicle; t, testis; u, uterus; v, vitellarium; vd, vitelline duct; vf, vitelline follicles; vgs, ventrogenital sac; vi, ventral invagination; vs, ventral sucker.

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